

SHORT COMMUNICATION

Dancing to her own beat: honey bee foragers communicate via individually calibrated waggle dances

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ABSTRACT

Communication signals often vary between individuals, even when one expects selection to favour accuracy and precision, such as the honey bee waggle dance, where foragers communicate to nestmates the direction and distance to a resource. Although many studies have examined intra-dance variation, or the variation within a dance, less is known about inter-dance variation, or the variation between dances. This is particularly true for distance communication. Here, we trained individually marked bees from three colonies to forage at feeders of known distances and monitored their dances to determine individual communication variation. We found that each honey bee possesses her own calibration: individual duration–distance calibrations varied significantly in both slopes and intercepts. The variation may incur a cost for communication, such that a dancer and recruit may misunderstand the communicated distance by as much as 50%. Future work is needed to understand better the mechanisms and consequences of individual variation in communication.

KEY WORDS: *Apis mellifera*, Waggle run, Calibration, Miscommunication, Individual variation

INTRODUCTION

Communication signals often vary between individuals (Maynard-Smith and Harper, 2003). Sometimes the nature of the signal is such that the function of the variation is clear, for example by providing a means of individual recognition in territorial interactions (Bee et al., 2001; Maynard-Smith and Harper, 2003; Antunes et al., 2011). However, variation also exists in communication signals that one would expect to be optimized for accuracy and possess little variation, for example the honey bee (*Apis mellifera*) waggle dance, where foragers communicate to nestmates the direction and distance from the colony to a profitable resource, usually nectar or pollen (von Frisch, 1967; Couvillon, 2012).

Direction is encoded in the orientation of the dancer's body from vertical during the waggle run, which is the information-rich portion of the waggle dance; and distance is encoded by the duration of the waggle run, which increases approximately linearly with distance (von Frisch, 1967; Schürch et al., 2013). Waggle dances are known to possess both intra-dance (within dance, between successive waggle runs) variation in both the distance and direction components (De Marco et al., 2008; Tanner and Visscher, 2010; Couvillon, 2012; Couvillon et al., 2012b; Preece and Beekman,

2014) and inter-dance (between dances) variation in the direction component (von Frisch and Lindauer, 1961; von Frisch, 1967; Schürch and Couvillon, 2013). However, less is known about inter-dance variation in the duration component (see descriptions of the phenomenon in Boch, 1957; Schweiger, 1958; von Frisch, 1967).

Here, we trained individually marked bees to forage at known distances and monitored their waggle dances to determine individual variation in duration–distance communication. Specifically, we used linear mixed effect models to compare the nature of the variation within and between bees in distance calibration. We hypothesized that individual honey bee foragers may possess (1) similar duration–distance calibrations, (2) duration–distance calibrations where the intercepts differ between individuals but the slopes are similar, or (3) duration–distance calibrations where the slopes and intercepts differ between individuals. Then we analysed within- versus between-colony inter-dance variation. Lastly, we examined the potential consequences of individual differences in communication.

MATERIALS AND METHODS

Data were collected from 8 August 2013 to 28 August 2013 on days with good foraging weather. We chose to work in high summer because bees will only train and recruit to feeders when there is a relative dearth of flowers in the landscape, which occurs at this time of year in the study location (Couvillon et al., 2014). Colonies were queenright and of mixed European race, predominantly *Apis mellifera mellifera*, and were housed in glass-walled observation hives that were located at the Laboratory of Apiculture and Social Insects (LASI) at the University of Sussex. The hives were connected to the outside through 3×30 cm plastic tubes. Supplemental syrup feeding is sometimes necessary with observation hives; however, we only fed the colonies on days when data were not collected.

Using the methods of Grüter and Ratnieks (2011) and Schürch et al. (2013), we sequentially trained ca. 20 marked honey bee foragers per colony from three colonies to collect 1 mol l⁻¹ sucrose syrup scented with linalool (10 µl l⁻¹) at five distances (200, 250, 312, 350 and 400 m, verified by GPS to ±2 m; Table 1). Foragers measure distance via optic flow (Srinivasan et al., 2000; Chittka and Tautz, 2003), which accumulates linearly with distance (Schürch et al., 2013). Therefore, we were interested in analysing the slopes and intercepts of individual honey bees' waggle run duration (in seconds) to distance (in metres) calibrations. Bees were only included at a particular distance if they performed at least three separate dances for that distance. If a bee performed fewer than 3 for a feeder (or did not appear at that feeder at all) but appeared and danced 3+ times at a subsequent feeder, we would still include the bee but leave out the feeder in which she did not meet the requirement. Ideally, we would have trained further, as honey bees in our location are known to forage at many kilometres (Couvillon et al., 2014); however, time constraints were severe, and given the linear nature of the honey bee calibration (Schürch et al., 2013) and

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Table 1. Selection of the eight candidate models demonstrating that each bee's calibration possesses its own slope and intercept

Fixed effects		Random effects	Model performance					
Intercept	Distance	Structure	d.f.	log-likelihood	AICc	Delta	Weight	Evidence ratio
0.02	1.74	Distance Bee ID	6	650.4	−1288.6	0.00	0.64	1
0.02	1.74	Distance Bee ID, 1 Colony ID	7	650.4	−1286.6	2.04	0.23	3
0.01	1.75	Distance Bee ID, Distance Colony ID	9	651.8	−1285.4	3.21	0.13	5
0.00	1.79	1 Bee ID, Distance Colony ID	7	638.2	−1262.2	26.41	0.00	5.4e+05
0.01	1.78	1 Bee ID	4	632.4	−1256.8	31.80	0.00	8.1e+06
0.01	1.78	1 Bee ID, 1 Colony ID	5	632.4	−1254.8	33.83	0.00	2.2e+07
0.01	1.77	Distance Colony ID	6	508.4	−1004.7	283.90	0.00	4.4e+61
0.01	1.77	1 Colony ID	4	504.9	−1001.8	286.87	0.00	2e+62

The fixed effect (distance) was the same for all models, and only the random effect structure changed. The three top-ranking models all allow for an individual slope per bee with feeder distance (indicated by 'Distance | Bee ID'), and the best-ranking model is in grey. Data from 753 dances from $N=75$ individuals from 3 colonies.

the spatial information it conveys (Schürch and Ratnieks, 2015), 400 m would be sufficient to test our hypotheses. Lastly, we repeated the experiment with the second and third colonies, which gave us a total of 753 dances from $N=75$ individuals.

Dances were decoded by hand on iMac computers using Final Cut Express (v4.0.1) and analysis was done using R 3.0.3 (R Core Team 2014, <https://www.r-project.org/>). We extracted and averaged for each dance the duration of four, consecutive, mid-dance waggle runs (Couvillon et al., 2012b). It is important to note that although we determined waggle run duration visually, the signal itself produced by the dancing bees is acoustic (Wenner, 1962; Esch, 1964). Therefore, inter-individual differences detected via our method may not exactly reflect the actual level of differences in the acoustic communication of information. However, because the bees dance at a frequency that is more rapid than the standard video frame rate, it is safe to assume that if we are to detect any significant differences between individuals, the differences must be large to be perceived by relatively coarse video analysis.

Based on previous experience (Schürch et al., 2013), we constructed eight candidate linear mixed effect models using restricted maximum likelihood estimation with lme4 (Bates et al., 2015) and using distance from colony to feeder as a fixed effect. For each candidate model, we considered different random effect structures, allowing for various combinations of random intercepts and slopes for bees and colonies (Table 1). We used the MuMIn package to calculate the corrected Akaike information criterion (AICc) and weights. From the latter we calculated

evidence ratios (Burnham et al., 2011), which we used for final model selection.

RESULTS AND DISCUSSION

Here, we report on individual honey bee duration–distance curves, demonstrating that each bee possesses her own calibration. Specifically, we found that each bee's calibration varied significantly, possessing its own slope and intercept (Table 1, Fig. 1), which supports the third hypothesis. The best model that uses this inter-bee variation is 540,000 times more likely than the best model that does not allow for individual slope (Table 1). While the evidence for individual calibration curves is overwhelming, making the honey bee waggle dance in possession of a large amount of signal variation, we did not find evidence for differences among colonies because the models allowing for random colony intercepts and slopes did not fit significantly worse (Table 1).

The potential consequences of individual differences in communication are illustrated with two example bees that we present as possessing different calibrations (Fig. 1B). We observed that one bee performed a waggle run of duration 0.4 s for a distance of 210 m. If she had communicated this duration to a nestmate with a different calibration, the potential recruit could misinterpret the distance as being ca. 310–320 m from the colony – a difference in this situation of almost 50% (Fig. 1B).

We did not test what underlying mechanisms are responsible for the observed individual differences in calibrations. Honey bee odometers are visually driven, where the distance is derived from how much the

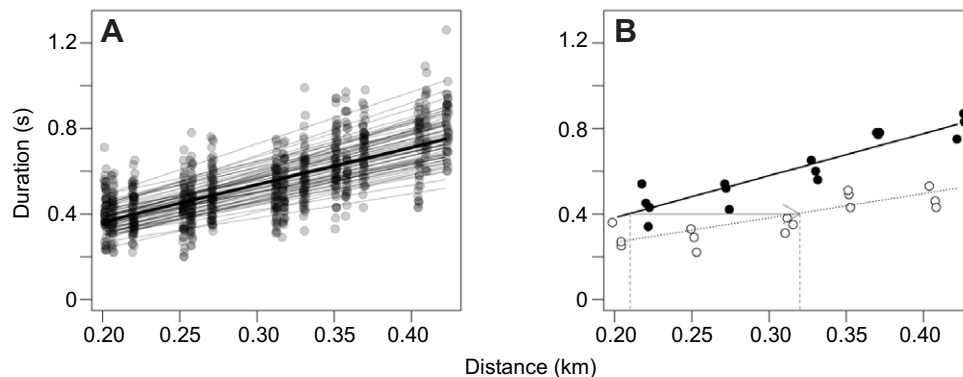


Fig. 1. Honey bees communicate via individually calibrated duration–distance dances. (A) Raw data (points), individual bee calibration curves (thin lines) for $N=75$ bees from 3 colonies performing 753 dances at one of five distances, and the overall calibration (thick line). Random jitter is added to the distance of the raw data to make individual data points more discernible, but distances are equal per feeder location (x -axis, Table 1). (B) Example data of two individual bees (black and white circles) selected for possessing different calibration curves (black and grey fitted lines). The horizontal arrow indicates the bees' distance miscommunication for the same duration, which here is approximately 100 m (50%).

world's image moved on their eyes during the flight (Srinivasan et al., 2000; Chittka and Tautz, 2003). Do individual bees differ in the neural coding of distance, such that some visually driven neurons are more sensitive than others? Alternatively, bees may not differ in their perception of how far they have flown, but they may simply struggle to communicate the distance precisely (i.e. are constrained). This alternative hypothesis, which has been examined in the context of intra-dance variation, is strongly supported by evidence (Tanner and Visscher, 2010; Couvillon et al., 2012a; Preece and Beekman, 2014).

However, less well understood is inter-dance variation, or dance inaccuracy, between dances of different bees for the same location. The few studies that do exist focus on the dance directional component (Schweiger, 1958; von Frisch and Lindauer, 1961; Schürch and Couvillon, 2013). Here, we report that honey bees, in addition to being imprecise (intra-dance variation), are also inaccurate (inter-dance variation) in their indication of distance. What would now be interesting to determine is whether inter-dance variation confers an adaptive benefit in distributing recruits, or whether inaccuracy, like imprecision, reflects a constraint of the honey bee physiology.

Of course, one important point to consider is that our honey bees, while predominantly *Apis mellifera mellifera*, are of mixed genetic origin (Carreck, 2008). Different subspecies possess slightly different duration–distance calibrations (Boch, 1957; von Frisch, 1967). Would we see such individual variation if we were to study a ‘pure’ race of honey bees?

Perhaps the fact that each forager's calibration is peculiar to herself and does not resemble that of other bees helps to explain the famous inefficiency of the waggle dance, where recruited bees often fail to find the advertised location: the likelihood that a newly recruited forager will locate the target, which is affected by the distance to the target, whether the target was a feeder or a patch of flowers, the presence or absence of floral odours, and how many waggle dances the recruit was allowed to follow (Esch and Bastian, 1970; Mautz, 1971; Gould, 1976; Seeley and Visscher, 1988; Tautz and Sandeman, 2003), is estimated to be 16–25% (Seeley and Visscher, 1988). Individual calibrations may also represent a significant challenge to the recruit's success (Fig. 1B). Our results also lead to many further questions. For example, when a recruit does find the target successfully, is this because she happens to possess a calibration that is similar to that of the dancing bee? More work is needed to examine individual calibration networks against the success of a particular recruitment event.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

R.S. and M.J.C. conceived, designed and conducted the experiment and wrote the manuscript; E.E.W.S. decoded the dances; R.S. analysed these data; F.L.W.R. contributed valuable discussions throughout the process and commented on the manuscript.

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