



## 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.

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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 & Hrcncir 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 Toufaily 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 Toufailya, 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 Toufailya 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).

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