ANIMAL
BEHAVIOUR

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

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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 & Hrncir 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

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& 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 ± SD = 6.14 ± 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 ± SD = 11.17 ± 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 ± 5.60 (range 1–35) dances and 40.03 ± 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

visited the empty F1 feeder 4.88 ± 3.27 times (range 0–15; 99% of all F1 foragers made ≥1 visit).

Figure 1 shows the percentage of F1 foragers visiting the F1 and F2 feeders during the experiment. No F1 forager was seen at F2 on the odour treatment day. By the end of test day 1, 13.5% (14 of 104) of the F1 foragers had switched from F1 to F2, doubling to 25% (21 of 84; Fig. 1) by the end of test day 2. This change in the proportions of F1 foragers visiting the two feeders across the 3 days is highly significant (GLMM with 'day' as fixed effect: $Z = 5.14$, $P < 0.001$). We found a significant positive relationship between the number of F2 dances followed and the number of times an F1 forager revisited the F1 feeder (GLMM: $Z = 3.22$, $P = 0.001$; Fig. 2). Figure 2 shows this relationship for F1 foragers recruited and nonrecruited to the F2 feeder. The different slopes of the two best fit lines suggest that bees recruited to F2 responded more strongly to waggle dances and did not merely follow more dances. Our previous model confirmed this by showing a significant interaction between the number of dances followed and whether an F1 forager was recruited to F2 or not ($Z = 2.4$, $P = 0.016$).

We then tested whether the number of times an F1 forager visited the empty F1 feeder on test days 1 and 2 was related to the number of waggle runs per dance followed subsequently. We included the total dance duration (in waggle runs), the experimental day and the number of waggle dances that an F1 forager had previously followed as additional explanatory variables in the model to control for any confounding effects these might have. We found a significant positive relationship between the number of previous visits to F1 and the number of waggle runs for F2 followed per dance (GLMM: $Z = 2.16$, $P = 0.031$; Fig. 3). Furthermore, F1 foragers tended to follow dances for longer on day 2 ($Z = 1.7$, $P = 0.089$) than day 1. Not surprisingly, the total length of a dance positively affected the number of waggle runs followed per dance ($Z = 7.77$, $P < 0.001$). The number of previous waggle dances followed had no effect on the number of waggle runs followed per dance ($Z = 0.21$, $P = 0.84$). The number of dances a bee followed in the interval between making two unrewarded visits to F1 was not affected by the number of previous unrewarded visits to F1 ($Z = 1.58$, $P = 0.11$).

Following Dances for Natural Food Sources

We analysed 107 dances for natural food sources (34 in Hive 1, 46 in Hive 2, 27 in Hive 3) with a total of 905 waggle runs (8.45 ± 7.4 waggle runs/dance). In 78 (72%) of these dances the dancing bee did not carry pollen. The waggle runs lasted 0.3–2.5 s (1.18 ± 0.48 s). Using von Frisch's (1967) distance curve, we estimate that the indicated distances are about 130–2500 m with
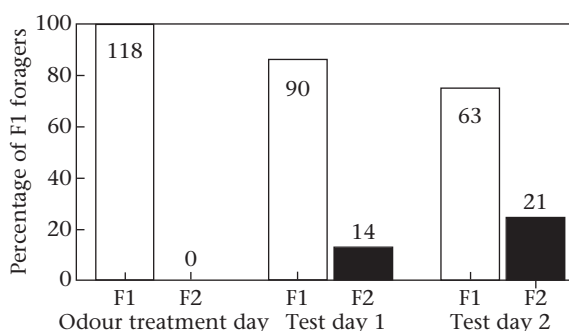

Figure 2. Relationship between the number of waggle dances followed and the number of times F1 foragers visited the familiar but now empty F1 feeder. Each circle represents one F1 forager. Black circles show the foragers that were successfully recruited to the F2 feeder, which was advertised by waggle dances; white circles show foragers that were not recruited.

a mean distance of about 1000 m. Although these dancers were often briefly touched by F1 foragers (head within one antennal length; 1.22 ± 1.63 contacts/dance) only 27 (25%) were followed by at least one F1 forager. Interest in these dances was visibly lacking. The dances that were followed were followed much less than F2 dances (1.33 ± 0.62 versus 3.46 ± 2.78 waggle runs; $Z = 6.5$, $P < 0.001$). We also recorded no trophallactic contacts between the dancers and the F1 foragers during the 27 instances of dance following. However, unmarked followers were seen receiving food from these dancers. We then tested whether the interest in natural dances increased from test day 1 to test day 2 by comparing the proportion of dances that were followed on both days. We found no significant effect of test day, type (with pollen versus without pollen) and waggle run duration (i.e. distance to the food source; test day: $Z = -0.05$, $P = 0.96$; type: $Z = -0.23$, $P = 0.82$; waggle run duration: $Z = 0.63$, $P = 0.53$).

F1 Foragers Recruited to the F2 Feeder

Overall, 21 F1 foragers that followed F2 dances were recruited to the F2 feeder over the 2 test days (Fig. 1). F1 foragers that visited the

Figure 1. The percentage of F1 foragers visiting their training feeder, F1, and the feeder advertised by waggle dances, F2, at different times during the experiment. Test day 1 is the day after the odour treatment and test day 2 is 2 days after the odour treatment. Numbers within the F1 bars show the number of bees that visited this feeder exclusively. Numbers above the F2 bars show the number of bees that switched to the F2 feeder by the end of that day of the experiment.
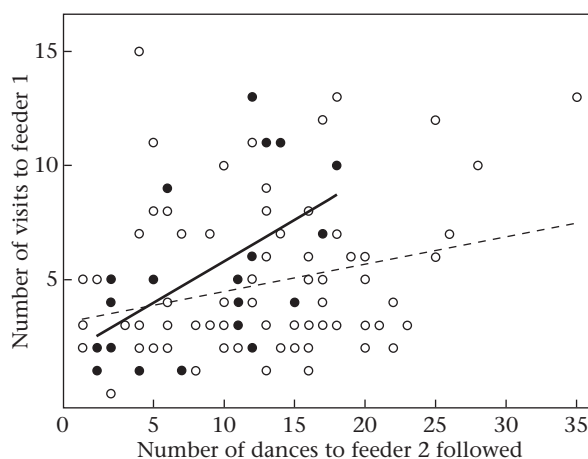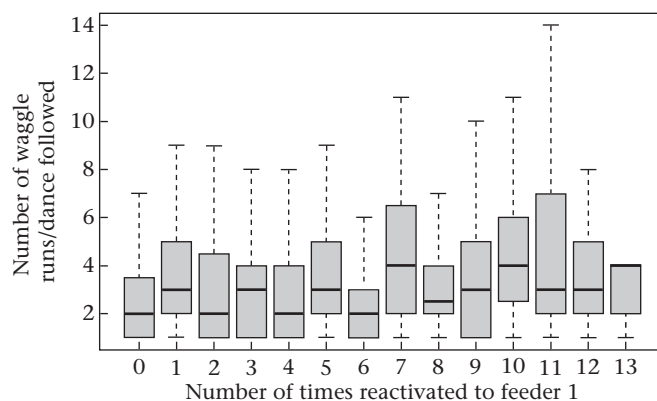

Figure 3. The relationship between the number of times F1 foragers visited the familiar but empty F1 feeder during the experiment and the number of waggle runs per dance followed after returning to the hive. The box plots show medians, quartiles, 5th and 95th percentiles.

F2 feeder followed more waggle runs per dance (LME: $t = 3.06$, $P = 0.003$; Fig. 4a) but fewer dances than those that did not visit F2 (LME: $t = -2.45$, $P = 0.016$; Fig. 4b).

How did F1 foragers locate the F2 feeder? Of these 21 bees, 19 (90.5%) followed one or several F2 dances after their last unsuccessful visit to the F1 feeder shortly before being captured at the F2 feeder. The average time between the last F2 dance followed and capture at F2 was 5.58 ± 3.58 min. On average, they followed 37.4 ± 9.2 waggle runs (range 3–71). The average time between the last unrewarded visit to the F1 feeder and capture at F2 was 30.24 ± 15.23 min.

Two bees (9.5%) flew to the F2 feeder shortly (3 and 5 min) after visiting the empty F1 feeder, without following dances after the last visit of the F1 feeder. They had, however, followed F2 dances before flying to the F1 feeder (3 and 14 waggle runs).

DISCUSSION

Foragers that repeatedly found that retrieving private information about feeding sites was unrewarded subsequently increased the number of waggle runs followed per dance for an alternative location of the same food type. As a consequence, foragers started switching from visiting the familiar but now unrewarding feeder, F1, to the unfamiliar but rewarding feeder, F2, advertised by F2 dancers (Fig. 1). F1 foragers did not increase their interest in dances advertising natural food sources. They followed these dances only briefly and had no trophallactic interactions with the dancing bee. Throughout the experiment, F1 bees preferred F2 dancers, which all had the familiar floral odour. The test feeders were relatively close to the hive, 150 m, but this proximity does not seem to be the reason why the natural food sources, which were generally at greater distances, 130–2500 m, were ignored: we found no effect of waggle run duration (which indicates distance) of natural dances on the dance-following behaviour of F1 foragers. However, a possible role of distance in the selection of dances should be addressed in future research. Of 21 successful recruits, 19 (90.5%) followed one or several F2 dances shortly (5.58 min) before being captured at the F2 feeder. However, two bees (9.5%) either flew directly from F1 to F2 or returned to the hive for a short while, but without following dances between visiting the two feeders. Both bees had followed dances earlier, so it is possible that they used the vector information of F2 dances before visiting F1 and combined this information with private spatial information acquired, for example, during orientation flights (see Menzel et al. 2006) or by path integration (Chittka et al. 1995) to fly directly from the

unrewarding feeder to the advertised one. More research is needed to confirm or refute this possibility.

Our results suggest that the process of switching from using private location information that yields no further foraging success to social location information can be relatively slow. During our experiment, F1 foragers followed an average of 11.6 dances (maximum 35) and 40 waggle runs (maximum 127) of F2 dances. The more F2 dances a bee followed the more it visited the familiar but now unrewarding feeder, F1 (Fig. 2). This shows a strong attachment of experienced foragers to food source locations that were profitable in the past even after repeatedly following waggle dances that provided information about currently profitable alternative food locations with the same food odour. In nature, honeybee foragers often visit the same food patch for days or even weeks (Ribbands 1949). The availability of natural nectar sources might not always be predictable and can be interrupted by bad weather, depletion, diurnal cycles, etc. Hence, finding that a food source is currently unrewarding does not mean that this location information is of no value because food might reappear later. As the number of times the forager finds no food at the known location increases, the incentive to use the alternative social vector information increases. This may explain the positive relationship between the number of unrewarded visits to a now unrewarding feeder and the interest in dances advertising the F2 feeder (Fig. 3). We also included time in the same model and found that foragers tended to follow dances for longer on test day 2 versus test day 1. This indicates that the time period between dance following and the last rewarded trip may also be a factor that favours the prioritization of social information.

What characterizes a successful recruit? Communication in animals is a probabilistic process and individual animals differ in their responsiveness to signals (Wilson 1971; Deneubourg et al. 1983). Our results show that recruits responded more strongly to waggle dances than nonrecruits. They visited the empty F1 feeder relatively more often in response to F2 dances (Fig. 2) and followed individual waggle dances for longer (39.5% more waggle runs per dance; Fig. 4a). Hence, these bees had both better social information about the location of the new food source and better knowledge about the diminished value of their old food source.

Overall, the strong initial attachment of honeybee foragers to a known food source and their subsequent switch to a location advertised by social information only after repeated unsuccessful foraging trips could be adaptive in an environment where food sources commonly become temporarily unrewarding for periods of up to a few days. If the food source reappears, dancing reactivates groups of experienced foragers working on the same plant species. Accordingly, previous studies have shown that experienced foragers frequently follow dances (under natural circumstances: Seeley & Towne 1992; Biesmeijer & Seeley 2005; in experiments: von Frisch 1967; Gil & Farina 2002; Grüter et al. 2008). Most (88%) of the F1 foragers in our study followed F2 dances. If food patches disappear completely, the spatial information encoded in the waggle dance provides foragers with an opportunity to switch to other high-quality food patches. Given that F1 foragers largely ignored dances for natural food sources, our results also suggest that foragers preferred to switch to another patch of the same food type. The reason might be that F1 foragers received rewards associated with the familiar odour while they were following F2 dances. Dancing bees often distribute small samples of food that function as rewards for social olfactory learning (Farina et al. 2005; Grüter et al. 2006). Hence, they would have acquired information that their food patch is no longer rewarding but other patches of the same food type are still around. More controlled experiments with multiple odours are needed to confirm or refute this hypothesis.

Our results raise a number of questions. An obvious one is why F1 foragers follow so many dances, given that dance followers can
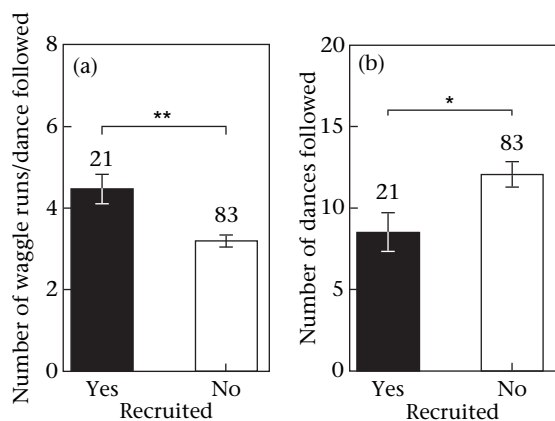
Figure 4. The dance-following behaviour of F1 foragers recruited and not recruited to the F2 feeder. (a) The number of waggle runs per dance followed. (b) The number of dances followed. The bar plots show the mean and SE. Numbers above bars show the number of bees. $*P < 0.05$; $**P < 0.01$.

acquire accurate location information from following just a few waggle runs (von Frisch 1967; Esch & Bastian 1970; Mautz 1971; Tanner & Visscher 2008). In addition, they only need about 200 ms to identify odours with high accuracy (Wright et al. 2009). The waggle dance has a strong motivational effect on surrounding bees (von Frisch 1967; Bozic & Valentincic 1991) and it has been argued that some foragers might need to interact longer with dancers to reach the necessary motivational state (Grüter & Farina 2009). Following several dances and many waggle runs could also be beneficial if it provides bees with better information about the overall foraging situation of the colony and, therefore, whether it is worth leaving the hive to undertake risky foraging trips (Visscher & Dukas 1997). Two studies suggest that the vector information conveyed by waggle dances does not enhance colony foraging success in many circumstances (Sherman & Visscher 2002; Dornhaus & Chittka 2004). However, our results suggest that the spatial information of the waggle dance might be particularly important when food sources suddenly disappear. Hence, we might find a significant role of the vector information in situations when the environment changes radically, such as by the disappearance of an important crop or after extended periods of bad weather. This possibility is also supported by a theoretical study showing that social information is particularly useful in a changing environment (Rendell et al. 2010).

In good foraging conditions, honeybees forage close to the hive, similar to the situation in our experiment. However, in less favourable conditions foragers fly to flower patches several km from the nest (Beekman & Ratnieks 2000). Would foragers that had previously collected nectar or pollen at greater distances also rely on private information after following a dance for a nearby food source? More experiments are needed to explore how foragers adjust their information use, and therefore their foraging strategy, according to the costs and benefits associated with using private and social information under naturally occurring foraging conditions such as distance variation. Many other social insects also use both social and private information to find food sources and foragers have to decide whether to rely on information provided by nestmates or self-acquired information (e.g. in ants: Rosengren & Fortelius 1986; Harrison et al. 1989; Quinet & Pasteels 1996; Grüter et al., in press; bumblebees: Leadbeater & Chittka 2009; stingless bees: Biesmeijer et al. 1998; Biesmeijer & Slaa 2004). These previous studies combined with the present study show that social insect foraging provides suitable experimental systems for investigating how the spatiotemporal availability of resources, the quality of information, and the costs and benefits associated with using information affect information choice strategies in animals.

Acknowledgments

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