

# Honey bee waggle dance communication: signal meaning and signal noise affect dance follower behaviour

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**Abstract** Returning honey bee foragers perform waggle dances to inform nestmate foragers about the presence, location and odour of profitable food sources and new nest sites. The aim of this study is to investigate how the characteristics of waggle dances for natural food sources and environmental factors affect dance follower behaviour. Because food source profitability tends to decrease with increasing foraging distance, we hypothesised that the attractiveness of a dance, measured as the number of dance followers and their attendance, decreases with increasing distance to the advertised food location. Additionally, we determined whether time of year and dance signal noise, quantified as the variation in waggle run direction and duration, affect dance follower behaviour. Our results suggest that bees follow fewer waggle runs as the food source distance increases, but that they invest more time in following each dance. This is because waggle run duration increases with increasing foraging distance. Followers

responded to increased angular noise in dances indicating more distant food sources by following more waggle runs per dance than when angular noise was low. The number of dance followers per dancing bee was also affected by the time of year and varied among colonies. Our results provide evidence that both noise in the message, that is variation in the direction component, and the message itself, that is the distance of the advertised food location, affect dance following. These results indicate that dance followers may pay attention to the costs and benefits associated with using dance information.

**Keywords** *Apis mellifera* · Waggle dance · Foraging · Honey bee · Communication · Signal noise

## Introduction

Many animals produce signals for directing conspecifics to feeding locations (Wilson 1971; Galef and Buckley 1996; Judd and Sherman 1996; Maynard-Smith and Harper 2003; Sumpter and Brännström 2008; Shettleworth 2010). These signals are especially well studied in social insects. In some cases successful foragers emit signals that simply increase foraging effort (Thom et al. 2007; Jarau and Hrncir 2009), including the vibratory signal in the honey bee, whose message is “increase your work rate” (Schneider and Lewis 2004). In other cases, the signals also send recruits to specific locations by direct guiding (Hölldobler and Wilson 1990; Nieh 2004; Jarau and Hrncir 2009), trail pheromones (Wilson 1971; Beekman et al. 2001; Nieh 2004; Jarau and Hrncir 2009), or the honey bee waggle dance (von Frisch 1967).

Honey bees, *Apis mellifera* and other *Apis*, are well known for using the waggle dance to provide nestmates with information about the presence, location, quality and odour of profitable food sources (reviewed in: von Frisch

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1967; Seeley 1995; Dyer 2002; Grüter and Farina 2009a; Couvillon 2012). During a waggle dance, a worker bee waggles her abdomen as she walks in a straight line (waggle run), then turns either to the left or right to return to the starting point (return phase), before she usually repeats another waggle run. This waggle run is the information-rich part of a dance (von Frisch 1967; Seeley et al. 2000; Michelsen 2003) and provides the direction and distance vector from the nest to the feeding location. A dancing bee may perform from 1 to 100 or more waggle runs, depending on the resource quality and nectar availability (von Frisch 1967; Seeley et al. 2000). Higher quality resources tend to elicit dances with more repeated waggle runs (von Frisch 1967; Seeley 1995). The dance signal is quite noisy in that successive, repeated waggle runs within a dance vary in direction and duration (Dyer 2002; De Marco et al. 2008; Couvillon 2012; Couvillon et al. 2012b; Schürch and Couvillon 2013), even if the mean is unaffected. Dance followers reduce the effect of signal noise by averaging several waggle runs to compute an overall vector (von Frisch and Jander 1957; Tanner and Visscher 2008). Consequently, the number of waggle runs followed positively correlates with the accuracy of the flight vector (Tanner and Visscher 2009). Therefore, following more waggle runs is beneficial in terms of information accuracy, but requires more time. Previous work has reported that foragers that were successfully recruited to a food location by a waggle dance followed on average eight (Judd 1994), 17 (Grüter et al. 2008), 15.5 (Wray et al. 2012) or 20–23 waggle runs (Menzel et al. 2011). It has been suggested that dance followers need to follow a minimum of approximately five waggle runs to acquire precise location information (von Frisch and Jander 1957; Esch and Bastian 1970; Mautz 1971; Biesmeijer and Seeley 2005; Grüter and Farina 2009a).

Dance following has mostly been studied in experimental situations with nearby *ad libitum* sucrose feeders in environments with few or zero good natural food sources (Grüter et al. 2008; Grüter and Ratnieks 2011; Menzel et al. 2011; Wray et al. 2012). This rather unnatural situation might affect how foragers use waggle dance information (Grüter and Farina 2009a). We know of only one study that investigated dance following behaviour in a naturally foraging colony (Biesmeijer and Seeley 2005). Interestingly, this study reported that dance followers followed on average only two to four (range 1–20+) waggle runs (Biesmeijer and Seeley 2005). The authors suggested that only in 12–25 % of cases did dance following lead to discovery of the advertised location. Some of the other follower bees might have resumed foraging at familiar food sources after perceiving a familiar flower odour on the dancer (von Frisch 1923; Ribbands 1954; von Frisch 1967; Wenner et al. 1969; Wenner and Wells 1990; Reinhard et al. 2004; Grüter et al. 2008). Reactivation does not require extensive dance

following but simply the detection of the familiar odour on the dancer. This might explain why reactivated foragers followed on average less than five waggle runs (Grüter et al. 2008; Grüter and Ratnieks 2011; Wray et al. 2012, but see Menzel et al. 2011, where reactivated bees followed >20 runs). Biesmeijer and Seeley (2005) found that many dance followers were active foragers, which led them to hypothesize that dance following provided “confirmation” of the continued availability of a familiar food source. However, the interpretations made by Biesmeijer and Seeley (2005) about how often dances are followed for the discovery of new food patches, reactivation or confirmation were based on assumptions about how foragers would behave after leaving the hive rather than actual observations. This is because it has not yet been possible to investigate what followers of natural dances do once they leave the hive due to the foraging distances and flight speed of foragers.

The aim of this study was to investigate how the characteristics of the waggle dances for natural food sources and environmental factors affect natural dance follower behaviour. We tested the hypotheses that the distance of the advertised food source and the informational noise in the waggle run affect dance follower behaviour. Foragers might follow more waggle runs for distant food sources because getting lost at a greater distance from the colony is potentially more costly. On the other hand, dances for more distant food sources might arouse less interest for several reasons, including the increased flight costs, the time it takes to follow the longer dance circuits, the increased chance that the food source disappeared before being located, or the lack of odour molecules on the dancers’ body after longer flight (von Frisch 1967), which function as orientation cues for followers (Díaz et al. 2007). We also tested whether the time of year and the overall dancing activity influence the number of dance followers and the number of waggle runs that a follower follows. Because signal noise might affect the attractiveness of a dance to the dance followers, we tested for an effect of the standard deviation of waggle run duration and angle on the dance followers. Our results show that workers follow fewer waggle runs as the food location distance increases, but that they invest more time in following each dance. The number of dance followers per dancing bee was also affected by the time of year and varied among colonies.

## Materials and methods

### Study organism and hives

We used three colonies (H1–H3) of honey bees (*A. mellifera mellifera*), each housed in an observation hive with three medium and one deep Langstroth frames. Hives were kept indoors at room temperature (c. 20 °C) at our laboratory on

the campus of the University of Sussex. Each colony had a queen, brood, c. 5,000 workers, and adequate honey stores but also vacant cells to store additional honey and pollen. Because the colonies were housed in glass-walled hives, we monitored these conditions through the course of the experiment to ensure good health and similarity between colonies. A plastic tube 3 cm in diameter and 30 cm long connected each hive to the outside, which allowed foragers free flying access.

#### Dance decoding

Dances were decoded for the location vector for another project (Couvillon et al. 2012a), and these dances were then used to study dance following behaviour in our investigation. Briefly, to decode dances, we videoed each observation hive for 1 h between 0900 and 1600 on each study day using camcorders (Canon Legria HV40, HDV 1080i). Cameras were placed 1 m from hives to reduce parallax and then zoomed to an area 25 cm wide × 20 cm high. Cameras were daily directed towards the area of most dances (the “dance floor”). Plumb lines of nylon fishing line with heavy metal washers at the end were hung at 5 cm intervals across the wall of outer glass. These appeared as thin white lines in the video and gave a vertical frame of reference.

Videos were analysed using Final Cut Express (Version 4.0). Dances were decoded frame by frame. We detected the beginning and end of each waggle run by observing whether or not the dancer’s body and wings were blurred on a single video frame. The exact beginning and end points (hour, minute, second, frame) were taken from the timer of the video software to a temporal resolution of 0.04 s (one frame). This provided both waggle run duration and circuit duration (waggle run + return phase). Each dance is composed of a variable number of runs (four to 32). Previous work has determined that it is sufficient to decode and to average at least four successive waggle runs, excluding the first and last run, as they are significantly more variable in both duration and angle (Couvillon et al. 2012b). Averaging four waggle runs provides a reliable mean estimate for the entire dance (Couvillon et al. 2012b). We calculated the mean and standard deviation for both duration and angle for all waggle runs within a bout of dancing. Additionally, we recorded whether a dancer carried pollen to test if the presence of pollen affects the attractiveness of a dance.

#### Dance follower behaviour

We analysed dance following behaviour in 4 months (September 2009; April, May and July 2010). These months were selected because food abundance and average foraging distance, as measured by waggle run duration, varied greatly among these months (Couvillon et al., unpublished results), which include spring, summer and autumn. For each

decoded dance, we determined the number of dance followers 10 s after the beginning of the dance (after Grüter and Farina 2009b) and then determined the number of waggle runs these followers followed from this moment on. Waiting for 10 s gave surrounding bees time to identify and approach the dance. Additionally, we also recorded how many other dances were occurring simultaneously in the video.

By analysing the movement of followers, we made sure that bees, which were merely standing near a dancer, were not counted as followers. Followers were identified as bees facing the dancer with their heads within antennal length during the waggle run and who followed the movement of the dancer (Tanner and Visscher 2008; Grüter and Ratnieks 2011). To quantify dance following duration, we recorded how many waggle runs each dance follower then followed. A follower was considered to have stopped following a dance if she turned from the dance and walked away. A dancer was considered to have stopped dancing if she interrupted a dance for >5 s, e.g., for nectar transfers. For statistical analysis, we averaged the number of waggle runs followed by all followers of a dance to obtain a mean value per dance.

#### Statistical analysis

We analysed the data using general linear models in Minitab (version 14). We first tested whether hive and the presence of pollen affected the number of followers and the average number of waggle runs followed. If not, we pooled the data across hives or dances with and without pollen to increase statistical power. If necessary, we transformed the response variable with log or square-root transformations to meet the assumptions of ANOVA (Grafen and Hails 2002). We centred continuous explanatory variables (the mean was subtracted from each value) to facilitate interpretation of interactions between them (Grafen and Hails 2002). Before including multiple continuous explanatory variables, we made sure that they correlated only weakly to avoid problems of co-linearity. Non-significant interactions between explanatory variables ( $P > 0.05$ ) were removed from the model. All tests are two-tailed. Descriptive statistics are given as mean ± standard deviation.

## Results

#### Descriptive statistics

We analysed the behaviour of 2,405 dance followers in 602 dances (Fig. 1a, b), 249 dances in hive 1, 185 in hive 2 and 168 in hive 3. We discarded 26 dances (4.1 %) either because foragers stopped dancing before the followers stopped following or because dancers left the videoed area before all dance

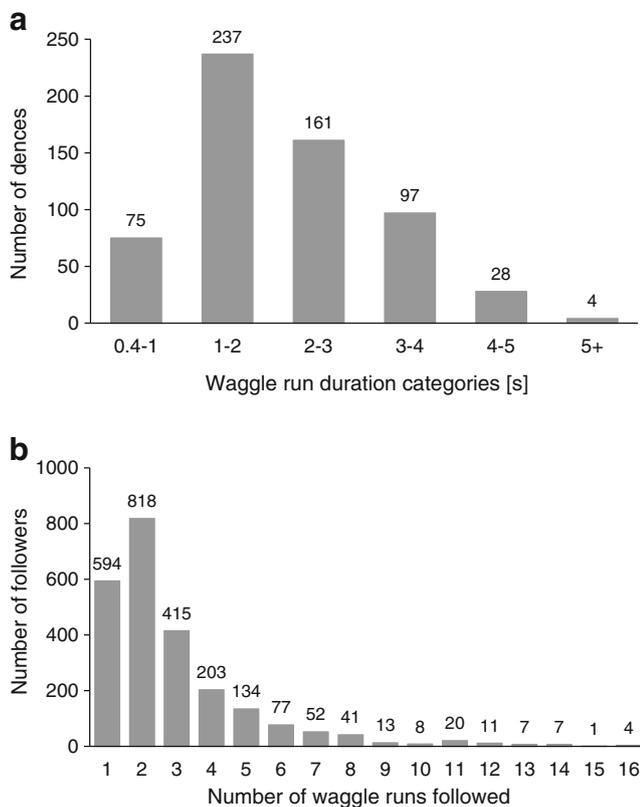
followers finished dance following. The average number of followers was  $3.98 \pm 0.92$  per dance (range 2–8). Of all dancers, 21 % were foragers carrying pollen.

The average number of waggle runs followed by each follower was  $2.80 \pm 1.38$  (range 1–16; Fig. 1b; hive 1,  $2.75 \pm 1.29$ ; hive 2,  $2.81 \pm 1.33$ ; hive 3:  $2.88 \pm 1.56$ ).

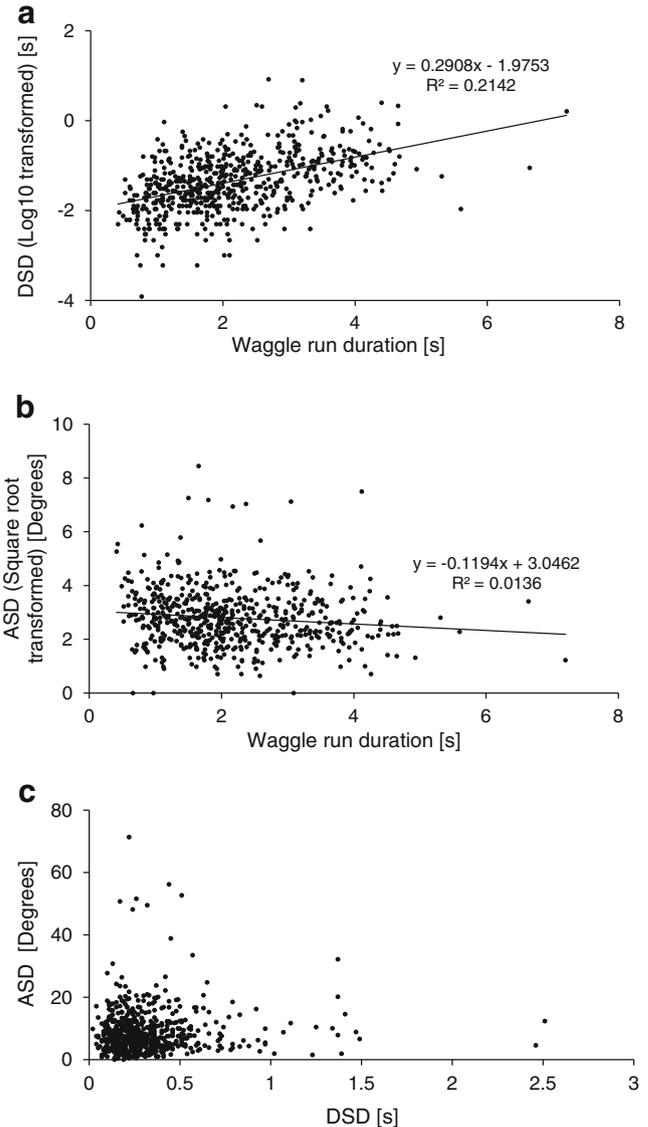
First, we tested whether the mean waggle run duration, which encodes foraging distance, affected the standard deviation of waggle run duration or waggle run direction within a dance. There was a significant positive effect of mean waggle run duration on duration standard deviation (DSD;  $F_{1,600}=162.20$ ,  $R^2(\text{adj})=21.18\%$ ,  $P<0.001$ ; Fig. 2a), and a significant negative effect of mean waggle run duration on angle standard deviation (ASD;  $F_{1,600}=7.80$ ,  $R^2(\text{adj})=1.12\%$ ,  $P=0.005$ ; Fig. 2b). There was no relationship between the ASD and DSD ( $F_{1,600}=1.30$ ,  $R^2(\text{adj})=0.05\%$ ,  $P=0.255$ ; Fig. 2c).

Experiment 1: factors affecting the number of waggle runs followed

We tested whether the number of waggle runs followed differed between hives and depended on whether dancers carried

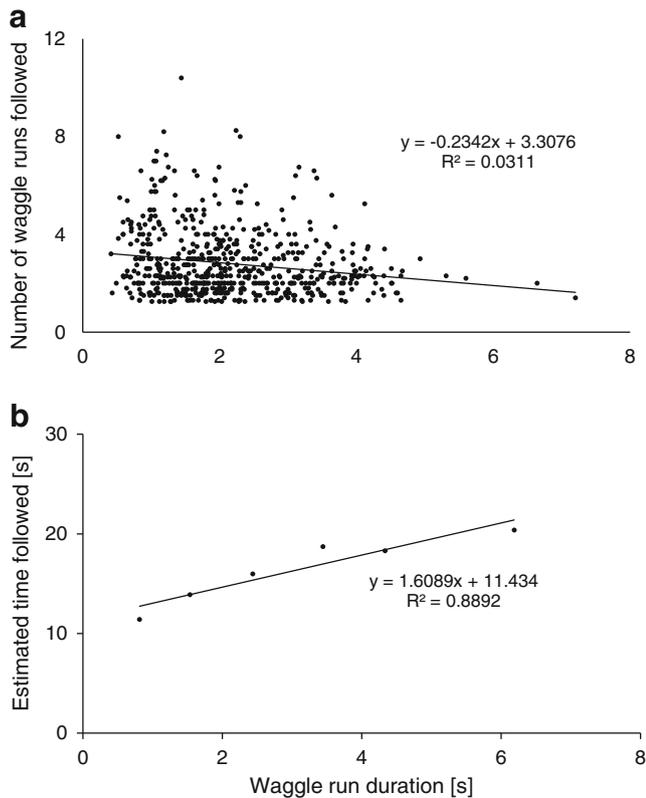


**Fig. 1** The frequency distribution of waggle run durations and the number of waggle runs followed per dance (maximum was 16). Most followers followed dances only briefly, for one or two waggle runs. **a** The distribution of waggle run durations for all 602 dances. **b** The number of waggle runs followed by followers per dance



**Fig. 2** **a** There is a positive relationship between waggle run duration and duration standard deviation (DSD). **b** There is a weak but significant negative relationship between waggle run duration and angle standard deviation (ASD). **c** There is no significant relationship between these two components of noise (DSD and ASD). We used log10 and square root transformation to transform the response variable when this was necessary to meet the assumptions of ANOVA. For each data set, the best transformation was chosen

pollen. We found a non-significant effect of hives ( $F_{2,596}=1.25$ ,  $R^2(\text{adj})=0.41\%$ ,  $P=0.287$ ), pollen versus non-pollen ( $F_{1,596}=0.09$ ,  $R^2(\text{adj})=0.01\%$ ,  $P=0.765$ ), and the interaction ( $F_{2,596}=2.36$ ,  $R^2(\text{adj})=0.78\%$ ,  $P=0.095$ ) between the two (entire model,  $R^2(\text{adj})=0.00\%$ ). Hence, we pooled the data across dance types and hives to increase statistical power. We ran a model including month, waggle run duration, DSD, ASD, and the number of simultaneous dances as explanatory variables. We found a significant effect of waggle run duration ( $F_{1,592}=4.08$ ,  $R^2(\text{adj})=0.67\%$ ,  $P=0.044$ ; Fig. 3a), but not



**Fig. 3** The number of wagggle runs followed decreases with increasing wagggle run duration of a dance, but with increasing wagggle run duration (further distance of the food source), bees follow a dance longer in terms of time. **a** The relationship between the wagggle run duration and the number of wagggle runs followers followed per dance. **b** The relationship between wagggle run duration and the estimated time (seconds) that followers follow the dancer. The estimated time of following was calculated by multiplying circuit duration and the number of wagggle runs followed for each category. The *line* represents a best-fit line of a regression analysis ( $R^2=0.889$ ) using the means of the categories

month ( $F_{3,592}=2.42$ ,  $R^2(\text{adj})=1.19\%$ ,  $P=0.065$ ), DSD ( $F_{1,592}=2.05$ ,  $R^2(\text{adj})=0.34\%$ ,  $P=0.152$ ), ASD ( $F_{1,592}=0.07$ ,  $R^2(\text{adj})=0.01\%$ ,  $P=0.785$ ) or the number of simultaneous dances ( $F_{1,592}=1.11$ ,  $R^2(\text{adj})=0.18\%$ ,  $P=0.292$ ). Additionally, the interactions between wagggle run duration and ASD was significant ( $F_{1,592}=4.09$ ,  $R^2(\text{adj})=0.67\%$ ,  $P=0.044$ ; entire model,  $R^2(\text{adj})=3.91\%$ ). This suggests that the angular noise also affected dance following but that this effect depends on the duration of the wagggle run and, therefore, the distance to the food source. The slope of the interaction was positive ( $y=0.0014x-0.640$ ). Figure 3a shows the relationship between the indicated wagggle run duration and the number of wagggle runs followed.

Our findings show that followers follow fewer wagggle runs for more distant food sources. However, as wagggle runs and return phases take longer for further distances (von Frisch 1967), followers might actually invest more time in following these fewer runs. To visualize this relationship,

we created six categories of wagggle run duration: <1 s, 1–2 s, 2–3 s, 3–4 s, 4–5 s, 5+s). We then multiplied the average number of wagggle runs followed for a particular distance category with the time it takes a dancer to make a circuit (wagggle run + return phase) for the corresponding distances. Figure 3b shows that there is indeed a strong positive relationship ( $R^2=0.8892$ ) between wagggle run duration and the estimated time invested by dance followers to follow a dance.

#### Experiment 2: factors affecting the number of dance followers

First, we again tested whether the number of dance followers differed between hives and depended on whether dancers carried pollen. There was a significant effect of hives ( $F_{2,596}=4.02$ ,  $R^2(\text{adj})=1.33\%$ ,  $P=0.018$ ), but not the presence of pollen ( $F_{1,596}=0.87$ ,  $R^2(\text{adj})=0.14\%$ ,  $P=0.351$ ) or the interaction ( $F_{2,596}=0.55$ ,  $R^2(\text{adj})=0.18\%$ ,  $P=0.579$ ) of the two (entire model,  $R^2(\text{adj})=2.31\%$ ). Hence, we analysed each hive separately but pooled pollen and non-pollen dances.

We hypothesised that the number of bees following a dance depends on the time of year (because of seasonal changes in overall foraging conditions and colony size), the number of other bees dancing (because this affects the ratio of dancers to potential followers) and wagggle run duration (because this affects the area required for a dance circuit). Therefore, for each hive we ran a model including month, wagggle run duration and the number of simultaneous dances as explanatory variables.

In hive 1, we found that month ( $F_{3,243}=11.11$ ,  $R^2(\text{adj})=8.75\%$ ,  $P<0.001$ ) and number of simultaneous dances ( $F_{1,243}=10.40$ ,  $R^2(\text{adj})=2.73\%$ ,  $P=0.001$ ) both had a significant effect on the number of dance followers, but that wagggle run duration did not ( $F_{1,243}=0.57$ ,  $R^2(\text{adj})=0.15\%$ ,  $P=0.453$ ; entire model,  $R^2(\text{adj})=11.50\%$ ). In hive 2, we found that none of the explanatory variables was significant (months:  $F_{3,175}=2.34$ ,  $R^2(\text{adj})=3.7\%$ ,  $P=0.075$ ; wagggle run duration:  $F_{1,175}=0.75$ ,  $R^2(\text{adj})=0.39\%$ ,  $P=0.389$ ; simultaneous dances:  $F_{1,175}=0.27$ ,  $R^2(\text{adj})=0.14\%$ ,  $P=0.604$ ; entire model,  $R^2(\text{adj})=3.00\%$ ). In hive 3, only month significantly affected the number of dance followers ( $F_{3,162}=9.66$ ,  $R^2(\text{adj})=15.06\%$ ,  $P<0.001$ ; wagggle run duration:  $F_{1,162}=0.00$ ,  $R^2(\text{adj})=0.00\%$ ,  $P=0.990$ ; simultaneous dances:  $F_{1,162}=1.38$ ,  $R^2(\text{adj})=0.72\%$ ,  $P=0.24$ ; entire model,  $R^2(\text{adj})=19.22\%$ ). For hives 1 and 3, we did a post hoc analysis including a sequential Bonferroni correction for multiple testing (Sokal and Rohlf 1995) to investigate which months differ from each other in the number of followers (Table 1; Fig. 4). The results suggested that dances attracted the most followers in September (early autumn).

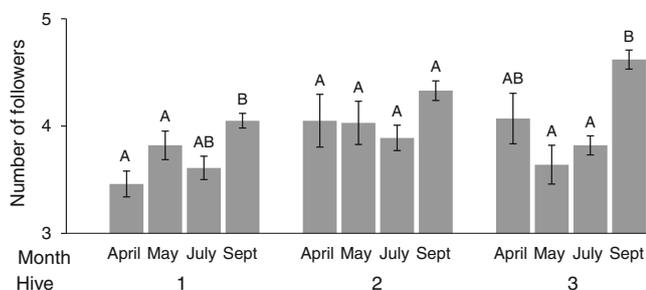
**Table 1** Pair-wise comparisons between months for hives 1 and 3

Pairwise comparisons between months	<i>P</i> values	
	Hive 1	Hive 3
April–May	0.148	0.661
April–July	0.265	1.000
April–September	<b>&lt;0.001</b>	0.029
May–July	1.000	1.000
May–September	<b>0.014</b>	<b>&lt;0.001</b>
July–September	0.222	<b>&lt;0.001</b>

*P* values were corrected for multiple testing with sequential Bonferroni in order to avoid inflation of type-I errors. **Bold** values passed the sequential Bonferroni correction

## Discussion

Our results show that the following of waggle dances for natural food sources is affected by the distance to that source. As foraging distance increases, bees follow fewer waggle runs (31 % reduction from waggle runs <1 s to waggle runs >5 s, Fig. 3a). However, since waggle run duration (and corresponding circuit duration) is longer for greater distances (von Frisch 1967), followers actually invest more time in dance following with increasing food source distance (c.10 s for a food source at c.1,000 m and c.30 s for a food source at c.10,000 m; Fig. 3b). Thus, although followers invest more time for distant food sources, they might acquire less information because they follow fewer waggle runs. Previous research indicates that the number of waggle runs followed has a significant effect on the accuracy of flights to the advertised source (Tanner and Visscher 2009). However, it is not known whether dance followers acquire the same amount of spatial information per waggle run for nearby food sources (short circuits, short waggle runs) as for distant food sources (long circuits, long waggle runs). The waggle run provides distance and direction information, and these two vector



**Fig. 4** The number of dance followers per dance in the different colonies and during different months. The letters above bars indicate statistically significant ( $P < 0.05$ ) differences between months in each hive. For example, *B* above September in hive 1 indicates that the numbers of followers differed significantly from April and May (*A*), but that September, April, and May are not significantly different from July (*AB*). Error bars present standard errors

components might differ in how easily or accurately they are decoded by dance followers. Interestingly, the two components are not equally prone to signal noise. Variation among waggle runs in the direction component depends on sensory and physical constraints that depend on the body position of the dancer (von Frisch and Lindauer 1961; Tanner and Visscher 2010; Couvillon et al. 2012a) and this angular noise tends to decrease with increasing waggle run duration (Weidenmüller and Seeley 1999; Beekman et al. 2008; Couvillon et al. 2012b) (Fig. 2b). On the other hand, noise in the duration component (distance) increases with increasing waggle run duration (Fig. 2a), which agrees with previous work (Beekman et al. 2008; Couvillon et al. 2012b). Hence, while bees might need to follow fewer waggle runs to acquire accurate direction information for distant food sources, they probably need to follow more waggle runs to acquire precise information about distance. Overall, bees might face a speed–accuracy trade-off and we would expect dance following to be long enough to acquire sufficiently accurate location information at different food distances. Feeder array studies (Tanner and Visscher 2009) or harmonic radar (Menzel et al. 2011) could be used in future studies to determine how dance following affects the angular and distance precision of foraging flights of varying distances.

Our results suggest that angular variation among waggle runs is related to dance following, but that this effect depends on the distance of the food source. Followers actually followed slightly more waggle runs for distant food sources when angular variation was greater (significant interaction between waggle run duration and ASD). This suggests that followers might compensate for low signal quality (low signal to noise ratio) for distant food sources by investing more time in dance following. Increasing angular noise translates into a much greater potential error (distance between indicated and actual food location) at larger distances and, hence, such a response could decrease the risk of getting lost while searching for the advertised food source. Alternatively, it might be easier for bees to evaluate angular scatter in longer waggle runs. Overall, this effect was relatively weak, suggesting that it might be difficult for followers to evaluate angular noise.

In general, dance following was short ( $2.80 \pm 1.38$ , range 1–16 circuits), confirming previously reported results (Biesmeijer and Seeley 2005). While most followers followed one to five waggle runs (90 %), only 2 % followed >10. This suggests that many instances of dance following are shorter than typical for bees that successfully use the waggle dance to locate food (Michelsen 2003; Grüter et al. 2008; Grüter and Farina 2009a; Menzel et al. 2011; Wray et al. 2012). Wray et al. (2012) showed that successful recruits followed on average 15.5 waggle runs and Menzel et al. (2011) showed that foragers leaving the hive in the direction of the advertised food location had followed on average more than 20 waggle runs.

So why do bees following dances under natural conditions follow so few waggle runs? One explanation is that some foragers have private information about other food sources and, therefore, are not interested in following dances extensively (Biesmeijer and Seeley 2005; Grüter et al. 2008; Grüter and Farina 2009a). Since our followers were not individually marked, it is also possible that these bees returned later to the same dances to acquire more information. However, this seems unlikely because subsequently followed dances are likely to advertise different food sources (Biesmeijer and Seeley 2005; their Fig. 4). It has also been shown that dancing attracts nectar receivers (Farina 2000). Hence, it is possible that some of the followers were nectar receivers not interested in the food source location. Lastly, it is possible that previous studies reporting high numbers of followed waggle runs are also reporting an artefact of the methodology. Bees train to feeders best when there are fewer natural floral resources available (Seeley 1995). Perhaps followers in those circumstances are more committed to following a dance because they have no information about profitable alternatives.

We found that the number of followers differed between colonies and between months in two of three colonies. Two other factors, waggle run duration and the number of simultaneous dances, had no large effects. The time of year might affect the number of dance followers for several reasons. For example, the number of followers could vary depending on colony size. This could also explain the inter-colony differences in the number of dance followers. Dances had more followers in September (Fig. 4). In this month, the foraging environment improved considerably compared to August due to the blooming of ivy (*Hedera helix*), and most foragers could be seen returning with the pollen from ivy (personal observation; Garbuzov and Ratnieks, unpublished results). It has been shown that foragers are attracted to dancers that carry familiar food odours, which in turn leads to a higher number of dance followers (von Frisch 1923; Grüter et al. 2008; Grüter and Farina 2009b; Grüter and Ratnieks 2011). It is possible that dances generally have more followers when most of a colony's foragers have experience with the same food type, as was the case in September with ivy, because the nearest dancer to an unemployed forager is likely to carry a familiar and attractive odour.

In summary, our results show that dance followers respond to the characteristics of the waggle dance. However, while dancing behaviour and the factors that cause a bee to perform this signal are better understood (reviewed in: von Frisch 1967; Seeley 1995; Dyer 2002; Couvillon 2012), we still have a limited understanding of how followers of natural dances use the different informational components in their foraging decisions. More research into follower behaviour (signal receivers) and information use-strategies under natural circumstances is needed to understand, for example,

why natural dance following is shorter than expected if follower bees were trying to decode the spatial information of a dance.

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