# Do honeybees have two discrete dances to advertise food sources?

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The honeybee, *Apis mellifera*, dance language, used to communicate the location of profitable food resources, is one of the most versatile forms of nonprimate communication. Karl von Frisch described this communication system in terms of two distinct dances: (1) the round dance, which indicates the presence of a desirable food source close to the hive but does not provide information about its direction and (2) the waggle dance, which indicates the presence of a desirable food source more than 100 m from the hive and its provides information about both its distance and its direction. The view that honeybees have two discrete recruitment dances has been widely accepted since its inception in the 1920s. However, there are few detailed examinations of the behavioural parameters of dances over the range of food-source distances represented by round dances and waggle dances. Here, we show that both the round dance and the waggle dance convey information about distance and direction and that there is no clear switch between the two. We conclude that it is most meaningful to view the round and waggle dances as the ends of a continuum and that honeybees have just one adjustable recruitment signal: the waggle dance.

For 50 years, Karl von Frisch investigated the dance language of honeybees, *Apis mellifera*, and so achieved a sparkling series of discoveries about animal communication. From his earliest reports on this communication system (von Frisch 1923), through his summary masterwork (von Frisch 1967), to his Nobel Prize lecture (von Frisch 1974), he always described the dance language in terms of two discrete dances: round dances and waggle dances. In producing the former, a bee steps excitedly in a circle, then suddenly turns to reverse her direction of travel, circles around again before reversing again, and so on (Fig. 1). In producing the waggle dance, a bee steps straight ahead for a short distance, then turns to travel back to her starting point, again walks through a straight length, then makes a turn in the opposite direction, and so on in regular alternation. A vigorous wagging of the body gives special emphasis to the straight part of the

waggle dance, so it is often called the 'waggle phase' (Tautz et al. 1996). The round dance is quite similar to the waggle dance, although it lacks an obvious straight stretch with conspicuous body wagging, but traditionally the round dance and the waggle dance have been viewed as two distinct dances, with only waggle dances providing information about the direction to the advertised food source (Michener 1974; Winston 1987; Alcock 2005). The present paper reports a detailed comparison of round dances and waggle dances and addresses the following question: do bees have two discrete recruitment dances?

Originally, Karl von Frisch thought that round dances and waggle dances are discrete signals because he believed that they are separate advertisements for two distinct types of food sources: round dances for nectar sources and waggle dances for pollen sources (von Frisch 1923, 1942). He held this view because in his early experiments he always placed his sugar water feeders close to his study hive, so his 'nectar'-collecting bees always performed round dances, whereas the flower patches providing pollen were far away, so his pollen-collecting bees always produced waggle dances. Evidently, his initial viewpoint that

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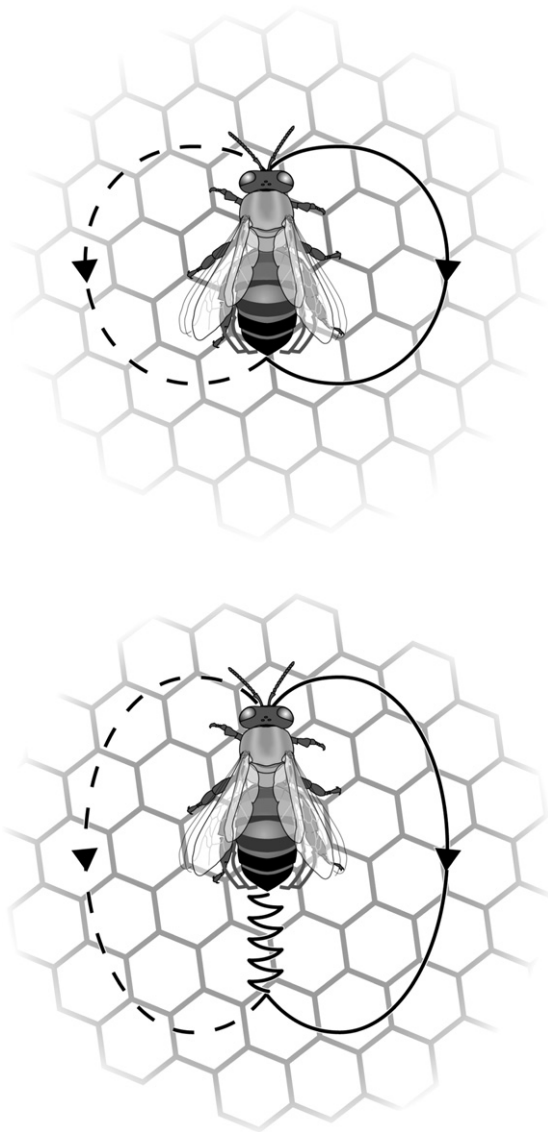
**Figure 1.** The forms of honeybee dancing that Karl von Frisch described as two discrete recruitment dances. Top: the round dance, wherein the dancing bee completes rapid circular manoeuvres, each one starting with a brief waggling of the abdomen, then a turn to the left or right, and finally a circle back to the starting point. Bottom: the waggle dance, wherein the dancing bee completes elongate manoeuvres, each one starting with a conspicuous and prolonged period of abdomen waggling, then a turn to the left or right, and finally a walk back to the starting point.

round and waggle dances are discrete signals representing distinct food types shaped his later thinking. Even after he had discovered that round dances and waggle dances represent food sources that differ in distance only, not in forage type (von Frisch 1946), he continued to write about 'the two forms of the dance' (von Frisch 1948, page 5) and he even devoted separate chapters to them in his masterwork (von Frisch 1967). Curiously, von Frisch did explain that both dances announce the existence of a profitable food source (von Frisch 1967, page 57), and he did describe a gradual transition from round dances to waggle dances when a feeder's distance from the hive is increased from

10 to 100 m (von Frisch 1967, page 61), but he never noted the basic similarity of form between round dances and waggle dances. Instead, he emphasized the distinction that waggle dances indicate the direction and distance to a desirable food source whereas round dances ostensibly indicate only the presence of an attractive food source somewhere nearby.

In recent years, several investigators have reported evidence that casts doubt on the round dance versus waggle dance dichotomy. Kirchner et al. (1988) reported that round dances, like waggle dances, contain distance information encoded in acoustical signals produced during (brief) waggle phases. They also reported that directional information is present in round dances when the food source is as close as 1 m from the hive (i.e. bees producing round dances show a preferred direction in their waggle phases). More recently, Jensen et al. (1997) also reported the presence of waggle phases in round dances but that these dances contain statistically significant directional information only for food sources greater than 15 m from the hive. Thus, both research groups concluded that round and waggle dances encode distance and direction information, but neither group concluded that round dances and waggle dances are simply different forms of the same communication signal.

Here, we report detailed findings on the behaviour of bees performing dances for near and far food sources and so take a systematic approach to comparing round dances and waggle dances. In particular, we investigated the presence of distance and direction information, which many have thought is contained only in waggle dances, by looking at dances for 10 food-source distances, ranging from 10 to 500 m. We confirm that both distance and direction information are present in both round dances and waggle dances. We also establish that both round and waggle dances can be modelled as a first-order Markov chain, and that the transition probabilities between left and right turns increase significantly with increasing distance to the food source. Finally, we propose that the round dance and the waggle dance are really just two variants of the same signalling behaviour, although there is more signal noise in dances for nearer food sources.

## METHODS

### Recording and Analysing Dances

Three unrelated colonies (A, B and C) were maintained in observation hives, as described by Seeley (1995, chapter 4). Working with one colony at a time, we trained foragers to a sugar water feeder at 10 distances (10, 30, 50, 70, 100, 150, 200, 300, 400 and 500 m) according to the methods of von Frisch (1967). Dances of individually marked bees were recorded upon their return to the hive. We recorded 15–21 dances per colony per distance (572 dances total) using a Sony mini-DV camcorder (DCR-TRV50). Only one dance per bee per distance was recorded, but an individual bee was sometimes observed and recorded at more than one distance. Feeders were supplied with 0.5–2 M sucrose solution scented with anise (60 µl/litre). Sucrose solution concentration was adjusted to promote a high,

but not overwhelming, level of dancing for the feeder. Only 5–10 bees at a time were allowed to visit the feeder, to prevent overcrowding and the inhibition of dancing (Fernández & Farina 2002; Thom 2003). All dances were recorded from 5 June 2005 to 10 August 2005 between 0800 and 1800 hours and contained a minimum of 10 waggle phases. However, in a few cases (8%, 46 of 572 dances) data from two dances with fewer than 10 waggles were combined provided they were performed by the same bee within 15 min of each other.

Since distance is indicated by the duration of the waggle phase, we calculated the average waggle-phase duration to the nearest 30th of a second for each dance. The duration of each waggle phase within a dance was measured by noting the first and last video frame that was part of each waggle phase. To investigate the relationship between waggle-phase duration in 'round' and 'waggle' dances, we divided the data into two groups based on food-source distance: 10–100 m and 100–500 m; 100 m is considered the beginning of the waggle dance (von Frisch, 1967) and was included in each group.

Directional information is conveyed by the waggle-phase angle, which was recorded with 0° as straight up and then normalized to the 'expected angle' (i.e. the difference between the sun's azimuth and the feeder's direction). This generated a circular distribution of the deviations of the observed waggle-phase angles from the expected waggle-phase angle (i.e. 0° indicates that the observed waggle-phase angle exactly matched the expected waggle-phase angle). Circular histograms were created by pooling all waggle-phase angles for each distance for each colony, as in Jensen et al. (1997). Mean vector bearing (MVB) is the mean direction of all waggle phases. Mean vector length (MVL) is a measure of dispersion about the mean direction in the circular data and can be considered a 'goal-oriented component' for each dance (referred to as 'r' in Jensen

et al. (1997) and Kirchner et al. (1988)). MVB and MVL were calculated for each colony at each distance using equations found in Fisher (1993). Rayleigh's $Z$ test was used to test for directionality with the null hypothesis that the circular distribution of all angles comes from a uniform circular distribution (Fisher 1993). Circular histograms and Rayleigh's $Z$ test were calculated using Oriana v. 2.02 (Golden, CO, U.S.A.).

## Markov Chain Analysis

The difficulty in discerning patterns in the round dance may be due to the low consistency with which foragers perform dances for nearby food sources. One measure of consistency can be derived from the patterns of left and right turns that follow sequential waggle phases. For each dance (sequence of left and right turns), we calculated first-order Markov transition probabilities using a program modified from Faraone (1986). Transition probabilities were evaluated using a $G$ test of independence. Since the sample sizes for each dance were small, data from all dances at each distance were pooled for analysis. Data from each combination of colony and distance were analysed separately. Second-order Markov transition probabilities were not calculated because there were almost no cases where a second-order model was found to apply (few cases of the following sequences: LLL or RRR; data not shown).

For each dance, we also calculated a predictability index (PI) from the first-order transition probability (TP) matrix: $PI = 1 - (TP_{RR} \times TP_{RL} + TP_{LR} \times TP_{LL})$. For example, $TP_{RL}$ denotes the transition probability of making a left turn after a right turn. This index has a value of 0.5 when the current state has no predictive value ($TP_{RR} = TP_{RL} = TP_{LR} = TP_{LL} = 0.5$) concerning the next act to be performed and a value of 1.0 when the current states provides
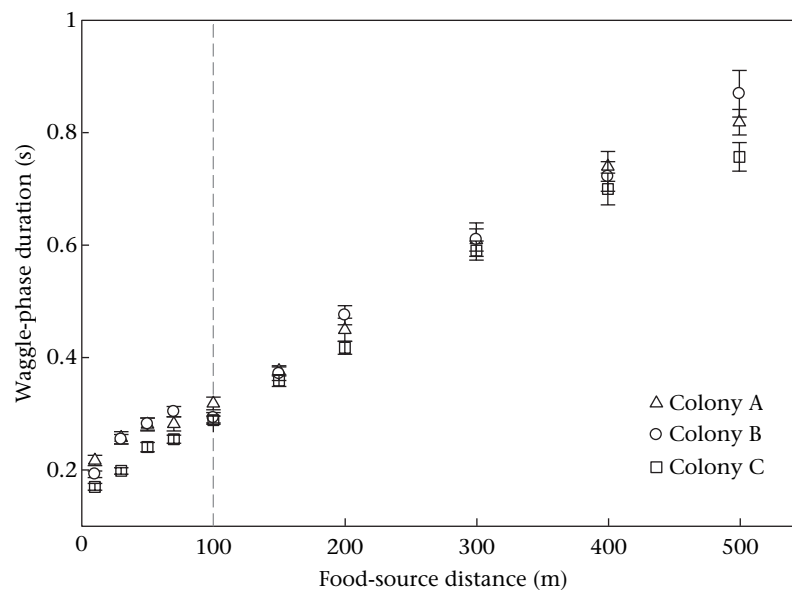


**Figure 2.** Waggle-phase duration for three colonies, mean ± SE, $N = 572$, dashed line indicates the presumed beginning of the waggle dance. Distance is encoded in the round dance in the same manner as in the waggle dance. The data point for Colony A at food-source distance of 300 m is hidden behind the data point for colony B.

complete certainty about the next act to be performed ($TP_{RR} = 0$; $TP_{RL} = 1$; $TP_{LR} = 1$; $TP_{LL} = 0$).

## Statistical Analysis

Waggle-phase duration was analysed with a repeated measures mixed model fitted with an unstructured co-variance matrix, random intercept and random slope using PROC MIXED in SAS (Littell et al. 1996). Colony was modelled as a fixed effect and distance was examined for both linear and quadratic effects. Individual bees (dancers) were treated as subjects for repeated measures. The data were transformed using the natural logarithm function to equalize variances. Separate analyses were conducted for three ranges: (1) the round dance range, 10–100 m; (2) the waggle dance range, 100–500 m; and (3) the combined range (10–500 m).

The predictability index (PI) derived from the Markov chain analysis was analysed using the same basic model just described, but without the unstructured covariance matrix, random intercept and random slope. The data were transformed using the arcsine ($\log(p)$) transformation and only a single model that included all data from 10 to 500 m was examined.

To determine whether the relationship between waggle-phase duration and food-source distance is better explained by two lines (one for round dances, i.e. for the 10–100 m data, and one for waggle dances, i.e. for the 100–500 m data) or by one line (one for both dances, i.e. for the 10–500 m data), waggle-phase duration was also analysed by fitting a quadratic equation ($Y = \text{intercept} + \beta_1 X + \beta_2 X^2$, where $Y$ is waggle-phase duration and $X$ is food-source distance) to the data by the least squares method. This regression analysis assumes that each data point (the mean duration of a bee's waggle phases for a given distance) is independent, an assumption that was violated because we observed 171 bees to get 572 data points. Nevertheless, we performed a regression analysis because this method of analysis yielded a coefficient of determination ($R^2$) that enabled us to see whether the relationship between waggle-phase duration and food-source distance is better explained by two lines or by just one. Because the estimates of the parameters (a, $\beta_1$, $\beta_2$) and associated $P$ values generated using this simple regression model were nearly identical to those generated using the repeated measures model, we only report the parameters and associated statistics from the repeated measures analysis. We report the $R^2$ values for the three models generated by the regression analysis.

## RESULTS

### Distance Information

Waggle phases were present in all recorded dances for food sources between 10 and 500 m from the hive. Figure 2 shows that in all three colonies there was a clear pattern of steady increase in waggle-phase duration with increasing food-source distance.

Over the distance range of the round dance, 10–100 m, there was a significant effect of colony on waggle-phase

**Table 1.** Parameter estimates for a quadratic line ($Y = \text{intercept} + \beta_1 X + \beta_2 X^2$) for data on waggle-phase duration as a function of food-source distance

| | | Colony A | | | Colony B | | | Colony C | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept | $\beta_1$ | $\beta_2$ | Intercept | $\beta_1$ | $\beta_2$ | Intercept | $\beta_1$ | $\beta_2$ |
| 10–100 m | Estimate±SE | 0.209±0.012 | 0.015±0.005 | −0.0004±0.0004 | 0.164±0.010 | 0.033±0.004 | −0.002±0.0004 | 0.145±0.011 | 0.022±0.004 | −0.0008±0.0004 |
| | $t$ | 31.12 | 3.16 | 1.25 | 39.84 | 8.17 | 5.64 | 41.43 | 6.87 | 3.47 |
| | $df$ | 142 | 220 | 212 | 142 | 202 | 195 | 142 | 192 | 176 |
| | $P$ | <0.0001 | <0.0018 | <0.21 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | $R^2$ | 0.34 | | | 0.52 | | | 0.64 | | |
| 100–500 m | Estimate±SE | 0.111±0.030 | 0.020±0.003 | −0.0001±0.00004 | 0.128±0.028 | 0.018±0.002 | 0.00006±0.00003 | 0.068±0.028 | 0.022±0.002 | −0.0002±0.00004 |
| | $t$ | 26.54 | 10.67 | 5.70 | 28.79 | 11.74 | 6.31 | 30.93 | 13.42 | 8.23 |
| | $df$ | 236 | 254 | 257 | 254 | 269 | 259 | 243 | 241 | 218 |
| | $P$ | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | $R^2$ | 0.82 | | | 0.77 | | | 0.82 | | |
| 10–500 m | Estimate±SE | 0.199±0.009 | 0.014±0.001 | 0.00002±0.00002 | 0.196±0.008 | 0.013±0.001 | 0.000008±0.002 | 0.146±0.008 | 0.016±0.001 | 0.00008±0.00002 |
| | $t$ | 57.32 | 17.01 | 7.18 | 59.79 | 19.79 | 8.41 | 67.19 | 25.20 | 13.13 |
| | $df$ | 220 | 541 | 520 | 168 | 490 | 503 | 170 | 488 | 462 |
| | $P$ | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | $R^2$ | 0.88 | | | 0.85 | | | 0.90 | | |

For each colony, estimates are presented for the data gathered with the feeder at 10–100 m, 100–500 m and 10–500 m. Each $P$ value indicates the probability that the estimate differs from zero simply by chance.
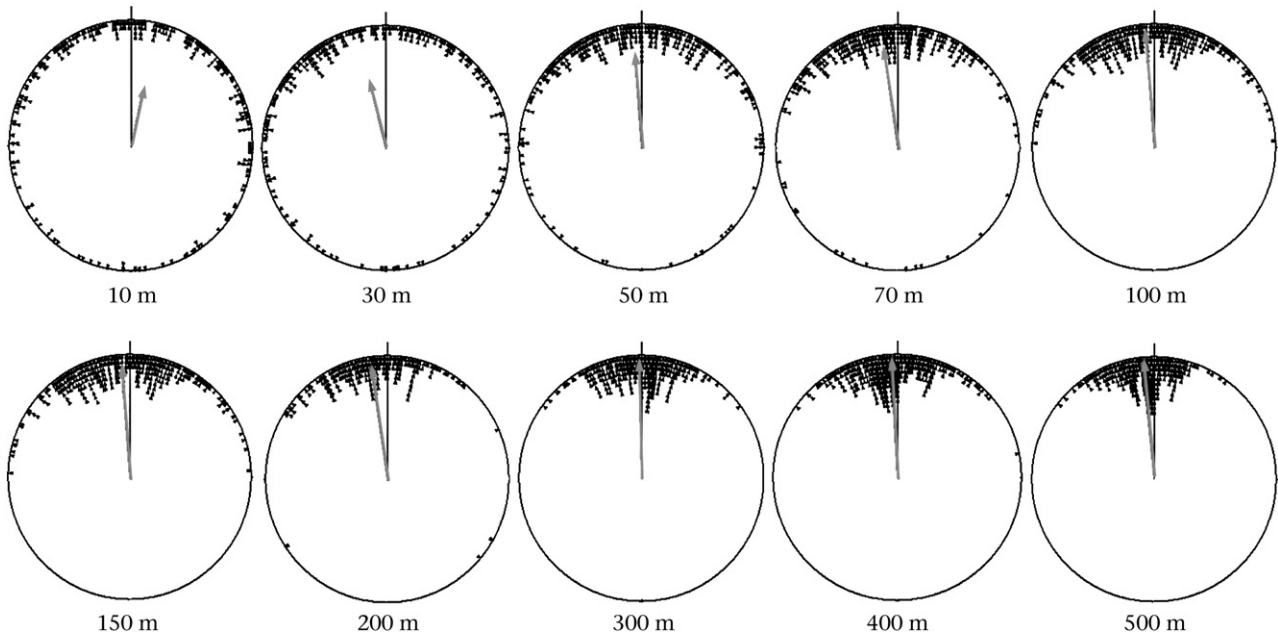
**Figure 3.** Indication of direction in the waggle phases of the dances in colony A. Statistical information for each circular histogram is provided in Table 3. For all distances, the directional component was significant ($P < 0.01$). The direction of the grey arrow indicates the MVB and the length of the grey arrow indicates MVL. The black solid line denotes the direction of the food source.

duration ($F_{2,142} = 13.24$, $P < 0.0001$); therefore, the results (parameter estimates and associated statistics) for each colony are presented separately in Fig. 2 and Table 1. There were significant linear ($F_{1,211} = 105.62$, $P < 0.0001$) and quadratic ($F_{1,198} = 34.34$, $P < 0.0001$) effects of distance on waggle-phase duration, and the interactions of colony

with both the linear ($F_{2,209} = 4.80$, $P = 0.0092$) and quadratic ($F_{2,197} = 4.16$, $P = 0.0170$) terms were significant. The linear coefficient ($\beta_1$) was highly significant in all three colonies, and the quadratic coefficient ($\beta_2$) was significant in colonies B and C, but not A (Table 1). In all colonies, the estimated quadratic coefficient was close
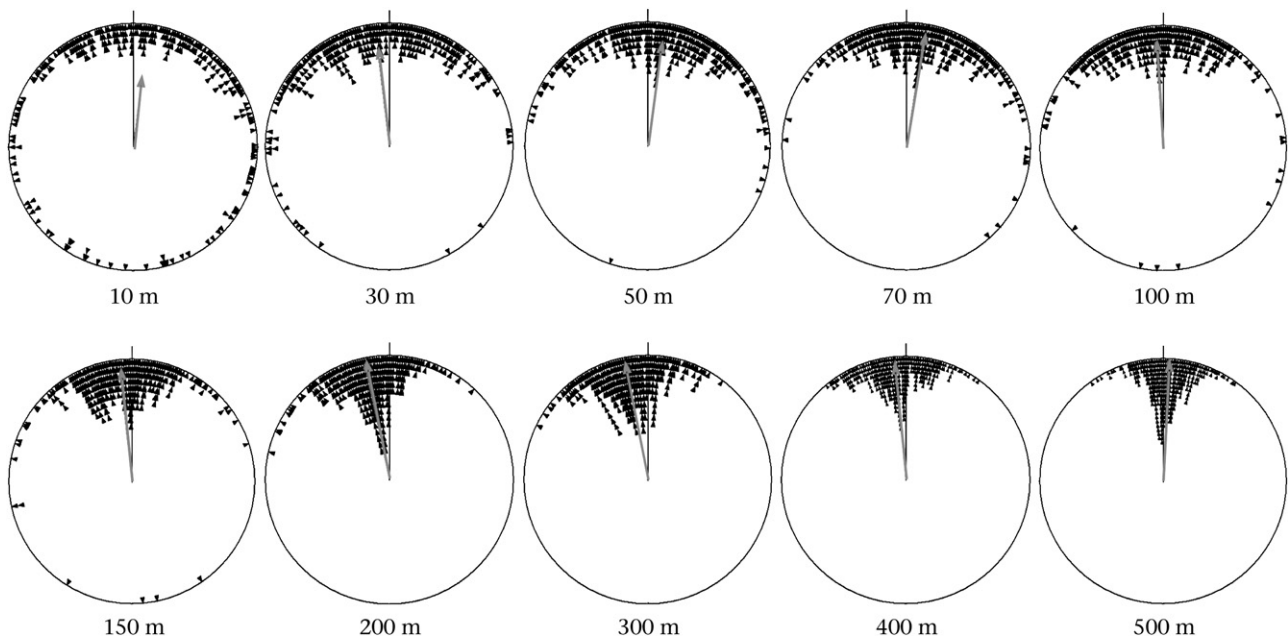


**Figure 4.** Indication of direction in the waggle phases of the dances in colony B. Statistical information for each circular histogram is provided in Table 4. For all distances, the directional component was significant ($P < 0.01$). The direction of the grey arrow indicates the MVB and the length of the grey arrow indicates MVL. The black solid line denotes the direction of the food source.

**Figure 5.** Indication of direction in the waggle phases of the dances in colony C. Statistical information for each circular histogram is provided in Table 5. For all distances, the directional component was significant ($P < 0.01$). The direction of the grey arrow indicates the MVB and the length of the grey arrow indicates MVL. The black solid line denotes the direction of the food source.
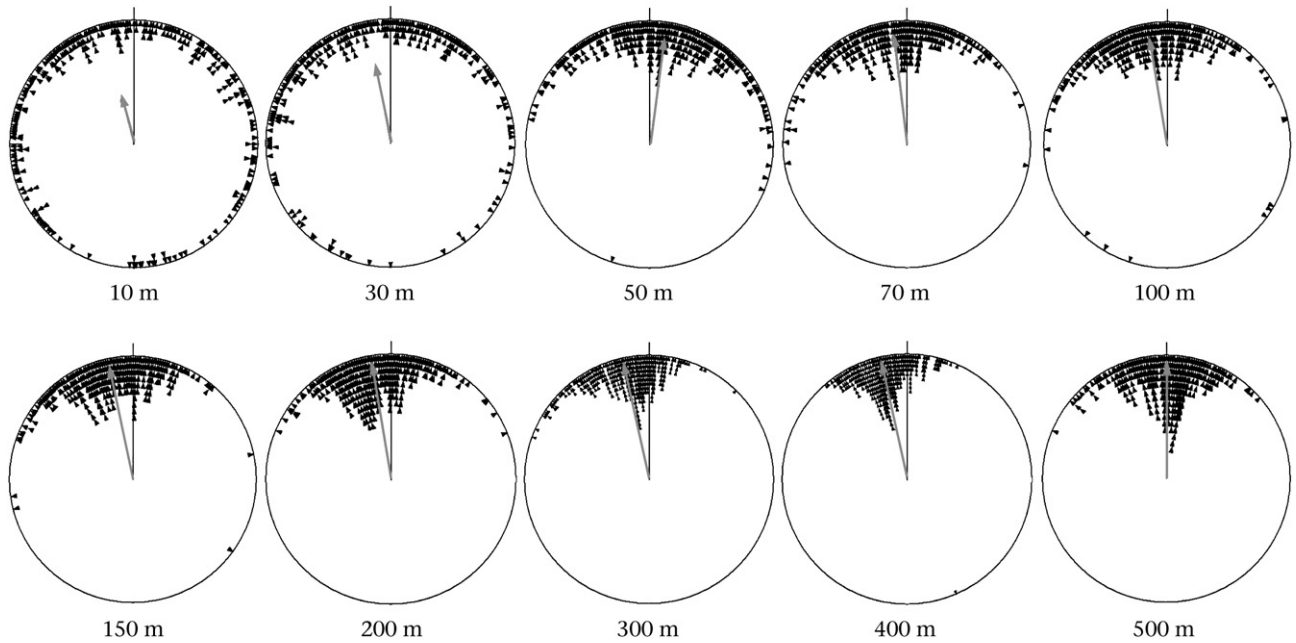
to zero, indicating that the relationship between food-source distance and waggle-phase duration was essentially linear.

Over the distance range of the waggle dance, 100–500 m, there was no significant effect of colony on waggle-phase duration ($F_{2,246} = 2.38$, $P = 0.0948$), but for consistency, the results for each colony are presented separately in Fig. 2 and Table 1. There were significant linear ($F_{1,261} = 425.11$, $P < 0.0001$) and quadratic ($F_{1,247} = 134.91$, $P < 0.0001$) effects of distance on waggle-phase duration, but the interactions of colony with the linear ($F_{2,260} = 0.91$, $P = 0.4049$) and quadratic ($F_{2,246} = 1.06$, $P = 0.3479$) terms were not significant. In all colonies, the linear ($\beta_1$) and quadratic ($\beta_2$) coefficients were highly significant (Table 1). And once again, in all colonies, the estimated quadratic coefficient was close to zero, indicating that the relationship between food-source distance and waggle-phase duration was essentially linear.

Over the distance range of both dances, 10–500 m, there was a significant effect of colony on waggle-phase duration ($F_{2,184} = 23.03$, $P < 0.0001$). There were

significant linear ($F_{1,510} = 1257.68$, $P < 0.0001$) and quadratic ($F_{1,499} = 268.01$, $P < 0.0001$) effects of distance on waggle-phase duration, and the interactions of colony with the linear ($F_{2,510} = 9.11$, $P < 0.0001$) and quadratic ($F_{2,498} = 7.07$, $P = 0.0009$) terms were also significant. In all colonies, the linear ($\beta_1$) and quadratic ($\beta_2$) coefficients were highly significant (Table 1). Yet again, in all colonies, the estimated quadratic coefficient was close to zero, indicating that the relationship between food-source distance and waggle-phase duration was essentially linear.

There was no indication that the pattern of increasing waggle-phase duration with greater food-source distance is better modelled by two regression equations, one for the distance range of the round dance (10–100 m) and one for the distance range of the waggle dance (100–500 m), than by one regression equation for the combined range (10–500 m). As is shown in Table 1, the coefficients of determination ($R^2$) for the three colonies were greater for the combined round and waggle dance range ($R^2 = 0.85$–$0.90$) than for either just the round dance range ($R^2 = 0.34$–$0.64$) or just the waggle dance range ($R^2 = 0.77$–$0.82$). This result strongly suggests

**Table 2.** Circular statistics for dances at 10 food-source distances for Colony A

| Distance (m) | 10 | 30 | 50 | 70 | 100 | 150 | 200 | 300 | 400 | 500 |
|---|---|---|---|---|---|---|---|---|---|---|
| $N$ (waggles) | 246 | 248 | 313 | 322 | 322 | 263 | 227 | 283 | 327 | 288 |
| Dances* | 17 | 15 | 17 | 20 | 17 | 18 | 16 | 19 | 20 | 20 |
| MVB (°) | 11.8 | −13.6 | −4.0 | −8.4 | −4.3 | −3.5 | −8.6 | −1.3 | −3.1 | −4.3 |
| MVL | 0.447 | 0.530 | 0.733 | 0.811 | 0.887 | 0.936 | 0.918 | 0.954 | 0.949 | 0.962 |
| Rayleigh's test ($Z$)† | 49.11 | 69.67 | 168.32 | 211.58 | 253.38 | 230.63 | 191.35 | 257.66 | 294.69 | 266.58 |

*The number of dances equals the number of dancers at each distance.
†All are significant at $P < 0.01$.

**Table 3.** Circular statistics for dances at 10 food-source distances for Colony B

| Distance (m) | 10 | 30 | 50 | 70 | 100 | 150 | 200 | 300 | 400 | 500 |
|---|---|---|---|---|---|---|---|---|---|---|
| N (waggles) | 288 | 325 | 350 | 339 | 342 | 350 | 341 | 335 | 341 | 350 |
| Dances* | 20 | 18 | 20 | 20 | 20 | 20 | 20 | 20 | 20 | 20 |
| MVB (°) | 6.8 | −6.7 | 8.3 | 8.8 | −3.9 | −6.1 | −11.9 | −10.7 | −5.1 | 2.3 |
| MVL | 0.544 | 0.791 | 0.850 | 0.879 | 0.864 | 0.906 | 0.959 | 0.956 | 0.969 | 0.982 |
| Rayleigh's test (Z)† | 88.5 | 203.1 | 252.6 | 261.8 | 255.4 | 287.1 | 313.5 | 306.5 | 320.1 | 337.2 |

*The number of dances equals the number of dancers at each distance.
†All are significant at $P < 0.01$.

that a single underlying process is responsible for the dance behaviour at all distances.

## Direction Information

To facilitate comparisons to prior studies, we plotted our directional data in the same manner as Kirchner et al. (1988) and Jensen et al. (1997). For each colony and for all distances, waggle phases showed a directional orientation and their dispersion decreased as distance increased (larger values of MVL; Figs 3−5). For all colonies at all distances, the goal-oriented component, MVL, was significant, indicating that the circular distributions of waggle phases are not uniform but instead show a preferred direction (Rayleigh's Z test, Tables 2−4).

## Markov Model

The mean and pooled transition frequencies for each distance and each colony, calculated for first-order Markov transition probabilities, and all associated statistics are given in Tables 5−7. At each distance, the transition frequencies fit a first-order Markov model. Data were analysed for a second-order Markov model but key cells in the second-order matrices do not exist, indicating that the dance does not fit a second-order process.

Analysis of the predictability index (PI) with distance as a continuous variable revealed significant effects of colony ($F_{2,440} = 21.74$, $P < 0.0001$), linear distance ($F_{1,502} = 84.59$, $P < 0.0001$), quadratic distance ($F_{1,448} = 7.95$, $P = 0.0050$) and colony by linear distance interaction ($F_{2,498} = 4.53$, $P = 0.0113$). The results for each colony are presented in Fig. 6. The

colony by quadratic distance effects were not significant ($F_{1,488} = 1.69$, $P = 0.1855$).

## DISCUSSION

Ever since its discovery by Karl von Frisch, the honeybee's dance language has captivated the attention of scientists from a range of disciplines. Furthermore, the initial terminology put forth by von Frisch to describe this communication behaviour has been broadly adopted. This study has investigated the long-standing view that there are two discrete dances, what von Frisch called the round dance and the waggle dance. Currently, it is widely believed that these are separate 'words' in the language of the bees (von Frisch 1967). However, we suggest that a revision to this terminology is needed because the round and waggle dances are merely two ends of a continuum; 'adjustable waggle dance' is sufficient. Distance and direction are encoded using the same mechanisms in both dances, and the predictability of dance behaviour gradually increases as the food-source distance increases.

This is the first report of the linear relationship between waggle-phase duration and food-source distance for round dances (Fig. 2). We also report that there is no discontinuity in the waggle-phase duration data between dances for nearby and distant food sources, which indicates that distance information is encoded in the same manner for food sources less than 100 m from the hive and for ones greater than 100 m from the hive. The slight differences between colonies, giving rise to significant colony effects, may be attributed to genetic differences (Arnold et al. 2002; Johnson et al. 2002), and possibly, to unidentified environmental factors.

**Table 4.** Circular statistics for dances at 10 food-source distances for Colony C

| Distance (m) | 10 | 30 | 50 | 70 | 100 | 150 | 200 | 300 | 400 | 500 |
|---|---|---|---|---|---|---|---|---|---|---|
| N (waggles) | 294 | 280 | 350 | 301 | 320 | 323 | 340 | 350 | 340 | 346 |
| Dances* | 19 | 18 | 21 | 20 | 20 | 20 | 20 | 21 | 20 | 19 |
| MVB (°) | −14.1 | −10.6 | 8.8 | −7.4 | −9.7 | −12.1 | −9.7 | −12.3 | −12.6 | 2.3 |
| MVL | 0.404 | 0.605 | 0.850 | 0.895 | 0.877 | 0.916 | 0.942 | 0.959 | 0.971 | 0.951 |
| Rayleigh's test (Z)† | 48.08 | 183.0 | 230.1 | 251.4 | 249.8 | 260.8 | 272.0 | 283.2 | 301.3 | 279.6 |

*The number of dances equals the number of dancers at each distance.
†All are significant at $P < 0.01$.

**Table 5.** Transition frequencies (lease square means ± SE), pooled transition frequencies (used for *G* test of independence) and first-order Markov transition probabilities for Colony A

| Distance (m) | 10 | 30 | 50 | 70 | 100 | 150 | 200 | 300 | 400 | 500 |
|---|---|---|---|---|---|---|---|---|---|---|
| Number of dances | 11 | 11 | 15 | 16 | 14 | 16 | 14 | 13 | 20 | 15 |
| $TF_{RR}$ ($PTF_{RR}$) | 1.18±4.33 (13) | 0.64±0.20 (7) | 1.40±0.32 (21) | 0.68±0.18 (11) | 0.43±0.17 (6) | 0.25±0.19 (4) | 0.43±0.20 (6) | 0.31±0.17 (4) | 0.40±0.13 (4) | 0.53±0.19 (8) |
| $TF_{RL}$ ($PTF_{RL}$) | 9.27±0.68 (102) | 7.45±1.08 (137) | 9.13±0.88 (137) | 7.94±0.59 (127) | 9.86±0.67 (138) | 6.75±0.56 (108) | 6.43±0.37 (90) | 6.85±0.61 (89) | 7.15±0.41 (143) | 6.93±0.54 (104) |
| $TF_{LR}$ ($PTF_{LR}$) | 9.27±0.68 (102) | 7.72±1.16 (85) | 9.20±0.88 (138) | 8.00±0.56 (128) | 9.71±0.61 (136) | 6.63±0.54 (106) | 6.00±0.33 (84) | 7.23±0.57 (94) | 7.20±0.57 (94) | 6.93±0.50 (104) |
| $TF_{LL}$ ($PTF_{RR}$) | 0.72±0.27 (8) | 2.27±0.41 (25) | 1.47±0.32 (22) | 1.19±0.29 (19) | 0.71±0.27 (10) | 0.31±0.15 (5) | 0.57±0.25 (8) | 0.46±0.18 (6) | 0.60±0.15 (12) | 0.40±0.13 (6) |
| $G*$ | 173.31 | 107.80 | 188.88 | 205.00 | 279.10 | 233.82 | 161.03 | 189.12 | 278.28 | 203.53 |
| $P>G$ | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| $TP_{RR}$ | 0.11±0.03 | 0.08±0.03 | 0.14±0.03 | 0.07±0.02 | 0.04±0.01 | 0.03±0.02 | 0.05±0.02 | 0.04±0.02 | 0.05±0.02 | 0.07±0.02 |
| $TP_{RL}$ | 0.89±0.03 | 0.92±0.03 | 0.86±0.03 | 0.93±0.02 | 0.96±0.02 | 0.97±0.02 | 0.95±0.02 | 0.96±0.02 | 0.95±0.02 | 0.93±0.02 |
| $TP_{LR}$ | 0.92±0.03 | 0.75±0.04 | 0.85±0.04 | 0.88±0.03 | 0.94±0.02 | 0.94±0.02 | 0.95±0.03 | 0.95±0.02 | 0.92±0.02 | 0.95±0.02 |
| $TP_{LL}$ | 0.08±0.03 | 0.25±0.04 | 0.15±0.04 | 0.12±0.03 | 0.06±0.02 | 0.06±0.02 | 0.05±0.02 | 0.05±0.02 | 0.08±0.02 | 0.05±0.02 |

*Test of independence. TF = transition frequencies (least square means ± SE); PTF = pooled transition frequencies calculated as the sum of all occurrences of the specified sequence at the specified distance; TP = transition probability (least square means ± SE); L = left turn; R = right turn.

**Table 6.** Transition frequencies (least square means ± SE), pooled transition frequencies (used for *G* test of independence) and first-order Markov transition probabilities for Colony B

| Distance (m) | 10 | 30 | 50 | 70 | 100 | 150 | 200 | 300 | 400 | 500 |
|---|---|---|---|---|---|---|---|---|---|---|
| Number of dances | 18 | 17 | 20 | 20 | 20 | 20 | 20 | 20 | 20 | 19 |
| $TF_{RR}$ ($PTF_{RR}$) | 2.23±0.37 (41) | 2.53±0.38 (43) | 1.8±0.29 (36) | 1.35±0.33 (27) | 1.6±0.29 (32) | 1.25±0.26 (25) | 0.65±0.21 (13) | 0.45±0.14 (9) | 0.40±0.13 (8) | 0.74±0.21 (14) |
| $TF_{RL}$ ($PTF_{RL}$) | 5.72±0.40 (103) | 6.88±0.32 (117) | 7.00±0.38 (140) | 7.60±0.40 (0.52) | 7.25±0.43 (145) | 8.00±0.33 (160) | 7.45±0.41 (0.49) | 8.15±0.44 (163) | 8.00±0.36 (160) | 8.32±0.39 (158) |
| $TF_{LR}$ ($PTF_{LR}$) | 5.94±0.42 (107) | 6.83±0.33 (116) | 7.10±0.38 (44) | 7.55±0.42 (151) | 7.15±0.41 (143) | 7.75±0.27 (155) | 7.50±0.41 (150) | 8.40±0.42 (168) | 7.80±0.39 (156) | 8.21±0.37 (156) |
| $TF_{LL}$ ($PTF_{RR}$) | 2.22±0.38 (40) | 2.2±0.37 (43) | 2.20±0.35 (44) | 1.85±0.39 (37) | 1.15±0.23 (23) | 1.45±0.29 (29) | 1.05±0.29 (29) | 0.20±0.09 (4) | 0.45±0.14 (9) | 0.42±0.16 (8) |
| $G*$ | 59.20 | 70.37 | 119.89 | 170.12 | 174.49 | 204.46 | 243.58 | 367.97 | 327.38 | 304.75 |
| $P>G$ | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| $TP_{RR}$ | 0.28±0.04 | 0.25±0.03 | 0.20±0.03 | 0.15±0.04 | 0.17±0.03 | 0.13±0.03 | 0.08±0.02 | 0.05±0.02 | 0.05±0.02 | 0.07±0.02 |
| $TP_{RL}$ | 0.72±0.04 | 0.75±0.03 | 0.80±0.03 | 0.85±0.04 | 0.83±0.03 | 0.87±0.03 | 0.92±0.02 | 0.95±0.02 | 0.95±0.02 | 0.93±0.02 |
| $TP_{LR}$ | 0.73±0.04 | 0.74±0.03 | 0.77±0.03 | 0.81±0.04 | 0.86±0.03 | 0.85±0.03 | 0.88±0.02 | 0.98±0.01 | 0.95±0.02 | 0.96±0.02 |
| $TP_{LL}$ | 0.27±0.04 | 0.26±0.03 | 0.23±0.03 | 0.19±0.04 | 0.14±0.03 | 0.15±0.03 | 0.12±0.02 | 0.02±0.01 | 0.05±0.01 | 0.04±0.15 |

*Test of independence; TF = transition frequencies (least square means ± SE); PTF = pooled transition frequencies calculated as the sum of all occurrences of the specified sequence at the specified distance; TP = transition probability (least square means ± SE); L = left turn; R = right turn.

**Table 7.** Transition frequencies (least square means ± SE), pooled transition frequencies (used for *G* test of independence) and first-order Markov transition probabilities for Colony C

| Distance (m) | 10 | 30 | 50 | 70 | 100 | 150 | 200 | 300 | 400 | 500 |
|---|---|---|---|---|---|---|---|---|---|---|
| Number of dances | 17 | 14 | 19 | 17 | 19 | 19 | 20 | 21 | 20 | 19 |
| $TF_{RR}$ ($PTF_{RR}$) | 1.53±0.37 (26) | 1.64±0.39 (23) | 1.10±0.24 (21) | 1.18±0.26 (20) | 0.74±0.26 (20) | 0.79±0.25 (15) | 0.60±0.23 (12) | 0.57±0.16 (12) | 0.20±0.12 (4) | 0.63±0.24 (12) |
| $TF_{RL}$ ($PTF_{RL}$) | 8.41±0.70 (143) | 7.64±0.53 (107) | 8.42±0.47 (160) | 8.65±0.56 (147) | 7.68±0.40 (146) | 7.32±0.39 (139) | 7.55±0.38 (151) | 7.86±0.37 (165) | 8.35±0.48 (167) | 8.79±0.48 (167) |
| $TF_{LR}$ ($PTF_{LR}$) | 8.29±0.70 (141) | 8.07±0.50 (0.07) | 8.68±0.47 (165) | 8.53±0..53 (145) | 7.47±0.43 (145) | 7.37±0.39 (140) | 7.75±0.35 (155) | 7.67±0.42 (161) | 8.25±0.46 (165) | 8.47±0.45 (161) |
| $TF_{LL}$ ($PTF_{RR}$) | 2.53±0.54 (43) | 1.86±0.43 (26) | 1.37±0.27 (26) | 0.59±0.21 (10) | 1.16±0.28 (22) | 0.89±0.25 (17) | 0.95±0.20 (19) | 0.76±0.23 (16) | 0.45±0.15 (9) | 0.42±0.15 (8) |
| $G^\ast$ | 143.14 | 117.57 | 233.79 | 249.64 | 224.47 | 225.11 | 261.45 | 295.39 | 369.34 | 329.96 |
| $P>G$ | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| $TP_{RR}$ | 0.16±0.04 | 0.17±0.04 | 0.11±0.02 | 0.11±0.03 | 0.08±0.03 | 0.08±0.02 | 0.06±0.03 | 0.06±0.02 | 0.02±0.01 | 0.05±0.02 |
| $TP_{RL}$ | 0.84±0.04 | 0.83±0.04 | 0.89±0.02 | 0.89±0.02 | 0.92±0.03 | 0.92±0.02 | 0.94±0.94 | 0.94±0.02 | 0.98±0.01 | 0.95±0.02 |
| $TP_{LR}$ | 0.77±0.05 | 0.82±0.04 | 0.86±0.03 | 0.94±0.02 | 0.87±0.03 | 0.90±0.03 | 0.90±0.02 | 0.92±0.02 | 0.96±0.01 | 0.95±0.02 |
| $TP_{LL}$ | 0.23±0.05 | 0.18±0.04 | 0.14±0.03 | 0.06±0.02 | 0.13±0.03 | 0.10±0.03 | 0.10±0.02 | 0.08±0.02 | 0.04±0.01 | 0.05±0.02 |

*Test of independence; TF = transition frequencies (least square means ± SE); PTF = pooled transition frequencies calculated as the sum of all occurrences of the specified sequence at the specified distance; TP = transition probability (least square means ± SE); L = left turn; R = right turn.
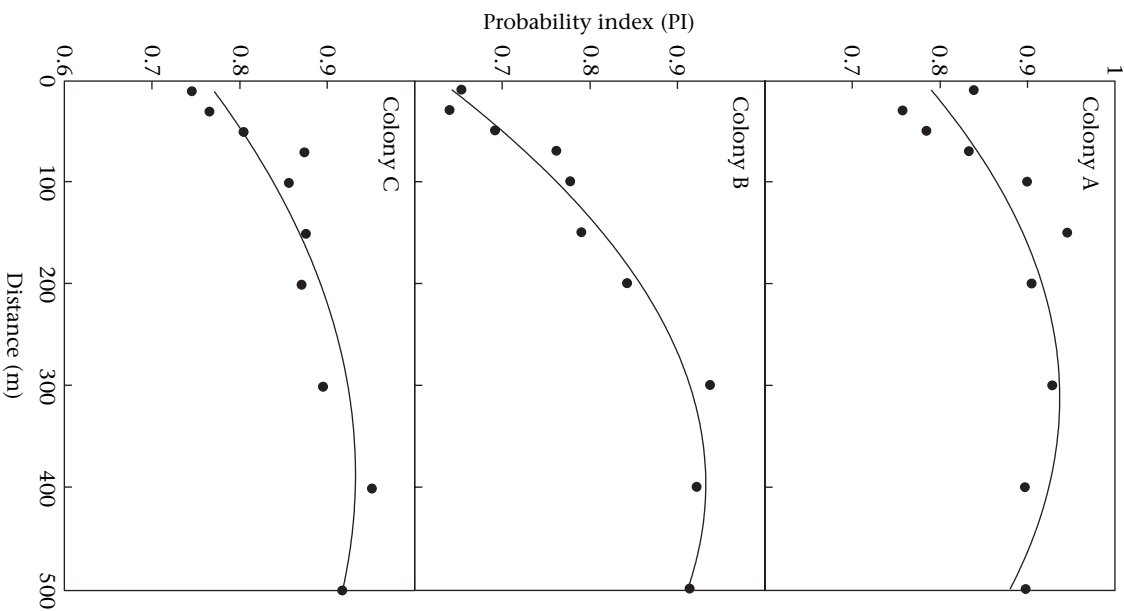


**Figure 6.** Average probability index (PI) at each distance for the three colonies. PI is a measure of consistency in alternating left and right turns. A PI of 1.0 indicates that a left turn always followed a right turn. A PI of 0.5 indicates that left and right turns are equally likely after a left or right turn.

The presence of waggle phases in round dances was described by von Frisch and others (see Jensen et al. 1997). However, it was believed that there is no information in the brief waggle phases of round dances. The linear relationship between waggle-phase duration and food-source distance from approximately 100 m up to 10000 m from the hive was already well documented (von Frisch 1967). Here, we extend those findings by showing that the linear relationship also exists for food sources between 10 and 500 m from the hive.

Kirchner et al. (1988) reported significant directionality in the waggle phases of dances for food sources just 1 m from the hive. However, they analysed the circular distributions of the mean waggle-phase angles of whole dances, each containing dozens of waggle phases. This method of analysis presumes that a bee following a waggle dance

follows the entire dance and then determines the mean waggle-phase angle of the dance. Although the mechanisms by which dance followers acquire information from dances are not fully understood (Judd 1995), the scenario presumed by Kirchner et al. (1988) is unlikely given that individual dances can contain up to 200 waggle phases (Seeley 1995) but that bees following a dance typically attend fewer than 10 waggle phases (Judd 1995). Our results are congruent with those of Jensen et al. (1997), who reported significant directionality for food sources as close as 15 m from the hive, based on an analysis of the circular distributions of individual (not mean) waggle-phase angles.

An interesting pattern emerged in the circular distributions: there appears to be a slight, left-directed bias in the waggle phases (negative MVB). Although unlikely, this could reflect the influence of an artificial light source outside the hive to which the bees were orienting during their dancing. Or, perhaps the dancers were compensating for the fact that recruit bees would be flying to the goal when the sun was in a position slightly different from that during the recruiting bee's dance, which would introduce a bias to the left of the expected orientation.

Our analysis reveals two possible reasons why most previous observers have not noticed the fundamental similarity of round dances and waggle dances. First, although dances advertising food sources far from the hive (>500 m) have a highly regular pattern of alternating left and right turns, which in a Markov chain analysis results in a PI of nearly 1.0, the regularity of this pattern decreases in a nonlinear fashion as the distance between hive and food source decreases. It is possible that previous observers overlooked the unitary nature of the dance language because the pattern of alternating left and right turns is much less apparent for food sources near the hive. Second, the large amount of 'noise' (small MVL) in dances for nearby food sources evidently led to an initial conclusion that there is no directional information within the round dance, as described by von Frisch (1967). However, the present examination of this signalling behaviour shows that both distance and direction information are encoded in dances for all distances. The signal-to-noise ratio, however, increases as distance increases (see Kirchner et al. 1988). We conclude that the bees have only one dance that always encodes distance and direction to the food source, but that the precision of expression of this information depends on the distance to the recruitment target.

## Acknowledgments

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