Working against gravity: horizontal honeybee waggle runs have greater angular scatter than vertical waggle runs

Margaret J. Couvillon1,*, Hunter L. F. Phillipps1, Roger Schürch2 and Roger L. W. Ratnieks1
1Laboratory of Apiculture and Social Insects, School of Life Sciences, University of Sussex, Brighton BN1 9QG, UK
2School of Life Sciences, University of Sussex, Brighton BN1 9QG, UK
*Author for correspondence (m.couvillon@sussex.ac.uk).

The presence of noise in a communication system may be adaptive or may reflect unavoidable constraints. One communication system where these alternatives are debated is the honeybee (Apis mellifera) waggle dance. Successful foragers communicate resource locations to nest-mates by a dance comprising repeated units (waggle runs), which repetitively transmit the same distance and direction vector from the nest. Intra-dance waggle run variation occurs and has been hypothesized as a colony-level adaptation to direct recruits over an area rather than a single location. Alternatively, variation may simply be due to constraints on bees’ abilities to orient waggle runs. Here, we ask whether the angle at which the bee dances on vertical comb influences waggle run variation. In particular, we determine whether horizontal dances, where gravity is not aligned with the waggle run orientation, are more variable in their directional component. We analysed 198 dances from foragers visiting natural resources and found support for our prediction. More horizontal dances have greater angular variation than dances performed close to vertical. However, there is no effect of waggle run angle on variation in the duration of waggle runs, which communicates distance. Our results weaken the hypothesis that variation is adaptive and provide novel support for the constraint hypothesis.

Keywords: honeybee; Apis mellifera; waggle dance; foraging; animal communication; signal noise

1. INTRODUCTION

Communication normally involves some imprecision in the information transfer from the signal producer to the signal receiver [1]. The reason for the presence of this imprecision, which may occur at different stages (e.g. signal production, transmission and reception), is a matter of debate. Specifically, is the imprecision an adaptive feature that has evolved to benefit the system [2,3] or does it reflect constraints [4]?

One communication system central to this debate is the honeybee (Apis mellifera) waggle dance, where a successful forager, upon returning to the hive, performs a stereotyped behaviour where she advances linearly in one direction on the comb while wagging her body at ca 15 Hz [5] from side to side (waggle run). She then turns to the left or right and usually circles back to the start (return phase) to repeat the waggle run. This circuit of waggle run + return phase may be repeated 1 to 100+ times, depending on resource quality [6,7]. The waggle run conveys the direction and distance vector from the nest to the resource location: distance is encoded in the duration of the waggle run and direction by the angle of the dancer’s body relative to the vertical [8]. The return phase is free of vector information [7,9]. For both angle and duration, there is a variation among the repeated waggle runs [10–12]. It has been hypothesized that this scatter is adaptive because it directs recruits to a general area, as opposed to a specific point [6,13–15], which is how scattered, floral resources sometimes occur in nature. In contrast to this tuned error hypothesis, under the physiological constraint hypothesis, the bees simply cannot dance more precisely [16,17] and the variation does not serve an adaptive function.

In this study, we investigated whether variation among waggle runs within a dance is affected by gravity. We hypothesized that angular variation would be greater when a bee is dancing horizontally (around 90° or 270°) on the vertical comb versus dancing vertically (around 0° or 180°). The reason for this is that when a bee makes a vertical waggle run, either up or down, the gravitational force is aligned to the waggle run (figure 1a). In contrast, a bee making a non-vertical waggle run will experience a gravitational force perpendicular to the waggle run and proportional to the absolute value of the sine of the angle from vertical (figure 1b,c). This force is at its maximum when the bee is dancing horizontally (figure 1d). In this way, we predict that angular variation will increase from 0° to 90° or from 180° to 270°, and decrease from 90° to 180° or from 270° to 360°. Conversely, we predict no effect of waggle run angle on variation in the duration of waggle runs (figure 1, d1–d3) because gravity should not affect the ability of a dancing bee to measure time.

2. MATERIAL AND METHODS

Using the methods of Couvillon et al. [10], we videotaped and decoded waggle runs within natural dances performed by foragers returning to three glass-walled vertical observation hives. Dances were decoded by hand on iMac computers using Final Cut Express (v. 4.0.1). To decode a waggle run, we extract two pieces of information: duration, which we obtained by noting the start and stop times of waggle run, and orientation clockwise from vertical, which we measured by making two marks on the screen over the dancer’s thorax near the start and end of a waggle run. We then measured the angle of the line running through these two points relative to vertical plumbline on the observation hive visible on the video (maximum measurement error approx. 1°). Previous work has shown that taking the mean of any four, preferably consecutive, mid-dance waggle runs gives a good estimate of the whole dance [10], so thus we did to obtain a single angle and duration mean per dance. As a measure of variation, we determined the standard deviation (s.d.) of angle and duration for the four waggle run sample.

We decoded and analysed 198 dances with angles ranged from 0° to 360°. We converted angles over 180° to their mirror equivalent angle between 0° and 180° clockwise from vertical (e.g. 300° become 60°). Although angles are graphed in degrees, they were analysed in radians. Waggle run durations ranged from 0.31 to 4.83 s, which correspond to resource distances of 200–5000 m [8]. These are typical foraging ranges for honeybees [18,19].

We built two linear models using Minitab (v. 14.2). In the first model, we analysed the response variable of angle s.d. (radians and square root-transformed) against the factors of angle average (between 0° and 180°, in radians), sine of this angle average and duration average. In the second model, we analysed the response...
variable of duration s.d. (square root-transformed) against the same factors. After transformation of the response variables, the models met modelling assumptions.

3. RESULTS
For angle s.d. (figure 2a), there was a small but significant effect of angle average ($F_{1,194} = 5.20, \ p = 0.02$) and large, significant effect of sine of angle average ($F_{1,194} = 16, \ p < 0.001$) and a non-significant effect of duration average ($F_{1,194} = 3.46; \ p = 0.065$). This means that angle s.d. significantly follows the absolute value of the sine function of waggle run angle (0–180°), where angular scatter is greatest around 90° (and 270°), but lowest around 180° and 0°. The significant negative linear influence of angle average (see regression equation in figure 2a) indicates that angular s.d. is a bit higher when the bees are dancing upwards (around 0°) compared with dancing downwards (around 180°). The insignificance of duration means that our effect cannot be explained by nearby resources happening also to be described by horizontal dances.

In contrast, for duration s.d. (figure 2b), the effects of both angle average and the sine of angle average are insignificant ($F_{1,194} = 0.020$ and 0.25; $p = 0.89$ and 0.62, respectively), and duration average is significant ($F_{1,194} = 60.22; \ p < 0.001$). This means that, as predicted, duration s.d. is not affected by either angle or the sine of the angle. Duration itself affects duration s.d. This is not surprising, as it has previously been shown that dances for greater distances (higher duration) were more variable in their intra-dance duration [10].

4. DISCUSSION
As predicted, our results show that angular variation significantly follows the sine of the mean waggle run angle. In contrast, duration variation does not. These data confirm that horizontal dances around 90° possess the most angular scatter compared with vertical dances around 0° or 180° and support the constraint hypothesis [17,20] that bees are dancing to the best of their ability.

In the tuned error hypothesis, the directional imprecision in both angle and duration components of the waggle dance is considered to be a colony-level adaptation because it ‘tunes’ the dance to the spatial distribution of resources [14,15]. One prediction of this hypothesis is that greater angular variation is needed to distribute recruits over a nearby flower patch versus over a same-sized patch located further from the colony. Consistent with this prediction, angular scatter decreases with increasing distance, and as a result, the absolute scatter of recruits does remain relatively constant from 100 to 1000 m [13] (but see [17]). However, 1000 m is less than 10 per cent of the maximum distance at which honeybees forage [18,19], so the above information may be non-representative. Additionally, although floral resources do sometimes

\[ \text{Figure 1. Under the gravity hypothesis, angular variability (s.d.) is predicted to be least when the bees are dancing vertically, (a) either up or down, on the vertical comb because the gravitational force is aligned to the waggle runs. (b,c) A bee making a non-vertical waggle run will experience a non-aligned gravitational force, which will generate varying amounts of s.d. (d) The non-aligned force is at maximum when the bee is dancing horizontally. In contrast, waggle run duration (d1–d3) variability (s.d., not shown) is unaffected by the angle at which the bee dances.} \]
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Figure 2. There was a significant effect of the sine of the angle on angular variability (1a, $p < 0.001$; $R^2_{adj} = 11\%$; back transformed line: (angle s.d. = $0.37 - 0.017 \times$ angle average + $0.088 \times$ sine (angle average) $- 0.016 \times$ duration average)$^2$) but not on duration variability (1b, $p = 0.615$; $R^2_{adj} = 25\%$; back transformed line: (duration s.d. = $0.30 + 0.002 \times$ angle average + $0.016 \times$ sine (angle average) + $0.093 \times$ duration average)$^2$). Angular variability is greatest around $90^\circ$ and $270^\circ$, but lowest around $180^\circ$ and $0^\circ$. Dance angles greater than $180^\circ$ were converted to their mirror equivalent. Variability is the s.d. among waggle runs ($n = 4$) per dance.

occur in large patches and may, in theory, benefit from spreading recruits, new nest sites, which are also advertised by waggle dances, are points. Dances for these should be more precise than dances for food. Although there have been attempts to test this [11,14], no one has yet been able to show less scatter in dances for nest sites [6,16,20].

Our study further weakens the tuned error hypothesis. In normal foraging, the angle of the waggle run on the comb for each resource location will change owing to solar azimuth movement (on average, $15^\circ$ per hour). Therefore, dances for the same resource location will be useful to a colony. Furthermore, our results show no effect on the variation in waggle dance duration, which we had predicted would not be affected by gravity.

A future test of the gravity effect could compare angular scatter in dances with and without the gravitational constraint. One way to do this would be to train bees from two hives to the same feeder. One hive would be horizontal (i.e. no gravitational challenge) with a strong, visual light source for orientation, while the other hive would be vertical (i.e. with gravitational challenge) [21]. We predict that angular variability in waggle runs would show $6\, \text{h}$ periodic fluctuations in the vertical hive but not in the horizontal hive.

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