



Honeybee foragers increase the use of waggle dance information when private information becomes unrewarding

Christoph Grüter*, Francis L.W. Ratnieks

Laboratory of Apiculture & Social Insects, School of Life Science, University of Sussex

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Social insect foragers often have access to both social and private information about the locations of food sources. In honeybees, *Apis mellifera*, foragers can follow waggle dances (social information) to obtain vector information about the location of profitable food sources or they can use route memories (private information) acquired during previous foraging trips. The relative use of social information versus private information is poorly understood and currently debated. It is hypothesized that social information should be prioritized when the use of private information has a low benefit. We tested this hypothesis by training foragers to a high-quality 2 M sucrose feeder, which subsequently became unrewarding. As foragers continued to experience zero reward from their private route information they increased the time spent following waggle dances advertising an alternative food source with the same odour. A significant proportion of foragers successfully switched to the food source indicated by dances. Overall, trained foragers showed a strong attachment to the known but currently unrewarding feeder, even after repeatedly following dances advertising a profitable alternative. Successful recruits to the novel food source advertised by the waggle dances had more social information about this source in that they had followed dances for longer. Our results suggest that honeybee foragers follow a strategy that is conservative in terms of switching from one food patch to another.

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In many social insects, successful foragers guide nestmates to food sources by providing route or location information (reviewed in Hölldobler & Wilson 1990; Hölldobler 1999; Franks & Richardson 2006; Leadbeater & Chittka 2007; Jarau & Hrcncir 2009). The best known example is the waggle dance of honeybees (*Apis*), by which a forager communicates the distance and direction vector to the food patch it has been visiting to nestmate workers that follow the dance (von Frisch 1967; Seeley 1995; Riley et al. 2005).

However, recent studies suggest that many workers that follow waggle dances ignore the vector information on leaving the nest (Biesmeijer & Seeley 2005; Grüter et al. 2008; Grüter & Farina 2009). Instead of recruiting bees to the indicated location, waggle dances often prompt experienced foragers to revisit food sources that they have previously used. It seems that the floral odours on the dancing bee are important for the reactivation of unemployed foragers (von Frisch 1967; Reinhard et al. 2004; Grüter et al. 2008; reviewed in Reinhard & Srinivasan 2009): if a dancing bee carries a particular floral odour, this preferentially attracts foragers that know this odour from their earlier foraging, and after following the

dance most followers return to the known food source (reactivation) rather than to the advertised location (recruitment; Johnson 1967; Grüter et al. 2008). Hence, social odour information can cause informational ambiguity if it is similar to private odour information linked to route memories. Route memory information enables forager honeybees and ants to return to known food locations for weeks or even months (Ribbands 1949; Rosengren & Fortelius 1986; Collett et al. 2003).

In several ant species, private location information overrides social information in experienced foragers (e.g. *Formica* sp.: Rosengren & Fortelius 1986; *Paraponera clavata*: Harrison et al. 1989; *Lasius neoniger*: Traniello 1989; *L. fuliginosus*: Quinet & Pasteels 1996; *L. niger*: Grüter et al. 2011), which ignore pheromone trails (but see *Linepithema humile*: Aron et al. 1993). In vertebrate species that have been tested, private information is prioritized if it is reliable and up-to-date (van Bergen et al. 2004; reviewed in Laland 2004; Kendal et al. 2005). What circumstances, therefore, result in the prioritization of the social vector information from waggle dances by forager honeybees? For example, is vector information predominantly used by workers that are beginning their foraging career, and hence lack private information about food sources, whereas experienced foragers predominantly use the dance as an indication that familiar types of food are still available and should be revisited (Biesmeijer & Seeley 2005; Grüter

* Correspondence: C. Grüter, Laboratory of Apiculture & Social Insects, School of Life Science, John Maynard-Smith Building, University of Sussex, Falmer BN1 9QG, U.K.

E-mail address: cg213@sussex.ac.uk (C. Grüter).

& Farina 2009)? However, it is unlikely that experienced foragers would enhance their foraging by using private information under all circumstances.

We investigated whether experienced honeybee foragers switch to prioritizing social information from waggle dances when their sucrose food source, which has the same odour as the source advertised by the dances, becomes unrewarding. We predicted that reactivated foragers finding that the feeder that they had previously been visiting was still unrewarding would return to the nest and pay closer attention to waggle dances, such as by increasing the number of waggle runs they follow, thereby indicating their interest and use of social vector information (a dance usually consists of one to several dozens of waggle runs; Biesmeijer & Seeley 2005; Grüter et al. 2008; Tanner & Visscher 2009). This would result in foragers switching from their familiar but unrewarding feeding location to a novel rewarding location that is advertised by waggle dances.

METHODS

Experiments were performed in September and October 2009. Ivy, *Hedera helix*, was the only important natural pollen and nectar source available at that time. We studied three colonies of *Apis mellifera* at the Laboratory of Apiculture and Social Insects, University of Sussex. Each colony was housed in an observation hive containing three deep Langstroth frames or the equivalent comb area in medium frames (H1–H3). Each colony was thriving with a queen, about 3000 workers, brood, pollen and honey reserves, and had been set up for several weeks prior to data collection.

Experimental Procedure

One hive at a time was studied. We used standard training procedures (von Frisch 1967; Seeley 1995) to train a group of 30–50 worker bees to a feeder (F1) offering unscented 2 M sucrose solution ad libitum 150 m from the hive. The training process took 1–2 days. The trained F1 foragers were individually marked with numbered tags glued to the notum (Opalithplättchen, Christian Graze KG, Weinstadt-Endersbach, Germany). A different group of 30–50 bees (F2 foragers) were trained to a second feeder (F2), 150 m from the hive and 180 m from F1, and individually marked. 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 F1 and F2 foragers knew of only one feeder location during the training period. Foragers visiting high-quality food sources show little interest in other waggle dances (Seeley & Towne 1992) and do not switch to other food sources. On the day after training, both feeders offered 2 M of identically scented sucrose solution (50 µl essential oil per litre sucrose solution; Farfalla Essentials AG, Uster, Switzerland) for 60 min, from about 1300 to 1400 h (henceforth: odour treatment day). During this period, foragers of both groups could learn the association between location and scent. The 60 min duration allowed foragers to make at least three foraging trips (mean \pm SD = 6.14 \pm 1.93), which is known to be 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 (Hive 1), peppermint (Hive 2) and lemon (Hive 3).

We trained a total of 118 F1 foragers. On the first day after the odour treatment (test day 1), we allowed F2 foragers to collect 2 M sucrose solution for 120 min (1100–1300 h) at F2. F1 was empty during the entire period. The syrup in the F2 feeder had the same scent as during the odour treatment day and was discovered within 20 min by F2 foragers. We allowed 10 F2 foragers to make repeated syrup-collecting trips and to perform waggle dances in the hive. F1

foragers that followed the dances of F2 foragers would therefore experience an informational conflict between the social vector information of the dance and the private location information, triggered by the familiar odour of the F2 dancers. This was repeated on the next day (test day 2). All other marked and unmarked foragers arriving at F2 were captured in plastic tubes and their arrival time noted; this was done to limit the number of dancers to 10. The arrival time and the number of F1 foragers visiting the F1 feeder during the 120 min test period were also noted. We counted two landings at the feeder as two different visits if the interval between them was ≥ 3 min. At the hive, interactions between the 10 F2 foragers and the F1 foragers were filmed 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). The numbered tag was readable in all but one of the 1252 instances of an F1 forager following an F2 dancer. A bee was defined as having followed a dance if her head was directed towards a dancer within one antennal length during at least one waggle run (Tanner & Visscher 2009). Following a dance does not imply that the follower acquired information or will use the information acquired. Simultaneously to the dances of F2 foragers, some unmarked foragers performed waggle dances for natural food sources on the dance floor. When these occurred, we recorded whether dancers carried pollen and measured the waggle run duration as a measure of the indicated distance (von Frisch 1967). We averaged three waggle runs to the nearest 0.1 s (except in cases where dancers performed < 3 waggle runs). We recorded when, how often and for how many waggle runs F1 foragers followed F2 dances for the F2 feeder and dances for natural food sources.

Statistical Analyses

We analysed the data using general and generalized linear mixed-effect models (LME and GLMM) in R 2.9 (R Development Core Team 2009). R fitted the models with the lmer and the lme functions (Zuur et al. 2009). Because we often had several observations per bee and always had several bees per hive we included both hive and bee (if applicable) as hierarchically nested random effects to control for the nonindependence of data from the same bee and bees from the same hive (Bolker et al. 2009; Zuur et al. 2009). For model selection we used the protocol proposed by Zuur et al. (2009). We first explored the optimal structure of the random components (comparing random intercept models with random intercept and slope models) before testing the fixed effects. Since we had no a priori interest in testing for differences between hives, we retained the random effects in the model (Bolker et al. 2009) when testing the significance of the fixed effects (see Results). Testing the fixed effects was done with Wald tests (Bolker et al. 2009; Zuur et al. 2009). Nonsignificant interactions between the fixed effects ($P > 0.05$) were removed for the final model.

RESULTS

Dance Following of F1 Foragers

Across the three trials, F2 foragers performed 472 waggle dances comprising 5272 waggle runs (mean \pm SD = 11.17 \pm 8.05 per dance,) for the F2 feeder during test days 1 (245 dances) and 2 (227 dances). F1 foragers showed a strong interest in these dances and most (104 of 118, 88.1%) followed dances (4203 waggle runs in total). On average, F1 foragers followed 11.59 \pm 5.60 (range 1–35) dances and 40.03 \pm 28.92 (range 1–127) waggle runs for the F2 feeder, with six (5.8%) following more than 100 waggle runs. In the 4 h of observation on test days 1 and 2 combined, each F1 forager

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