

Original Article

How dancing honey bees keep track of changes: the role of inspector bees

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How do honey bees track changes in their foraging environment? Previously, 2 complementary mechanisms have been identified by which bees can effectively switch between food sources when their relative quality changes. First, an increase in profitability of a food source elicits an increase in waggle dances (the bees' recruitment mechanism) for that source. Second, bees that have retired from foraging at a food source make occasional inspection visits to that food source and resume foraging if its quality improves. Here, we investigate, using both field experiments and a mathematical model, the relative importance of these 2 mechanisms. By manipulating dance information available to the bees, we find that when food sources change quality frequently, inspector bees provide a rapid response to changes, whereas the waggle dance contributes to a response over a longer time period. The bees' ability to switch feeders without dance language information was found to be robust with respect to the spatial configuration of the feeders. Our results show that individual memory, in the form of inspector bees, and collective communication can interact to allow an insect colony to adapt to changes on both short and long timescales. *Key words:* *Apis mellifera*, collective memory, dynamic environment, foraging, honey bee, mathematical modeling. [*Behav Ecol*]

INTRODUCTION

Many animals live in groups. Benefits of group living include protection from predators (Hamilton 1971), social learning (Alcock 2005), cooperative care for the young (Gilchrist and Russell 2007), and cooperative foraging (Dussutour and Simpson 2009). Cooperative foraging allows group-living animals to exchange information about the location and profitability of food sources. This can be vital in environments where food is scarce or hard to find. Under such conditions, a single animal living alone has a low probability of finding a food source, but the chances that at least one member of a large group of searching individuals finds food are much higher (Seeley 1995; Beekman and Ratnieks 2000). Being able to share the information about the discovered food with other group members is the key to successful collective foraging.

A variety of mechanisms for sharing information have evolved across the animal kingdom. Some of the most sophisticated of these arose among the social insects, especially the ants and bees (Camazine et al. 2001). Many species of ants are known to share information with their nestmates by modifying their local environment. On the discovery of food, trail-laying ants lay a chemical, or pheromone, trail back to the nest that allows nestmates to follow the trail to the food source (Hölldobler and Wilson 1990). This mechanism allows foragers to rapidly recruit colony mates, leading to quick exploitation of a newly discovered food source. Even more sophisticated is the method of communication used by the honey bees (*Apis* spp.). The only nonhuman animal known to have a symbolic

language, the honey bee encodes information about the location and quality of food sources and potential nest sites in a recruitment dance (von Frisch 1967; Seeley 1995). Location information is encoded in the dance itself, while the intensity and duration of the dance indicate the quality of the food source or nest site being danced for.

There has been much debate about the specific benefits of the dance language with regard to foraging. The suggested benefits to the colony include rapid recruitment of foragers to newly discovered food sources (Seeley and Visscher 1988; Beekman and Lew 2008), greater foraging success in conditions when food is scarce and not easily discovered through independent search (Sherman and Visscher 2002; Dornhaus and Chittka 2004; Dornhaus et al. 2006; Beekman and Lew 2008), or conditions where food source locations change frequently (Dornhaus and Chittka 2004). However, the potential benefits of dance language in a changing environment have not been tested experimentally or via modeling. In tropical regions, where the honey bee dance is thought to have evolved, the foraging environment changes rapidly as many tropical trees only flower for a few days. In such a dynamic foraging environment, rapid communication about short-lived resources may be of crucial importance (Dornhaus and Chittka 2004).

Much of our current understanding of the mechanisms behind the dynamic foraging of honey bees stems from the seminal study of Seeley et al. (1991). They showed that worker bees make individual assessments of a food source's absolute quality and adjust their dance behavior accordingly without making direct comparisons between food sources. When the quality of a food source is high, the foraging bees react by dancing longer and more vigorously for that food source (Seeley et al. 2000). Longer and more vigorous dances attract more dance followers resulting in most bees being recruited toward the better quality food source. These changes in

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dancing response allow the colony to effectively track changes in food quality.

Much of the empirical work on honey bee foraging has been complemented by mathematical modeling reflecting different hypotheses about how memory of food sources is stored within a colony. In these models, bees are assigned to behavioral states, such as exploiting a food source or waiting for a dance to follow. They can switch between the states with experimentally determined rates. The modeling approach was first introduced by Camazine and Sneyd (1991) in order to simulate the experimental results of Seeley et al. (1991). The model of Camazine and Sneyd is based on the hypothesis that the collective memory of the colony is communicated via the dance language. Their model accurately predicted the rapid shift of the bulk of foragers to the rich food source shortly after the quality of the feeders had been switched. This model has been refined to account for scout bees and to introduce states for bees following dances for the different feeders (Sumpter and Pratt 2003). There are, however, several aspects of the honey bee foraging process missing from these models. de Vries and Biesmeijer emphasize the importance of individual behaviors; worker bees have multiple behavioral states from which they can go to exploiting a food source (de Vries and Biesmeijer 1998; Biesmeijer and de Vries 2001; de Vries and Biesmeijer 2002). In addition to switching to exploiting from scouting or recruiting, bees can also start foraging as inspectors or reactivated foragers. Inspector bees are former foragers who have retired from a food source but continue to make occasional visits to that food source and check on its quality. They resume foraging if the food source becomes profitable once again. Reactivated foragers are those bees that retired from a food source but return to it after receiving additional external information, such as an olfactory cue, about the quality of that source. Biesmeijer and Seeley (2005) followed bees through their entire foraging careers and determined that inspectors account for 63% of resumed foragers, while reactivated foragers constitute the remaining 37%.

Despite these studies, it remains unclear in what foraging situations reactivation and inspection are important and in what cases the dance language is the primary mechanism for communicating memory. Here, by investigating these mechanisms under rapidly changing foraging conditions, using a combination of experiment and modeling, we come to a better understanding of how honey bee colonies track changes in their environment. If dance language is the main mechanism allowing reallocation of a colony's foraging resources after a change in food source quality, then eliminating it should prevent the colony from being able to switch to a better quality food source. Conversely, if inspection plays a major role, then the colony should be able to reallocate its resources to the better food sources even in the absence of dance language.

We also investigate the spatial generality of our findings. If our results are robust with respect to food source distribution, then we expect the removal of dance information to have the same effect irrespective of the feeders' spatial configuration.

MATERIALS AND METHODS

Experimental methods

We conducted experiments in a grass paddock at the University of Western Sydney's Hawkesbury Campus in Richmond, New South Wales, Australia. A colony of *Apis mellifera* containing approximately 5000 bees was placed in an observation hive in a specially constructed bee hut. The hut was itself placed in the center of the field. We used 2 feeder configurations: a semicircular configuration and a sparse configuration, both using 3 feeders. This was done in order to determine whether

a bee colony is able to respond to changes in its environment under different food source distributions. Due to the directional imprecision of the dance, a bee following a dance for an isolated food source is likely to fail to find any food if she misses the particular food source that is being danced for (Towne and Gould 1988). In a more clustered foraging environment, where food sources are located close together, a recruited bee is likely to end up at a nearby food source even if she misses the intended one.

In the clustered arrangement, feeders 1 and 2 were only 15 m apart, whereas feeder 3 was 80 m from feeder 2. During the waggle phase of the dance, bees have a 15° error in waggle orientation (Towne and Gould 1988). Hence, feeders 1 and 2 were within the error of the dance. In the sparse configuration, all 3 feeders were 250 m from the hive and ~430 m from each other to form an equilateral triangle. The experimental layout is shown in Figure 1.

To ensure that the colony was aware of all 3 feeders at the start of the experiment, bees were initially trained to the 3 feeders containing 2 M sugar syrup. The feeders were placed together at the hive entrance until at least 8 bees were observed feeding. We then moved the feeders incrementally toward their final positions, 250 m from the hive. The training process took between 1 and 2 days, at the end of which the feeders were covered up to prevent attracting feral bees. Bees were not marked during training because we were only interested in the bees, which knew the final location of the feeder. The morning of the experiment, we refilled all 3 feeders with 2 M sugar water and waited until at least 5 bees had returned to each feeder. We then marked all visiting bees with feeder-specific colors for 15 min. This gave us a measure of the baseline number of foragers at each feeder.

We started the experiment by refilling 2 of the feeders with 1 M sugar syrup. These became the "low-quality" feeders. The remaining "high-quality" feeder was emptied and refilled with 2 M sugar syrup. Every 15 min, we counted the number of returning bees (defined as a bee already marked with the color of that feeder), recruits (unmarked bees), and switchers (bees carrying the color of a different feeder) that landed on the feeder within 2 min. All new recruits were marked. Every 105 min, a new randomly selected feeder was designated the high-quality feeder and the other 2 were designated the low-quality feeders. This continued until all 3 feeders had been designated as high quality once.

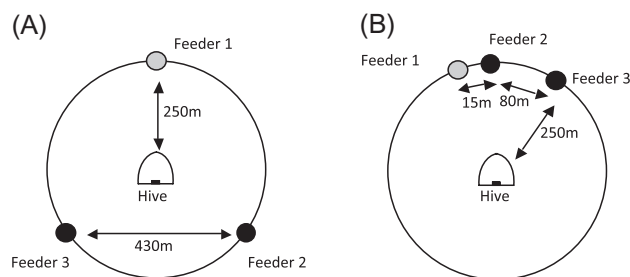


Figure 1

Experimental setup. In the experiments, feeders containing sugar solution were placed 250 m away from the hive in 2 different spatial configurations, sparse (A) and clustered (B). In the clustered configuration, a bee following a recruitment dance for one of the feeders is equally likely to end up at any of the feeders due to error in the dance's spatial accuracy. One feeder (gray) started out with a sucrose concentration of 2 M, whereas the others (black) contained 1 M solution. Some bees were trained to each of the feeders prior to the start of the experiment. During the experiment, feeder quality was switched every 105 min, with each of the 3 feeders becoming the profitable food source once.

Dance versus no dance

To test the importance of dance language on the colony's ability to adapt to changing foraging conditions, we needed to prevent the bees from transferring directional information. We achieved this by eliminating the cues dancing bees usually use to orient the dance. When a bee dances, the angle of the waggle phase relative to the direction of gravity on the vertical comb shows the direction of food relative to the azimuth of the sun (von Frisch 1967). In the absence of gravitational cues, bees orient the waggle dance toward the sun or polarized light (von Frisch 1967). We used a white sheet to diffuse light and prevent the bees from orienting toward polarized light and placed the hive on its side (horizontally) to eliminate gravitational cues. A similar method was used by Dornhaus and Chittka (2004) and Sherman and Visscher (2002) to disorient honey bee dances. Our treatment resulted in disoriented bees that wagged in random directions over the course of a single dance rather than the more focused oriented waggle normally observed. It is worth noting that while this treatment removes the directional component of dance information, it does not affect information about quality and distance to the food source being danced for.

We tested the efficacy of the treatment by videotaping the dances of bees in a normal hive and a treatment hive. We measured the angle of each "waggle" in the waggle dance for 15 bees from each hive. Only 30% of bees in the no dance treatment had oriented dances (Rayleigh's test: dances were considered disoriented if $P > 0.05$).

Statistical methods

The combination of configuration and dance/no dance led to 4 treatment groups: sparse/dance, sparse/no dance, clustered/dance, and clustered/no dance. We had 3 replicates for each treatment group with the exception of the clustered/no dance, which had 4 replicates. A different colony was used for each treatment.

Our central goal was to determine if disrupting dance language would prevent the colony from being able to shift its foraging force to the newly rich feeder. We used a signed-rank test to determine if a greater than expected proportion of honey bees were foraging on the high-quality feeder relative to the 2 low-quality feeders (expected probability = 0.33) in the time interval immediately before each quality change (at 105, 210, and 315 min). The proportion of honey bees was calculated by dividing the number of bees on the high-quality feeder by the total number of bees on all 3 feeders.

To increase our sample size for the statistical comparison of the dance and no dance treatments, we combined data from the sparse and clustered configurations.

We were also interested in the effect of spatial configuration on the colonies' ability to respond to changes in food quality. We used repeated measures analysis of variance (ANOVA) to analyze the effects of feeder configuration on the proportion of honey bees exploiting the high-quality feeder. We conducted separate analyses on each 105-min time period (period 1 = 0–105 min, period 2 = 105–210 min, and period 3 = 210–315 min). Note that the first measurement in each time period comes 15 min after the switch. Dance and no dance treatments were also analyzed separately, resulting in 6 analyses: dance (period 1, period 2, and period 3) and no dance (period 1, period 2, and period 3). Huynh-Feldt corrected P values and degrees of freedom are reported where assumptions of sphericity were not met.

All statistical analyses were done using JMP 8 (SAS, Cary, NC). All mean values are presented with standard errors.

EXPERIMENTAL RESULTS

Prior to the start of the experiment, all 3 feeders were of equal quality. Once 2 of the feeders were refilled with lower quality sugar solution, the highest quality feeder rapidly accumulated the largest proportion of foraging bees. Following the switch of food source quality (105 min after the beginning of the experiment), the number of bees visiting the highest quality feeder built up gradually.

Eventually, the most profitable feeder had the highest proportion of foraging bees in each of the experimental setups (Figure 2). We observed the same gradual build-up of bees on the 2 M feeder following the second switch (210 min after the start of the experiment). On average, it took 52.5 min after the switch for the most profitable feeder to attract the highest proportion of foraging bees.

Generally, the majority of the bees foraging at any particular feeder at a given time were returning bees, with the recruits and switchers making up the rest (Figure 3). Switchers made up the smallest proportion of foragers, never exceeding 30% of the total bees. Following a decrease in feeder quality, the total number of bees visiting that feeder went down. Of the bees still foraging at this feeder a lower proportion were now recruits and switchers (Figure 3). This supports the idea that those bees remaining at the low-quality feeder are "inspecting" it. Figure 4 shows the experimental results for a representative trial, including the total number of bees and the number of returns, recruits, and switchers on each feeder over time.

Dance versus no dance

In the dance treatments, colonies showed a significant preference for the high-quality feeder in all 3 time periods (one-sided

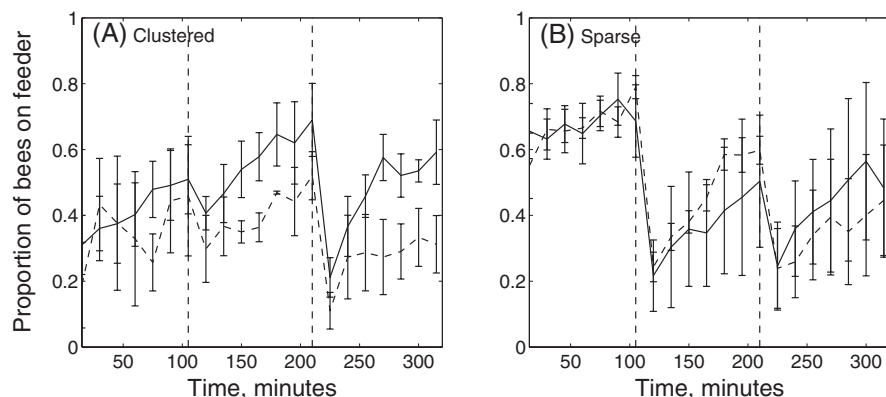


Figure 2

Proportion of bees on the highest quality feeder. This figure shows the percentage of foraging bees that are exploiting the most profitable feeder at any given time, for both the dance and the no dance experimental treatments. Panel (A) shows the clustered feeder setup and (B) shows the sparse. The solid line shows the dance treatment and the dashed line shows the no dance treatment. The vertical dashed lines indicate feeder quality switching times. Error bars denote standard errors.

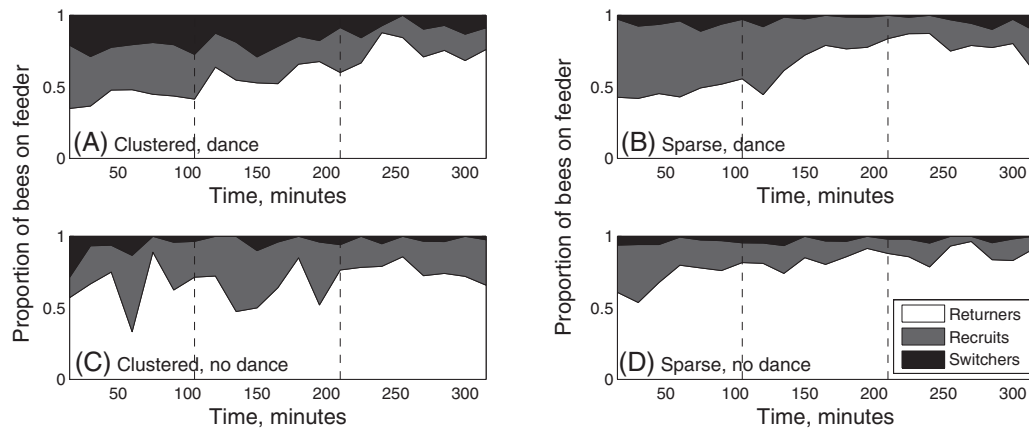


Figure 3

Proportion of returns, recruits, and switchers. Mean proportion of foraging bees on a feeder made up by returns, recruits, and switchers over the course of the experiment. The particular feeder shown in the figure was the high-quality feeder for the first 105 min of the experiment and became a low-quality feeder for the duration of the experiment after that point. All feeders showed similar qualitative patterns (data not shown). The dashed vertical lines represent the switching times. The clustered and sparse configurations with the dance language information are shown in (A) and (B), respectively, and clustered and sparse without dance are shown in (C) and (D). The white part of the graph represents returning bees, the gray part shows recruits, and the black shows switchers.

signed-rank: all $P < 0.05$, $N = 7$). The mean proportions of bees exploiting the high-quality feeder were 0.58 ± 0.078 , 0.61 ± 0.10 , 0.53 ± 0.087 at the end of time periods 1, 2, and 3, respectively. In the no dance treatment, bees allocated a higher proportion of their workforce to the high-quality feeder at 105 and 210 min (one-sided signed-rank: $P < 0.05$, $N = 6$). At the end of the third time period (315 min), colonies did not allocate a significant proportion of the workforce to the high-quality feeder (one-sided signed-rank: $P = 0.28$, $N = 6$). In the no dance treatment, the mean proportions of bees exploiting the

high-quality feeder were 0.62 ± 0.11 , 0.56 ± 0.04 , 0.38 ± 0.089 at the end of time periods 1, 2, and 3, respectively.

Configuration

In dance trials, configuration did not have a significant effect on the proportion of bees on the high-quality feeder in periods 1, 2, and 3 (repeated measures ANOVA, period 1: $F_{2,58,12.96} = 0.44$, $P = 0.70$; period 2: $F_{2,6,13.19} = 0.215$, $P = 0.86$; and period 3: $F_{6,30} = 1.0$, $P = 0.44$). In the no dance trials, configuration also did not have a significant effect in periods 1, 2, and 3 (period 1: $F_{4,0,16.0} = 0.61$, $P = 0.66$; period 2: $F_{6,24} = 1.12$, $P = 0.38$; and period 3: $F_{6,24} = 0.87$, $P = 0.53$).

Without dance language information, bees should not be able to track changes in their environment at the colony level. Our results, although based on a small number of replicates, suggest that even a large reduction in the ability of bees to pass on directional information has a negligible effect on colony-level response to changes in food quality. Furthermore, our result holds irrespective of feeder arrangement.

MODEL

We based our model on the framework proposed by Sumpter and Pratt (2003) for modeling social insect foraging. It is a state-based model, where each bee occupies 1 of 6 possible behavioral states at any given time. Rates of switching between states are taken from experimental data and previous work. Table 1 describes the behavioral states of the model and their biological meanings.

We now describe these states and the interactions between them in turn, while the Appendix contains the underlying differential equations. The overview of the model and the flows between the states are shown in Figure 5.

The first state, waiting (W), consists of bees that are waiting for a dance to follow at the dance floor in the nest. From here, there are 2 possible pathways the waiting bees can take to get to the exploiting state (E_i). One way is to follow a dance for a particular feeder (F_i) and then arrive at that feeder using information from the dance. The other way is to start searching for a food source (S) and then successfully discover a feeder. Searching bees are those that are independently looking for food, such as scout bees who have failed to locate

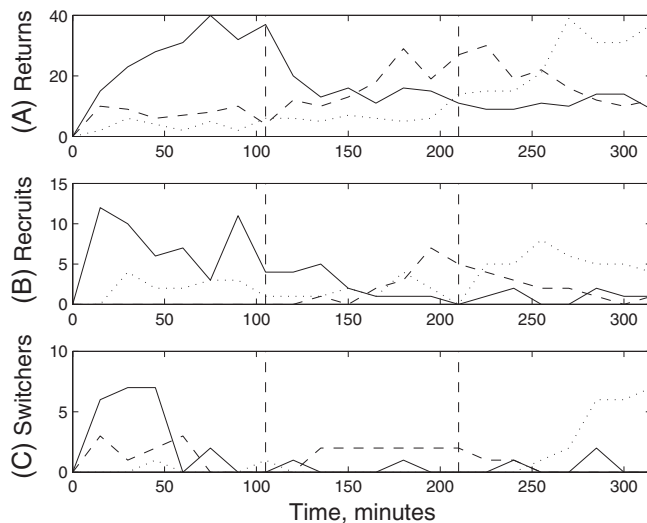


Figure 4

Results of a representative experimental trial. This figure shows the number of returning bees (A), recruits (B), and switchers (C) at each feeder over the course of an experiment at 15-min interval. This particular trial was done in the sparse configuration with the no dance treatment. Feeder 1 was the rich feeder for the first 105 min, followed by feeder 2, and then feeder 3 for the final 105 min. The solid line represents feeder 1, the dashed line feeder 2, and the dotted line feeder 3. The vertical dashed lines indicate the times at which feeder quality was swapped.

Table 1
Summary of the behavioral states that are used in the model

State name	Description
Waiting (W)	Bees waiting for a dance to follow at the dance floor in the nest
Searching (S)	Bees independently searching for food, such as scout bees
Following (F_i)	Bees attempting to find feeder i by following information they received from a recruitment dance for that feeder
Exploiting (E_i)	Foragers exploiting feeder i
Recruiting (R_i)	Bees recruiting others to feeder i by using the waggle dance
Inspecting (I_i)	Foragers that retired from feeder i but make occasional return trips to inspect its quality

a recruitment dance (Beekman et al. 2007). A searching bee can successfully discover feeder i with rate α_i or give up searching and return to wait for a dance at the nest with rate γ .

The rates at which waiting bees start following dances for a particular food source or searching depend on the proportion of recruiting bees dancing for each source. Waiting bees begin following a dance for food source i with rate $\lambda p \frac{R_i}{\sum_i R_i + K}$, where λ is the overall rate at which waiting bees leave the nest and R_i is the number of bees dancing for feeder i . K is a constant that determines the number of bees that search instead of following dances and p is the parameter that determines the percentage of waggle dance information that is preserved. The fact that the rate at which bees begin following a dance for a particular food source is directly proportional to the number of bees dancing for that food source reflects the observation that bees on the dance floor attempt to follow the first dance they sample (Seeley and Towne 1992). Waiting bees begin independently searching for food sources with rate $\lambda \frac{K}{\sum_i R_i + K} + \lambda (1-p) \frac{\sum_i R_i}{\sum_i R_i + K}$. This term includes the scout bees that did not follow any recruitment dances (Seeley 1995), as well as the bees that followed dances that were disoriented in the experimental setup. Note that the total rate of bees leaving the nest to search or follow, given by adding the 2 rates given above, is λ .

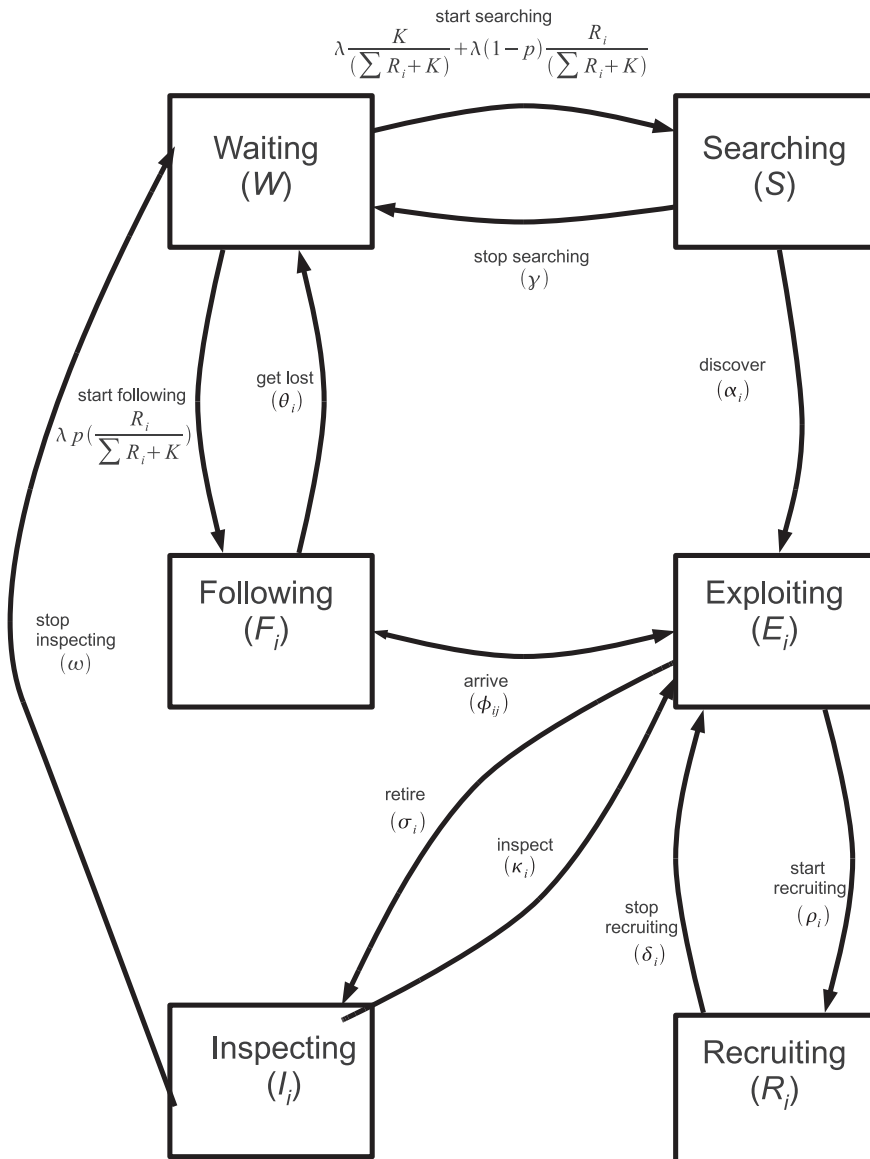


Figure 5
Model structure. Different behavioral states are represented by boxes, with connecting lines and arrows indicating possible ways in which individuals can switch between states. Rates at which the switches occur are shown next to the connecting lines.

Once following a dance for a particular feeder (F_i), a bee can get lost and return to waiting at the nest with rate θ_i or start exploiting a feeder, either the one she was following a dance for (with rate $\phi_{i,i}$) or one of the other feeders (with rate $\phi_{i,j}$, $i \neq j$, where the first subscript indicates the feeder which is being sought and the second subscript indicates the feeder that is actually found). This error term for dance following reflects a lack of precision in the dance language. The error makes it likely for a bee following a dance for an isolated food source to miss it and have to return to the hive. At the same time, if the food source the bee is heading toward is located in close proximity to other food sources, then the dance follower may end up on one of the other food sources and be able to start foraging (Towne and Gould 1988).

Foragers that are exploiting a feeder (E_i) can start recruiting for it (R_i) by dancing with rate ρ_i and return to exploiting that feeder with rate δ_i . Exploiting bees can also retire from a food source with rate σ_i . This retirement rate is higher for lower quality food sources (Seeley et al. 1991), and the retired bees move on to the inspecting state (I_i). This state is a modification of the original model of Sumpter and Pratt (2003) that helps account for the relatively small differences in foraging success with and without the use of dance language that we saw in our experiments. Inspection was proposed in the model by Biesmeijer and de Vries (2001), who introduced additional behavioral states for inspector bees and reactivated foragers. In their framework, inspectors are foragers that retire from an unprofitable food source but continue to make occasional trips to it. They resume foraging at this food source with rate κ_i if they discover that its quality has improved. The bees continue inspecting their abandoned food sources for a limited time period and return to waiting for a recruitment dance at the nest with rate ω . We include this inspector state in our framework. The other additional state of Biesmeijer and de Vries is reactivated foragers, bees that stop inspecting after a certain period of time and return to waiting for dances to follow at the nest. We rule out this state as a general explanation of the colony's rapid response to feeder switch because in the model of Biesmeijer and de Vries, this response requires reactivation by dance.

The parameter values used in the model are taken from the literature (Seeley et al. 1991; Seeley 1995) and are given in Table 2.

MODEL RESULTS

We started by looking at the outcome of the model without the inspector state, as in Sumpter and Pratt (2003). In accordance

with our empirical results, this model predicted that the spatial configuration of the food sources would not significantly affect the colony's foraging success. However, the model predicted a clear difference between colonies with and without the dance language information in terms of the number of bees exploiting the most profitable food source. Such a difference was not seen in the experiment. Instead, the model predicted that the colony would be virtually unable to make the switch to the rich food source when 70% of dance information is incorrect, as was the case in the no dance treatment.

Given these results, the model was modified as described above, with the addition of the inspecting state. The model of Sumpter and Pratt (2003) now becomes a special case of our revised model, in which retired foragers go directly from exploiting to waiting. This is equivalent to letting ω go to infinity.

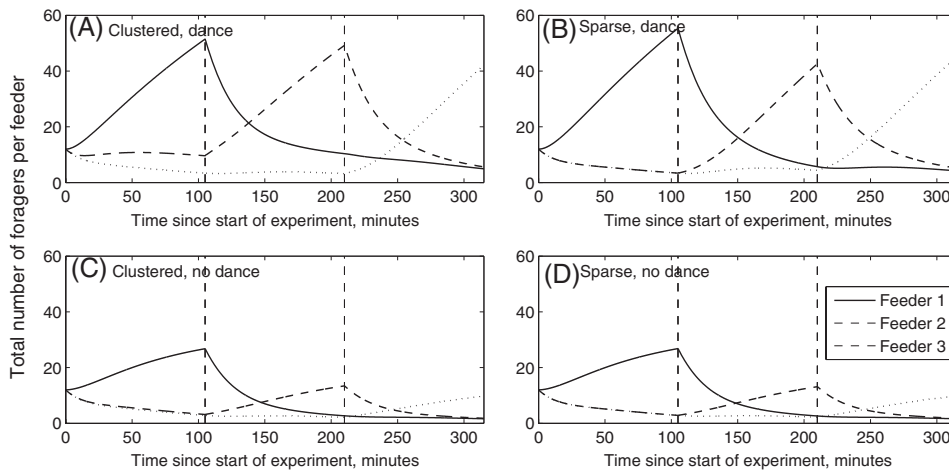
In order to investigate the relative roles of inspection and dance language in the experimental setup, we ran the model for different combinations of ω (inspector retirement rate) and p (dance effectiveness). We found that the model best reflects the experimental results for $\omega \approx 0$ or when inspector bees remain active for the longest time. This is most readily visible in the differences between the colony's foraging success with and without dance language. In the experiment, the drop in total foraging success when the use of dance language was removed was not as drastic as would be anticipated by the models of Sumpter and Pratt (2003) and Seeley et al. (1991). Setting $P = 0$, we see that the colony is still able to switch to the rich food source. This suggests that even if the 30% of dance language information that is still available to the colony in the no dance experimental treatment is reduced to 0%, the colony would still be able to switch. Figures 6 and 7 show the results of simulation runs for both clustered and sparse food source distributions for the dance and no dance treatments. Figure 6 shows these results for $\omega = 1/1440$, corresponding to 24 h of inspection, and Figure 7 shows the results for $\omega = 1$, corresponding to minimal inspection.

We performed a parameter scan in order to get a more thorough picture of the influence of inspecting and the dance language on a colony's foraging success in a dynamic environment. Figure 8 shows a colony's total foraging success over time, taking into account the relative quality of the feeders, for a range of values of ω for both the dance and the no dance treatments. The 3 subfigures correspond to different switching times for the feeders, with (A) corresponding to the 105-min switching time used in the experimental setup.

The parameter scan confirms the results seen in Figures 6 and 7 and shows that the experimental results are only

Table 2
Model parameters

Parameter	Meaning	Value
λ	Rate at which bees leave the nest, both to search and to follow dances	0.05
γ	Rate at which searching bees give up and return to the nest	0.0083
α_i	Rate of independent discovery of site i	0.0083
ρ_i	Rate at which exploiting bees start recruiting for site i	0.286 for rich site, 0.122 for poor site
δ_i	Rate at which bees stop recruiting for site i	0.667 for rich site, 3.333 for poor site
$\phi_{i,j}$	Rate at which bees following a dance for site i arrive at site j	In the sparse configuration: 0.0167 when $i = j$, 0 otherwise in the clustered configuration: $\phi_{12} = \phi_{21} = 0.0167$, $\phi_{ij} = 0.0167$ when $i = j$, 0 otherwise
θ_i	Rate at which bees following a dance for site i get lost and return to the nest	0.067
σ_i	Rate at which bees exploiting site i retire and return to the nest	0.00 for rich site, 0.04 for poor site
κ_i	Rate at which inspector bees begin exploiting site i	0.1 for rich site, 0.0 for poor site
ω	Rate at which bees stop inspecting and return to waiting	6.94×10^{-4}
K	Number of recruiters at which half departing foragers begin searching	3

**Figure 6**

Outcome of the model without inspection. Four panels showing the total number of foragers exploiting each feeder for both the clustered and the sparse spatial configurations, with and without dancing. For each configuration, feeder 1 is the high quality at the beginning, followed by feeder 2, and then feeder 3. The vertical dashed lines show feeder quality switching times. The configurations are (A) clustered, dance; (B) sparse, dance; (C) clustered, no dance; and (D) sparse, no dance.

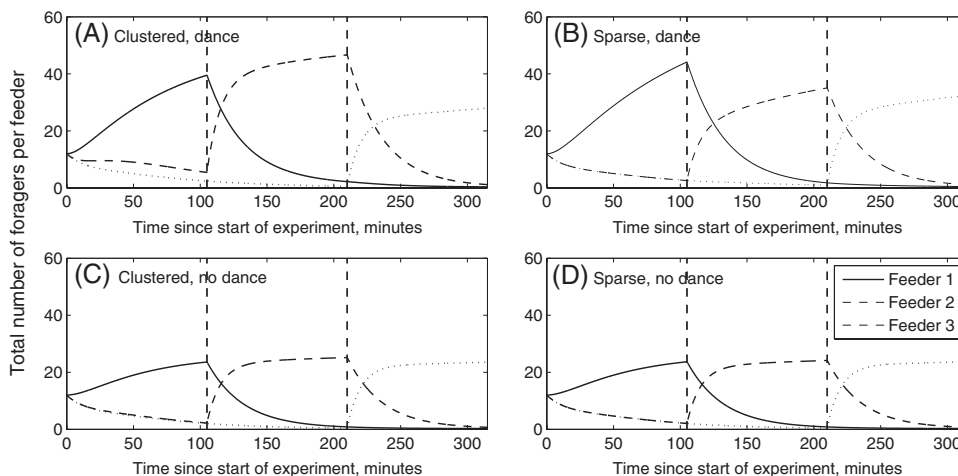
consistent with the model for low ω values. This means that inspector bees can explain the colony's ability to adjust to the changing foraging conditions in the short term. Looking at longer timescales, we see that this argument no longer holds, and low ω is no longer sufficient to maintain a high level of foraging success with limited dance language information. Parameter scans for switching times of 210 and 420 min are shown in Figure 8B,C, respectively. Since inspector bees only continue to visit formerly profitable food sources for a maximum of several days before giving up (Beekman 2005), we predict that the colony would not be able to successfully switch to the richer feeder without dance language information if the switches took place with longer intervals. This suggests that inspection is a mechanism that allows a honey bee colony to react to changes in its environment in the short term, while dance information benefits the colony on a longer timescale.

DISCUSSION

We found no clear difference in the dynamic foraging patterns of colonies with and without access to dance information, nor did we find an effect of feeder configuration. In all cases, the bees were able to track quality changes effectively. Given the established importance of dance language to a colony's foraging success in a static environment (von Frisch 1967; Seeley

et al. 1991), our results are initially surprising. However, a number of other authors have suggested that the importance of the directional component of the honey bees' dance language depends on the availability and distribution of forage and its variability in time (Sherman and Visscher 2002; Dornhaus and Chittka 2004). Our experiments show that a bee colony is able to successfully reallocate its foraging resources in dynamic environments even when dance language information is limited. This suggests that another explanation besides dance language is needed in order to completely understand dynamic foraging success by bee colonies.

Our explanation for the ability of the colony to react to rapid changes in their environment is that inspector bees act as the colony's short-term memory (Biesmeijer and de Vries 2001). These bees allow the colony to quickly begin utilizing previously abandoned food sources once they become profitable again. In our experiment, returners made up the vast majority of visitors to a feeder; independent discovery was relatively rare. This indicates that inspection is an important mechanism for reallocating foragers when food sources are hard to find. Our model supports this observation. By introducing an inspector state in to the "standard" model of honey bee foraging, we were able to reproduce our experimental results. Since there are large energetic costs to scouting, inspecting is probably less costly than rediscovering the food sources when they change profitability relatively frequently.

**Figure 7**

Outcome of the model with inspection incorporated. Four panels showing the total number of foragers exploiting each feeder for both the clustered and the sparse spatial configurations, with and without dancing. For each configuration, feeder 1 is the high quality at the beginning, followed by feeder 2, and then feeder 3. The vertical dashed lines show feeder quality switching times. The configurations are (A) clustered, dance; (B) sparse, dance; (C) clustered, no dance; and (D) sparse, no dance. In each panel, the inspector bees are assumed to return to the low-quality feeder for up to 24 h ($\omega = 1/1440$).

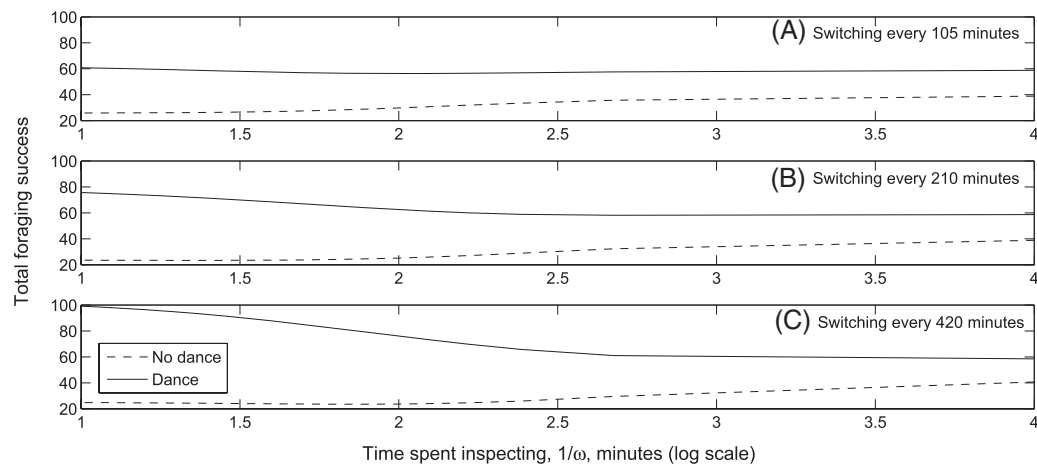


Figure 8

Parameter scan showing the colony's total foraging success over the course of the experiment for the values of P (the fraction of dance information made available to the colony) corresponding to the no dance ($P = 0.3$) and dance ($P = 1$) treatments and $1/\omega$, the amount of time the bees spend inspecting a food source after it becomes unprofitable. In the experiments, the value of $1/\omega = 1440$, corresponding to inspecting a feeder for 24 h after its quality changes. Parameter scans for 3 different times of feeder switches are shown, (A) 105 min (corresponding to the experimental setup), (B) 210 min, and (C) 420 min. Total foraging success of a colony is computed by adding up the number of foragers exploiting each food source at each time step, taking into account the sugar concentrations of the solutions.

Although we labeled the bees “inspectors,” they can also be viewed as foragers altering their foraging tempo and rate of recruitment. A forager bee controls 3 aspects of the foraging process: tempo, retirement rate, and recruitment (Bartholdi et al. 1993; Seeley 1995). The inspector bees can thus be thought of as foragers that make visits to the food sources at a lower rate and tune their recruitment rates to zero for the duration of inspection. Regardless of the exact label used to describe these behavioral states, models that include some form of inspection better match experimental results.

One factor that may have a strong influence on the effect of dance language in the colony's ability to reallocate resources is the distance between the hive and the food sources. At closer distances, the rate of independent discovery will likely increase, meaning that the colony would be able to switch to the rich food source even without the presence of waggle dance or inspectors. At longer distances, the independent discovery rate will be so low as to prevent switching from occurring without dance. In our experiments, the majority of bees foraging on the rich feeder were inspectors, indicating that the independent discovery rate is quite low. This suggests that inspectors, and not independent discoverers, are the major force influencing the colony's ability to redistribute foraging effort in the absence of dance language.

The honey bee waggle dance is known to be imprecise (Towne and Gould 1988). Previous work has discussed the possibility of this imprecision being adaptive, where the error can be viewed as a mechanism of increasing exploration of potential nearby food sources (Weidenmüller and Seeley 1999). Under this hypothesis, one might expect that when the feeder qualities were changed the build up of bees at the better feeder would be faster in the clustered configuration than the sparse configuration. The model reflects this prediction in that it shows that there are slightly more bees on the best quality feeder directly after the switch in the clustered configuration. For example, compare the (A) panels of Figures 6 and 7. This difference is small because the number of returning bees and independent discoveries is greater than the number of bees that land on the wrong feeder by following

a dance. Our experimental results did not show a difference between the colonies' ability to switch in the clustered and sparse configurations, although the power of our analysis did not allow us to detect more subtle effects. We therefore tentatively conclude that adaptive dance error plays a minimal role in our setup.

There is an ongoing debate about whether emergent behavior in insect societies is due to individual capabilities or mass recruitment mechanisms (Aron et al. 1993; Seeley 2002; Detrain and Deneubourg 2006). Detrain and Deneubourg (2006) provide examples of both: in one example, an ant colony's decision about which food sources to explore emerges out of the individual scouts' decisions about the exploitability of the prey based on a number of simple but “intelligent,” criteria for each scout. On the other hand, they also show examples where a colony's foraging decision to focus on one out of a number of possible food sources is facilitated via the mass recruitment mechanism of trail pheromones. Seeley (2002) also provides examples of rather complex and versatile behaviors, such as the large number of different signals that worker bees can make and interpret, which can influence emergent behavior at the colony level. Here, we have shown that the relative degree to which individual or social complexity determines foraging strategy depends very much on time-scale. Individual memory provides a response when foraging conditions change over the course of hours, dancing provides a response over the course of days, and rediscovery provides a longer term response.

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APPENDIX

Model equations and parameters

Waiting = get lost from following + stop searching + stop inspecting – start searching – start following

$$\frac{dW}{dt} = \theta_1 F_1 + \theta_2 F_2 + \theta_3 F_3 + \gamma S + \sum_i \omega I_i - \lambda W.$$

Searching = start searching – stop searching – start exploiting

$$\frac{dS}{dt} = \lambda \frac{K}{\sum_i R_i + K} W + \lambda(1-p) \frac{\sum_i R_i}{\sum_i R_i + K} W - \gamma S - \sum_i \alpha_i S.$$

Exploiting = start exploiting after following a dance + start exploiting after searching – retire from exploiting – (start recruiting – stop recruiting) + start exploiting after inspecting

$$\begin{aligned} \frac{dE_i}{dt} = & \phi_{1,i} F_1 + \phi_{2,i} F_2 + \phi_{3,i} F_3 + \alpha_i S - \sigma_i E_i \\ & - (\rho_i E_i - \delta_i R_i) + \kappa_i I_i. \end{aligned}$$

Recruiting = start recruiting – stop recruiting

$$\frac{dR_i}{dt} = \rho_i E_i - \delta_i R_i.$$

Following = start following – get lost – start exploiting

$$\frac{dF_i}{dt} = \lambda p \frac{R_i}{\sum_j R_j + K} W - \theta_i F_i - (\phi_{i,1} + \phi_{i,2} + \phi_{i,3}) F_i.$$

Inspecting = start inspecting by retiring from exploiting – start exploiting – stop inspecting

$$\frac{dI_i}{dt} = \sigma_i E_i - k_i I_i - \omega I_i.$$

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