

Original Article

Honey bees use social information in waggle dances more fully when foraging errors are more costly

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Social animals can obtain valuable information from group members, but sometimes experience conflicts between this social information and personal information obtained through their own experience. Experienced honey bee foragers (*Apis mellifera*) have personal information about familiar food sources, and can also obtain social information by following waggle dances. However, it is unclear whether temporarily unemployed foragers whose visits to a food source have been interrupted make full use of social information from dancers or rely primarily on their own personal information to determine whether their familiar food source is active again. We hypothesized that experienced foragers should pay more attention to the social information in waggle dances when foraging errors that can arise from ignoring social information are more costly. We manipulated the cost of mistakenly flying to a familiar but unprofitable food source by training bees to visit feeders that were either close (100 m) or far (1000 m) from the hive and found that temporarily unemployed foragers who had been trained to forage at more distant feeders were more likely to pay attention to social information about food source location. Our findings demonstrate that experienced forager bees can flexibly alter the extent to which they rely on social, as opposed to personal, information and are more likely to fully utilize social information from dancers when foraging errors are more costly. *Key words:* *Apis mellifera*, communication, dance language, reactivation, social information, waggle dance. [*Behav Ecol* 23:125–131 (2012)]

INTRODUCTION

Accurate information can increase an organism's fitness by enabling it to respond more effectively to challenges and opportunities. An animal's own experiences and trial-and-error interactions with the environment can provide it with "personal information" about its surroundings (Danchin et al. 2004; Dall et al. 2005), and group-living animals can also obtain "social information" by interacting with and observing other group members (Wagner and Danchin 2010). However, sometimes animals can face a situation in which the social information they obtain from group members conflicts with their own personal information (e.g., Kendal et al. 2004; van Bergen et al. 2004), and they must choose which one to use (reviewed by Kendal et al. 2005; Rieucau and Giraldeau 2011). In such situations, individuals tend to rely more on social information when it is especially persuasive (Rieucau and Giraldeau 2009) or when personal information is difficult to acquire (Boyd and Richerson 1988), unreliable or outdated (van Bergen et al. 2004), or costly to use (Kendal et al. 2004).

Honey bees (*Apis mellifera*) live in large kin groups in which social information is constantly exchanged via both inadvertent social cues and intentional signals (Seeley 1998). The most sophisticated of these signals is the waggle dance—perhaps the most complex form of communication in non-

human animals—which provides worker bees with valuable social information about high-quality resources. Although some of the bees who follow waggle dances are naïve foragers with no personal information about nearby food sources, nearly 80% of dance followers are experienced foragers whose visits to a rich food source have been interrupted by nightfall or bad weather (Biesmeijer and de Vries 2001; Biesmeijer and Seeley 2005). These experienced bees already possess personal information about the scent and location of their familiar food source (Reinhard et al. 2004, 2006; Beekman 2005), and by following waggle dances they can also obtain social information about the scent and location of profitable food sources. However, if the social information provided by waggle dancers does not match their personal information, foragers will be forced to choose between these 2 sources of information. Paying attention to social information about the scent and location of the food sources dancers are advertising could reduce a dance follower's chance of mistakenly making a risky and energetically costly trip back to their familiar food source when it is still unrewarding (a "reactivation error"). But following dances takes time, which may not be worthwhile if personal information is cheap and reliable.

Previous research suggests that temporarily unemployed foragers often rely on social scent and/or location information obtained from waggle dancers. Contacting a dancer carrying a familiar scent can prompt temporarily unemployed foragers to return to their familiar food source (Johnson 1967; von Frisch 1967, p. 32–33; von Frisch 1968), whereas contact with a dancer carrying an unfamiliar scent generally does not have the same effect (von Frisch 1967 p. 33, 43). von Frisch (1967) also reports that temporarily unemployed foragers trained to unscented food sources are less likely to be reactivated (see

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Table 2) by dances advertising a food source at an unfamiliar distance (p. 152), and less than 20% respond to dances for an unfamiliar direction (p. 153). He observed that some of these dance followers, rather than leaving the hive,

“turn[ed] decisively away from the dancer—one of them not until she had run along after her for a few circuits—as if after the sudden realization: ‘That is none of my affair.’ Thereafter they remained at rest on the comb. They had understood and heeded the indication of direction.” (von Frisch 1967, p. 153)

These observations suggest that experienced bees who are familiar with a food source’s location can distinguish between dances advertising familiar and unfamiliar locations after following only a few dance circuits, and are less likely to respond to dances for unfamiliar locations. Although dance followers may be able to detect a dancer’s scent more rapidly (Biesmeijer and Seeley 2005), the location a dancer advertises will be a more reliable source of information if food sources in multiple locations share the same scent.

These previous findings suggest that experienced bees frequently use social information from waggle dancers, although they may use different information (scent or location) depending on the circumstances. However, under some conditions, dance followers seem to ignore social information completely. In a study by Grüter et al. (2008), temporarily unemployed foragers almost always ignored social information provided by waggle dancers and instead simply used personal information to return to their familiar food source. The extent to which bees rely on social information from waggle dances, as opposed to their own personal information about the location and availability of familiar food resources, is likely to be affected by a factor such as the quality and reliability of personal and social information (Brockmann and Sen Sarma 2009; Grüter and Farina 2009a, 2009b) and the costliness of errors that could result from using inaccurate or out-of-date personal information.

Grüter and Ratnieks (2011) recently showed that honey bee foragers who experience unrewarding conditions at their familiar feeder are more likely to rely on location information from waggle dances, which suggests that bees pay more attention to social information when their personal information no longer accurately indicates the location of valuable food sources. Our study asks whether the costliness of errors that can arise from relying solely on personal information also affects an unemployed forager’s tendency to rely on social information about food resources. We hypothesized that temporarily unemployed foragers should follow dances more carefully and rely more fully on location information from waggle dances when reactivation errors are more costly. To test this hypothesis, we trained bees to visit one of 2 identically scented feeders located in opposite directions from the hive, shut off both feeders for several hours, turned on only one of the feeders again, and monitored the responses of temporarily unemployed trained foragers who followed waggle dances advertising the active feeder. The bees with foraging experience at the nonadvertised feeder faced a choice between relying on their personal information about food source location and the social information about food source location provided by the waggle dancers. Bees who relied on their personal information or paid attention only to the scent information from waggle dancers should tend to return to their familiar food source after following a dance. But bees who paid attention to the location information in the waggle dances should tend to either remain in the hive (waiting for news that their familiar food source is again rewarding) or fly out to the location indicated by the dancer. We predicted that bees trained to more distant feeders (1000 vs. 100 m) would use the social information in the waggle dance more fully and therefore would be less likely to make errors when deciding where and when to resume foraging.

METHODS

Study site and colonies

Tests were performed with 2 colonies of honey bees (*A. mellifera*) housed in 2-frame observation hives (Seeley 1995, Figure 4.2) that we transported to the Cranberry Lake Biological Station (CLBS) in the Adirondack State Park (lat 44°09’N, long 74°48’W) on 7 July 2007. The CLBS is surrounded by forests that contain few flowers, so there are no local bee colonies, and it is relatively easy to train bees to forage at artificial feeders. During each test, one colony was housed in a small wooden hut at the CLBS (Seeley 1995, Figure 4.4) and the other was kept in reserve at a marina approximately 6.5 km away.

Training

We began each experimental trial by training groups of 30–60 bees to visit each of 2 artificial feeders located 100 m (Trials 1 and 3) or 1000 m (Trials 2 and 4) north and south of the hive (Table 1) using techniques described by von Frisch (1967). Different groups of bees were used for each testing trial. Trained foragers were individually marked using shellac-based paints. The paint mark on each bee’s thorax indicated the feeder she was trained to visit, and 1–3 marks on her abdomen indicated her identity. Any bee who switched feeders during the training process was captured in a freezer bag (Seeley 1995, p. 78).

To train bees to 100 m, we placed 2 feeders next to the hive and then gradually moved each feeder and its group of foragers farther away until one was 100 m to the north and the other was 100 m to the south of the hive (Figure 1). To train bees to 1000 m, we began with the feeders at 100 m and then moved them gradually to 1000 m. To obtain a new group of bees for the 1000 m trials, we allowed the foragers who had been trained to 100 m feeders to recruit a new group of bees to the feeders as they were moved farther from the hive and then captured the bees from the 100 m test. Training to 100 m took 2 days, and training to 1000 m took 5–6 days.

On the day after feeders reached their final destinations, trained bees were allowed to forage freely from 09:00 to 16:00 (Figure 1). Throughout the day, the sucrose concentrations were adjusted so that trained bees kept returning to the feeder but did not perform dances to recruit additional bees to the feeder. Sucrose concentrations ranged from 0.5 to 2.5 M and were always equal at both feeders. During training and testing periods, both feeders were scented using anise extract, which was present in the sugar solution (50 µl/l) and in a reservoir on top of which the jar of solution rested (Seeley 1995, Figure 4.5 and 4.6). The scent levels approximated what bees encounter at natural food sources (Seeley 1995) and ensured that dance followers were exposed to both external and internal fragrances as is typical for bees foraging on flowers (von Frisch 1967, p. 224–227).

Testing

On testing days (Table 1; Figure 1), we filled both feeders with sucrose solution and allowed bees to forage freely from

Table 1
Colony, feeder distance, and food location during the 4 experimental trials

Trial	Colony	Test date	Distance to feeders (m)	Food location during testing
1	1	12 July	100	South
2	1	17 July	1000	North
3	2	31 July	100	North
4	2	9 August	1000	South

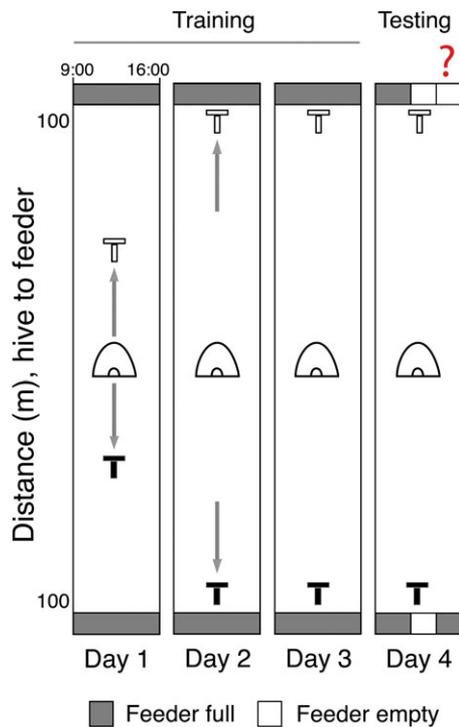


Figure 1

Diagram of experimental set-up during Trial 1, when feeders were 100 m from the hive. The horizontal bar by each feeder is a timeline indicating when the feeder was filled (gray) and when it was empty (white). During the testing period, only the south (black) feeder contained food; the feeder to the north (white) was empty. During Trial 2 (not shown), a new group of bees was trained to the feeders on days 5–9, the feeders were moved from 100 to 1000 m, and the north feeder had food during the testing period. During trials 3 and 4, the location of food during the testing periods was reversed (Table 1). Figure by B.A.K.

approximately 09:00–12:00. We based our initial sucrose concentrations on the levels that had been necessary to keep bees visiting the feeder during the previous training day (0.5 M in Trials 1 and 2, 1.0 in Trial 3, 2.0 in Trial 4) and adjusted them if necessary to keep trained bees visiting without attracting additional recruits. If multiple unmarked bees arrived at the feeder within a given 10-min interval, sucrose solution was lowered by 0.5 M at both feeders to prevent additional recruitment. After the morning feeding period, we removed the feeders with sucrose solution and replaced them with clean, empty feeders. Trained bees periodically returned to inspect these empty feeders, but the frequency of their visits soon decreased. We monitored each empty feeder and recorded the number and identity of inspecting bees until there was an average of one inspector arriving at the feeders every 15 min. At that time (~14:00), we removed the empty feeder from one feeding station (“food” location) and replaced it with a feeder containing concentrated sugar solution (2.5 M); the other feeder (“no food” location) remained empty. The location with food alternated between trials (Trials 1 and 4: south feeder; Trials 2 and 3: north feeder; Table 1). The testing period began when the first marked bee to return to the food location flew back to the hive and performed a waggle dance for her feeder.

During the testing period, an observer at each feeder recorded the arrival time and identity of each marked bee who arrived and also captured every bee, with the exception of 2–3 bees at the “food” location who were designated as dancers. The anise scent of the waggle dancers was familiar to all the temporarily unemployed foragers in the hive, regardless of the feeder they had been trained to visit. However,

the location information in the waggle dances was only familiar to bees who had been trained to visit the advertised feeder.

Throughout each testing period, we videotaped (AGDVC 30; Panasonic) the area of the hive in which bees were performing and following dances (the “dance floor”; von Frisch 1967, p. 36–37). An observer at the hive (M.K.W.) pointed at, and announced the identity of, each marked bee in the vicinity of a dancer. Testing continued until no more marked bees were observed following dances in the hive (~2 to 3 hours). All captured bees were released at the end of each testing period.

Video coding and analysis

After the experiment, one of us (M.K.W.) reviewed the video recordings from Trials 1 and 2 to quantify the behavior of marked bees inside the hive. Technical difficulties prevented us from obtaining video data from our recordings of Trials 3 and 4, so for these trials, we report only the feeder data (where and when trained bees were captured). The behavior of each marked bee who was pointed out on the video recordings was monitored throughout the testing period, and the times (if any) when the bee entered or exited the hive, performed trophallaxis, or followed a dance were noted. Each bee who was less than one bee length from a dancer and faced the dancer for at least one complete dance circuit (waggle run + return phase) was classified as a dance follower. We counted the number of dance circuits a bee followed as the number of circuits during which she was no more than one bee width from a dancer, was facing the dancer, and was actively following the dancer’s movements by running alongside or behind her. The end of a following bout occurred when the dancer stopped dancing, the follower turned $\geq 90^\circ$ away from the dancer and walked away from her, or the follower was pushed away from the dancer and did not resume following her for 2 or more dance circuits (Girard et al. 2011). All trained bees from Trials 1 and 2 were classified according to the definitions in Table 2.

We excluded from our analysis any bees who did not visit a feeder on the day before and on the morning of the test day because they were likely to have died or switched to visiting a different food source (77 of 345 trained bees). However, we did not exclude bees who visited a feeder on the day before testing but not on the morning of the test day (39 of 345 bees). Even after an entire day without food rewards, approximately 85% of bees remember the scent and location of a feeder they have regularly visited (Beekman 2005), so bees who had visited a feeder on the day before testing presumably still remembered its location on the test day.

Statistical Methods

Statistical tests were performed using SAS v9.2. Categorical data were tested using chi-square tests (proc FREQ), comparisons among group means were performed using 2-tailed *t*-tests for 2 groups (Proc *t*test) or 2-way analysis of variance (ANOVA) tests for multiple groups (Proc GLM), and means for significant effects were separated using a Tukey–Kramer post-hoc test. Dance-following data were log transformed before performing Tukey tests to meet homogeneity of variance assumptions. All reported *P* values are for 2-tailed tests ($\alpha = 0.05$), and average values are reported as mean \pm standard error.

RESULTS

Did bees pay attention to the location information in waggle dances?

Among the bees from all 4 trials for whom the dances indicated an unfamiliar location, 65% of them (51 of 78) returned to their familiar food source, whereas 35% of them (27 of 78

Table 2
Categories that were used to classify marked bees from Trials 1 and 2 based on their behavior during testing periods

Behavioral category	Definition
Reactivated bee	A bee who returned to her familiar feeder in response to external information (from a waggle dance)
Recruit	A bee who followed a dance for an unfamiliar feeder and subsequently arrived at that feeder
Unresponsive follower	A bee who followed a dance but did not subsequently leave the hive
Uncaptured follower	A bee who followed a dance and left the hive but was not captured at either feeder
Inspector	A bee who arrived at her familiar feeder during the testing period without obtaining new external information (from waggle dances)
Scout	A bee who arrived at the unfamiliar feeder during the testing period without obtaining new external information (from following dances)
Inactive bee	A bee who was observed in the hive but never followed a dance
Unobserved bee	A bee who was not observed in the hive or at the feeder during the testing period

Temporarily unemployed foragers who returned to a familiar feeder after following a dance were classified as reactivated bees, whereas bees who followed a dance for an unfamiliar feeder and then arrived at that feeder were classified as recruits. Descriptions of reactivated bees, recruits, inspectors, and scouts are based on definitions from Biesmeijer and de Vries (2001) and Fernandez et al. (2003).

bees) went to the unfamiliar location advertised by the dancers (Figure 2). In contrast, nearly all of the bees (79 of 80 bees; 99%) for whom dances indicated their familiar feeder returned to that location, with the exception of one scout bee who arrived at the empty, unfamiliar 100 m feeder without having followed any dances in the hive. Bees from both colonies and at both distances were more likely to return to their familiar feeder when the dances in the hive were advertising their familiar feeder (chi-square: Colony 1: $\chi^2_{df=1} = 14.4$, $P = 0.0001$; Colony 2: $\chi^2_{df=1} = 15.3$, $P < 0.0001$; 100 m: $\chi^2_{df=1} = 19.9$, $P < 0.0001$; 1000 m: $\chi^2_{df=1} = 9.22$, $P = 0.0024$).

Waggle dances advertising unfamiliar locations were less effective at stimulating bees to return to their familiar feeder. Bees who followed dances advertising an unfamiliar location were less likely to be reactivated (see Table 2) to their familiar site (36%, 19/53) than bees who followed dances advertising a familiar location (100%, 23/23; chi-square: $\chi^2_{df=1} = 12.2$, $P = 0.0005$). A quarter (13/53; 25%) of the bees who followed dances for an unfamiliar feeder used the location information in the waggle dance and arrived at the advertised feeder before the end of the testing period. The remaining 39% of bees who followed dances for unfamiliar locations but did not arrive at a feeder either did not leave the hive in response to these dances (6/53; 11%) or left the hive but did not arrive at a feeder (15/53; 28%). Because bees who followed dances advertising their familiar feeder always returned to that feeder, the 64% of bees who did not return to their familiar feeder after following dances for an unfamiliar location presumably paid attention to the location information and recognized that these dances were not advertising their familiar food source.

Effects of distance

Among the bees who followed dances for unfamiliar locations (Trial 1: 100 m, 30 bees; Trial 2: 1000 m, 23 bees), the fraction

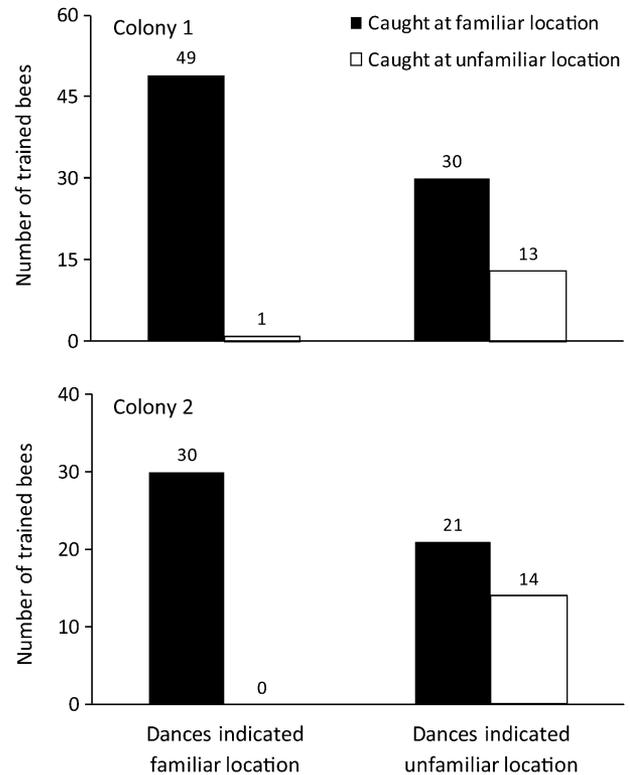


Figure 2

Locations where trained bees from colony 1 and colony 2 were captured during testing periods. Nearly all bees whose familiar feeder was advertised during the testing period were caught at that location. In contrast, some of the bees who were unfamiliar with the advertised location returned to their familiar feeder, whereas others flew to the unfamiliar feeder advertised by the dancers.

of bees who did not leave the hive in response to these dances was higher at 1000 m than at 100 m (22% vs. 3.3%; chi-square $\chi^2_{df=1} = 4.39$, $P = 0.036$; Figure 3) and the fraction of bees who arrived at either of the 2 feeders was lower at 1000 m than at 100 m (43% vs. 73%; chi-square: $\chi^2_{df=1} = 4.85$, $P = 0.028$). If we assume that bees who followed dances for unfamiliar locations but did not return to their familiar feeder were paying attention to the location information in the dances—and therefore never left the hive, left the hive but did not arrive at a feeder, or flew to the advertised feeder—then we can conclude that 57% of these bees (17 of 30) attended to location information at 100 m (Figure 3a), whereas 74% (17 out of 23) attended to location information at 1000 m (Figure 3b).

In comparison, distance had no effect on the behavior of bees who followed dances advertising familiar locations (Figure 3). All of these bees responded to dances by leaving the hive, and all of them were caught at their familiar feeder, both at 100 m (10 bees) and 1000 m (13 bees).

Dance-following behavior

Waggle dance followers who relied only on scent or personal information and were reactivated to their familiar, but unprofitable, feeder followed dancers for an average of 3.9 ± 1.2 dance circuits (Figure 4), left the hive 1.5 ± 0.2 times, and arrived at their familiar feeder 49 ± 5.6 min after the start of the testing period ($n = 20$). In contrast, bees who paid attention to the location information in the dance and were recruited to an unfamiliar feeder actively followed

dances for an average of 15.5 ± 2.3 dance circuits (Figure 4), left the hive an average of 2.4 ± 0.3 times, and took 73.7 ± 39.6 min from the start of the testing period to successfully locate the advertised feeder ($n = 13$). Among bees who followed dances for an unfamiliar location, those who were reactivated, recruited, uncaptured, or unresponsive differed in the number of dance circuits they followed (ANOVA: $F_3 = 6.94$, $P = 0.0004$; Figure 4). Bees who were recruited to an unfamiliar feeder spent more time following dances than those who were reactivated to a familiar feeder (11.6 ± 5.0 vs. 5.7 ± 1.3 min; $t_{53} = 4.58$, $P < 0.0001$) and followed dancers for more dance circuits (15.5 ± 2.3 vs. 3.7 ± 0.7 circuits; Tukey post-hoc test: $P = 0.004$).

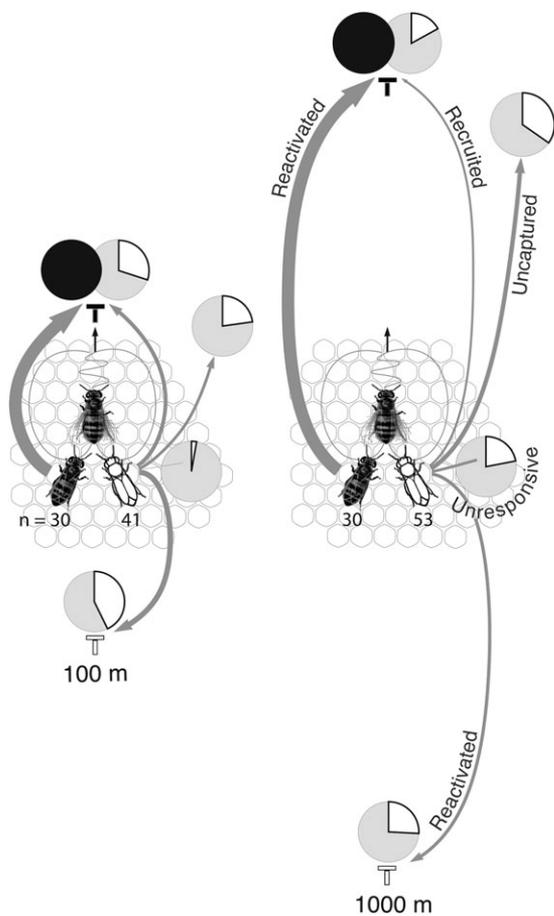


Figure 3
 Responses of bees from Trials 1 and 2 who followed dances for feeders located either 100 m (shown on left) or 1000 m from the hive. In each trial, there were 2 types of dance followers: bees who were familiar with the feeder that the dancers were advertising (indicated in black), and bees who had been trained to visit the other feeder and were thus unfamiliar with the advertised location (indicated in white). Pie symbols and arrow thicknesses represent the fraction of bees in each group who returned to their familiar feeder (“reactivated”), flew to an unfamiliar feeder (“recruited”), left the hive but were not caught (“uncaptured”), and followed a dance but did not leave the hive (“unresponsive”). The number beneath each type of dance follower indicates the size of that group of bees. During testing periods, a reservoir of anise scent was present at both feeders, but the advertised feeder (indicated in black) contained concentrated 2.5 M sucrose solution, whereas the nonadvertised feeder (indicated in white) was empty. Figure by B.A.K.

DISCUSSION

There are 2 main results of this study. First, we found that temporarily unemployed foragers were more likely to be reactivated to their feeder if the dances performed in the hive indicated a familiar location rather than an unfamiliar location. This finding shows that many of these bees must have paid attention to location information in the dances. Second, we found that temporarily unemployed foragers who followed dances indicating an unfamiliar location were less likely to leave the hive and less likely to return to their familiar feeder when the feeders were farther from the hive. This finding shows that these bees must have paid more attention to the location information in the dances when the distance to their familiar food source—and, thus, the cost of making a reactivation error—was greater. In contrast, the temporarily unemployed foragers who followed dances indicating a familiar location always left the hive and always returned to their familiar feeder, regardless of the feeder’s distance from the hive. The strong reactivation of these bees probably reflects the fact that for these bees, there was no conflict between personal information and social information; both stimulated them to return to their familiar feeder.

These results support previous studies showing that individuals are less likely to ignore social information and rely solely on personal information when the potential costs of doing so are greater. For example, Kendal et al. (2004) showed that guppies with experience feeding from one of 2 feeders typically preferred to continue feeding at that location even after observing group members feeding elsewhere. But when visiting their familiar feeder became costly because it required them to go behind a barrier and lose sight of the rest of their shoal, individuals were more likely to pay attention to social information and visit the feeder where they had observed group members feeding. Our findings suggest that—like guppies—honey bees can evaluate the relative cost of using personal as opposed to social information, and can increase their reliance on social information when using personal information becomes more costly. These results add to our understanding of social learning in insects (reviewed by Leadbeater and Chittka 2007) by demonstrating that honey bee foragers are able to flexibly alter their reliance on social as opposed to personal information under different conditions.

Interestingly, even when the feeders in our study were close to the hive, so the cost of making a reactivation error (i.e., returning to their familiar feeder when it remained empty) was low, some bees still paid attention to the socially provided location information in the waggle dance and were not reactivated by dances that advertised an unfamiliar location. Over 40% of the bees who followed dances for an unfamiliar feeder

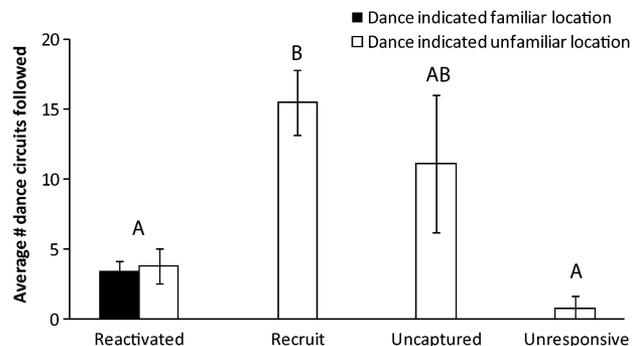


Figure 4
 Average number of dance circuits followed by different categories of bees as defined in Table 2. Groups with different letters were significantly different based on post-hoc Tukey tests ($P \leq 0.004$).

100 m from the hive arrived at the location advertised by the dancers, and 25% of them either did not leave the hive in response to dances or left the hive but never arrived at either feeder. Bees who followed dances for familiar locations always arrived at their familiar feeder, so these uncaptured bees presumably had paid attention to the location information waggle dancers advertised and were searching for the advertised feeder. These findings suggest that even when the errors that could arise from relying solely on personal information were not particularly costly, many bees (about 70%) preferred to rely on social information from waggle dancers when deciding where and when to resume foraging.

Our results differ markedly from those of Grüter et al. (2008), who found that most temporarily unemployed foragers relied only on personal information after following waggle dances, and returned to their familiar feeder regardless of the scent or location advertised by the dancers. One possible reason for this difference is that our study was performed in an environment with fewer alternative food sources, and foragers in such locations may place greater emphasis on socially acquired information from waggle dances if personal information is consequently less reliable (Grüter et al. 2008) or more difficult to obtain. The difference in the lengths of our testing periods could also account for some of the difference in our results. Previous studies suggest that it can take hours for bees following waggle dances to find the locations that dancers are advertising (Seeley 1983), and the bees in our study who were recruited to an unfamiliar feeder took an average of 74 min to locate it. Indeed, several bees in our study who had left the hive but had not yet arrived at either feeder were probably still searching for the advertised feeder when we ended the testing period. Because Grüter et al. (2008) used 40-min testing periods, it is possible that some of the dance followers in their study who did not arrive at either feeder were searching for the advertised feeder but were unable to find it by the end of the testing period.

Previous studies of temporarily unemployed foragers have had conflicting results. Numerous researchers have found that bees pay attention to social information provided by waggle dancers (odor information: Johnson 1967; Biesmeijer and Seeley 2005; location information: von Frisch 1967), but others have found that bees can be reactivated equally well by any waggle dance, regardless of its odor or location information (Grüter et al. 2008). Our results, and those of Grüter and Ratnieks (2011), suggest that experienced dance followers are able to flexibly adjust the degree to which they rely on social as opposed to personal information, and presumably also the type of social information they use (scent or location information), in response to the costs and benefits associated with these strategies. This may explain why previous studies of dance-following behavior have produced such different results, and why “even small changes in experimental design can lead to very different recruitment patterns” (Grüter and Farina 2009a).

Interestingly, even under the same experimental conditions, we observed a significant amount of variability among bees in their responses to the waggle dances they followed. Although some dance followers returned to their familiar feeder regardless of the location dancers were advertising, other bees paid attention to the socially provided location information in the dance and flew out in search of the advertised feeder. Because we used different bees in each testing trial, we do not know if these differences in workers' dance-following behavior are consistent over time. Recent studies have shown that some honey bees are more impulsive than others (Burns and Dyer 2008) and tend to make faster but less accurate foraging decisions. If these decision-making strategies are consistent across contexts, then more impulsive foragers might also tend

to adopt the faster but potentially less accurate strategy of ignoring social information about scent and location when following waggle dances as temporarily unemployed foragers. Kurvers et al. (2010) recently demonstrated that personality and social information use are correlated in barnacle geese, and investigating whether this is also true of honey bees could be a promising area for future study.

In conclusion, our results show that, at least under some conditions, many temporarily unemployed foragers do pay attention to the social information in waggle dances. Moreover, our results show that temporarily unemployed foragers pay more attention to the social information in waggle dances when their familiar food sources are farther away. Previous studies have shown that honey bee foragers are sophisticated in how they produce waggle dances, and alter the duration and tempo of their dances in response to environmental factors such as the food source's overall profitability, the abundance of other food resources, and the risk of predation (Seeley 1994; Seeley et al. 2000; Abbott and Dukas 2009). Our findings suggest that experienced honey bee foragers display a similar level of sophistication in how they follow waggle dances, and pay more attention to the social information in waggle dances when the cost of making a reactivation error is higher.

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