

Intra-dance variation among waggle runs and the design of efficient protocols for honey bee dance decoding

Article (Published Version)

Couvillon, Margaret J, Riddell Pearce, Fiona C, Harris-Jones, Elisabeth L, Kuepfer, Amanda M, Mackenzie-Smith, Samantha J, Rozario, Laura A, Schürch, Roger and Ratnieks, Francis L W (2012) Intra-dance variation among waggle runs and the design of efficient protocols for honey bee dance decoding. *Biology Open*, 1 (5). pp. 467-472. ISSN 2046-6390

This version is available from Sussex Research Online: <http://sro.sussex.ac.uk/id/eprint/38761/>

This document is made available in accordance with publisher policies and may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the URL above for details on accessing the published version.

Copyright and reuse:

Sussex Research Online is a digital repository of the research output of the University.

Copyright and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable, the material made available in SRO has been checked for eligibility before being made available.

Copies of full text items generally can be reproduced, displayed or performed and given to third parties in any format or medium for personal research or study, educational, or not-for-profit purposes without prior permission or charge, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.

Intra-dance variation among waggle runs and the design of efficient protocols for honey bee dance decoding

Margaret J. Couvillon^{1,*}, Fiona C. Riddell Pearce¹, Elisabeth L. Harris-Jones¹, Amanda M. Kuepfer¹, Samantha J. Mackenzie-Smith², Laura A. Rozario¹, Roger Schürch³ and Francis L. W. Ratnieks¹

¹Laboratory of Apiculture and Social Insects and ³Social Evolution Research Group, School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK

²Department of Geography, School of Global Studies, University of Sussex, Brighton BN1 9QJ, UK

*Author for correspondence (M.Couvillon@sussex.ac.uk)

Biology Open 000, 1–6
doi: 10.1242/bio.20121099

Summary

Noise is universal in information transfer. In animal communication, this presents a challenge not only for intended signal receivers, but also to biologists studying the system. In honey bees, a forager communicates to nestmates the location of an important resource via the waggle dance. This vibrational signal is composed of repeating units (waggle runs) that are then averaged by nestmates to derive a single vector. Manual dance decoding is a powerful tool for studying bee foraging ecology, although the process is time-consuming: a forager may repeat the waggle run 1–>100 times within a dance. It is impractical to decode all of these to obtain the vector; however, intra-dance waggle runs vary, so it is important to decode enough to obtain a good average. Here we examine the variation among waggle runs made by foraging bees to devise a method of dance decoding. The first and last

waggle runs within a dance are significantly more variable than the middle run. There was no trend in variation for the middle waggle runs. We recommend that any four consecutive waggle runs, not including the first and last runs, may be decoded, and we show that this methodology is suitable by demonstrating the goodness-of-fit between the decoded vectors from our subsamples with the vectors from the entire dances.

© 2012. Published by The Company of Biologists Ltd. This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial Share Alike License (<http://creativecommons.org/licenses/by-nc-sa/3.0>).

Key words: Waggle dance, Honey bee, *Apis mellifera*, Animal communication, Social insect recruitment

Introduction

In the decades since Karl von Frisch discovered that honey bee workers (*Apis mellifera* spp.) communicate foraging locations to nestmates via the waggle dance (von Frisch, 1946; von Frisch, 1967), researchers have studied many aspects of the dance language. Some of these aspects have included mechanisms and evolution of message production (Seeley et al., 2000; Dornhaus and Chittka, 2004; Couvillon, 2012); message reception (Riley et al., 2005; Tanner and Visscher, 2008; Tanner and Visscher, 2009); the role of odour, memory, and acoustics (Kirchner et al., 1988; Reinhard et al., 2004; Grüter and Ratnieks, 2011); and how honey bees measure distance (Srinivasan et al., 2000; Esch et al., 2001; Chittka and Tautz, 2003; Tautz et al., 2004). Additionally, the dance has been used as a tool to investigate honey bee foraging ecology (von Frisch, 1967; Visscher and Seeley, 1982; Waddington et al., 1994; Seeley, 1995; Beekman and Ratnieks, 2000; Steffan-Dewenter and Kuhn, 2003; Beekman et al., 2004; Seeley and Visscher, 2004). In this last field, biologists use the waggle dance to determine where bees collect food or find new nest sites.

In the waggle dance, a worker bee vibrates her abdomen from side to side as she advances linearly in one direction (the waggle run), then turns either to the left or right to circle back to the start (the return phase), at which point she usually repeats the

waggle run with the return to the opposite side. The dancer is communicating a distance and direction vector from the nest site to a useful resource (nectar, pollen, water, propolis, or a new nest site). Distance and direction are encoded in the waggle run duration and orientation relative to vertical, respectively (von Frisch, 1946; von Frisch, 1967). The circuit of waggle run and return phase is made a variable number of times (1–>100) in a single dance bout, depending on resource quality (Seeley et al., 2000). Variation in angle and duration exists within these runs (Dyer, 2002; De Marco et al., 2008). Dance followers (recruits) take an average to derive a single distance and direction (von Frisch and Jander, 1957; Tanner and Visscher, 2008).

Quantifying and decoding waggle dances present certain experimental challenges, and the methodology used has changed with technological advances. von Frisch mostly analysed dances in real time but sometimes used motion film cameras. He used a clock to obtain duration, usually of complete dance circuits (waggle phase + return phase), and a protractor (accurate to 5°) to obtain orientation (von Frisch and Jander, 1957; von Frisch, 1967). Live dance decoding with timers, protractors (accurate to 2–11°), and the use of complete dance circuits as a duration measurement remained common practice in the decades after von Frisch (Visscher and Seeley, 1982; Waddington et al., 1994; Seeley, 1995; Steffan-Dewenter and

Kuhn, 2003). The advent of video recording made it possible to review footage easily, allowing for after-the-fact dance decoding, the decoding of simultaneous dances, and more accurate measurement of orientation. The use of digital video and computers makes it technically easy to analyse dances frame by frame, improving resolution. However, even with these improvements, dance decoding is time-consuming: a single forager bee may make waggle runs for over an hour in real time. Therefore, there is a need for protocols to optimise dance decoding. Specifically, how do we select the waggle runs to decode or not within a dance, and how many decoded waggle runs are necessary to obtain a good estimate of the location vector?

In this study we made a detailed analysis of intra-dance variation in waggle run duration and angle for dances to natural food sources in order to design time-efficient protocols for dance decoding. This involved the decoding and analysis of $n=3753$ waggle runs for 273 dances. We found consistent and significant trends in waggle run variability. These we use to design a new, systematic protocol for dance decoding. Lastly, we demonstrate that our sub-sampling technique generates angle and duration means that are good estimates of the entire waggle dance angle and duration mean, confirming the suitability of our recommendations.

Results

The first and last waggle runs are significantly more variable than the middle run

Within a dance, the deviation in duration among the first, middle, and last waggle runs differed significantly (First circuit = 0.98 SDs; Middle circuit = 0.65 SDs; Last circuit = 0.86 SDs; One-way ANOVA, $F=17.01$, $p<0.001$; Fig. 1). This significance was maintained using non-parametric statistics (Kruskal-Wallis, $H=34.6$, $p<0.001$). The first and last waggle runs did not differ significantly in deviation (Tukey's Post Hoc Test, $p=0.510$) but both had significantly higher deviation than the middle circuit ($p<0.001$).

Within a dance, the deviation in angle among the first, middle, and last waggle runs also differed significantly (First circuit = 0.90 SDs; Middle circuit = 0.57 SDs; Last circuit = 0.77 SDs; One-way ANOVA, $F=20.39$, $p<0.001$; Fig. 1). This significance

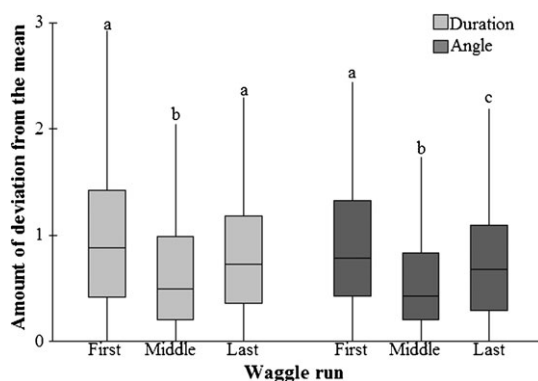


Fig. 1. For both duration and angle, the middle waggle run within a dance is significantly less variable than either the first or last waggle run. The deviation, shown in standard deviations from the mean for the whole dance, was calculated for each circuit within a dance, and the absolute value of these was compared across all dances ($n=273$ dances).

was maintained using non-parametric statistics (Kruskal-Wallis, $H=41.79$, $p<0.001$). The first waggle run angle was the most deviant, followed by the last waggle run (Tukey's Post Hoc Test, $p=0.02$ for first vs. last). Both had significantly higher deviation than the middle circuit ($p<0.001$).

Variability across waggle runs, excluding first and last, is constant throughout a dance

There was no significant increase or decrease in waggle run deviation in duration with waggle run order within a dance from second to penultimate (Regression analysis, $R^2=2.9\%$, $p=0.21$) (Fig. 2). Similarly, there was no significant increase or decrease in angle. (Regression analysis, $R^2=4.6\%$, $p=0.11$; Fig. 2). Therefore, as long as one excludes the first and last waggle runs, there is no trend in the remaining waggle run variability.

Duration variability is positively correlated with waggle run duration; angle variability is negatively correlated with waggle run duration

Across all dances, mean waggle run duration was positively correlated with the standard deviation of duration within a dance and mean waggle run duration was negatively correlated with the angle standard deviation (Duration: Spearman's Rank Correlation, $\rho=0.58$, $p<0.001$; Angle: Spearman's Rank Correlation, $\rho=-0.36$, $p<0.001$; Fig. 3). That is, dances for greater distances (higher mean duration) were more variable in their intra-dance waggle run durations. Dances for greater distances (higher mean duration) were less variable in their intra-dance waggle run angles, confirming what has previously been shown for shorter durations (see Discussion).

Replacing an errant waggle run does not improve fit between the four waggle run sample and all the waggle runs of a dance There was no significant improvement when the most deviant waggle run was replaced with the next waggle run from the same side (Regression analysis: Angle: $R^2=0.06\%$, $p=0.31$; Duration: $R^2=1.5\%$, $p=0.10$; Fig. 4). This indicates that highly errant

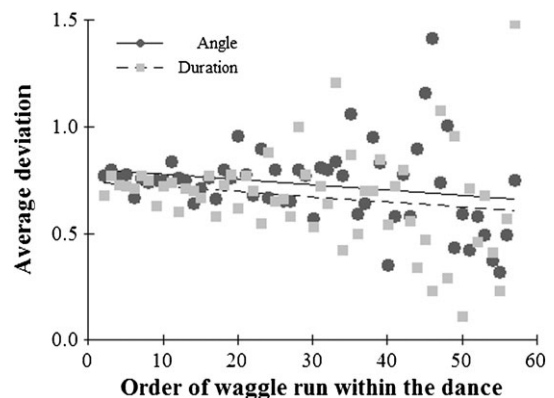


Fig. 2. For both duration and angle, there is no significant increase or decrease in variability, in units of standard deviation, with the order of the waggle run within a dance. Each data point shows the average absolute value of the deviation for the second to penultimate waggle run, for all dances with that made that number of waggle runs (i.e., the sample size reduces). This means that the data points around $x=2$ represent an average of 273 dances, data points around $x=20$ represent an average of c. 70 dances, and data points $x=40$ represent an average of c. 7 dances.

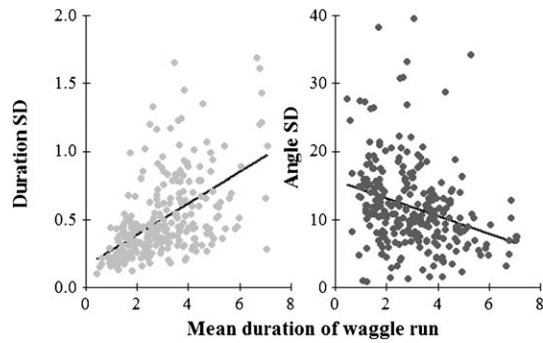


Fig. 3. Within a dance, mean waggle run duration (seconds) is positively correlated with duration standard deviation (Spearman's Rank Correlation, $\rho=0.58$, $p<0.001$) and negatively correlated with angle standard deviation (Spearman's Rank Correlation, $\rho=-0.36$, $p<0.001$). That is, waggle dances describing resources located at a greater distance are more variable in the duration but less variable in angle.

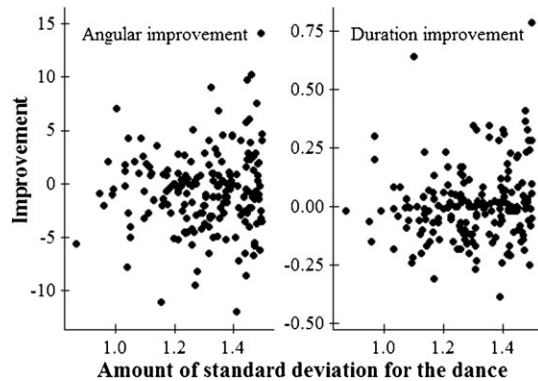


Fig. 4. For both angle and duration, replacing the most deviant waggle run of the four waggle run sample does not significantly improve the fit of the sample mean to the overall mean of all waggle runs in a dance. The Y axis represents whether or not replacing an errant run improves the fit and is in units of degrees (panel 1) and seconds (panel 2). A positive number is an improvement, and a negative number is a worsening. There was no significant trend in either direction for both angle ($p=0.31$) and for duration ($p=0.10$).

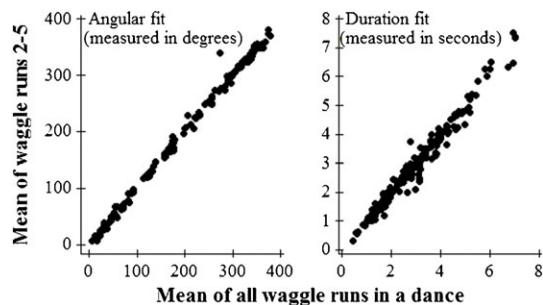


Fig. 5. A sample of 4 waggle runs, not including the first or the last run, from a dance generates a mean that is highly significantly correlated with the mean of all the waggle runs. This is true for both angle ($p<0.001$, $R^2=99.7\%$), which was measured as degrees, and for duration ($p<0.001$, $R^2=97.3\%$), which was measured in seconds.

waggle runs (not including the first and last waggle run), whose substitution would have an effect on the mean, are rare.

Our methodology generates angle and duration means that are good representation of the mean for the whole dance. For both angle and duration, there was a highly significant correlation between our four waggle run sample (\bar{x}_1) and the mean of all the waggle runs within a dance (\bar{x}_i) (Regression analysis: Angle: $R^2=99.7\%$, $p<0.001$; Duration: $R^2=97.3\%$, $p<0.001$; Fig. 5).

Discussion

Our results clearly show consistent trends in the variability of waggle runs within a dance that are relevant to waggle dance decoding. In particular, the first and last waggle runs are more variable than the middle run. However, there was no significant trend in variability as a function of waggle run order for both waggle run duration (distance) and angle (direction) when the first and last runs were excluded. In addition, our results show that waggle dances for more distant locations (with longer average waggle run durations) are significantly more variable for duration, even as they are significantly less variable for angle.

What recommendations for dance decoding protocols arise from our results? The fact that the first and last waggle runs are more variable means that these should ideally be avoided. In contrast, the lack of any trend in variability from the second to the penultimate waggle run shows that any of these should be suitable for decoding. Previous studies on angular variability have shown the importance of decoding an even number of waggle runs because angles within a dance cluster around the left and the right of the average direction (Towne and Gould, 1988; Weidenmüller and Seeley, 1999; Gardner et al., 2007; Tanner and Visscher, 2008). These left and right-sided clusters result from alternating waggle runs in which the bee makes its return to the left or right (Towne and Gould, 1988). Therefore, when decoding dances, it is recommended to have equal numbers of left and right-hand circuits to even out any angular biases.

How many waggle runs should be decoded given that a bee may perform from 1- >100 waggle runs within a dance? There is a trade-off between the number of waggle runs per dance and the total number of dances that can be decoded in a given time period. Sometimes it will be more important to decode more dance locations and sometimes it will be more important to obtain more accuracy per dance, even at the expense of total numbers of dances decoded. Ultimately, this decision depends on the type of question being addressed.

For studies that require the decoding of many dances, we recommend that four consecutive waggle runs be decoded. We selected four because the confidence interval of the mean, which is important for both duration and for angle, depends on the square root of the sample size. Therefore, decoding four compared to two runs halves the estimated deviation from the mean. However, to halve it again, sample size would need to increase from four to sixteen. This not only results in a fourfold increase in the time it would take to decode the dance but also decreases the proportion of dancing bees that make this many waggle runs in a single bout. For example, in our 273 dances, 206 of them (75%) made at least 6 waggle runs and would therefore be suitable for our methodology (i.e., ignoring first and last waggle runs to decode middle four). However, only 64 of 273 dances (23%) had the 18 or more waggle runs necessary to sample 16 runs. Four, being an even number, also takes into account

the alternating angular biases. Therefore, decoders should find a bee performing a minimum of six waggle runs, ignore the first and last, and decode the middle four. Duration and angle are then averaged to obtain a single duration and a single angle.

Although we did observe some errant waggle runs that were not the first or the last within the dance, these occurred in less than 2% of the dances. For example, in the first panel of Fig. 5, there is one point that does not fall on the line for angular goodness-of-fit. This dance possessed an errant middle run in our subsample (waggle run 2–5 measured angles: 352°, 247°, 350°, 337°), and therefore our sample average angle did not represent the overall average angle. Usually the reason for these truly errant middle waggle runs was because a bee was bumped by a nestmate during the dance. When this happens it is immediately clear to the researcher who is quantifying the waggle run. Hence, the run can be excluded prior to decoding and replaced with a subsequent run on the same side. Here we verify the relative rareness of these errant waggle runs by demonstrating that replacing the most deviant waggle run of four with the next subsequent waggle run on the same side does not improve the fit between the sample mean and the total mean (Fig. 4). As it does not significantly help to replace the most deviant run, we recommend against any systematic detection and discarding of waggle runs.

Waggle runs for greater distances tended to be more variable in duration but less variable in angle (Fig. 3). This effect of decreasing angular variability with increasing waggle run duration has previously been reported (Beekman et al., 2005) and is attributed to a physical constraint (Beekman et al., 2005; Tanner and Visscher, 2010a; Tanner and Visscher, 2010b). A bee dancing for a nearby location makes short duration waggle runs (<1 sec), which necessitates turning her body almost immediately to begin the next waggle run. This results in less angular precision (more variability) for nearby resources. In contrast, previous reports did not find any effect of waggle run duration on variability of waggle run duration (Beekman et al., 2005), whereas we found increasing variability with increasing duration. The probable reason for this discrepancy is that the previous study used feeders at distances under 233 m, whereas we studied dances that described locations up to c.12 km distant. In general, the idea that a bee making longer duration waggle runs has greater difficulty with durational precision makes logical sense: estimating 10 seconds is easier than estimating 70 seconds. Lastly, we show here that our methodology, in addition to increasing the efficiency of dance data collection, also provides an estimate of the resource location that is not significantly bettered when the entire dance is decoded (Fig. 5).

That there is intra-dance variation is not surprising, as communication systems sometimes possess a form of error in information transfer (Shannon, 1949; Levin and Miller, 1996; Maynard Smith and Harper, 2003; Dussutour et al., 2009). As variation seems therefore to be inevitable in waggle dances, it is interesting to note that bees, especially recruits, have evolved some compensatory features. Dance followers take the successive, scattered waggle runs and “average”, which is a common method of noise reduction (von Frisch and Jander, 1957; Tanner and Visscher, 2008). Averaging is also what biologists do to determine foraging locations. Here we have just streamlined the process of collecting the data to average.

The decoding of waggle dances can be a powerful tool for studies of honey bee conservation, pollination, and ecology. However, existing technology does not yet allow for automated

dance decoding, although this may eventually come (A. Mitchell, Detection of dancing honey bees, MSc thesis, University of Bristol, UK, 2005). For now, measurements must be made manually, which is time-consuming. Nevertheless, the honey bee is the only animal that tells a researcher where it has been foraging. To gather comparable ecological data from other species to help in their conservation requires the use of animal-borne radios (Jouventin and Weimerskirch, 1990; Rutz et al., 2007; Burger and Shaffer, 2008) or GPS loggers (Gagliardo et al., 2007; Schofield et al., 2007; Cagnacci et al., 2010), the trackers of which are too big for insects (Wikelski et al., 2007). The use of harmonic radar (Riley et al., 2005; Menzel et al., 2011) with honey bees is limited in the distance it may transmit (<1 km) and the terrain over which it must be used (flat). As honey bees may collect food 12–14 km from the hive, their foraging range is >450 km², making harmonic radar and extensive markings/field observations untenable. Here we have shown that the dance decoding process may be streamlined, and we provide a method that is quicker and cheaper than previously used methods.

Materials and Methods

Study organism and hives

We used 3 honey bee colonies of mixed European race, predominantly *Apis mellifera mellifera*, housed in glass-walled observation hives located at the laboratory. Each colony had a queen and contained approximately 5000 workers on 1 deep and 3 medium Langstroth frames. Care was taken to maintain similar-sized patches of brood (roughly one side of one medium frame) and stored honey (1 medium frame) in each colony to control for foraging motivation via food storage quantity and brood nutritional needs. When supplemental feeding was needed, colonies were given sucrose solution on Friday afternoons. Data collection (videoing dances) was not done over the weekends, and the sugar solution was consumed by Monday morning. A 3 cm diameter × 30 cm plastic tube gave foragers access to the outside.

As bees dance relative to vertical, we placed plumb lines made of nylon fishing line with heavy metal washers at the ends at 5 cm intervals across the outer glass wall. These appeared as thin white lines in the video. Additionally, we placed a digital clock (radio controlled for accuracy) on each observation hive within the video area. We repositioned the clock as needed so that the time was visible within the video. Time of day is needed to determine the solar azimuth for each dance, as the sun moves approximately 15 degrees per hour. We adjusted the zoom of each camera so that a “dance floor” area c. 25 cm wide × 20 cm deep was recorded. This included most of the dances on one side of the frame but still gave enough definition to quantify individual dances with ease from the video.

Data collection

Video data were collected from 11 August 2009 to 13 October 2009 on days when the bees were foraging. We filmed each observation hive for one hour per study day using camcorders (Canon Legria HV40, HDV 1080i) and mini-DV tapes. The camera was set back 1 m from the hive to reduce parallax effects. Our goal was to film all three hives simultaneously around the same time each day (10–11am GMT), although sometimes one of the hives was inactive or bad weather prevented foraging. We uploaded tapes to external hard drives connected to iMac computers running Final Cut Express (Version 4.0.1). Videos were played until we observed a bee making a waggle dance. In this study, we decoded every dance we saw for as many waggle runs as were made. As it takes several minutes to decode each waggle run, dances with many waggle runs could take several hours to decode.

To decode dances, it is necessary to extract two pieces of information per waggle run: the duration of the waggle run (von Frisch, 1967; Seeley et al., 2000), which is a function of distance to the advertised location, and the direction of the waggle run relative to vertical, which gives the direction from the nest relative to the solar azimuth. Previous work on waggle dance decoding used the duration of the entire circuit (waggle run + return phase) or the several entire circuits that is then averaged (von Frisch, 1946; von Frisch, 1967; Waddington et al., 1994; Beekman and Ratnieks, 2000). However, the waggle run is actually the information-rich portion of the dance (Michelsen et al., 1992), while the return phase (or more specifically, the quickness of the return phase) depends on resource quality (Seeley et al., 2000) and can be noisy. Therefore, we only used the waggle run, not the entire circuit, in our dance decoding.

We measured duration by noting the beginning and end of each waggle run, which was determined by the start and end of the blurring of the dancer's body and wings, which could easily be seen on a still frame of the video. Beginning and end

times (hour, minute, second, frame) were taken from the timer of the video software, which provides a temporal resolution of 0.04 sec (1 frame). Thus, our maximum measurement error was approximately 0.08 s. To determine foraging locations, duration must be transformed to distance. However, this transformation was not necessary in this study, as our aim was to investigate variation among waggle runs and not actual foraging locations. Therefore, all analysis is done on duration, not distance.

To determine the angle of the dancer's body relative to vertical during the waggle run, we taped acetate sheets on the computer screen and made dots above the centre of the dancing bee's thorax twice during the waggle run. Usually we found it best to make these dots during the middle portion of the waggle run, as sometimes the bee began to waggle when it was still turning its body. A line was drawn to connect the dots and was extended to the nearest vertical plumbline on the video. Using a 360° protractor, the angle of this line clockwise from vertical was determined to the nearest degree. Thus, our maximum measurement error was approximately 1°. We determined the azimuth using the Excel Macro (© W.F. Towne) Sun2007 and the time (GMT in minutes) for each waggle run. Ultimately, to determine foraging locations the dance angle is added to the azimuth to get a final direction. However, this was not necessary in this study, as our aim was to investigate variation among waggle runs and not actual foraging locations. Therefore, all analysis is done on measured angles, not angle + azimuth.

Data analysis

While decoding the dances we had the impression that the first and last waggle runs were more variable than those in the middle of the dance. To test this possibility, we first calculated the mean and standard deviation for both duration and angle for all waggle runs within a bout of dancing (i.e., for all repeated waggle runs in a single continuous period of dancing). Then, we determined how many standard deviations each individual waggle run deviated from the mean, e.g., [(individual waggle run duration in a dance – mean waggle run duration for that dance)/standard deviation for that dance]. Lastly we took the absolute value of this number. In this way, we compared how the first, last, and the middle run deviated from the mean. For dances with an even number of waggle runs, and therefore two middle runs, we randomly selected one of these.

We also investigated whether waggle run variation increased or decreased for dances with more total waggle runs. Do bees, for example, become more consistent the more repetitions they make? To test this we calculated, as above, the mean and standard deviation for both duration and angle for all waggle runs within a bout of dancing. Then, we determined how many standard deviations each individual waggle run deviated from the mean for each run from second to penultimate. We averaged this across all dances to obtain a single value for second through penultimate waggle run variability. As our dances had a variable number of waggle runs (range 4–72 waggle runs, n=273 dances), the sample size decreased with circuit number.

We determined whether waggle run duration was correlated, either positively or negatively, with both duration standard deviation and with angle standard deviation. We also investigated whether replacing an “errant” waggle run (as measured by its difference from the mean for that dance) improves the fit of the mean of four waggle run sample compared to the overall mean of all waggle runs in a dance. To do this, for both angle and duration, we took the mean (\bar{x}_1) of waggle runs 2–5, which does not include the more variable first and last waggle runs. Within these four waggle runs, we replaced the most deviant waggle run, relative to the mean, with the next waggle run on the same side, left or right. Therefore, this analysis was only done on dances with >6 waggle runs (n=186). Then we calculated the mean of these four waggle runs (\bar{x}_2) and the total mean of all the waggle runs (\bar{x}_1). We took the absolute value of ($|\bar{x}_1 - \bar{x}_2|$) and subtracted the absolute value of ($|\bar{x}_1 - \bar{x}_2|$). If the resultant number is positive, this indicates that there has been an improvement, as \bar{x}_2 would be nearer than \bar{x}_1 to \bar{x}_1 . If the resultant number is negative, this indicates that there has been a worsening of the fit, as \bar{x}_1 would be nearer to \bar{x}_2 than \bar{x}_1 . If the resultant number is zero, this indicates neither an improvement nor a worsening. This was done for angles and durations and was plotted against the SD for that dance.

Lastly, we compared the goodness-of-fit of four waggle runs (\bar{x}_1) which did not include either the first or the last waggle run with the total mean (\bar{x}_1). The better the correlation, the stronger the fit between our estimated mean based on four waggle runs and the total mean of all the waggle runs in a dance. This was done for both angle and duration.

Acknowledgements

This research was funded by the Nineveh Charitable Trust (MJC), Waitrose (FCRP), and the Swiss National Science Foundation (Grant No. PBBEP3_133529 to RS).

Competing Interests

The authors declare that there are no competing interests.

References

- Beekman, M. and Ratnieks, F. L. W. (2000). Long-range foraging by the honey-bee, *Apis mellifera* L. *Funct. Ecol.* **14**, 490–496.
- Beekman, M., Sumpter, D. J. T., Seraphides, N. and Ratnieks, F. L. W. (2004). Comparing foraging behaviour of small and large honey-bee colonies by decoding waggle dances made by foragers. *Funct. Ecol.* **18**, 829–835.
- Beekman, M., Doyen, L. and Oldroyd, B. P. (2005). Increase in dance imprecision with decreasing foraging distance in the honey bee *Apis mellifera* L. is partly explained by physical constraints. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **191**, 1107–1113.
- Burger, A. E. and Shaffer, S. A. (2008). Application of tracking and data-logging technology in research and conservation of seabirds. *The Auk* **125**, 253–264.
- Cagnacci, F., Boitani, L., Powell, R. A. and Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 2157–2162.
- Chittka, L. and Tautz, J. (2003). The spectral input to honeybee visual odometry. *J. Exp. Biol.* **206**, 2393–2397.
- Couvillon, M. J. The dance legacy of Karl von Frisch. *Insectes Soc.* [Epub ahead of print]
- De Marco, R. J., Gurevitz, J. M. and Menzel, R. (2008). Variability in the encoding of spatial information by dancing bees. *J. Exp. Biol.* **211**, 1635–1644.
- Dornhaus, A. and Chittka, L. (2004). Why do honey bees dance? *Behav. Ecol. Sociobiol.* **55**, 395–401.
- Dussutour, A., Beekman, M., Nicolis, S. C. and Meyer, B. (2009). Noise improves collective decision-making by ants in dynamic environments. *Proc. R. Soc. B.* **276**, 4353–4361.
- Dyer, F. C. (2002). The biology of the dance language. *Annu. Rev. Entomol.* **47**, 917–949.
- Esch, H. E., Zhang, S., Srinivasan, M. V. and Tautz, J. (2001). Honeybee dances communicate distances measured by optic flow. *Nature* **411**, 581–583.
- Gagliardo, A., Ialø, P., Savini, M., Lipp, H.-P. and Dell’Omo, G. (2007). Finding home: the final step of the pigeons’ homing process studied with a GPS data logger. *J. Exp. Biol.* **210**, 1132–1138.
- Gardner, K. E., Seeley, T. D. and Calderone, N. W. (2007). Hypotheses on the adaptiveness or non-adaptiveness of the directional imprecision in the honey bee waggle dance (Hymenoptera: Apidae: *Apis mellifera*). *Entomol. Gener.* **29**, 285–298.
- Grüter, C. and Ratnieks, F. L. W. (2011). Honeybee foragers increase the use of waggle dance information when private information becomes unrewarding. *Anim. Behav.* **81**, 949–954.
- Jouventin, P. and Weimerskirch, H. (1990). Satellite tracking of Wandering albatrosses. *Nature* **343**, 746–748.
- Kirchner, W. H., Lindauer, M. and Michelsen, A. (1988). Honeybee dance communication: acoustical indication of direction in round dances. *Naturwissenschaften* **75**, 629–630.
- Levin, J. E. and Miller, J. P. (1996). Broadband neural encoding in the cricket cercal sensory system enhanced by stochastic resonance. *Nature* **380**, 165–168.
- Maynard Smith, J. and Harper, D. (2003). *Animal Signals*. Oxford, UK: Oxford University Press.
- Menzel, R., Kirbach, A., Haass, W.-D., Fischer, B., Fuchs, J., Koblösky, M., Lehmann, K., Reiter, L., Meyer, H., Nguyen, H. et al. (2011). A common frame of reference for learned and communicated vectors in honeybee navigation. *Curr. Biol.* **21**, 645–650.
- Michelsen, A., Andersen, B. B., Storm, J., Kirchner, W. H. and Lindauer, M. (1992). How honeybees perceive communication dances, studied by means of a mechanical model. *Behav. Ecol. Sociobiol.* **30**, 143–150.
- Reinhard, J., Srinivasan, M. V., Guez, D. and Zhang, S. W. (2004). Floral scents induce recall of navigational and visual memories in honeybees. *J. Exp. Biol.* **207**, 4371–4381.
- Riley, J. R., Greggers, U., Smith, A. D., Reynolds, D. R. and Menzel, R. (2005). The flight paths of honeybees recruited by the waggle dance. *Nature* **435**, 205–207.
- Rutz, C., Bluff, L. A., Weir, A. A. S. and Kacelnik, A. (2007). Video cameras on wild birds. *Science* **318**, 765.
- Schofield, G., Bishop, C. M., MacLean, G., Brown, P., Baker, M., Katselidis, K. A., Dimopoulos, P., Pantis, J. D. and Hays, G. C. (2007). Novel GPS tracking of sea turtles as a tool for conservation management. *J. Exp. Mar. Biol. Ecol.* **347**, 58–68.
- Seeley, T. D. (1995). *The Wisdom Of The Hive: The Social Physiology Of Honey Bee Colonies*. Cambridge, MA, USA: Harvard University Press.
- Seeley, T. D. and Visscher, P. K. (2004). Group decision making in nest-site selection by honey bees. *Apidologie (Celle)* **35**, 101–116.
- Seeley, T. D., Mikheyev, A. S. and Pagano, G. J. (2000). Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **186**, 813–819.
- Shannon, C. E. (1949). *Communication In The Presence Of Noise*. New York, NY, USA: Institute of Radio Engineers.
- Srinivasan, M. V., Zhang, S., Altwein, M. and Tautz, J. (2000). Honeybee navigation: nature and calibration of the “odometer”. *Science* **287**, 851–853.
- Steffan-Dewenter, I. and Kuhn, A. (2003). Honeybee foraging in differentially structured landscapes. *Proc. Biol. Sci.* **270**, 569–575.
- Tanner, D. and Visscher, K. (2008). Do honey bees average directions in the waggle dance to determine a flight direction? *Behav. Ecol. Sociobiol.* **62**, 1891–1898.
- Tanner, D. and Visscher, K. (2009). Does the body orientation of waggle dance followers affect the accuracy of recruitment? *Apidologie (Celle)* **40**, 55–62.
- Tanner, D. A. and Visscher, P. K. (2010a). Adaptation or constraint? Reference-dependent scatter in honey bee dances. *Behav. Ecol. Sociobiol. (Print)* **64**, 1081–1086.

- Tanner, D. A. and Visscher, P. K.** (2010b). Does imprecision in the waggle dance fit patterns predicted by the tuned-error hypothesis? *J. Insect Behav.* **23**, 180-188.
- Tautz, J., Zhang, S., Spaethe, J., Brockmann, A., Si, A. and Srinivasan, M.** (2004). Honeybee odometry: performance in varying natural terrain. *PLoS Biol.* **2**, e211.
- Towne, W. F. and Gould, J. L.** (1988). The spatial precision of the honey bees' dance communication. *J. Insect Behav.* **1**, 129-155.
- Visscher, P. K. and Seeley, T. D.** (1982). Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* **63**, 1790-1801.
- von Frisch, K.** (1946). Die Tänze der Bienen. *Österr. Zool. Zh.* **1**, 1-48.
- von Frisch, K.** (1967). *The Dance Language And Orientation Of Bees*. Cambridge, MA, USA: Belknap Press of Harvard University Press.
- von Frisch, K. and Jander, R.** (1957). Über die Schwänzeltanz der Bienen. *Z. Vgl. Physiol.* **40**, 239-263.
- Waddington, K. D., Herbert, T. J., Visscher, P. K. and Richter, M. R.** (1994). Comparisons of forager distributions from matched honey bee colonies in suburban environments. *Behav. Ecol. Sociobiol.* **35**, 423-429.
- Weidenmüller, A. and Seeley, T. D.** (1999). Imprecision in waggle dances of the honeybee (*Apis mellifera*) for nearby food sources: error or adaptation? *Behav. Ecol. Sociobiol.* **46**, 190-199.
- Wikelski, M., Kays, R. W., Kasdin, N. J., Thorup, K., Smith, J. A. and Swenson, G. W., Jr.** (2007). Going wild: what a global small-animal tracking system could do for experimental biologists. *J. Exp. Biol.* **210**, 181-186.