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Social learning strategies in honeybee foragers: do the costs of using private information affect the use of social information?

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Individual honeybee foragers often need to decide between using private versus social information when choosing where to forage. Social information is provided by the waggle dances made by successful foragers. Experienced foragers also have private information about the feeding sites they have previously visited. Previous work has shown that honeybees are flexible in their information use strategy. However, the conditions that favour the use of one information source over the other remain poorly understood. It has been suggested that foragers rely more on social information when use of private information becomes more costly. We tested this by training two groups of foragers to two feeding sites, 120 or 600 m from the hive, both providing a sucrose solution identical in concentration. We then made these two locations unrewarding and observed whether foragers trained to the further, and therefore more costly to check, site paid more attention to dances for a third, closer site (120 m in a different direction) than foragers trained to the 120 m site. Contrary to prediction, foragers trained to the 600 m feeder followed dances for the novel feeder less (25% fewer waggle runs) than foragers trained to 120 m feeder. Foragers from the distant feeding site were also not more likely to arrive at the food source advertised by dances. Our results suggest that higher costs of private information do not increase the use of social information as long as bees are satisfied with their original food source (i.e. they use a 'copy-if-dissatisfied' strategy). Additionally, we show that switching from private to social information is preceded by a rapid motivational change. Minutes before switching to the advertised resource, the foragers increased their dance-following time by 65% compared with earlier dances.

Social insects have evolved remarkable methods of communication to provide nestmates with information about good food sources (reviewed in: von Frisch 1967; Seeley 1995; Hölldobler & Wilson 2009; Jarau & Hrncir 2009). In the honeybee, *Apis mellifera*, successful foragers perform waggle dances inside the nest to provide nestmates with information about the presence, location and odour of profitable food sources (reviewed in: von Frisch 1967; Gould 1976; Seeley 1995; Dyer 2002; Michelsen 2003; Grüter & Farina 2009a; Couvillon 2012; Farina et al. 2012). The number of waggle runs, each of which repeats the same vector information, made by a returning forager varies from 0 to >100 and is positively correlated with the profitability of the food source, such as its sugar concentration or distance from the hive. In this way, recruits are directed to the better feeding locations, without the necessity of having first to sample suboptimal ones (von Frisch 1967; Seeley 1995; Grüter et al. 2010).

Although the use of social information can reduce costs, such as those caused by individual learning (e.g. time, energy, predation), individuals should not always rely on others: an animal that already possesses private or personal information, for example, might do better by ignoring social information because it can be less reliable (Laland 2004; Kendal et al. 2005, 2009; Rieucau & Giraldeau 2011). Accordingly, a waggle-dancing bee provides location information with considerable noise; that is, repeated waggle runs of the same dance vary in both distance and direction information (Weidenmüller & Seeley 1999; Tanner & Visscher 2010; Couvillon et al. 2012; Al Toufailia et al. 2013), and recruits often require several exploratory trips before locating the advertised food source (Seeley 1983; Visscher & Seeley 1988). Theoretical models support this by indicating that animals should have flexible information use strategies and use social information under specific circumstances (Boyd & Richerson 1985; Laland 2004; Kendal et al. 2005, 2009; Rendell et al. 2010; Rieucau & Giraldeau 2011). In general agreement with these predictions, social insect foragers do not follow their

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nestmates blindly (reviewed in Leadbeater & Chittka 2007). In both ants and honeybees, foragers often use private information about the location of food sources even if they have access to social information in the form of pheromone trails or waggle dances (ants: Rosengren & Fortelius 1986; Harrison et al. 1989; Aron et al. 1993; Grüter et al. 2011; Elizalde & Farji-Brener 2012; honeybees: Johnson 1967; Grüter et al. 2008; Grüter & Ratnieks 2011; Menzel et al. 2011; Wray et al. 2012). In honeybees, waggle dances can trigger spatial memories and cause dance followers to fly to familiar feeding sites rather than to the location advertised by the dance (Grüter & Farina 2009a).

What are the strategies foragers use to decide between social and private information about feeding locations? This is a relatively unexplored area (Kendal et al. 2009), but a recent study suggested that honeybee foragers use a ‘copy-if-asocial-information-is-costly’ strategy (Wray et al. 2012) (‘asocial information’ may include private information about known feeding locations and asocial learning of new feeding locations). Foragers trained to a food source at 1000 m were more likely to switch to an alternative food source at the same distance than foragers trained to 100 m. The idea here is that checking a previously used food source at 1000 m is more costly in time and energy than checking one at 100 m. In agreement with this, honeybee foragers respond to increased foraging distances by abandoning more distant food sources quicker if they become unrewarding (H. Al Toufailia, C. Grüter & F. L. W. Ratnieks, unpublished data) and by dancing less (Boch 1956; von Frisch 1967; Seeley et al. 1991). A copy-if-asocial-information-is-costly strategy has also been found in fish (Kendal et al. 2004; Webster & Laland 2008): minnows (*Phoxinus phoxinus*) rely more on social information about where to feed if acquiring asocial information is associated with increased predation risk. However, since the two distance treatments in Wray et al. (2012) differed in two factors (both in the costs of using private information and in the costs of using social information), it is not clear how each factor contributed to the observed treatment effects. Both types of costs have the potential to affect dance follower behaviour and information use (see Wray et al. 2012; Al Toufailia et al. 2013). It is also not immediately obvious why foragers with costly private information should be more likely to use costly social information than foragers with cheap private information and access to cheap social information. Alternatively, the results are compatible with a copy-if-dissatisfied strategy (Laland 2004; Galef et al. 2008; Kendal et al. 2009). This strategy is considered to be simple to implement because it does not require the animal to assess the relative profitability, or the costs and benefits, of alternatives (Laland 2004; Kendal et al. 2009). Rather, the payoff from using private information determines a forager’s ‘satisfaction’ in relation to an internal threshold that influences the probability of using social information. Norway rats, *Rattus norvegicus*, have been shown to follow such a strategy (Galef et al. 2008): individuals kept on an unpalatable, energetically dilute diet were more likely to rely on social information about what to eat than individuals receiving a more ‘satisfactory’ food source. Furthermore, Grüter & Ratnieks (2011) found that if a familiar food source becomes unrewarding, honeybee foragers start to invest more time in following waggle dances.

The copy-if-dissatisfied and the copy-if-asocial-information-is-costly strategies lead to different predictions under specific conditions (Laland 2004; Kendal et al. 2009). We tested whether higher costs of using private information increased the use of social information (copy-if-asocial-information-is-costly strategy). We trained honeybee foragers to a food source at either 120 or 600 m from the hive. Subsequently, both groups of foragers were exposed to dances for a novel food source at 120 m, in a different direction. If honeybee foragers follow a copy-if-asocial-information-is-costly strategy, we predicted that foragers trained to 600 m would pay more attention to these dances than foragers from the 120 m treatment because using private information (i.e. checking the feeder at the training location) is more costly for foragers trained at 600 m than for foragers trained to a feeder that is five times closer (120 m). However, if foragers use a copy-if-dissatisfied strategy, then foragers trained to the more distant food source would not be predicted to switch to social information if their old food source is ‘satisfactory’ (i.e. if it meets some threshold of profitability). Therefore, we trained bees using profitable rewards. An additional aim of the study was to investigate the behavioural dynamics of the switch from private information use to social information use.

METHODS

We used four colonies (H1–H4) of *Apis mellifera* located at the Laboratory of Apiculture and Social Insects, University of Sussex. Experiments were performed in September and October 2010 and 2011, a time of year when bees can more easily be trained to feeders at longer distances from the hive in this area. Each colony was housed in an observation hive containing three deep Langstroth frames or the equivalent comb area in medium frames. Each colony had a queen, about 3000–4000 workers, brood, pollen and honey reserves. Colonies had been set up for several weeks prior to data collection.

Experimental Procedure

We studied one hive at a time and performed two trials per hive. In one trial, the feeder distance was 120 m, and in the other, 600 m. Honeybees can forage at up to 12 km (von Frisch 1967), but foraging distances are usually considerably less (Seeley 1995; Beekman & Ratnieks 2000). In the study area, approximately 40% of all dances for natural food sources indicated a distance of less than 600 m from the hive (August 2010 to July 2011, $N = 2745$; M. J. Couvillon, F. C. Riddell Pearce & F. L. W. Ratnieks, unpublished data). The two trials were separated by approximately 1 week. For each trial we used standard procedures (von Frisch 1967; Seeley 1995) to train a group of 30–50 foragers to a feeder (training feeder, TF) offering unscented 2M sucrose solution ad libitum. This reward represents an above-average, indeed highly profitable, food source (see Figure 2 in Seeley 1986). In one trial, the TF was located 120 m from the hive, and in the other, 600 m. Training took 1–2 days. Trained foragers at the feeder were individually marked with numbered tags glued to the notum (Opalithplättchen, Christian Graze KG, Weinstadt-Endersbach, Germany). Simultaneously, a second group of bees (20–40 per trial) was trained to a second feeder (dance feeder, DF), which was always 120 m from the hive. DF foragers were individually marked as described above. Both TF and DF were placed on blue 30×30 cm platforms to help bees discover and learn them. The angle between the two vectors from hive to feeder was about 80°. The training procedure and the spatial arrangement of the feeders made it almost certain that the TF and DF foragers knew of only one feeder location during the training period. On the day after training, both feeders offered 2M of identically scented sucrose solution (50 μl of essential oil per litre of sucrose solution; Farfalla Essentials AG, Uster, Switzerland) for 60 min, from about 1300 until 1400 hours (henceforth: odour treatment day). When the TF feeder was 600 m from the hive, food was offered for slightly longer, 70 min, to allow TF foragers of both treatments to make a similar number of visits to the feeders. During this period foragers of both groups could learn the association between reward, location and scent. The duration allowed foragers to make at least three foraging trips (mean ± SD: 120 m: 5.6 ± 2.6, range 1–13; 600 m: 6.3 ± 1.9, range 2–10), which is a sufficient number of positively reinforced events to form a long-term olfactory memory (Menzel 1999). We used a different odour for each hive: jasmine (H1), peppermint (H2), lemon (H3) and eucalyptus (H4).

We trained a total of 359 TF foragers, 197 at 120 m and 162 at 600 m (see Results, Table 1). On the day after the odour treatment, we allowed DF foragers to collect 2M sucrose solution for 120 min (ca. 1100–1300 hours) at DF (test day). TF was empty on this day. The solution in the DF feeder had the same scent as during the odour treatment day and was discovered within 20 min by inspecting DF foragers. We allowed 10 DF foragers to make repeated foraging trips and to perform waggle dances inside the hive. Dances for natural food sources were rare during this period, and trained foragers show little interest in these food sources (Grüter & Ratnieks 2011). TF foragers that followed the dances of DF foragers would, therefore, face a choice between the social vector information of the dance (advertising DF) and the private location information (feeder TF), triggered by the familiar odour of the DF dancers. TF foragers could determine the distance to the DF feeder because this information is provided by the duration of the waggle run phase of the dance (von Frisch & Jander 1957; Seeley et al. 2000). Thus, TF foragers could potentially compare the distances of TF and DF. To limit the number of dancing bees advertising DF to 10, we captured other marked (both DF and TF foragers) and unmarked foragers arriving at DF with plastic tubes and detained them for the rest of the day and then released them. Their arrival time was noted. The arrival times and number of TF foragers visiting the TF feeder during the 120 min test period were also noted. TF foragers visiting the TF feeder were not captured. We counted two landings at the TF feeder as two distinct visits if the interval between them was at least 3 min.

At the observation hive, the dances of DF foragers and the dance-following behaviour of both DF and TF foragers was recorded using a high-definition video camera (Sony HDR-HC3). Returning foragers were directed to one side of the observation hive so that all dances were visible (see Seeley 1995). A bee was defined as having followed a dance if her head was directed towards a dancer within one antennal length for at least one waggle run (Tanner & Visscher 2009; Grüter & Ratnieks 2011). Occasionally, bees stopped dancing to unload their food or to walk around on the comb. We considered a bee as having performed two dances (i.e. two separate bouts of dancing) within a visit to the hive if the dance was interrupted by mouth-to-mouth feeding or walking for more than 5 s.

Statistical Analyses

We analysed the data using general and generalized linear mixed effect models (LME and GLMM) in R 2.13 (R Development Core Team 2011). R fitted the models with the lmer, lme and glmmPQL functions (Zuur et al. 2009). Depending on the error distribution of the response variable, we used normal (log and square root transformed), binomial or Poisson distribution. We used quasi-Poisson and the glmmPQL function if overdispersion was detected in the response variable (Crawley 2007). Random effects: we included hive and trial as hierarchically nested random effects to control for the nonindependence of data collected from the same hive or during the same trial (Zuur et al. 2009). We tested random effects by comparing a model with both random effects with a model with just one random effect (χ^2 and P values for random effects are given in the Results). Nonsignificant random effects were removed from the model (Bolker et al. 2009; Zuur et al. 2009). We then compared random intercept models with random intercept and slope models (Zuur et al. 2009). If no random effect was significant, we used generalized linear models (GLM) to confirm the results of the mixed models. Fixed effects: after deciding on the appropriate random effects structure, we tested the fixed effects with Wald tests (Bolker et al. 2009; Zuur et al. 2009). Nonsignificant interactions between fixed effects ($P > 0.05$) were removed from the final model.

RESULTS

Across the eight trials (two × four colonies), DF foragers performed 741 dances comprising 9430 waggle runs (mean ± SD = 12.7 ± 10.5/dance; Table 1). Approximately 80% of the trained TF foragers followed DF dances during the 120 min testing period (120 m: 82%, 600 m: 78%; Table 1). The following analysis focuses on the behaviour of these TF foragers.

TF foragers followed on average 6.3 ± 5.2 (range 1–37) dances comprising 26.1 ± 25.8 (range 1–181) waggle runs. Individual dances were followed for 4.4 ± 2.2 waggle runs. In 78.5% of dance-following events, following ended before the dance. During the 120 min of observation, TF foragers visited the familiar TF feeder, which was empty, 2.6 ± 1.9 times.

The Effect of Training Distance on Feeder Choice

By the end of the test period, 77 of the 359 (21.4%) trained TF foragers had been recruited to the DF feeder. We predicted that more TF foragers would switch to the DF feeder if their own feeder was further away. However, Table 1 shows that there was no clear

Table 1

Summary data on the behaviour of honeybee foragers trained to two feeders (TF foragers), either at 120 m or 600 m, in all eight trials (two distances × four colonies)

Hive	Distance (m)	DF dances	Waggles[*]	TF trained[†]	Followed DF[‡]	Sum waggle runs[§]	Average[**]	Dances[††]	Waggle runs[‡‡]	TF recruited 1[§§]	TF recruited 2[***]	Visited TF[†††]
1	120	101	1258	29	28	977	3.4±1.2	10±5.7	34±25.6	3	14	3.2±1.6
1	600	113	1431	31	23	305	2.0 ±0.9	5.7±4.5	11.4±13.1	0	1	3.5±1.8
2	120	76	969	38	31	1324	5.2±2.2	8.6±5.6	45.3±29.3	4	7	1.9±1.2
2	600	84	1089	51	45	1084	4.5±1.5	5.2±3.5	23.3±17.4	15	25	1.5±1.2
3	120	74	625	82	57	786	4.5±2.1	3.2±2.1	14.5±11.0	6	12	2.8±2.1
3	600	96	1189	35	19	271	3.1±2.1	4.7±2.8	14.6±10.5	1	2	4.2±1.5
4	120	57	674	48	39	811	5.5±2.8	3.7±2.9	20.4±20.2	1	1	2.3±1.7
4	600	140	2195	45	44	1940	4.8±2.0	9.6±7.2	46.3±38.6	4	15	3±2.3

Data are given as sample size or mean ± SD. TF: training feeder; DF: dance feeder.

[*] Total number of waggle runs performed by DF foragers at DF (novel feeder being advertised by dances).

[†] Number of TF foragers trained during the odour treatment day.

[‡] Number of trained TF foragers that followed DF dances during the 120 min testing period.

[§] Total number of DF waggle runs followed by TF foragers (foragers previously trained to a feeder at 600 or 120 m at locations different from DF).

[**] Mean number of waggle runs followed by TF foragers.

[††] Mean number of DF dances followed by TF foragers during the 120 min testing period.

[‡‡] Mean number of waggle runs followed by TF foragers during the 120 min testing period.

[§§] Number of TF foragers recruited to the DF feeder after following the first DF dance.

[***] Number of TF foragers recruited to the DF feeder during the entire 120 min testing period.

[†††] Mean number of times TF foragers visited the TF feeder during the 120 min testing period.

effect of training distance on the probability of being recruited to the DF feeder. In two colonies, H1 and H3, a higher proportion of 120 m than 600 m TF foragers were recruited to DF, but vice versa in colonies H2 and H4. There was no statistically significant effect of treatment distance (GLMM with binomial response variable: recruited to DF; predictor variable: treatment distance: $z = 0.2$, $P = 0.83$; random effects: colony: $\chi^2 = 0$, $P = 1$; trial: $\chi^2 = 22.5$, $P < 0.001$). This model showed that trial day had a big effect. This could be caused by unidentified environmental effects (e.g. weather) on a trial day.

Only 10.5% of TF foragers were captured at the DF feeder after following DF dances, without having visited the TF. Most foragers, 76%, were first observed at TF. Only 13.5% were not observed at either DF or TF (Fig. 1). The proportion of foragers recruited to DF (using social information) versus being reactivated to TF (using private information) after following the first DF dance did not differ between the two treatments (9.2% versus 74.7% at 120 m, and 11.7% versus 77.2% at 600 m; GLMM with binomial response variable: recruited to DF; predictor variable: treatment distance: $z = -0.2$, $P = 0.81$; random effects: colony: $\chi^2 = 0.1$, $P = 0.73$; trial: $\chi^2 = 2.2$, $P = 0.14$; GLM without random effects; treatment: $z = -1.3$, $P = 0.19$).

The Effect of Training Distance on Dance-following Behaviour

We predicted that foragers trained to the 600 m feeder would pay more attention to the DF dances than foragers trained to the 120 m feeder. However, we found the opposite effect (Table 1, Fig. 2). In all four colonies, TF 600 m foragers followed, on average, 24.6% fewer waggle runs per dance (Fig. 2). This effect was highly significant (LME with log-transformed normal response variable: waggle runs/dance followed; predictor variable: treatment distance: $t = -4.6$, $P < 0.001$; random effects: colony: $\chi^2 = 5.0$, $P = 0.026$; trial: $\chi^2 = 0.53$, $P = 0.47$). There was no treatment effect on the number of dances followed (GLMM with quasi-Poisson response variable: number of dances followed; predictor variable: treatment distance: $t = 0.2$, $P = 0.83$; Table 1) or on the total number of waggle runs followed (GLMM with 'quasi-Poisson' response variable: total number of waggle runs followed; predictor variable: treatment distance: $t = -0.5$, $P = 0.67$; Table 1).

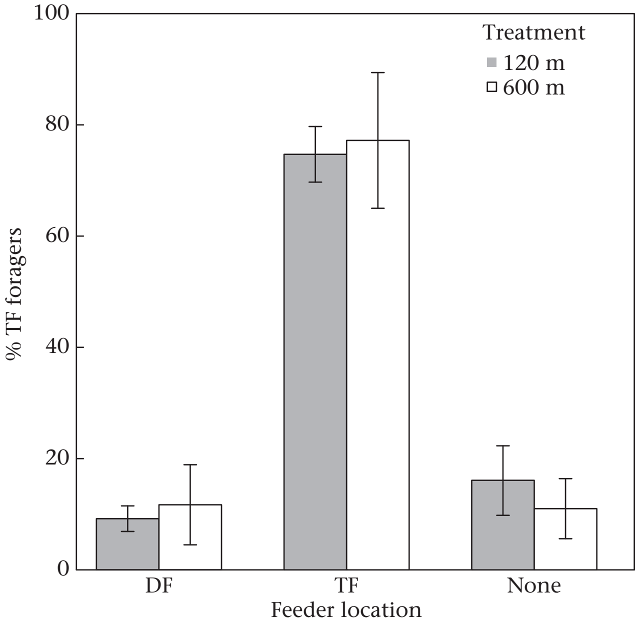

Figure 1. Percentage of foragers trained to a feeder (TF), at either 120 or 600 m from the hive, that were observed at either the feeder being advertised by dances (DF), the now unrewarding training feeder (TF), or neither feeder (none) after following the first dance for the DF. Bars show means ± SD of the four colonies studied.

Comparing the Dance-following Behaviour of DF and TF Foragers

We tested whether DF foragers followed DF dances for fewer waggle runs (4.72 ± 2.4 waggle runs) than TF foragers that were also trained to 120 m (4.71 ± 2.2 waggle runs; $N = 155$) but found no difference (LME with log-transformed normal response variable: number of waggle runs/dance followed; predictor variable: training feeder (DF versus TF): $t = -0.054$, $P = 0.59$; random effects: colony: $\chi^2 = 2.3$, $P = 0.12$; trial: $\chi^2 = 0.05$, $P = 0.99$; GLM without random effects; DF versus TF: $t = -0.2$, $P = 0.86$).

TF Foragers Successfully Recruited to DF

To explore whether TF foragers that were eventually recruited to the DF feeder increased their interest in DF dances gradually or abruptly (i.e. just before being seen for the first time at the DF feeder, that is, before being recruited), we ranked the DF dances followed by a TF forager according to their order before the forager was recruited and averaged, for each of these ranks, the number of waggle runs that were followed (Fig. 3). For example, the last dance followed before being recruited to DF (dance 1) is shown at the right end of the *X* axis in Fig. 3. Foragers slowly increased their attendance at DF dances with an abrupt and substantial increase in the number of waggle runs followed just before being observed foraging at the DF feeder: +65.4% at the last dance followed (dance 1) compared with the penultimate dance (dance 2). The mean ± SD interval between attending these two dances was 6.1 ± 8.5 min ($N = 65$). Statistical analysis confirmed that the number of waggle runs followed increased as the dance rank decreased (Fig. 3) (GLMM, with Poisson response variable: number of waggle runs/dance followed; predictor variable: dance rank: $z = -10.3$, $P < 0.001$; random effects: colony: $\chi^2 = 0$, $P = 1$; trial: $\chi^2 = 4.4$, $P = 0.036$; bee: $\chi^2 = 19.0$, $P < 0.001$). However, when analysing only the last three dances we found no difference between dance 3 and dance 2, but significant differences between the last dance, 1, and the previous two dances (GLMM, with Poisson response: day 1 versus day 2: $z = 7.1$, $P < 0.001$; day 1 versus day 3, $z = 7.1$: $P < 0.001$; day 2 versus day 3: $z = 0.35$, $P = 0.72$; random effects: colony: $\chi^2 = 0$, $P = 1$; trial: $\chi^2 = 2.6$, $P = 0.1$; bee: $\chi^2 = 3.6$, $P = 0.058$).

Figure 3 also shows the dance-following behaviour of TF foragers that were not recruited to the TF feeder by the end of the observation period (white bars). Here, we ranked the DF dances followed by a TF forager according to their order before the end of the observation period with dance 1 being the last dance observed. The number of followed waggle runs also increased with decreasing dance rank (GLMM, with poisson response variable: number of waggle runs/dance followed; predictor variable: dance rank: $z = -4.0$, $P < 0.001$; random effects: colony: $\chi^2 = 0.57$, $P = 0.45$; trial: $\chi^2 = 12.1$, $P < 0.001$; bee: $\chi^2 = 250.0$, $P < 0.001$).

To test whether bees were affected by previous attendance at dances, and in particular whether bees that had not followed many dances compensated in the last dance (dance 1), we tested whether the number of dances followed before recruitment was inversely related to the number of waggle runs followed during the last dance before recruitment. We found no significant effect (LME with square-root transformed normal response variable: number of waggle runs of last dance followed; predictor variable: number of dances followed before last dance: $t = 0.78$, $P = 0.44$; random effects: colony: $\chi^2 = 0.65$, $P = 0.42$; trial: $\chi^2 < 0.1$, $P = 0.99$; linear

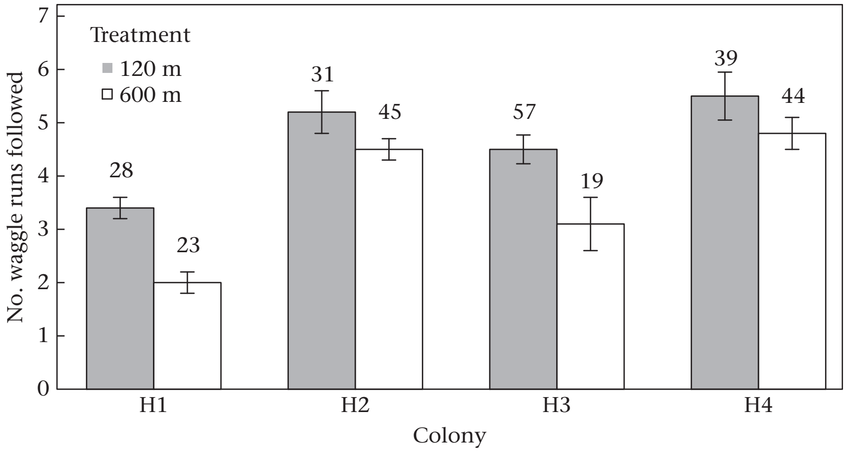

Figure 2. Numbers of waggle runs per dance advertising the dance feeder (DF) location followed by foragers previously trained to a feeder (TF) at 120 m (grey bars) or 600 m (white bars) for the four study colonies. Bars show means ± SD per bee over the entire observation period. Numbers above bars give the number of bees.

model without random effects; number of dances followed: $F_{1,75} = 0.07$, $P = 0.79$). In addition, the increase in the number of waggle runs followed between the last two dances was not affected by the total number of dances followed before being recruited (LME with normal response variable: difference between last two dances in number of waggle runs followed; predictor variable: number of dances followed before last dance: $t = 0.56$, $P = 0.57$; random effects: colony: $\chi^2 = 0.45$, $P = 0.50$; trial: $\chi^2 < 0.1$, $P = 0.99$; linear model without random effects; number of dances followed: $F_{1,63} = 0.1$, $P = 0.74$).

DISCUSSION

Contrary to expectation, we did not find that a greater cost of using private information causes foragers to increase their use of social information. Foragers trained to a food source 600 m from the hive that was currently unrewarding were not more likely to use social information for a novel location when compared to foragers trained to a 120 m food source. This is contrary to expectation if foragers were using either a copy-if-asocial-information-is-costly or a copy-if-better strategy (Laland 2004; Kendal et al. 2009). We suggest that our results and the results of two previous studies (Grüter & Ratnieks 2011; Wray et al. 2012) are more consistent with a copy-if-dissatisfied social learning strategy. Here, foragers would continue to use private information even if costs increase, as long as the overall profitability of a food source is ‘satisfactory’. We created a ‘satisfactory’ food source at both locations, TF and DF, by offering an above-average reward at both. That is, both feeders allowed bees to quickly collect high-concentration sucrose solution. The 1000 m foragers in Wray et al. (2012) might have been more dissatisfied because the quality of the TF food source was deliberately kept lower during the training period to avoid recruitment during training (Wray et al. 2012). Our statistical analysis found significant effects of trial days (see also Table 1). This suggests that other unknown factors specific to a trial (e.g. wind conditions at the training feeder) might also influence the decision of a forager to use private versus social information.

Foragers trained to the more distant food source actually followed dances for the closer alternative food source less (ca. 25% fewer waggle runs per dance; Fig. 2). How can this be explained? There is evidence that experienced foragers pay more attention to dances indicating a known food source, such as when there is a

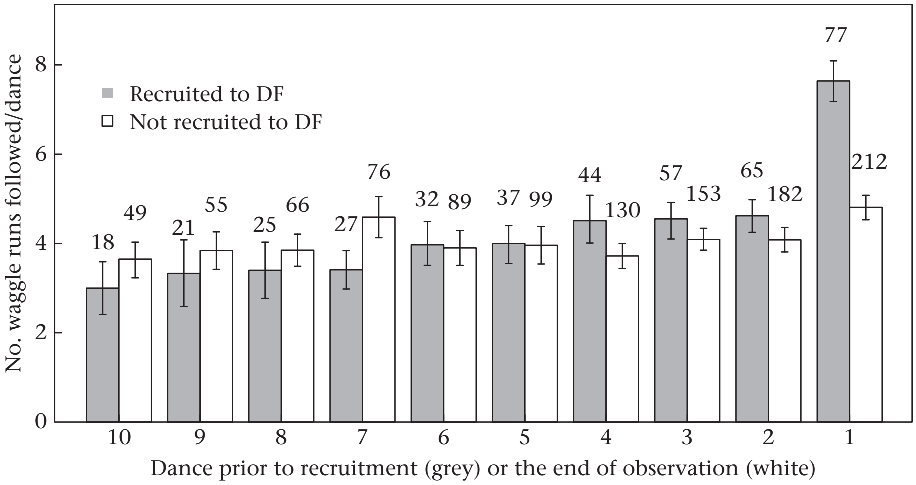

Figure 3. Number of waggle runs per dance advertising a novel feeding location (dance feeder: DF) followed by foragers previously trained to a different location (training feeder: TF) that were (grey bars) or were not (white bars) recruited to the new location by the end of the observation period. The *X* axis shows the order of dances prior to recruitment (grey bars) or prior to the end of the observation (white bars), with 1 being the last dance before the bee was seen at the new feeder (grey bars). Bars show means ± SD. Numbers above bars indicate the number of bees.

match between the memorized and the advertised locations (von Frisch 1967; Wray et al. 2012; but see Grüter et al. 2008). This could be adaptive because matching dances may indicate that a familiar food source that had become unrewarding may now be rewarding again. This can be valuable information. Possibly, the 600 m TF foragers recognized more quickly than the 120 m TF foragers that DF dances did not match their memorized location due to a difference in distance (see also von Frisch 1967, page 152) and, hence, showed less interest. A mismatch in the direction alone had no effect, at least at 120 m, because there was no difference in dance following between foragers following a dance for a familiar location (DF foragers) versus unfamiliar locations (TF foragers at 120 m) (see also Grüter et al. 2008). The effect of this mismatch in distance and direction information on dance-following behaviour is still poorly understood and different studies have provided contrasting results (von Frisch 1967; Grüter et al. 2008; Wray et al. 2012; this study). This interesting aspect of waggle dance communication deserves further investigation.

Our results confirm a previous study (Menzel et al. 2011) by showing that, even at foraging distances of around 600 m, a majority of foragers with experiences at a profitable food source will initially ignore social location information about an alternative profitable food source and use private information instead. In our study, only 10.5% of foragers used social information, but 76% used private information (Fig. 1). In Wray et al. (2012), the proportion of foragers using social versus private information was higher, 40% at 100 m, which might also be due to the fact that the food source in the feeder during training was kept below the dancing threshold. Menzel et al.'s (2011) study provides an intriguing twist to the question of social versus private information use. Their results suggest that at least some of the bees that initially ignored the social location information after following a dance none the less learned and stored dance vector information and used this information after finding their TF location unrewarding. These bees were then able to fly from the TF location to the DF location using a novel shortcut (Menzel et al. 2011).

Honeybee foragers clearly are flexible in how they use information. If a familiar food source remains unrewarding, foragers increasingly follow dances advertising alternative food sources (Grüter & Ratnieks 2011). Grüter & Ratnieks (2011) found a slow and gradual increase in the number of waggle runs followed per dance as foragers experienced the continued unavailability of their familiar food source (their Figure 3). However, these authors did not distinguish between successful recruits to the new food source and foragers that did not switch. In the current study, we found that arrival at the novel feeder advertised by waggle dances was characterized by a sudden and substantial increase in the number of waggle runs followed by the recruited bee (Fig. 3). The last dance (dance 1) before recruitment was followed for 65% more waggle runs than the previous dance (dance 2). In contrast, the increase was only 16% from dance five to dance two. The time interval between dance 2 and dance 1 was only 6.1 ± 8.5 min. This suggests that the switch from using private information to using social information is preceded by an abrupt motivational change, with bees nearly doubling their attendance at a dance within minutes. After following this last dance, foragers located the food source relatively quickly, being captured at the feeder a mean ± SD of 5.0 ± 2.7 min later. This suggests that foragers recruited by a waggle dance can locate a nearby food source quickly after following a dance carefully (see also Grüter & Ratnieks 2011; but see Wray et al. 2012). We found no effect of the number of previously followed dances on the following of the last dance before recruitment. One interpretation of this result is that TF foragers learned the vector information of the dance only during the following of the last dance.

The process of switching to a new food source that we observed shows parallels, but also some differences, compared to the earlier descriptive account of Seeley & Towne (1992). Our results confirm an initial period of 'cursory dance following' (dances 2–10; Fig. 3) followed by an event of 'thorough dance following' just before successful recruitment. During the phase of 'cursory dance following', foragers respond to dances by occasionally visiting familiar food locations, usually ignoring the location advertised by the dance. Subsequently, foragers increase the number of waggle runs they follow per dance even before 'thorough dance following' (Grüter & Ratnieks 2011; this study). During this period, foragers do not follow dances at random to find a new patch, but preferentially follow dancers that carry a familiar food odour (Balbuena et al. 2012; Grüter & Farina 2009b; Grüter & Ratnieks 2011).

What circumstances favour the use of private over social information in honeybee foraging? Bees that follow dances for natural food sources probably need substantially more time to locate a new patch than foragers flying to a known patch or bees that scout independently for new food sources (Seeley 1983; Seeley & Towne 1992; Seeley & Visscher 1988). Hence, it makes sense to prioritize private information when a familiar feeding site is profitable and also when it has a high chance of being rewarding again at the time of dance following (Grüter & Farina 2009a; Grüter & Ratnieks 2011). Since flowers of the same species bloom and offer food more or less in synchrony during certain hours of the day (Linnaeus 1751; Beutler 1930; Kleber 1935), the presence of a familiar food odour on a dancer should be a useful indication that this particular flower species is currently rewarding.

Recent research has demonstrated that honeybee foragers do not blindly follow the instructions of their successful nestmates after following a dance. Rather, they have a flexible information use strategy and use the waggle dance information in a context- and content- dependent way (Grüter et al. 2008; Grüter & Ratnieks 2011; Menzel et al. 2011; Wray et al. 2012; Al Toufailia et al. 2013). The honeybee is proving to be a practical experimental system for investigating information use in different circumstances. Future research is needed to determine how the different individual strategies lead to adaptive responses at both individual and colony level.

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