Searching for a new home—scouting behavior of honeybee swarms

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Honeybee scouting, where individual bees search the environment without prior information about the possible location of food sources or nest sites, is notoriously difficult to study. Yet, understanding scouting behavior is important as it provides insights into how social insects trade-off exploitation with exploration. The use of simulation models is an ideal way to investigate the possible mechanisms behind the regulation of scouting at the group level as well as the ways in which the swarm searches its environment. We used an individual-based simulation model to study the scouting behavior of honeybee swarms. In our model, we implemented a simple decision rule that regulates the number of scouts: individual bees first attempt to find a dance to follow but become scouts if they fail to do so. We show that this rule neatly allows the swarm to adjust the number of scouts depending on the quality of the nest sites known to the swarm. We further explored different search strategies that allow the swarm to select good-quality nest sites independent of their distance from the swarm. Assuming that it is costly to move to a site that is far away, the best search strategy would be to give precedence to nearby sites while still allowing the discovery of better sites at distances farther away. *Key words: Apis*, decentralized decision making, honeybees, individual-based model, nest-site selection, swarming. *[Behav Ecol 18:384–392 (2007)]*

A swarm of honeybees choosing a new home out of several possible nest sites is one of the most impressive examples of decentralized decision making in animal groups. Honeybee swarms consist of one queen and several thousand workers and are normally produced in spring as part of the colony's reproductive cycle. A honeybee swarm is temporarily homeless as the old nest site has been left to one of the daughter queens (the biology of swarming is reviewed in Winston 1987). Therefore, soon after the swarm has formed, several hundred scout bees fly off to explore the surroundings for a suitable new home. On finding a suitable nest site, scouts perform recruitment dances in order to try to recruit other bees to their discovered site. Other scouts decode the dances, visit the sites themselves, and may dance in turn. There ensues a process of competition among the scouts dancing for the different sites, at the end of which one site comes to dominate in visitation and dancing (Lindauer 1955; Seeley and Visscher 2004a). Once this agreement is reached, a process that can span a few hours up to several days, the swarm takes flight and moves to the chosen site, which can be several kilometers away (Seeley and Morse 1977; Villa 2004).

The choice of a new home is critical. The swarm needs to choose quickly as any delay will deplete the swarm's resources and increase the chance of predation or being washed away by rain. At the same time, the swarm should ensure that no better nest site is available before deciding on a mediocre site. Hence, a decision should not be made too quickly. A decision also needs to be unanimous to prevent the swarm from breaking up as most swarms contain only one queen and can therefore form just one functioning colony.

The process in which the swarm decides on a new home has been studied empirically (e.g., Camazine et al. 1999; Seeley and Buhrman 1999; Seeley 2003; Seeley and Visscher 2003, 2004b). As a result, the behavioral rules followed by the bees involved in the nest-site selection process are relatively well known. Less well known, however, is how the actions of individual bees lead to the swarm's ability to choose the best nest site out of several potential nest sites. Such translation from individual behavior to collective behavior is best made using mathematical or simulation modeling (e.g., Beekman et al. 2001; Sumpter and Beekman 2003; Sumpter and Pratt 2003; Janson et al. 2005; Pratt et al. 2005; Sumpter 2005).

So far 3 models have been published that describe the decision-making process of a honeybee swarm while selecting a new home. Britton et al. (2002) modeled the spread of information about possible nest sites among swarm members in a manner analogous to the spread of an infectious disease. In their model, "susceptible" individuals are those that do not have information about the location of nest sites, whereas the "infected" individuals do. Via dancing for their site, infected individuals "infect" susceptible ones, hence, the number of individuals that have information about a particular site increases. This model suggests that individual bees do not need to directly compare nest sites for the swarm to choose the best available site.

Myerscough (2003) used a population matrix model in which scouts dancing for different sites were modeled as different populations. Individuals within a population die (cease dancing), whereas new individuals are born (are recruited to a particular site and dance for that site). Critical to a decision being made is scouts ceasing to dance for their site, irrespective of the quality of that site. Scouts that have visited a superb site will perform more dances compared with scouts that have visited a mediocre site, but all will ultimately stop dancing for

their site. This allows the swarm to choose a better site even if dancing is already taking place for a mediocre site.

Whereas the differential equation formulation of Britton et al. (2002) gives us an overall idea of the decision-making process involved, Myerscough's (2003) approach allows one to pinpoint crucial individual behaviors underlying nest-site selection. However, her approach still does not allow the modeling of the different tasks involved in the swarm's decision making. Passino and Seeley (2006) constructed an individual-based simulation model to explore how certain behaviors have been tuned by natural selection to achieve a trade-off between the speed of the decision-making process and the accuracy of the decision. One aspect explored by Passino and Seeley is the regulation of the number of scouts searching for new nest sites (exploring) and scouts dancing for known nest sites (exploiting). However, the model of Passino and Seeley is rather coarse as it progresses in steps of 30 min. Moreover, their model does not incorporate spatial dimensions of the landscape so that each site, regardless of distance, has the same probability of being discovered and travel times do not play a role.

The iterative models of Myerscough and those of Passino and Seeley disregard the concurrency in the distributed decision-making process. In every simulation step, all committed bees (bees that are dancing for a site) perform their dances synchronously and the available followers are distributed over the available dances. All bees that were scouting in the previous simulation step are available to be recruited by dancing bees. This simplifies the regulation of scouts because it is ensured that dances will be read, regardless of the number of bees sent scouting. In a concurrent system, however, dancing bees may not be able to find dance followers if a large number of bees are already scouting for nest sites or are committed to nest sites. Also, no account is given to the different durations of the various tasks performed by bees within one step of the model.

In our model, we focus on a realistic representation of the individual behaviors involved in this distributed system. Like Passino and Seeley, we were interested in how the swarm balances the exploitation of known sites (scouts dancing for sites) against the exploration of new sites (searching for sites without having followed a dance). In particular, we wanted to investigate how the relative quality of the site affects this trade-off, as it seems likely that when the only sites known to the swarm are of poor quality, the swarm should invest more in exploring its environment for better quality sites. Likewise, when a superb site has been found, not much can be gained from further investment in exploration. We therefore created an individual-based simulation model of the honeybee swarm's decision-making process. To investigate the trade-off between exploration and exploitation, we implemented a simple decision rule that regulates the number of scouts: individual bees first attempt to find a dance to follow but become scouts if they fail to do so. We were also interested in the possible search strategies employed by the swarm while searching the surroundings for potential nest sites present at varying distances from the swarm. The relative distance of a nest site from the swarm is important as it affects the probability that it will be discovered by scouts. We therefore included in our model the time spent on the different tasks involved in the decision-making process. This allowed us to investigate different search strategies employed by scouts. We tested our model by determining if our swarms could choose between 2 identical nest sites and if they could decide on a better quality site when this site is discovered after an inferior site has already been found.

MODEL

We use an individual-based simulation to model the nest-site selection process of a honeybee swarm. The simulation is exe-

cuted in discrete time steps at a fine timescale of $\Lambda = 6$ s per simulation step. This allows us to capture the high degree of concurrency inherent to the natural system. At each simulation step, each bee acts according to the current state it is in. If there is a dependency between bees in certain states (e.g., the probability of finding a dance depends on the number of dancing bees), the dependent ones (bees searching for a dance) will be delayed until the others (the dancing bees) are done. Otherwise the order in which the bees perform their actions is random.

All the durations T_E of specific tasks (SCOUT, ASSESS, MISS) are varied with a scalar factor $\lambda = \mu/10$, where μ is taken from a chi-square distribution $\mu \sim \chi^2(10)$; consequently λ has an expected value of 1.0. Hence, the duration $T(E)$ of each task execution is determined as $T(E) = \lambda \cdot T_E$. In the following, we give the mean durations T_E.

The bees fly at a speed of 5 m/s between the swarm and a nest site, see Beekman, Fathke, and Seeley (2006). Therefore, the time spent traveling ranges from 50 s (for a site at 250 m) to 3 min 20 s (for 1 km) one way.

The decision-making process is presented in the form of a state diagram in Figure 1. A bee involved in nest-site selection can be in one of the following states:

REST The bee is on the swarm but currently not involved in nest-site selection.

SEARCH The bee is on the swarm and tries to find a dance to follow.

FOLLOW The bee is on the swarm and has found a dance and follows it.

SCOUT The bee searches the surroundings of the swarm for a potential nest site without having followed a dance, that is, it has no prior information about the location of potential nest sites.

ASSESS The bee is at a potential nest site and assesses its quality.

MISS The bee misread a dance and searches the surroundings of the swarm unsuccessfully for some time before returning to the swarm.

DANCE The bee is on the swarm and dances for its preferred site.

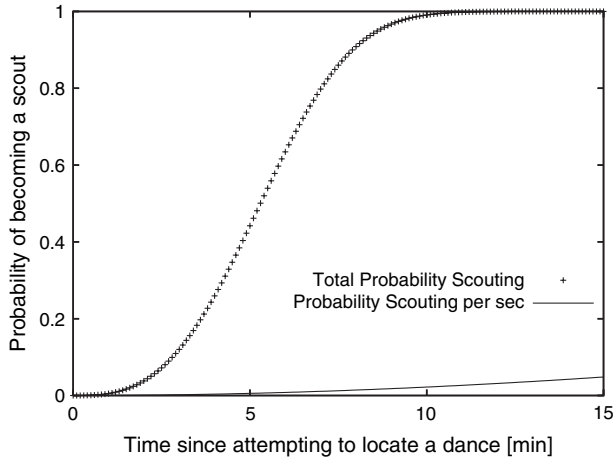TRAVEL The bee flies from the swarm to the candidate nest site or back to the swarm.

We modeled only the bees that are actively involved in the decision-making process. Seeley and Buhrman (1999) found that in swarms comprising 4000 bees, 2–4% of the bees were seen dancing at least once. As there may still be more bees involved in the decision-making process that did not dance because they never found a nest site good enough to recruit to, and because we wanted to work with swarms within the normal size range (10 000–15 000 bees), we used 500 bees in our simulations. At the beginning of the simulation, 80% of the bees are in the searching and 20% in the resting state. Details of the bees' behavior while in a certain state as well as the rates at which bees change states are given below.

Scouting

To regulate the number of scouts (bees searching independently for new sites), we assumed that a bee will first try to locate a dancing bee. The longer a bee searches unsuccessfully for a dance to follow, the more likely it is to leave the swarm and scout. The following response function is used to model the scouting probability of an individual searching bee:

$$r_\Theta(t) = \frac{t^2}{t^2 + \Theta^2}.$$

The input stimulus t is the duration in seconds that a bee has not found a dance to follow, and the response $r_\Theta(t)$

Figure 1
State diagram of the decision-making process. A searching bee tries to find a dance to follow. The longer it has to search for a dance, the higher the probability that it will start to scout. If a searching bee finds a dance to follow, it will follow that dance until the dancer ceases dancing. The dance follower then tries to find the advertised site. Its probability of success depends on the number of waggle runs it has followed. If it finds a potential nest site, it will assess its quality. If the quality exceeds the bee's internal threshold Φ, it returns to the swarm and dances for it. Depending on the quality of the nest site, the bee makes a number of return trips after which it will advertise the location of that site by dancing. The time spent dancing during each return trip is reduced until the bee no longer dances for that site. Nest sites of high quality will be danced for longer (more waggle runs per dance) and more often (more return trips) than nest sites of lesser quality. Hence, the higher the quality of the nest site, the more it is advertised on the swarm and the more likely it is to attract dance followers.

returns the probability per second of starting to scout. This probability is applied at each simulation step and scaled by the step length. The probability that a searching bee will start scouting after time t or at step $k = t/\Lambda$ is

$$P_{\text{scout}}(k) = 1 - \prod_{i=0}^{k}(1 - \Lambda \cdot r_{\Theta}(\Lambda \cdot i)).$$

The number of iterations i is scaled by Λ to elapsed seconds. The $r_{\Theta}(\Lambda \cdot i)$ is then scaled with Λ to account for the fact that the probability is applied only every Λ s. We used $\Theta = 4000$ for the response function. The probability of becoming a scout after a given duration as a result of the accumulated probabilities over the number of iterations ($\Lambda = 6$ s) is given in Figure 2.

Scouting trip success

The success of a scouting trip (i.e., whether or not the scout found a site) is modeled by a probability distribution for the discovery of potential sites. Initially, the case is considered in which all sites are found at equal distance from the swarm and these sites have an equal probability of being discovered. When we wanted to investigate the effect of distance of sites

on the decision-making process, we consider different probability distributions that describe the chance of being discovered depending on the distance of the sites from the swarm. These probability distributions correspond to different search behaviors employed by the swarm, as described later in this section.

A bee will search for time T_{scout} and, depending on the probability for finding a site, will either discover a site and assess it or return to the swarm and search for a dance again. Based on Lindauer (1955), we set the time spent per scouting trip at $T_{\text{scout}} = 20$ min.

Dance following

The probability of finding a dance is scaled by the number of dances currently available, $P_{\text{find}} = \Lambda \cdot 0.005 \cdot D$, where D is the total number of currently available dances. Which dance a searching bee finds is selected uniformly from the available dances. Whether the bee is able to follow the selected dance depends on the number of other bees currently following the dance. This is determined by $0.2^{\min\{f,2\}}$, where f is the number of other bees already following the dance, up to a maximum number of 7 followers.

The probabilities for finding and following a dance were assigned such that the resulting behavior resembles the

Figure 2
Probability that an individual bee in search state will start to scout relative to the time searching for a dance. Given are the probability per second $r_\Theta(t) = t^2/(t^2 + \Theta^2)$ and the cumulative probability that an individual will scout at a given time after it started searching for a dance; $\Theta = 4000$, $\Lambda = 6$ s.

Figure 3
Probability of finding the advertised nest site depending on the number of waggle runs followed for that site (successful dance following); the curve is obtained by combining both the observed success rate (successful) and the rate of unsuccessfully finding the site (unsuccessful) for a given number of waggle runs followed based on observations by Mautz (1971).

number of dance followers for forage as found by Tautz and Rohrseitz (1998).

A bee follows a dance until the dancer finishes after which the dance follower flies out to find the advertised site. The probability of successfully finding the site depends on the number of waggle runs the bee has followed for that site. If the bee has visited the site previously, it will definitely find it again. Otherwise, the probability is modeled according to observations made on the success rate for foraging in relation to the number of waggle runs followed (Mautz 1971).

Mautz (1971) recorded the number of waggle runs each bee has followed before attempting to locate the advertised site and whether or not it was then successful in finding the site.

From these data, we determined the cumulative distributions of the number of waggle runs followed by successful and unsuccessful followers, respectively.

We reproduced these 2 distributions to obtain a probability for finding a site depending on the number of waggle runs followed. The relative number of unsuccessful dance followers that have followed w waggle runs and could not find the advertised nest site afterward is modeled using $u(w) = 1 - 1/\sqrt{(w+1)}$; for the successful followers, $s(w) = w^2/(w^2 + \theta^2)$ is used, where $\theta = 60$. From both curves, the probability of success of a bee following a certain number w of waggle runs for a given site (the total number of unsuccessful attempts was roughly 1.5 times the number of successful ones) is extrapolated using Equation 1, compare Figure 3.

$$P_{\text{findSite}}(w) = \frac{s(w)}{1.5\, u(w) + s(w)}. \qquad (1)$$

If a bee is unsuccessful in finding the advertised site, it will spend time T_{miss} searching for the site and then return to the swarm. The maximum time spent scouting was set to 20 min (1200 simulation steps), and the maximum time searching unsuccessfully is one-third of this time (400 steps $\approx$ 7 min).

Site assessment

When a bee first arrives at a nest site, either by scouting or because it successfully followed a dance, it will assess its quality. Each visit to the site lasts about 10 min, Lindauer (1955),

$T_{\text{assess}} = 10$ min. The quality Q_S of a nest site is taken from [0; 100] and corresponds to the number of waggle runs a bee would perform for that site after its return to the swarm. The perceived quality $Q(S)$ of a site S is $Q(S) = Q_S + \delta$, where $\delta \sim N(0, \sigma^2)$ is drawn from a normal distribution with standard deviation $\sigma = 10$. If the perceived quality is greater than a predefined dance threshold Φ, a bee will dance for this nest site on return to the swarm. This threshold is set to $\Phi = 50$ for all bees. A bee that decided to dance for a site will perform $Q(S)$ waggle runs at the swarm at its first return and $Q(S) - 16(k - 1)$ at the kth return, as observed by (Seeley 2003). When a bee ceases dancing, it will search for another dance again.

The duration of a waggle run depends on the location of the promoted site, as the length of the waggle run encodes the distance to the advertised site. We used values based on the observations by Seeley and Buhrman (2001), using the distance–waggle dance duration curve from von Frisch (1967). One dance circuit (half of the figure-of-eight as described by von Frisch 1967) comprises a waggle run that lasts 2.4 s/km of distance to the site, and a return phase, which we fixed at 1.5 s regardless of the distance (for forage, it is known that the return phase is shorter the more profitable the discovered site is [Seeley et al. 2000] but it is unknown if this is also the case for the nest sites). Hence, one dance circuit for a site located at 250 m from the swarm takes 2.1 s, and one for a site at 1000 m takes 3.9 s.

Resting

The probability that a searching bee will start to rest is $P_{\text{rest}} = 0.002$/s. This is equal to the probability that a bee will turn from resting into searching for a dance. The expected time until a bee switches between these 2 states is thus $1/P_{\text{rest}} = 500$ s. This probability is based on Visscher and Camazine (1999).

Search strategy

How should the swarm search its environment to ensure that the best site is chosen when sites are present at different distances? When the choice is between sites of equal quality but

unequal distances, the swarm should choose the site closest to the swarm because of the shorter travel time (unless there are other reasons why a more distant site should be preferred, but we have no reason to believe that is the case). However, when a better quality site is present, this site should be selected regardless of its distance (presumably up to a certain maximum distance). Which site is chosen depends on the way in which scouts search their environment, that is, the probability that a site at a particular distance is discovered. Ideally, the scouts should search such that nearby sites are given preference, without loosing the option to choose a site farther away if this site is of better quality. How are these requirements reflected in the swarm's search strategy?

We describe a swarm's search strategy using a particular probability distribution for discovering a nest site at a given distance. Three different search strategies were used: "uniform," "distance," and "distance squared." For all 3, the probability of finding a site at 250 m is fixed at $P = 1/250$ per trip made by an individual bee. In the uniform probability distribution, each site, irrespective of its distance, is discovered with the same probability of $P_u = 1/250$. In the distance probability distribution, the probability of being found depends on the distance to the respective site, that is, the probability is given as $P_d = 1/d$. Lastly, in the distance-squared distribution, closer sites are preferred even more strongly. The probability is then given as $P_s = 250/d^2$. All the probabilities are given in Figure 4.

We formulated the search strategies, that is, their corresponding probability distributions, at the level of the swarm so that we could easily apply and compare them. Nevertheless, these probability distributions can be translated into individual search behaviors. Assuming that with each scouting trip, a circular patch of equal size is covered, the total area to be searched at a certain distance increases linearly with distance (the space to be searched at distance d is a ring of area $2\pi dw$, where w is the diameter of a search patch). Hence, if an individual scout chooses a random angle and a random distance when leaving the swarm and searches at this location, the probability for each location to be searched is inversely proportional to its distance to the swarm and corresponds with the distance distribution. Furthermore, if a scout is more likely to search at closer locations, the distance-squared distribution is obtained. The uniform distribution is included because it was used in all previously published nest-site selection models. For such a distribution, a scout would have to prefer searching at distances farther away to compensate for the increasing area that needs to be covered. Obviously, this is hard to realize for large scouting distances.

EXPERIMENTS

We used several experimental setups to explore different aspects of the decision-making process. In Experiments 1–3, we used nest sites that were all located at distance $d = 250$ m from the swarm. Hence, the search strategy employed is irrelevant in these experiments. In Experiments 4 and 5, we did include the different search strategies. In these experiments, we investigated the effect of distance of the nest sites on the swarm's ability to choose the best site. We performed 50 runs for Experiments 1–3 and 100 for Experiments 4 and 5. Details of the different experiments are outlined below. All experiments were run for 20 000 simulation steps, corresponding to 33 h and 20 min.

Experiment 1

Here the trade-off between the number of scouts (bees searching for a potential nest site without having followed a dance) and the number of bees committed to a site (assessing and dancing for that site) is investigated. The bees should recruit to a known site depending on its quality such that when only a poor site has been discovered, the bees retain the ability to recruit to a better site if such a site is found later. At the same time, a decision should be made quickly when a site of good quality has been discovered. We offered the swarm one nest site of 3 different qualities $Q \in \{45, 50, 70\}$. Hence, we tested the swarm's allocation of bees to scouting and recruiting to a poor, a mediocre, and a good site.

Experiment 2

In this experiment, we explored the swarm's ability to choose one nest site when nest sites of equal quality and located at the same distance but in opposite directions are present in pairs. We used pairs of poor, mediocre, and good sites ($Q \in \{45, 50, 70\}$).

Experiment 3

While recruiting to a mediocre site, a swarm has to retain the ability to discover a better site and eventually choose that better site. At what stage can the better quality site still be selected after the swarm has already discovered the mediocre site? In this experiment, we offered the swarm 2 sites of unequal quality, one of quality 50 (mediocre) and the other of quality 70 (good). In this experiment, the time of discovery for each nest site was set explicitly. The mediocre site was discovered immediately, whereas the good site was discovered t h after the mediocre site, $t \in \{0, 0.5, 1, 2, 4, 6\}$.

Experiments 4 and 5

In Experiments 4 and 5, we explore how the swarm can use different search strategies to balance the trade-off between distance of potential nest sites and their quality. In each experiment, we considered the 3 different probability distributions for discovering a site that were introduced in the Model section uniform $P_u = 1/250$, distance $P_d = 1/d$, and distance-squared $P_s = 250/d^2$. Again, 2 sites were offered to the swarm. The nearest site was fixed at $d = 250$ m, and the farther site was placed at $d \in \{400, 550, 700, 850, 1000\}$. In Experiment 4, the 2 sites were of equal quality, $Q = 50$, whereas in Experiment 5, the far site was of higher quality, $Q = 70$.
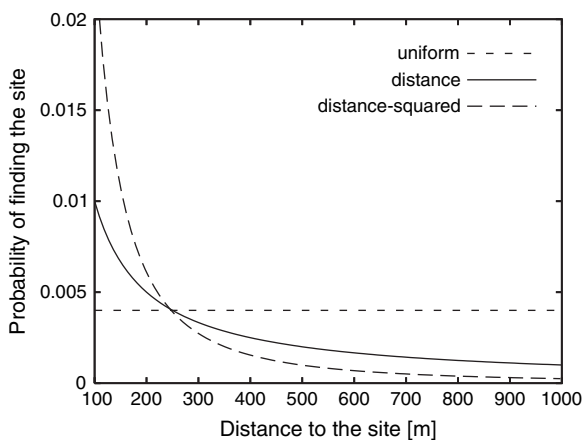

Figure 4
Probability for finding a site at a given distance for the 3 search distributions used.

RESULTS

We required the swarm to reach near consensus (all or most bees dancing for the same site) about which nest site would be chosen, even though real swarms rely on a quorum to perceive the completion of the decision-making process (Seeley and Visscher 2003, 2004b). The exact size of the quorum is of critical importance if we want to use it to determine when our simulated swarms have finished their deliberations. As quorum size has so far been estimated by counting the number of bees visible at the outside of the nest site (Seeley and Visscher 2003, 2004b), we do not have reliable information about the total number of bees necessary to form a quorum. In addition, we do not know if, and if so how, quorum size depends on the size of the swarm. We therefore decided to let the process run until the maximum simulation duration was reached. In this way, we do not run the chance of inadvertently assuming that a decision has been made. As an alternative, we could have used a conservative estimate (i.e., large) of quorum size, but this would not be different from waiting until consensus or near consensus was reached (as this also uses a large quorum size).

In the following, we considered a choice between 2 sites successful if 10 or fewer bees are still present at the nonchosen site at the end of a simulation run. When more than 10 bees were found at the nonchosen site, we assumed that the swarm did not reach a unanimous decision. This only occurred sporadically in the simulation runs, and these cases are not incorporated into the presented averages.

Number of dance followers

To verify that our dancing bees attracted a realistic number of dance followers, we used the experimental setup of Experiment 1 to determine the average number of dance followers for the first dance a bee makes for a site. We chose the first dance because this dance is the longest dance the bee will perform for that site and therefore potentially attracts the maximum number of dance followers. Figure 5 shows the average number of dance followers for nest sites of different quality. Because dances for sites of higher quality are longer, dances for better sites have a higher probability of being found by a bee searching for a dance. As time progressed, more and more dances became available and thus the average number of followers decreased. This decrease was more rapid the higher the quality of the site because the number of dances for a high-quality site builds up more quickly.

Experiment 1

The number of bees assessing the nest site and the number of bees scouting for new sites is shown in Figure 6. The higher the quality of a site, the faster the buildup of bees to this site. This is due to several factors. A bee discovering a site of high quality is more likely to dance for it on return to the swarm. In addition, dances for better sites last longer (more waggle runs per dance) which enable more bees to follow a dance for a high-quality site. Moreover, because a dance follower can follow more waggle runs, the chances of finding the advertised site increases (see Figure 3). Lastly, a bee that has discovered a superb site makes more return visits and thus the overall amount of dancing is higher the better the quality of the site.

For a site of quality 70, the swarm reached a decision after about 4 h, whereas this took about twice as long for a site of quality 50 (see Figure 6). Importantly, even a poor site of quality 45 (which is just below the dance threshold $\Phi = 50$) was chosen if no other site is discovered. This can only happen through the accumulation of assessment errors, as each bee
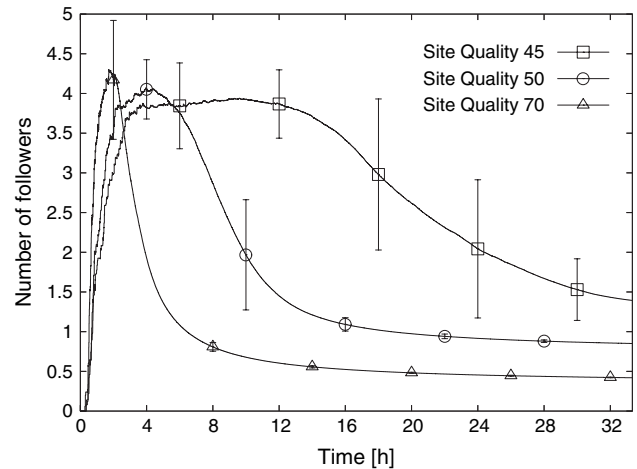

Figure 5
Average number of dance followers per dance for the first dance that a scout performs for a particular site; the vertical bars indicate standard deviation. Number of runs was 50.

has to overestimate the site by 5 points. (Alternatively, the bees could lower their dance threshold the longer the decision-making process takes, but this is not included in our model.)

The relationship between the buildup of bees at the site and the number of scouts is clear. When a site of high quality has been discovered, the number of bees at that site builds up rapidly. Because many dances are taking place, most bees searching for a dance will be able to find and follow one. As a result, the number of bees searching independently is low. Conversely, if the discovered site is of mediocre quality, the number of dances at any time is lower, resulting in more bees missing out on finding a dance and, hence, becoming scouts searching for new sites.

Experiment 2

As a swarm should not split, it needs to select just one nest site even if more than one site of the same quality has been discovered. When we offered the swarm 2 sites of equal quality,
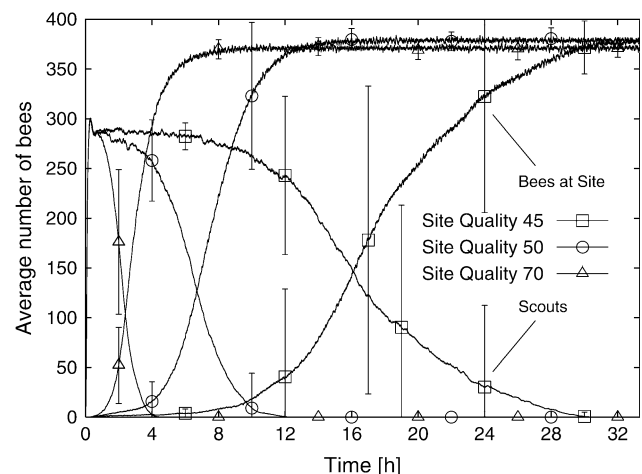

Figure 6
Average number of bees scouting for a site and the average number of bees assessing a site when a single nest site of different quality is present; the vertical bars indicate standard deviation. Number of runs was 50.
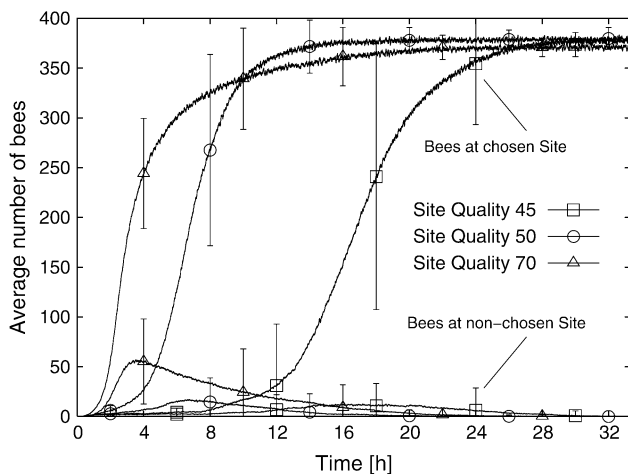
Figure 7
Average number of bees assessing a site when 2 nest sites of equal quality, and at the same distance but in opposite direction, are present. Both the number of bees at the chosen site and the number of bees at the nonchosen site are given; the vertical bars indicate standard deviation. Number of runs was 50. However, runs in which no unanimous decision was made were excluded (1 run for quality 45 and 70).

the swarm was able to choose between 2 sites in all but 2 occasions (once for quality 45 and 70) (Figure 7). When both sites were of high quality, both sites attracted a large number of bees rapidly. Only when the number of dance followers became limiting, did the 2 sites compete directly and a choice was made. This suggests that if a swarm is facing an abundance of high-quality sites, choosing between sites may become problematic, particularly if a quorum is used to terminate the decision-making process as more than one site can reach the quorum. Obviously, this problem would only arise if the sites are of equal quality, found at the same distance and discovered at the same time, a scenario that is highly unlikely under natural conditions.

Experiment 3

Ideally, a better site should be chosen even if it is discovered after a mediocre site has already been found. How long after the discovery of the mediocre site can the swarm still select the better site? In Table 1, we present the number of times that the site of quality 50 and the site of quality 70 was chosen depending on when the better site was discovered. The swarm chose the better site in all runs when it was discovered up to 2 h after the mediocre site was discovered. When the better site was discovered four or more hours later, the swarm could also settle for the mediocre site.

Whether or not the swarm is still able to select the better site most likely depends on the number of bees already present at the mediocre site at the time of discovery of the better site. When the better site was discovered after 4 h, the average number of bees present at the mediocre site was 11 ± 11 in the runs in which the better site was ultimately chosen. This number was significantly higher in the 4 cases in which the mediocre site was selected: 68 ± 27 (Wilcoxon Rank Sum Test, 2-sided, P value $\ll 0.001$). For the runs in which the better site was found after 6 h, these numbers were 13 ± 17 when the better site was ultimately selected and 169 ± 101 when the swarm settled for the mediocre site (Wilcoxon Rank Sum Test, 2-sided, P value $\ll 0.001$).

Table 1
Number of runs in which the swarm chose the mediocre (quality 50) and good (quality 70) site when the good site is discovered after the swarm has already found the mediocre site

	0 h	0.5 h	1 h	2 h	4 h	6 h
Mediocre site	0	0	0	0	4	30
Good site	50	50	50	50	46	20

Time refers to the time at which the good site was discovered after the discovery of the mediocre site.

Experiments 4 and 5

When 2 sites of equal quality are present but one is located much farther away, the swarm should choose the site closest to the swarm unless there are no costs involved in moving to a farther site. However, when the farther site is of better quality, this site should be selected. Which site is chosen depends on the way in which the swarm searches its environment, that is, the probability that a site at a particular distance is discovered.

In Experiment 4, we considered the scenario in which the sites were of equal quality. Table 2 (Distance of far site) shows the number of times in which each site was chosen by the swarm for the different search strategies. When the probability of discovery is independent of the site's distance ($P_u = 1/250$), we see a trend toward preference for the far site. This is most likely caused by dances for the farther site lasting longer therefore attracting more dance followers. Using probability $P_d = 1/d$ for the discovery of a site, the nearby site was chosen in the majority of runs. Only when the probability of discovery of a site depends on the squared distance, $P_s = 250/d^2$, was the nearby site clearly preferred. Moreover, only when using the squared distance probability were far sites less likely to be chosen the farther they were. The costs involved in making a suboptimal choice (i.e., moving into the farther site) is obviously not as great when both sites are of equal quality, unless the far site is so far from the swarm that travel times become costly.

When sites are of unequal quality, choosing the lower quality site is likely to impose a more serious cost to the swarm. Hence, in Experiment 5, the swarm should show a clear preference for the far site, as this site is of better quality. For both $P_u = 1/250$ and $P_d = 1/d$, the far site was clearly the most likely to be chosen (see Table 2, Distance of good-quality site). When the chance of discovery became smaller with increasing distance, $P_s = 250/d^2$, the far site was less likely to be selected the farther it was away from the swarm (see Table 2, Distance of good-quality site). But even when it is 4 times as far (1000 m), the chances are still high that the far site is chosen.

DISCUSSION

In this study, we explored how a swarm of honeybees trades off the exploitation of known nest sites with searching for sites that are not yet known to the colony. A swarm needs to decide quickly on a new home, but not so quickly that it is likely to settle on a nest site of low quality although better sites are available. How does the individual behavior of the bees involved in the decision-making process ensure that the best possible collective decision is made?

In our model, we used a simple mechanism to regulate the number of scouts. A bee involved in the nest-site selection process will first try to locate a dance to follow. If it succeeds, it will become a dance follower. If, however, it fails to follow a dance, it will fly out and search independently, thereby becoming a scout. A similar mechanism is thought to underlie

Table 2

Number of runs in which each site was ultimately chosen by the swarm for different search strategies employed by scouts

	Uniform		Distance		Distance squared	
	Near	Far	Near	Far	Near	Far
Distance of far site[a]						
400 m	36	64	76	24	80	20
550 m	51	48	73	25	90	10
700 m	20	79	69	29	93	7
850 m	31	68	65	34	94	6
1000 m	28	71	84	16	97	2
Distance of good-quality site[b]						
400 m	0	100	0	100	1	99
550 m	0	100	1	99	7	93
700 m	0	100	2	98	22	78
850 m	0	100	0	99	27	73
1000 m	0	100	3	97	39	61

[a] In this experiment, the sites were of equal quality (quality 50), but the nearby site was placed at distance 250 m, whereas the far site was farther away, at distances varying from 400 to 1000 m. The number of runs does not add up to 100 if in some runs the swarm did not reach a unanimous decision.

[b] Here the sites were of different quality. The nearby site was placed at distance 250 m and of quality 50, whereas the far site was of quality 70 but farther away.

the regulation of scouting for forage (Beekman, Gilchrist, et al. 2007).

This simple mechanism appears to be sufficient to regulate the number of scouts relative to the quality of the site already known (i.e., danced for) to the swarm and results in adaptive behavior at the level of the swarm. When the swarm only "knows" of a site of poor quality, the presence of a large number of scouts maximizes the chance of discovering a better quality site (see Figure 6). The reverse is true when a good-quality site has already been discovered. As it is not likely that an even better site will be found, the buildup of the number of bees dancing for the known site is rapid and the number of scouts low. Our results also show that if a better site is not found, the swarm will ultimately settle on the lesser quality site (Figure 6; site of quality 45). Again, this behavior is adaptive as a low-quality site is better than no site at all.

The discovery of new nest sites depends on 2 factors: the number of scouts sent out by the swarm and the searching strategy employed by the swarm. The latter is especially important when sites are present at different distances from the swarm, as is likely under natural conditions. How should scouts search?

We used 3 different search strategies that differ in the likelihood that sites farther from the swarm will be discovered by a scout. Which of the 3 different search strategies is the best depends on the costs of traveling to a site far away and the costs of moving into an inferior site nearby. A farther site can be costly in different ways. Travel time of scouts can be energetically costly, it may take longer to reach a decision, and the actual move to the new site may be more hazardous as it will require the swarm to fly a longer distance. It therefore seems likely that, unless all nearby sites are of inferior quality, scouts should search in such a way that sites that are farther from the swarm are less likely to be discovered. Otherwise, the swarm might move to a far site even if a good-quality site is found nearby, see Table 2 (Distance of far site). At the same time, the discovery of sites farther away should not be too unlikely, as

the swarm will otherwise be unable to choose a higher quality site at a distance from the swarm, see Table 2 (Distance of good-quality site).

Lindauer (1955) suggested that swarms show a preference for distant nest sites as this may reduce competition with the maternal colony. If this is the case, scouts should increase the chances of discovering far away sites first, as otherwise the swarm is more likely to settle on a nearby site of equal or comparable quality. However, subsequent authors failed to repeat Lindauer's observations and concluded that swarms, all else being equal, prefer nearby sites (Seeley and Morse 1977; Jaycox and Parise 1980, 1981). One study at first sight appears to refute the idea that swarms have a preference for nearby sites (Schmidt 1995). Schmidt (1995) performed an elegant experiment in which he, over 3 swarming seasons, offered a total of 63 swarms identical nest sites placed at different distances (100, 250, 500, and 1000 m) arranged in 4 concentric rings. Interestingly, he did not find any preference for a particular distance. Instead, the swarms distributed themselves rather evenly over the different distances.

This experimental setup could have yielded valuable insights into the actual searching behavior employed by individual scouts were it not that it contains a serious flaw. To ensure an equal number of nest sites at all distances, Schmidt (1995) placed 2 nest sites close together within the 2 innermost circles. This means that it becomes harder for the swarm to choose the nearby nest sites as the number of bees is divided over 2 nest sites, thereby doubling the required number of bees necessary to reach the quorum (Seeley and Visscher 2004b). So, instead of suggesting that swarms do not have a preference for sites located at a certain distance, Schmidt's results in fact support the idea that swarms prefer nearby sites.

Even though we did not include a quorum as a means to end the decision-making process, we strongly suspect that the quorum is a way to speed up the process. In most of our simulations, consensus in dances was reached for the site with the highest buildup of bees (data not shown), an observation that has also been made on real swarms (Seeley and Visscher 2003). Although the use of a quorum will avoid wasting time on continuous deliberations when a site of good quality had been found, using a quorum most likely increases the chance that the wrong decision is made. This is especially likely when there is a time delay between the discovery of sites such that a high-quality site is only discovered some time after a low quality site has been found. Moreover, to be accurate, the quorum should be relative to the size of the swarm because otherwise large swarms will easily reach a quorum at many different sites, or make the decision too quickly. This then raises the question: how do bees know the size of the swarm?

Collective behavior of animal groups is best understood by using a combination of theoretical modeling and field observations. Field observations are essential to understand the individual behaviors that most likely underlie the collective behavior. However, without modeling, it is not necessarily clear how this individual behavior results in adaptive collective behavior.

We built our model using extensive data obtained from field studies on how individual bees behave during the swarm's selection of a new home. But, in constructing our model, we also made some assumptions about how bees could behave, in particular how an individual decides to become a scout and how it then searches the environment. Simulated decisions made by in silico swarms suggest that our mechanism behind the regulation of scouts leads to the required behavior at the collective level. Our simulations also suggest what a successful search strategy could look like. Both assumptions should now be tested in the field, using real honeybee swarms.

REFERENCES

Beekman M, Fathke RL, Seeley TD. 2006. How does an informed minority of scouts guide a honey bee swarm as it flies to its new home? Anim Behav. 71(1):161–171.

Beekman M, Gilchrist AL, Duncan M, Sumpter DJT. Forthcoming 2007. What makes a honeybee scout? Behav Ecol Sociobiol.

Beekman M, Sumpter DJT, Ratnieks FLW. 2001. Phase transition between disorganised and organised foraging in pharaoh's ants. Proc Natl Acad Sci USA. 98(17):9703–9706.

Britton NF, Franks NR, Pratt SC, Seeley TD. 2002. Deciding on a new home: how do honeybees agree? Proc R Soc Lond ser B. 269:1383–1388.

Camazine S, Visscher PK, Finley J, Vetter RS. 1999. House-hunting by honey bee swarms: collective decisions and individual behaviors. Insectes Soc. 46:348–362.

Janson S, Middendorf M, Beekman M. 2005. Honey bee swarms: how do scouts guide a swarm of uninformed bees? Anim Behav. 70:349–358.

Jaycox ER, Parise SG. 1980. Homesite selection by Italian honey bee swarms, *Apis mellifera ligustica* (Hymenoptera: Apidae). J Kans Entomol Soc. 53:171–178.

Jaycox ER, Parise SG. 1981. Homesite selection by swarms of black-bodied honey bees, *Apis mellifera caucasica* and *A. m. carnica* (Hymenoptera: Apidae). J Kans Entomol Soc. 54:697–703.

Lindauer M. 1955. Schwarmbienen auf Wohnungssuche. Z vgl Physiol. 37:263–324.

Mautz D. 1971. Der Kommunikationseffekt der Schwänzeltänze bei *Apis mellifica carnica* (Pollm.). Z vgl Physiol. 72:197–220.

Myerscough MR. 2003. Dancing for a decision: a matrix model for nest-site choice by honeybees. Proc R Soc Lond ser B. 270:577–582.

Passino KM, Seeley TD. 2006. Modeling and analysis of nest-site selection by honeybee swarms: the speed and accuracy trade-off. Behav Ecol Sociobiol. 59:427–442.

Pratt SC, Sumpter DJT, Mallon EB, Franks NR. 2005. An agent-based model of collective nest choice by the ant *Temnothorax albipennis*. Anim Behav. 70:1023–1036.

Schmidt JO. 1995. Dispersal distance and direction of reproductive European honey bee swarms (Hymenoptera: Apidae). J Kans Entomol Soc. 68(3):320–325.

Seeley TD. 2003. Consensus building during nest-site selection in honey bee swarms: the expiration of dissent. Behav Ecol Sociobiol. 53:417–424.

Seeley TD, Buhrman SC. 1999. Group decision making in swarms of honeybees. Behav Ecol Sociobiol. 45:19–31.

Seeley TD, Buhrman SC. 2001. Nest-site selection in honey bees: how well do swarms implement the "best-of-n" decision rule? Behav Ecol Sociobiol. 49:416–427.

Seeley TD, Mikheyev AS, Pagano GJ. 2000. Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. J Comp Physiol A. 186:813–819.

Seeley TD, Morse RA. 1977. Dispersal behavior of honey bee swarms. Psyche. 84(3–4):199–209.

Seeley TD, Visscher PK. 2003. Choosing a home: how the scouts in a honey bee swarm perceive the completion of their group decision making. Behav Ecol Sociobiol. 54(5):511–520.

Seeley TD, Visscher PK. 2004a. Group decision making in nest-site selection by honey bees. Apidologie. 35:101–116.

Seeley TD, Visscher PK. 2004b. Quorum sensing during nest-site selection by honeybee swarms. Behav Ecol Sociobiol. 56(6):594–601.

Sumpter DJT. 2005. The principles of collective animal behaviour. Philos Trans R Soc Lond ser B. 361:5–22.

Sumpter DJT, Beekman M. 2003. From non-linearity to optimality: pheromone trail foraging by ants. Anim Behav. 66:273–280.

Sumpter DJT, Pratt SC. 2003. A modelling framework for understanding social insect foraging. Behav Ecol Sociobiol. 53:131–144.

Tautz J, Rohrseitz K. 1998. What attracts honeybees to a waggle dancer? J Comp Physiol A. 183:661–667.

Villa JD. 2004. Swarming behavior of honey bees (Hymenoptera: Apidae) in southeastern Louisiana. Ann Entomol Soc Am. 97(1):111–116.

Visscher PK, Camazine S. 1999. The mystery of swarming honey bees: from individual behaviors to collective decisions. In: Detrain C, Deneubourg JL, Pasteels JM, editors. Information processing in social insects. Basel (Switzerland): Birkhaser. p. 355–378.

von Frisch K. 1967. The dance language and orientation of bees. Cambridge (MA): Harvard University Press.

Winston ML. 1987. The biology of the honey bee. Cambridge (MA): Harvard University Press.