Foraging in honeybees—when does it pay to dance?

Madeleine Beekman* and Jie Bin Lew

*Behaviour and Genetics of Social Insects Lab, School of Biological Sciences A12 and Centre for Mathematical Biology, The University of Sydney, Sydney, NSW 2006, Australia

Honeybees are unique in that they are the only social insects that are known to recruit nest mates using the waggle dance. This waggle dance is used by successful foragers to convey information about both the direction and distance to food sources. Nest mates can use this spatial information, increasing their chances of locating the food source. But how effective is the bees’ dance communication? Previous work has shown that dancing does not benefit a honeybee colony under all foraging conditions and that the benefits of dancing are small. We used an individual-based simulation model to investigate under which foraging conditions it pays to dance. We compared the net nectar intake of 3 types of colonies: 1) colonies that use dance communication; 2) colonies that did dance but could not use the dance’s spatial information; and 3) colonies that did not dance. Our results show that dancing is beneficial when the probability of independent discovery of food sources is low. Low independent discovery rates occur when patches are very small or very far away. Under these conditions, dancing is beneficial as only a single individual needs to find a patch for the whole colony to benefit. The main benefit of the honeybee’s dance communication, however, seems to be that it enables the colony to forage at the most profitable patches only, ignoring forage patches that are of low quality. Thus, dancing allows the colony to rapidly exploit high-quality patches, thereby preventing both intra- and interspecific competitors from using that same patch.

Key words: Apis, central-place foraging, communication, recruitment, scouting, waggle dance. [Behav Ecol 19:255–262 (2008)]

Living in groups provides many benefits to individual group members. Individuals within a group are less vulnerable to predators (Hamilton 1971; Sword et al. 2005), their locomotion may be enhanced when moving as a group (Krause and Ruxton 2002), territories can be defended better (Packer et al. 1990), and a group can effectively modify the environment, for example, nest thermoregulation in social insects (Jones and Oldroyd 2007). Another important benefit of being in a group is that an individual can obtain information from other members of the group about their environment (Lachmann et al. 2000). When individual group members have accurate information about predation risk and food availability of a habitat, other group members can use this social information to decide whether to stay or leave their current foraging range (King and Cowlishaw 2007). Similarly, naive Bechstein’s bat females obtain information about the location of roosting sites (Kerth and Reckardt 2003), dwarf mongooses are warned of approaching predators (Rasa 1987), and naive fish can respond to information provided by a majority of individuals with pertinent directional information (Reebs 2000; Couzin et al. 2005).

Probably, the best-known examples of information sharing are found in the social insects (the ants and termites and some species of bees and wasps) in which many species have evolved complex signaling mechanisms that are used to recruit group members to food sources (Beekman and Dussutour, forthcoming). Many species of ant mark the route between their nest and discovered food sources with a chemical, thus indirectly leading nest mates to the food (Holldobler and Wilson 1990) allowing the colony to exploit food sources that are too large to be exploited by a single individual (Beckers et al. 1990; Detrain and Deneubourg 2002).

Honeybees are unique among the social bees because they are the only bees that have evolved a recruitment mechanism that relies on the direct transfer of information: the waggle dance. The honeybee’s waggle dance encodes both the direction and the distance to the advertised source. This source can either be a food patch (von Frisch 1967) or a new nest site (Lindauer 1955). During a typical dance, the dancer strides forward while vigorously shaking her body from side to side (Tautz et al. 1996). This is known as the “waggle phase” of the dance. After the waggle phase, she makes an abrupt turn to the left or right, circling back to start the waggle phase again. This is known as the “return phase.” At the end of the second waggle, the dancer turns in the opposite direction so that with every second circuit of the dance she will have traced the famous figure-of-8 pattern of the waggle dance (von Frisch 1967). Directional information is contained in the angle of the waggle phase such that the alignment of the dancing bee’s body relative to vertical is similar to the angle of the goal from the sun’s current azimuth. Distance information is encoded in the duration of the waggle phase (Esch et al. 2001).

The scientific study of the honeybee’s dance has been controversial (Wenner and Wells 1990). This controversy was not helped by the absence of unambiguous proof of the dance’s ability to increase the amount of food collected by a colony. It is only recently that experimental studies have focussed on quantifying the benefits, in terms of resources collected, of the honeybee’s dance by comparing colonies that could and could not utilize dance information (Sherman and Visser 2002; Dornhaus and Chittka 2004). By turning a colony on its side, dance communication is scrambled so that although successful foragers continue to perform dances, dance followers cannot extract spatial information from them. Both studies suggest that the benefits of dance communication depend on the distribution of forage and are most beneficial to a colony when forage is hard to find, variable in richness, and...
We developed an individual-based simulation model of foraging honeybees using Simulink in Matlab 7.3.1. Simulations were run in discrete time steps (\(t\)) in which 1 simulation time equals 10 s real time. Total simulation time was 2880 time steps representing 8 h. We calculated the net nectar intake of the colony at the end of the simulation. Bees only consumed nectar while in flight at a rate of 1 mg per kilometer flown. Bees are known to fly at a speed of 7 m/s (Beckman et al. 2006); hence, a bee that spends 16 min on a trip will have flown a total distance of 6.72 km during which she will have consumed 6.72 mg of nectar. Similarly, a bee visiting a patch at a distance of 4 km from the colony flies a total distance of 8 km per trip thereby consuming 8 mg. Successful foragers bring back to the colony 40 mg of nectar (note that the net amount of nectar will depend on the distance to the patch, as the further a patch, the more nectar a bee consumes in flight). We simulated a total of 260 bees, all of which were either active or potential foragers. The number 260 is sufficient to ensure that there are always bees available to be recruited to the different tasks associated with foraging.

We used 4 equal food patches per experiment. We varied the likelihood that patches were discovered by independent search (scouting) by changing the distance of the patch and the size of the patch. Patches were located at 2, 4, 6, 8, or 10 km from the hive. Patch size was measured in degrees: 5, 15, 30, 45, and 60. We did not include crowding, so that even at “small” patches all bees that had found the patch could collect nectar. Patches were depleted as bees collect nectar at a rate of \(P_o R_o\), where \(P_o\) is the patch’s initial profitability, \(K\) is a constant set at 0.999, and \(R_o\) is the total number of foragers that have visited that patch. Thus, the profitability of a patch decreases as the number of bees visiting that patch increases.

We used 3 variations on the model: 1) bees perform recruitment dances when foraging at a profitable patch, and dance followers can use this spatial information to help them locate the advertised site (costs and benefits of dancing); 2) bees perform recruitment dances, but dance followers are unable to use this information and instead search for food patches independently (costs but no benefits); and 3) bees do not perform recruitment dances (no costs and no benefits). All 3 variations are illustrated in Figure 1. Bees active in foraging can be in one of the 6 following states.

**Novices**: Bees without previous foraging experience; all bees start their foraging day as novices. Novices will go to the dance floor to attempt to find a dance to follow.

**Dancing bees**: Bees that judge the profitability of their patch high enough to recruit to that patch.

**Recruits**: Bees that have followed a dance and attempt to locate the advertised patch.

**Scouts**: Bees that have failed to find a dance. Scouts fly out in a random direction. (Note that in the 2 model variations in which dance information cannot be used or is not available, all foragers leave the colony as scouts.)

**Employed foragers**: Bees that have located a profitable food patch, either as scouts or as recruits.

**Retired foragers**: Bees that no longer forage at their patch because the patch’s profitability has declined.

**Novices**

Novices entered the system one at a time every 6 time steps so that all bees were in the system at \(t = 1560\). Bees were staggered to mimic the natural situation where not all potential foragers will leave the colony in the morning together. This also avoided them being treated by the model as a group instead of individual bees. Novices first attempt to locate a dance. In the absence of dancing (see Dancing bees below), novices directly entered the scout subsystem.

**Dancing bees**

Dancing bees convey information about the location of food patches by performing dances on an area in the colony called...
Figure 1
State diagram of the structure of the model and the flow between the different bee subsystems. Solid arrows denote the transfer of bees from one state to another; the dashed arrow signifies the flow of information. Bees start their foraging day as novices and then move through the system. In (A), successful foragers are able to use dance communication to transfer spatial information to nest mates ("dance with communication"). In (B), successful foragers dance, but this information cannot be used by nest mates ("dance no communication"). Instead, all dance followers enter the scout subsystem. In (C), no dancing takes place, and all bees search in a random direction on leaving the colony ("no dance").

The main difference between (B) and (C) is that, in model variation (B), dancing and dance following does take place before bees become scouts. Hence, the difference in net nectar intake between (B) and (C) is an estimate of the time costs associated with dancing. See text for further details.
the “dance floor.” As the distance to a patch is coded in the duration of the waggle phase (von Frisch 1967), dances for farther patches took longer to finish (assuming equal profitability). The number of time steps needed to perform 10 waggle phases was set at 1, 2, 3, 4, and 5 for patches at distances 2, 4, 6, 8, and 10 km, respectively.

Only dances for one particular patch could be witnessed by dance followers at any one time step. To decide which dance was witnessed, a random number between 1 and 100 was assigned to each patch in each time step. This number was then multiplied by the total number of bees dancing for that patch, and a dance for the patch with the highest number was read. In doing so, we ensured that the probability of a particular patch being witnessed increased as more bees were dancing for that patch without completely excluding patches for which only a small number of bees were dancing.

Novices, retired bees, and failed recruits (termed unemployed bees) attempt to witness dances. If at least one dance was available on the dance floor, the unemployed bee would follow it and enter the recrui subsystem. If no dance information was available, she entered the scout subsystem. Successful witnesses spent 1 time step reading the dance before becoming a recrui.

In the model variation in which dances do take place but dance followers cannot utilize this information, dance followers were sent to the scout subsystem after finishing witnessing a dance (Figure 1B). In the absence of dancing, all novices entered the scout subsystem without delay (Figure 1C).

Recruits
Recruited bees are known to make 4.1 ± 2.8 failed trips before locating the advertised patch (Seeley and Visscher 1988). Hence, the number of failed trips, x, was generated using a normal distribution with a mean of 4.1 and a variance of 2.8 (when the value returned was negative, we set this at zero). Each failed trip took 96 time steps (16 min real time that is similar to what has been found in real bees [Seeley and Visscher 1988]). Approximately 60% of recruits successfully locate the advertised patch after their failed trips (Seeley and Visscher 1988). We therefore assigned a random number between 0 and 1, γ, to each recruit after she has made her allocated number of failed trips. If γ > 0.4, she successfully found the advertised patch; otherwise, she returned to the dance floor.

Scouts
Scouts are bees that failed to find a dance (Beckman et al. 2007) and search for food independently. In our model, the success of a single scouting trip was proportional to the linear direction (in degrees) and distance (in kilometers) that the scout had flown leaving the colony. (Note that the assumption of a linear flight direction is a simplification.) Each scout exited the colony in a random direction, and this direction remained the same throughout her flight. She flew a random distance sampled from a normal distribution with mean and variance of 4. This random flight distance had to be at least equal to the distance of the patch from the colony for the scout to discover that patch. Therefore, the closer the patch was to the colony, the more likely the scout would encounter the patch. As a result, patches that were distant from the colony could still be discovered but with a lower probability than those closer to the colony. In addition, the larger the patch (measured in degrees), the more likely the scout’s flight would intercept that patch. If the scout did not find a patch, she returned to the colony and attempted another scouting flight.

Employed foragers
Successful recruits and scouts as well as retired bees that revisit a patch they have previously foraged at (see further) become employed foragers if their patch was of sufficient profitability. (The profitability of a patch decreases when bees visit that patch because they remove food from the patch.) If the patch’s profitability is too low, the probability that she abandoned that patch (become retired) increased (see Supplementary Figure S1). If she decided to continue foraging at that patch, she next had to decide whether or not to dance for that patch. The decision to dance depended on the patch’s profitability and on the bees’ influx rate b (number of employed bees that returned to the colony in the last 6 time steps) (e.g., Seeley 1994). The returning forager first decided whether or not to dance depending on patch profitability. When patch profitability was high, she would dance irrespective of the bees’ influx rate. However, when patch profitability was not very high, she would only perform a dance when the bees’ influx rate was low (Supplementary Figure S2).

Employed foragers always carried the maximum amount of nectar back to the colony (40 mg). Once a bee had become an employed forager, she continued foraging at that patch (provided patch profitability remained high); hence, she remembered the location of the patch.

Retired bees
Retired bees are employed foragers that abandoned their patch because its profitability has decreased. A retired bee inspects her patch to determine if its profitability has increased as often occurs under natural conditions where nectar and pollen are renewed. The probability to become a reactivated forager (a previously retired bee that resumed foraging when its patch is again profitable [Biesmeijer and de Vries 2001]) depended on the patch’s profitability (Supplementary Figure S3). When patch profitability remained low, the bee completely abandoned the patch (Supplementary Figure S1) and returned to the dance floor. Even though our patches never became profitable again (as we only simulate one foraging day), we needed to include retired bees for 2 reasons. Firstly, retired bees consume nectar when inspecting their patch. Secondly, when performing inspection flights, retired bees do not follow dances and can therefore not be recruited to other food patches. Only when a retired bee has completely abandoned its patch, will she start following dances again and be either recruited to a new patch or become a scout.

Experiments
In each experiment, we determined the net nectar intake of our 3 model variations for the different patch distances and patch sizes (4 distances, 5 patch sizes: 20 experiments per model variation). Patch profitability was set at 1 (maximum) for all patches at the beginning of the simulation. To specifically study the effect of patch variability on the relative success of dance communication, we also performed experiments in which we used 4 patches of size 15° located at 4 km that differed in their initial profitability (1, 0.5, 0.2, and 0.2 in the first experiment; 1, 0.4, 0.1, and 0.1 in the second experiment). The aim of these experiments was to determine how the different model variations allocate their foraging force over patches that differ in their initial profitability.

For all experiments, we performed 20 runs per model variation. We compared the net nectar intake among our 3 different model variations using 1-way analysis of variance. To determine which model variations were significantly different, we performed post hoc least square difference tests on the observed mean nectar intakes.

RESULTS
Our results clearly show that dance communication benefits the colony, measured in net nectar intake, when food patches
are hard to find independently. When we offered small patches (5°), colonies that used dance communication always collected more nectar than colonies that could not communicate the location of forage (Figure 2; see figure and legend for details of the statistical tests). Similarly, when patches were hard to find independently because they were far away (8 km), dance communication increased the colony's net nectar intake relative to colonies that could not communicate (Figure 2). Conversely, as patch size increased (and food was thus easier to find), dance communication no longer benefited the colony when patches were relatively close to the colony (2 and 4 km). In fact, when patch size was greater than 15°, using dance information actually disadvantaged colonies when the patches were found at a distance of 2 or 4 km. This is because bees are sent to search in a random direction (and hence become scouts) in the model variations that cannot use dance communication, and this facilitated the finding of relatively large and nearby patches. The chance that dance followers successfully find the advertised site is lower compared with randomly searching scouts in real honeybee colonies (Seeley and Visscher 1988), something that we explicitly incorporated into our model.

When patches were relatively small (15°) and neither very far nor very close (4 km), all 3 model variations collected a similar amount of nectar (Figure 2). We therefore used these foraging conditions to see if dance communication does benefit the colony when patches differ in their initial profitability. And indeed, when 1 patch is of superb quality, 1 of mediocre, and 2 of poor quality, the ability to communicate significantly increased the colony's net nectar intake (Figure 3). This is because colonies that made use of dance communication allocated a larger number of foragers to the most profitable patch whereas mostly ignoring poor patches (Figure 4). Even though colonies that could not use dance information still allocated more foragers to the best patch, this difference was not as pronounced as when bees were able to communicate.

![Figure 2](https://example.com/image.png)

**Figure 2**
Net nectar intake of our 3 model variations “dance with communication,” “dance no communication,” and “no dance” for all patch sizes and all patch distances. Bars represent the mean of 20 simulation runs, error bars the standard error of the mean (sometimes the standard errors are so small they cannot be seen). We compared the net nectar intake among the 3 model variations per patch size and per distance using a univariate analysis of variance. Means that share the same letter are not statistically different at α = 0.05 (post hoc least square difference).
Our results show that when all patches are of equal profitability, dance communication benefits the colony as soon as the average success of scouts in locating food patches falls below the average success of recruits. Thus, when food patches are easily discovered by independent search, a colony does best to send its foragers out on a random search instead of attempting to recruit them to a particular site, whereas recruitment is beneficial when patches are difficult to locate, for example, when they are far away (Figure 2). In fact, only in the presence of dance communication does it pay for scouts to search over long distances, as otherwise the potential benefits of locating a forage site far away will never outweigh the costs of long-distance scouting (Beekman and Ratnieks 2000).

When food patches were easy to find, net nectar intake was higher in the absence of dancing compared with the nectar intake of colonies in which the bees did dance but could not use this information (Figure 2). This is because no time was wasted on dancing and dance following so that a larger number of bees were sent out as scouts. However, the difference between the model variations with and without such “wasted” time was not great (Figure 2).

Notwithstanding the benefit of dancing when scouting success is low, our results show that the dance’s main benefit is the ability to rapidly exploit the most profitable patches when patch quality is variable. When we offered our colonies patches that varied in their initial profitability, colonies that utilized dance communication collected more nectar than those that could not use such information (Figure 3). The ability to communicate the location of food patches to nest mates leads to a rapid increase in the number of individuals that forage at that site (Figure 4) (Seeley and Visscher 1988) so that the discovery of a profitable food source by just one scout is, in theory, sufficient to allow a colony to rapidly exploit that food source. Without the use of dance communication, scouts will continue to find food patches of low profitability and the forager force will be more evenly spread over the available patches. Thus, contrary to earlier studies which concluded that the honeybee’s dance communication evolved as an adaptation to boom and bust foraging conditions typical of the tropics (Sherman and Visscher 2002; Dornhaus and Chittka 2004; Dornhaus et al. 2006), it seems more likely that it is competition for food sources that has driven the evolution of information transfer in social insects (Nieh 1999, 2004).
One potential role for dancing that we did not include in our model is the possibility that dances serve as a signal aimed at increasing the number of bees departing to search for food without communicating spatial information. Returning foragers can either arouse unemployed individuals (“there is something out there”) or transfer floral scents (“look for something that smells like this”). Such arousal signals are indeed used by bumblebees (Dornhaus and Chittka 1999), several species of stingless bees (Nieh 2004), and by honeybees when food is found close to the colony (von Frisch 1967; Weidenmüller and Seeley 1999; Beekman et al. 2005). Floral scents play an important role in reactivating honeybee foragers (Lindauer 1963; Reinhard et al. 2004; Beekman 2005).

It is interesting that honeybees are the only social bees that have evolved an intranidal spatially explicit recruitment mechanism. In many species of social insects, recruitment toward profitable food sources occurs outside the nest, for example, via odor trails or the marking of food sources. This allows other species as well as conspecifics to “eavesdropping” on these signals (Nieh et al. 2004) thus severely reducing the benefits of recruitment. Such eavesdropping can be avoided when recruitment takes place inside the nest (Nieh 1999; Nieh 2004). Hence, the honeybee’s dance communication prevents eavesdropping, whereas the transfer of spatial information allows the colony to rapidly monopolize highly profitable food sources thus making the honeybee a superior competitor.

The stingless bees (Meliponini) share many traits with honeybees such as relatively large colonies and food storage within the nest. They also evolved in a similar environment as honeybees, the tropics (Michener 2000; Oldroyd and Wongsiir 2006). Could it therefore be that honeybees suffer more intra- and interspecific competition compared with stingless bees and that this has driven the evolution of the dance communication? This seems unlikely given the apparent competition between stingless bee species (Hubbell and Johnson 1978; Nieh et al. 2004) and between stingless bees and honeybees (Koeniger and Vorwöhl 1979), as well as the high densities in which stingless bees are often found (Eltz et al. 2002; Eltz et al. 2005).

A possible alternative hypothesis for the evolution of the honeybees’ dance communication is an original function in communicating the location of new nest sites after reproductive swarming. Once the dance communication had evolved in the context of nest site selection (as the location of a potential nest site is also encoded in the dance [Lindauer 1955], a situation unique to honeybees), it could then be adapted to foraging, thus giving the honeybee an extra competitive advantage. Obviously, this hypothesis remains speculative.

SUPPLEMENTARY MATERIAL
Supplementary Figures 1–3 can be found at http://www.beheco.oxfordjournals.org/.

FUNDING
Australian Research Council (DP0345360 to M.B.); University of Sydney (to M.B.).

We would like to thank Ben Oldroyd, Sharon Shafir, Anne Houdé, Andrew King, and an anonymous reviewer for helpful comments on an earlier version of the manuscript.

REFERENCES


