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Original article

Comparison of two methods for decoding honeybee waggle dances

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Abstract – Honeybees communicate the locations of profitable resources using waggle dances. Researchers have used two manual dance decoding methods to infer the spatial foraging patterns of the bees. The 'waggle run method' infers foraging distance from waggle duration, representing the actual distance signal of the bees, and the 'circuit method' infers foraging distance from the duration of complete dance circuits, including both waggle and return phases. The circuit method enables decoding dances by real-time observation and is likely quicker, but it might give inaccurate distance estimates due to variations in the return phases. Here, we decoded 200 natural waggle dances from four *Apis mellifera* colonies using both methods to test how well inferences about foraging locations would match and compared the time required for dance decoding. We found a high linear correlation between foraging distances inferred from waggle duration and circuit duration (R^2, 0.793). However, the circuit method systematically overestimated foraging distances by about 86 m. Both methods provided similar results with respect to relative differences in spatial foraging patterns between the four test colonies. Decoding the dances using the circuit method was three to four times faster than the waggle run method (2 versus 7.3 min per dance). We conclude that the circuit method can be used for many research questions that require manual dance decoding to minimize time costs. However, when aiming to maximize the accuracy of inferred foraging locations, systematic errors of the circuit method should be accounted for, or the waggle run method should be used.

Waggle dance / Foraging range / Social information / Forage mapping / Eavesdropping / Dance language

1. INTRODUCTION

Honeybees are among the most abundant pollinators in both natural and agricultural landscapes (Hung et al. 2018; Rollin and Garibaldi 2019). Central to their foraging behaviour is the waggle dance, a highly sophisticated mode of communication through which a successful forager, upon returning to the nest, conveys information about profitable resource locations to fellow worker bees (von Frisch 1967). Since the 'dance language' can be decoded by human observers, it offers a distinctive perspective into the foraging behaviour of honeybee colonies. Researchers have used waggle dance information to study the bees' spatio-temporal patterns of resource collection (Visscher and Seeley 1982), their habitat preferences (Bänsch et al. 2020; Rutschmann et al. 2023; Sponsler et al. 2017), and their responses to anthropogenic changes (Danner et al. 2016; Garbuzov et al. 2015; Samuelson et al. 2022; Steffan-Dewenter and Kuhn 2003). Moreover, the waggle dance serves as a valuable tool in pollinator conservation more

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generally, as honeybees effectively provide insights into floral foraging grounds that can also be important for other flower-visiting insects (Balfour et al. 2015).

The waggle dance is composed of repetitive units of dance circuits that alternate between the waggle phase and the return phase. During the waggle phase, a dancing bee moves forward in a straight line on the vertical combs of the hive, waggling or shaking its abdomen. Then, in the return phase, it turns either left or right to return to the starting position in a semicircle, completing a dance circuit, which may be repeated several times (Figure 1). The duration of the waggle phase correlates to the distance to a resource patch, while the angle of the waggle phase relative to the vertical correlates to the flight angle relative to the sun's current azimuth (Michelsen et al. 1992; von Frisch 1967). In a waggle dance, the angle and duration may vary between waggle runs (Couvillon et al. 2012; De Marco et al. 2008). Therefore, dance followers average these variations to obtain a single distance and direction (Tanner and Visscher 2008; von Frisch and Jander 1957). Furthermore, the duration of the return phase exhibits an inverse relationship with the profitability of a resource, suggesting that the return phase itself and/or the rate of waggle-run production encode relative differences in food-source profitability (Łopuch and Tofilski 2020; Seeley et al. 2000).

For their pioneering studies of the waggle dance in the 1940s, Karl von Frisch and his collaborators directly measured the movements of dancing bees through the glass windows of observation hives. By observing the dancing bees in real time, researchers timed the duration of a series of consecutive circuits (waggle run plus return phase) using a stopwatch and counted the number of dance circuits performed. This made it possible to calculate the average circuit duration of dances, a measure that correlates well with foraging distance. The directional information of dances, represented by the average dance orientation, was directly determined using a protractor (von Frisch and Jander 1957; von Frisch 1967). Given the accessibility of these measuring techniques, the 'circuit method' (Figure 1) has been adopted for many studies that required decoding the waggle dances (e.g. Beekman and

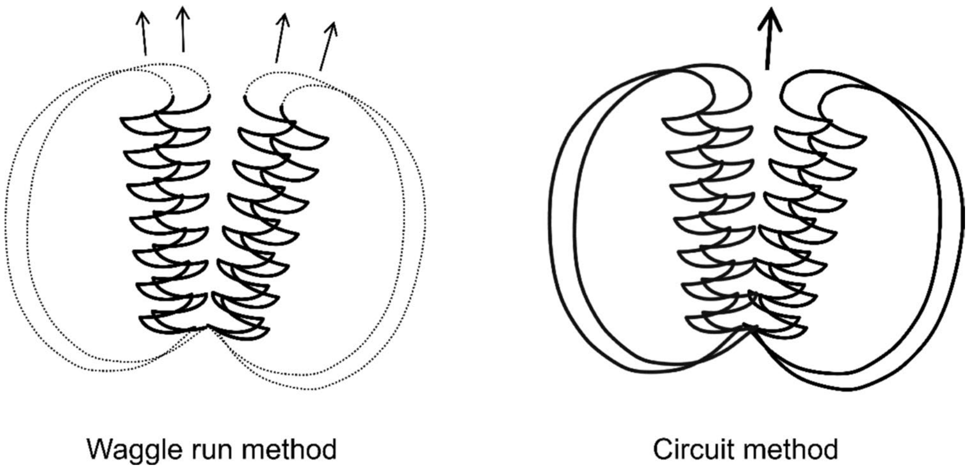

Figure 1. Illustration of the two dance decoding methods. Potential trajectory of a bee performing a waggle dance (direction: upwards) with four dance circuits, i.e. four directed waggle runs (zig-zag lines) each followed by return runs to the left or to the right. In the waggle run method (left), direction (indicated by arrows) and duration are measured for each waggle run (shown as bold zig-zag lines). In the circuit method (right), the duration of the whole dance, from the start of the first circuit to the end of the fourth circuit, is timed, and the average orientation (indicated by the bold arrow) is determined by aligning a protractor by eye.

Ratnieks 2000; Park and Nieh 2017; Rutschmann et al. 2023; Steffan-Dewenter and Kuhn 2003; Visscher and Seeley 1982). However, it is assumed that only the waggle run duration is the main distance signal used by the bees. The return phase correlates only slightly with foraging distance (Kohl and Rutschmann 2021) but varies with the resource quality (Michelsen et al. 1992; Seeley et al. 2000). Thus, relying on circuit duration (waggle plus return phase duration) could lead to significant over- or underestimation of foraging distances depending on the advertised food patch, potentially causing errors in inferred habitat use when dances are plotted on a land use map. Today, digital video recordings and computer analysis allow researchers to inspect video recordings of dances frame by frame, thereby enabling the analysis of the waggle times and the angles of individual waggle runs within dances (the average of which is obtained by calculation) (Figure 1). To ensure greater accuracy in estimating the foraging distances, it has thus become a standard method to utilize the waggle runs for dance decoding (the 'waggle run method') (Couvillon et al. 2012).

Despite significant improvements, automatic decoding technologies, as opposed to manual decoding methods, either require expensive experimental setups (Wario et al. 2017) or remain error-prone (Okubo et al. 2019), making them currently unsuitable for ecological studies that rely on data from multiple colonies at various field sites. As a result, dance decoding often remains a labour-intensive and time-consuming task, as it is still being done manually using some video analysis software on computers. The circuit method for decoding dances may be less accurate but could be significantly more time-saving compared to the waggle run method, even when analysing dances from video recordings. The circuit method requires only a single time and angle measurement per dance, whereas multiple waggle runs need to be timed separately for the waggle run method. Therefore, a trade-off likely exists between the decoding accuracy and the number of dances that can be decoded within a given time. Depending on the research question being addressed, one method might be preferred over the other. However, no study to date showed a detailed comparison of these methods. To quantify the potential time-accuracy trade-off in manual dance decoding, we decoded the same set of honeybee dances using both dance decoding methods and compared the inferred distance and directional information of the food resources, as well as the corresponding times required to analyse these dances.

2. MATERIAL AND METHODS

2.1. Dance data

We based our method test on video recordings of dances performed by normally sized colonies of *Apis mellifera carnica* housed in observation hives in the Steigerwald, in Germany. The recordings were performed as part of a larger study on honeybee foraging in a central European forest landscape (Rutschmann et al. 2023). We selected videos from four study colonies placed at four locations differing in landscape contexts to ensure observation of dances across a range of different natural foraging conditions. The recordings were all made simultaneously on March 31, 2019 (for a detailed description of colony preparation, refer to Rutschmann et al. (2023)).

2.2. Dance decoding

Recorded videos were screened for bees performing waggle dances. We decoded the dances of each consecutive bee observed dancing on the comb until we had decoded 50 dances for each of the four colonies, totalling 200 unique dances. We used the utilius fairplay 5 software (ccc software, Leipzig, Germany) for dance decoding. We chose this software because it required no preprocessing of video files or programming and offered the three key features for video-based dance decoding: (1) option to navigate videos at various speeds and frame by frame (in both directions), (2) a stopwatch and (3) a protractor. As suggested by Couvillon et al.

(2012), only dances with at least four consecutive waggle runs, excluding the first and the last runs (because of their variability), and with an equal number of right and left turns (to compensate for any angular biases caused by honeybee turning left or right) were analysed. Two commented example videos demonstrating the procedure for both the circuit method and the waggle run method are provided as supplementary files alongside this article.

Dance decoding was first done with the circuit method and then with the waggle run method. For the circuit method, the start frame of a circuit was identified (i.e. the start of a waggle run), and the stopwatch was activated. Then, videos were played back at normal speed, and consecutive dance circuits were counted. Playback was only interrupted intermittently to align the protractor tool with the longitudinal axis of the dancing bee during the waggle phases. The protractor was updated several times to align it along the visually estimated average dance angle with respect to the vertical. Eventually, the end frame of the *n*th consecutive circuit (number of consecutive circuits timed: 4–10) was identified, and the time duration of the whole sequence, the number of circuits and the (single) dance angle were entered into a data sheet. The duration of the sequence was divided by the number of circuits to obtain the mean circuit duration per dance.

When using the waggle run method for decoding dances, we measured the duration and the angle of four waggle runs for each dance separately. After the start frame of a waggle run was identified, the stopwatch function was activated, and the first of two markers of the protractor tool was dragged to the centre of the thorax. The video was then forwarded to identify the end frame of the waggle phase, after which the second position of the thorax was labelled with the second marker of the protractor tool. Finally, the time and the angle displayed by the program were copied and pasted into a data sheet. This was repeated three more times to obtain information on four consecutive waggle runs. The four measurements were then averaged to determine mean waggle duration and mean dance angle per dance.

We inferred foraging distances (d_c and d_w, in meters) from both circuit duration (t_c, in seconds) and waggle run duration (t_w, in seconds) using non-linear distance-duration calibration functions based on feeder training experiments that had been conducted with the same bees in the same forest landscape (Kohl and Rutschmann 2021).

To calculate foraging distance from circuit duration, we used the following:

for $t_c \leq 4.439852$: $d_c = \ln(-0.2253179 \bullet t_c + 1.3305467) \bullet (-1534.086)$, and

for $t_c > 4.439852$: $d_c = 1242.8536 \bullet t_c - 3818.086$.

To calculate foraging distance from waggle run duration, we used the following:

for $t_w \leq 2.2281747$: $d_w = \ln(-0.3355543 \bullet t_w + 1.0668888) \bullet (-1488.6951)$, and

for $t_w > 2.2281747$: $d_w = 1496.334 \bullet t_w - 1611.1028$.

We also inferred the Cartesian coordinates of the advertised foraging locations for both the circuit and the waggle run methods relative to the hive locations. The compass direction of the resource indicated by each dance was determined by adding the measured dance angle to the solar azimuth angle at the respective hive location and time of day. Solar azimuth data was obtained from the NOAA Solar Calculator for all dances.

2.3. Time taken to analyse dances

We measured the time it took to decode waggle dances with both the circuit and waggle run methods using a stopwatch for $N = 60$ waggle dances. First, we adjusted the video to the frame where a bee starts to shake its abdomen, i.e. the video frame where we started analysing a dance. We then started the timer and decoded the dance, as detailed above, with the circuit method. Upon completion, we stopped the timer, reverted the video to the video frame where the bee started to shake its abdomen and repeated the process for the waggle run method by starting the timer again and capturing waggle durations and dance angles for four consecutive waggles. To minimize experimenter bias, a formerly inexperienced decoder (A. Arra), blind to potential differences in the time required to analyse dances, conducted the analyses, with the question of time costs introduced by the co-authors only after sufficient decoding experience (approx. 50 dances analysed using both methods) was gained.

2.4. Statistics

All statistical analyses described below were performed using R 4.3.1 (R Core Team 2024), and all data figures were created using the R package ggplot2 (Wickham 2016). A commented R script is provided with the supplementary material to allow full replication and the same analysis with other data sets.

2.4.1. *Foraging distances*

We expected that the decoding method would primarily affect the estimated distances, not the direction, of advertised forage patches, with foraging distances translated from circuit duration (d_c) to be potentially biased compared to those inferred from waggle duration (d_w). For any given resource patch advertised, even the distance inferred from the waggle duration will randomly deviate from the 'true' distance due to natural variation inherent to the dance (Rutschmann et al. 2023; Schürch et al. 2013) and some noise introduced by the observer. However, we formerly considered the distance information from waggle durations to be accurate to use it as the independent variable in a linear regression analysis. The distance inferred from circuit duration was considered the dependent variable. In the ideal case, the waggle run method and circuit method would perfectly correspond so that $d_c = d_w$ and a linear model of d_c as a function of d_w would have a y-intercept of zero and a slope of one. Since this linear regression model tests the null hypothesis that the slope differs from zero, we also used a model of the difference between d_c and d_w as a function of d_w to formally test whether the slope of d_c as a function of d_w significantly differs from one.

Although each decoded dance was from a different bee, colony identity might have influenced the relationship between d_c and d_w. We therefore used a linear mixed effect model to account for random colony effects (function 'lmer' from the 'lme4' package) (Bates et al. 2015). A first model, built to account for random intercepts and slopes among colonies with the formulation 'lmer($d_c \sim d_w + (d_w \mid \text{colony ID})$', was not able to estimate the random effects ('singular fit'). We therefore present the result of the next less complex model that accounted for random intercepts only (formula of main model: 'lmer($d_c \sim d_w + (1 \mid \text{colony ID})$'; formula of ancillary model to test whether slope differs from 1: 'lmer($d_c - d_w \sim d_w + (1 \mid \text{colony ID})$'). p-values and marginal (pseudo) R-squared values for linear mixed models were produced using the packages 'lmerTest' ('summary' function) (Kuznetsova et al. 2017) and 'MuMIn' ('r.squaredGLMM' function) (Kamil Bartoń 2010), respectively. In addition to the formal comparison of d_c and d_w using linear models, we also compared the inferred distributions of foraging distances using descriptive statistics.

2.4.2. *Dance angles*

For testing the relationship between dance angles obtained using the circuit and the waggle run methods, we used a circular correlation test (package 'circular'; Lund et al. 2023).

2.4.3. *Foraging maps*

To investigate colony-specific variations in spatial foraging patterns among dances decoded using both the circuit and waggle run methods, foraging maps were created. Approximate foraging locations were generated using the foraging distances and angles of the decoded dances from each of the four colonies, with the central point being the location of the respective hive. Maps were constructed using QGIS software (QGIS Development Team 2021).

2.4.4. Time taken to analyse dances

The variations in the time taken to analyse an individual dance unit (i.e. one waggle run in the waggle method and one circuit in the circuit method) were compared between both methods using a paired *t*-test (function 't.test'). Moreover, we also compared the time taken to analyse a complete waggle dance (i.e. four waggle runs for each dance in the waggle run method, and four to ten dance circuits for each dance in the dance circuit method) using a paired *t*-test.

3. RESULTS

3.1. Direct comparison of foraging distances

Foraging distances obtained from the waggle run and the circuit methods were highly linearly correlated ($p < 0.0001$, marginal $R^2 = 0.7927$, Figure 2). The slope of the relationship did not significantly deviate from one (slope estimate = 1.0511, standard error = 0.0391; $p = 0.1953$). Notably, the intercept of the linear regression model was significantly different from zero (intercept estimate = 0.0856, standard error = 0.0361; $p = 0.0373$). This implies that foraging distances were systematically overestimated by approximately 86 m when decoded using the circuit method compared to the waggle run method, but this difference remained stable across foraging distances.

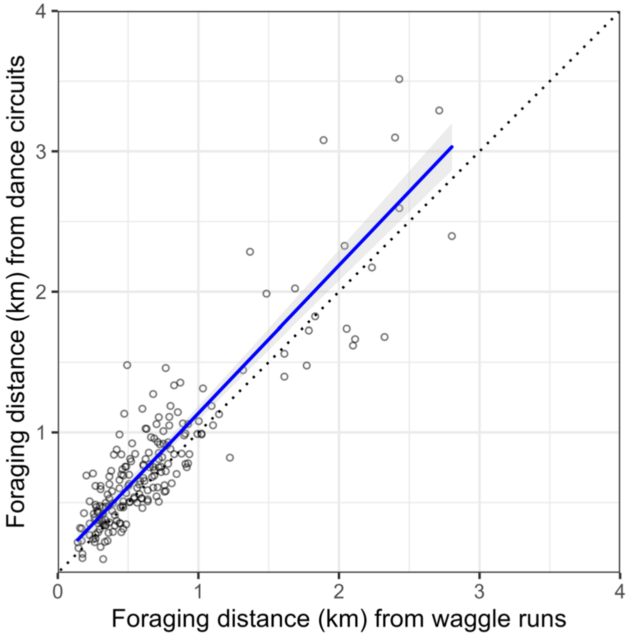

Figure 2. Comparison of foraging distances communicated by bee dances ($N = 200$) decoded using the waggle run and the circuit method. An outlier ($x = 2.5$, $y = 4.6$) lies beyond the plot's margins. The fitted linear regression model and the 95% confidence range is represented by a blue line and grey shading, while the perfect fit ($y = x$) is shown as a dotted black line.

3.2. Comparison of foraging distance distributions

In line with the linear regression analysis, the overall distribution of foraging distances (*N* = 200 dances) obtained using both methods were generally similar, but the distribution parameters were marginally higher for foraging distances calculated using the circuit method. Using the waggle run method, the mean and median foraging distances obtained were 0.71 km and 0.58 km, respectively (Figure 3). In comparison, for the circuit method, the mean and median foraging distances were 0.83 km and 0.69 km, respectively (Figure 3). Furthermore, most decoded dances (90%) fell within a range of 1.38 km for the waggle run method and 1.48 km for the circuit method. However, certain extreme values of foraging distances obtained from the circuit method were much larger compared to those from waggle run method, with the maximum foraging distance from the circuit method reaching approximately 4.58 km, significantly exceeding the maximum of approximately 2.8 km obtained from the waggle run method (Figure 3).

When comparing results for each colony separately, the mean and median foraging distances showed close similarity between both methods. These findings consistently revealed colony differences in foraging distance distributions (Figure 4). However, notable discrepancies were observed in the inferred maximum foraging ranges. For example, in colony 4, the maximum foraging distance was approximately 3 km when the waggle run method was used, whereas it extended well beyond 4 km when using the circuit method (Figure 4).

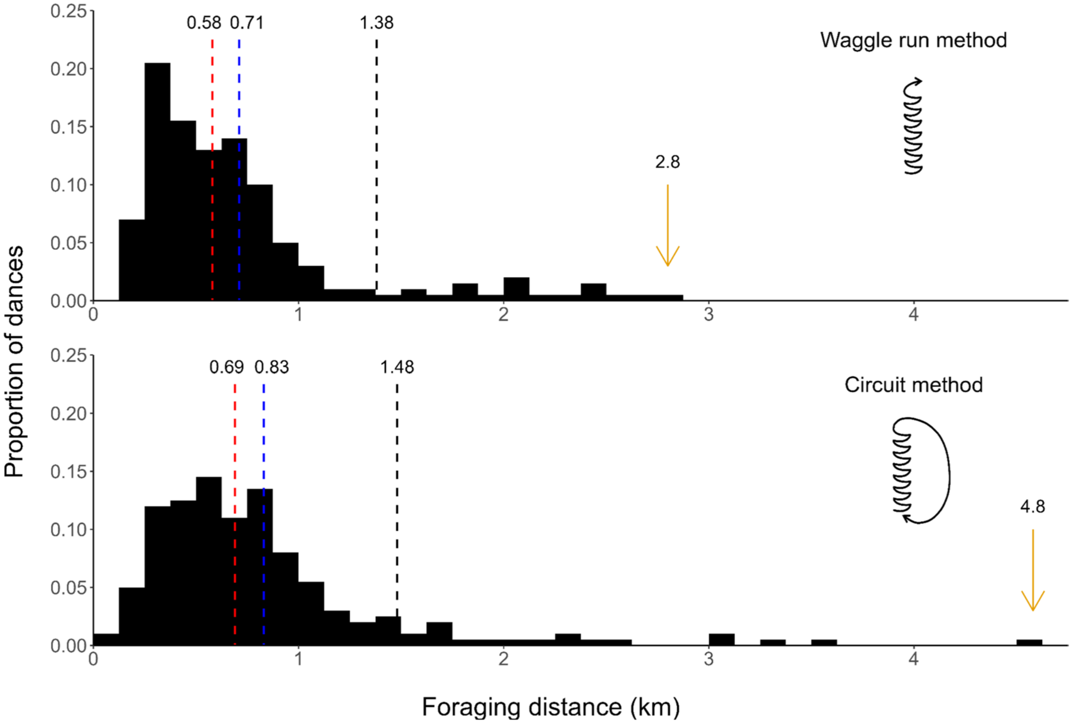

Figure 3. Comparison of foraging distances of dances (*N* = 200) calculated using the waggle run method (top row) and the circuit method (bottom row). Dashed lines represent various parameters of the foraging distance distributions (blue, mean; red, median; black, 90th percentile; yellow arrow, maximum foraging distance).

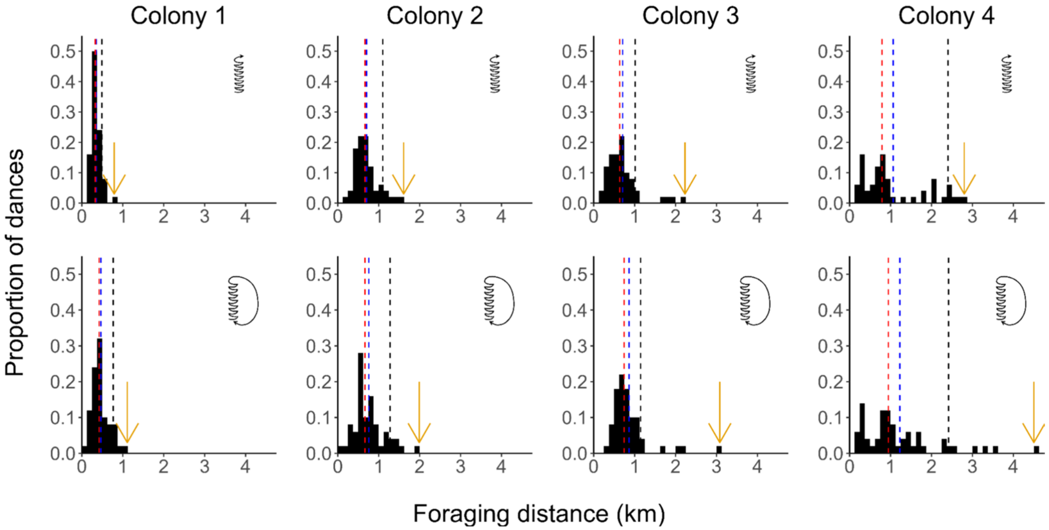

Figure 4. Comparison of foraging distances of dances ($N=50$ each) from the four distinct colonies (1–4), inferred using the waggle run method (top row) and the circuit method (bottom row). Dashed lines represent various parameters of the foraging distance distributions (blue, mean; red, median; black, 90th percentile; yellow arrow, maximum foraging distance).

3.3. Comparison of dance angles

The circular correlation analysis conducted between the mean dance angles decoded from both methods yielded a strong positive correlation coefficient ($r=0.982$, $p<0.001$, Figure 5).

3.4. Comparison of forage maps

Both decoding methods were consistent in revealing the variations in the range and distribution of foraging sites among the four study colonies (Figure 6). While minor discrepancies were observed in individual foraging sites (each corresponding to a single dance), the heat map highlighting foraging hotspots revealed consistent agreement between the waggle run and the circuit method (Figure 6).

3.5. Comparison of time taken to analyse dances

The time taken to analyse each waggle dance, regardless of the number of consecutive dance circuits timed, was three to four times higher for the waggle run method (median: 7 min 17 s per dance) compared to the circuit method (2 min per dance) (paired t.test: $\mathrm{Df}=59$, $t=-21.599$, $p<0.001$, Figure 7). When considering the time taken to decode per individual dance unit (single waggle run or single circuit), the difference was even greater. The waggle run method took almost six times longer than the circuit method (median: 109.4 s per waggle run versus 18.4 s per circuit) (paired t.test: $\mathrm{Df}=59$, $t=-25.881$, $p<0.001$, Figure 7).

4. DISCUSSION

Our study revealed considerable agreement in foraging distances estimated using the waggle run and the circuit methods. The similarity in mean dance angles measured using both methods further suggests that either method can be employed for decoding directional information. Moreover, we show that a trade-off exists between decoding investment and decoding accuracy, with the less accurate circuit method being significantly less time-consuming. Although it is known that the waggle

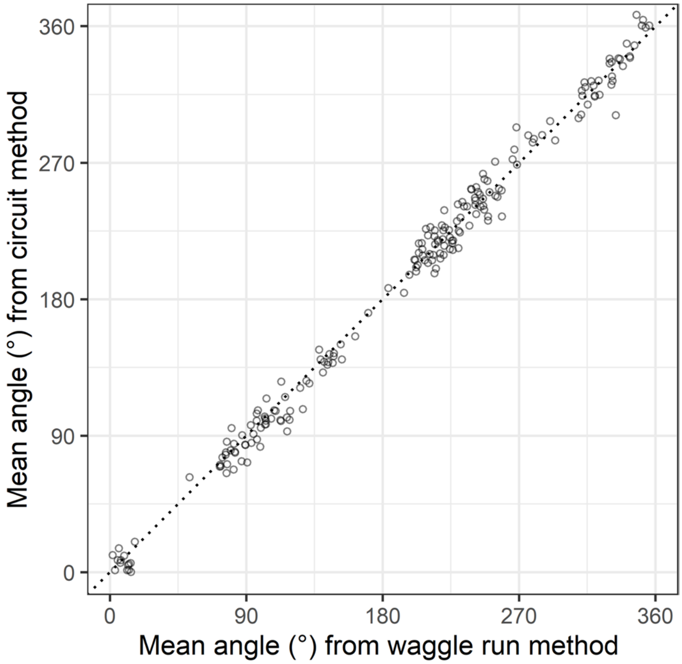

Figure 5. Linear representation of a correlation between the mean dance angles ($N=200$) determined using both the waggle run method and the circuit method. The line of perfect fit ($y=x$) is shown as a dotted line.

runs are the information-rich part of a waggle dance with respect to the distance and direction of foraging sites (Michelsen et al. 1992; Seeley et al. 2000), our results suggest that decoding from dance circuits instead of waggle runs would not substantially alter the conclusions about honeybees' spatial foraging patterns for many research questions.

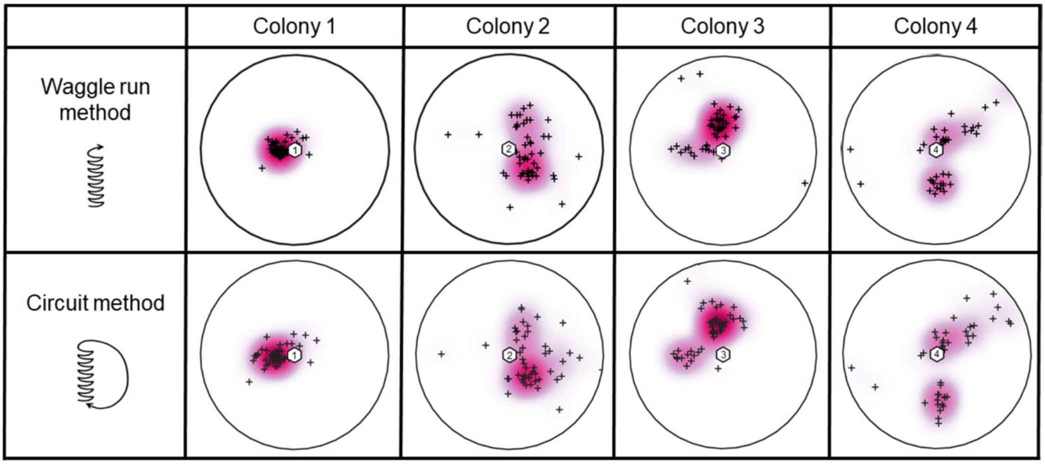

Figure 6. Comparison of forage maps for the four colonies generated by analysing dances using either the waggle run method (top row) or the circuit method (bottom row). The maps show foraging site information (crosses) extracted from 50 waggle dances per colony relative to the hive location (hexagons with colony number). A purple heat map highlights foraging hotspots. Variations in hive locations between the four colonies resulted in considerable differences in the range and distribution of foraging sites on the observation day (March 31, 2019).

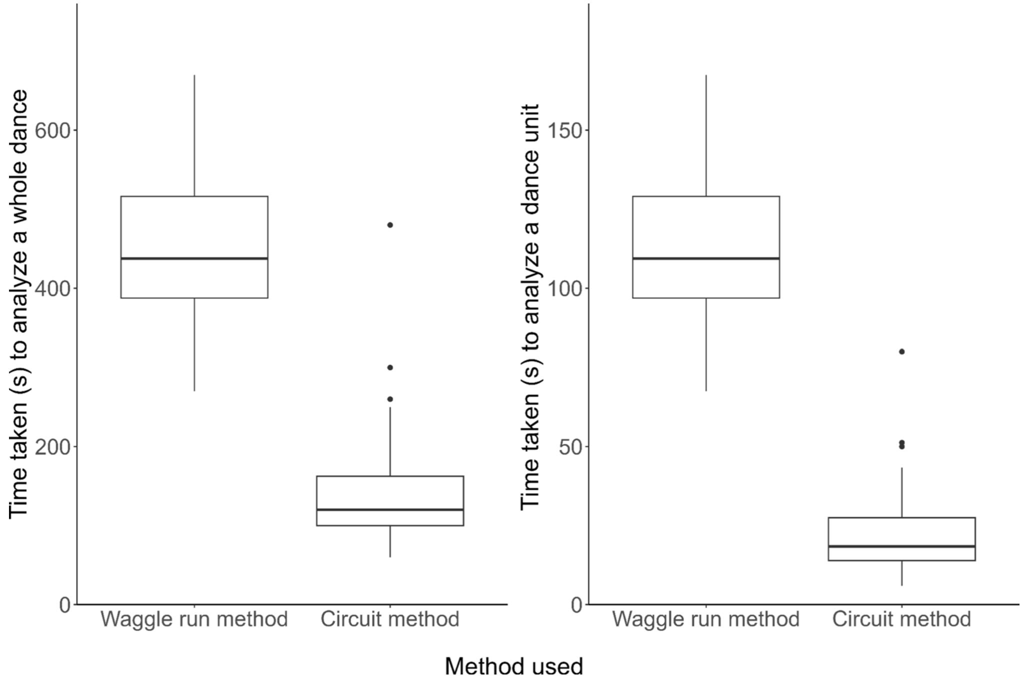

Figure 7. Comparison of time taken to analyse complete waggle dances (left) and for single dance units of honeybee dances (right), using both the waggle run method and circuit methods for the same set of waggle dances ($N = 60$).

The recognition that the duration of the return phase of the waggle dance is inversely correlated with the relative quality of a resource was a strong argument for shifting from the classical dance decoding protocol, which uses whole dance circuits (including the return phase) to decoding from waggle runs only (Schürch et al. 2013; Seeley et al. 2000). Since any given forage patch advertised by dancers may be relatively more or less rewarding than the average food patch, decoding from circuits can lead to an underestimation (high rewarding patches–shorter return phases) or an overestimation (low rewarding patches–longer return phases) of the actual distance to these patches. When considering that the statistics reported on foraging behaviour (e.g. foraging distance distribution) are typically based on many decoded dances, the circuit method could introduce noise or imprecision compared to the waggle run method, but the estimated mean values should remain unaffected. Interestingly, we show that the circuit method may not only introduce noise but also a systematic bias in inferred foraging distance, leading to inaccurate estimations of mean foraging parameters. The observed overestimation of foraging distance in our study by, on average, 86 m, indicates that the dances for natural food sources had slightly longer circuit duration than expected given the actual foraging distances (inferred from waggle durations, which we assume were accurate). A potential explanation for this overestimation is the artificial food source used for the experimental calibration of how circuit duration relates to foraging distance. To establish the distance code of the bees, they are trained to artificial feeders at varying distances from the hive, marked with colour for individual recognition, and observed back at the observation hive (von Frisch 1967). Such feeder training experiments typically rely on concentrated sucrose solution to guarantee that the bees stay highly motivated to forage at the feeders. The feeder experiment that led to the distance-duration calibration used in this study had been conducted in summer, when there was little natural forage for the bees (Kohl and Rutschmann 2021). It is thus likely that the artificial feeders were more rewarding than the average food source naturally encountered by the bees. If that was the case, bees advertising the feeders would have been likely to dance with relatively short return phases, leading to a systematic bias of the resulting distance-circuit duration calibration function.

Although the overestimation of foraging distance by the circuit method of about 86 m in our study was statistically significant, it is relatively small compared to the typical foraging distances of the bees. The median and mean foraging distance of *Apis mellifera carnica* honeybees in forest-dominated landscapes in Germany were found to be 861 and 1257 m (Rutschmann et al. 2023), so the uncorrected circuit method would overestimate these statistics by only 10% (947 m) and 6.8% (1343 m), respectively. Therefore, inferences of median or mean honeybee foraging distance obtained using the circuit method can be regarded as biologically relevant.

In the presented method test, we considered honeybee dances from four different colonies to account for colony differences in foraging patterns (Waddington et al. 1994), and both the waggle run method and the circuit method revealed variations in foraging distances and maximum foraging ranges between these colonies. However, while the central tendencies of foraging distances remained consistent across methods, maximum foraging ranges varied considerably. Colony 1, with relatively short-range foraging, showed comparable maximum foraging ranges across both methods (Figure 4). In contrast, Colony 4, which displayed notably long-range foraging, demonstrated a maximum foraging range more than 1.5 times longer when decoded using the circuit method compared to the waggle run method. Therefore, the use of the circuit method may lead to substantial overestimation of *maximum* foraging distances, particularly in colonies with larger foraging ranges. Unfortunately, accurately inferring maximum foraging distances is challenging with any method because only a few feeder training studies have trained bees beyond 1 km, meaning that inferences of foraging distances for long waggle durations are always based on extrapolations (Kohl and Rutschmann 2021). Regardless of whether the waggle run, or the circuit method is employed, we therefore recommend considering more robust measures, such as the 90th percentile foraging distance or the mean of the top 10% of foraging distances when analysing ‘maximum’ foraging distances.

In the context of long foraging distances, it also needs to be stressed that when the goal is to analyse honeybee habitat use via foraging maps, one should generally exclude dances indicating long foraging distances, regardless of the dance decoding method used. This is because, with a given error in a decoded dance direction, be it due to inherent noise in direction communication or decoding error (Schürch and Couvillon 2013), the deviation between inferred and true foraging locations rises linearly with increasing foraging distance (Rutschmann et al. 2023). Beyond a given foraging distance (the threshold is arbitrary and needs to be chosen by the investigator), the uncertainty of inferred locations usually becomes too large for forage mapping to be practical.

In addition to decoding accuracy, the time required to analyse dances is a crucial factor in method selection. Our findings indicate that the circuit method is more time-efficient than the waggle run method, which is important to consider, particularly when dealing with large datasets. For instance, imagine the task of analysing 2000 dances, a typical number for an ecological study. Following the procedures used in this study, analysing these many dances requires about 250 working hours just for decoding when using the waggle run method, but only around 67 working hours when using the circuit method.

Another neglected advantage of the circuit method is that it can be used in real time. Since only a single time and angle measurement need to be taken per dance, a researcher looking through the window of an observation hive can directly decode dances using a hand-held stopwatch and a protractor of plexiglass (von Frisch 1967). In fact, several previous studies demonstrated that such real-time decoding can fit an experimental design (Danner et al. 2014;

Steffan-Dewenter and Kuhn 2003; Visscher and Seeley 1982). It not only eliminates the need for expensive video recording and storage devices but also the burden of managing video files. Beyond research, real-time waggle dance decoding using the circuit method is an excellent educational tool for demonstrating honeybee communication and its research applications in practical courses at schools or universities.

Generally, there is a trade-off between the time required and the accuracy acquired by the method used. Therefore, the selection of decoding methods should be based on specific research objectives and constraints. In studies that focus solely on variations in foraging distances by season (Couvillon et al. 2015), landscape context (Danner et al. 2017) or comparisons between colonies (Waddington et al. 1994), the use of the circuit method may be sufficient. Similarly, in studies exploring spatio-temporal foraging patterns without direct reference to land use maps (Steffan-Dewenter and Kuhn 2003), the circuit method can be used. Whereas in studies where mapping dances on explicit land use maps is essential (Couvillon et al. 2014; Danner et al. 2014, 2016), using the waggle run method should be preferred. However, even in such cases, employing the circuit method can be acceptable if adjusted for its biases. For example, based on the data of this method test, Rutschmann et al. (2023) adjusted the distance-circuit duration function, as experimentally established by Kohl and Rutschmann (2021), to enhance the accuracy of their forage mapping.

Whether there is a systematic bias in the foraging distances inferred from circuit duration, as demonstrated here for *Apis mellifera carnica*, might depend on which *Apis* species or subspecies is considered because there are (sub) species-specific distance-duration calibrations (‘dance dialects’) (Kohl et al. 2020). It might also depend on the specific ecological circumstances of the feeder experiments that were used to obtain distance-duration calibrations (see above). We therefore recommend that researchers who choose the circuit method first evaluate its suitability for their study based on the factors discussed above. If the circuit method is applied to a bee population with a different distance-duration calibration than the one used in this study, they should follow the procedure of the presented method test to account for any potential systematic bias.

Despite being a sophisticated communication behaviour, a certain amount of error in information transfer is inevitable and is considered integral to the communication systems of social insects, playing an important functional role, such as increasing the foraging flexibility (Dussutour et al. 2009; Okada et al. 2014). While variation in the waggle dances is evident, dance followers minimize this variation by averaging the dances, similar to researchers attempting to reduce noise while decoding them (Tanner and Visscher 2008; von Frisch and Jander 1957). Various factors may be responsible for these errors in waggle dances, with many possible explanations for their occurrence (Preece and Beekman 2014). However, the presence of these errors in the waggle dance communication is undeniable (Schürch et al. 2013). Nevertheless, waggle dance decoding remains a powerful tool for studying honeybee foraging ecology from a colony-level perspective. Therefore, optimizing existing methods and carefully considering methodological trade-offs can enhance the efficacy of waggle dance decoding in various research applications until automatic dance decoding becomes widely available with high accuracy.

SUPPLEMENTARY INFORMATION

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AUTHOR CONTRIBUTION

PLK and BR conceived the study. BR collected the video recording data. AA decoded dances. AA, PLK, and BR analysed the data. AA authored the first draft. All authors contributed to the final version.

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DATA AVAILABILITY

The following information was supplied regarding data availability: The raw data is available in the Supporting Data.

DECLARATIONS

Competing interests The authors declare no competing interests.

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