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Modeling and analysis of nest-site selection by honeybee swarms: the speed and accuracy trade-off

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Abstract Nest-site selection in honeybees is a process of social decision making in which the scout bees in a swarm locate several potential nest sites, evaluate them, and select the best one by means of competitive signaling. We develop a model of this process and validate that the model possesses the key features of the bees' decision-making process, as revealed by prior empirical studies. Next, we use the model to study the "design" of the nest-site selection process, with a focus on how certain behavioral parameters have been tuned by natural selection to achieve a balance between speed and accuracy. First, we study the effects of the quorum threshold and the dance decay rate. We show that evolution seems to have settled on values for these two parameters that seek a balance between speed and accuracy of decision making by minimizing the time needed to achieve a consensus and maximizing the probability that the best site is chosen. Second, we study the adaptive tuning of the tendency of bees to explore for vs be recruited to a site. We show that this tendency appears to be tuned to regulate the positive feedback process of recruitment to ensure both a reasonably rapid choice and a low probability of a poor choice. Finally we show that the probability of choosing the best site is proportional to its quality, but that this proportionality depends on its quality relative to other discovered sites.

Keywords *Apis mellifera* · Honeybee · Nest-site selection · Social decision making

Introduction

For many years, biologists have studied decision making by animal groups. Such decision making typically emerges from the actions of individuals that, despite being rather poorly informed, are able to share information, influence one another, and eventually choose a course of action for the entire group (reviewed by Camazine et al. 2001; Franks et al. 2002). Examples of this group-level decision making include selecting the best travel route (Deneubourg and Goss 1989), choosing among food sources (Beckers et al. 1990; Seeley 1995), and deciding where to nest (Mallon et al. 2001; Pratt et al. 2002). Here, we develop a stochastic discrete-time model of one form of social decision making: nest-site selection by honeybee swarms. Our primary goal is to use this model to study the functional "design" of this decision-making process, that is, to see how the behaviors of individual bees have been tuned by natural selection so that the swarm as a whole achieves a good balance between speed and accuracy in its choice of a new home.

Nest-site selection by honeybee swarms is a highly distributed decision-making process that usually occurs in the spring when a colony outgrows its hive and divides itself by swarming (the biology of swarming is reviewed in Winston 1987). The mother queen and approximately half the worker bees leave the parental nest to establish a new colony, while a newly reared daughter queen and the remaining workers stay behind to perpetuate the old colony. The swarm bees leave en masse, forming a cloud of bees just outside the parental hive, but within about 20 min, they coalesce into a cluster at an interim site, usually a nearby tree branch. From here they choose their future nest site. Several hundred scout bees fly from the swarm cluster and search out tree cavities and other potential dwelling places. The dozen or so scouts that find suitable cavities report these locations by means of waggle dances on the surface of the swarm, and other scouts decode the dances, visit the sites themselves, and may dance in turn. A process of recruitment and selection ensues in which one site comes to dominate in visitation and dancing, and the swarm takes

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flight again and moves to the selected cavity (reviewed by Seeley and Visscher 2004a).

Two mathematical models of the bees' nest-site selection process have already been published. Britton et al. (2002) introduced an ordinary differential equation model, like ones used to model the spread of diseases and beliefs, and they studied how swarms can make decisions even without any bees comparing the various possible home sites. Myerscough (2003) used a population biology model in which dances reproduce via recruitment and die by decaying away. She introduced a discrete-time synchronous "matrix model" and used the theory of Leslie matrices to analyze the ability of swarm bees to produce unanimous decisions.

Also relevant to the present study are the many models developed to analyze the food-source selection process of honeybee colonies (Camazine et al. 1990; Camazine and Sneyd 1991; Camazine 1991; Jenkins et al. 1992; Bartholdi et al. 1993; de Vries and Biesmeijer 1998; Biesmeijer and de Vries 2001; Cox and Myerscough 2003; Schmickl and Crailsheim 2003). While the models of Cox and Myerscough 2003 and Schmickl and Crailsheim (2003) may be the most comprehensive, we have benefited most in building a model of the nest-site selection process from the way Camazine and Sneyd (1991) modeled the dance floor in a hive and from the arguments of de Vries and Biesmeijer (1998) on why an "individual-oriented" model (i.e., one that represents some of the behaviors of individual bees) is useful in tracing the connections between individual actions and emergent group behavior. We will model the dance floor (the surface of the swarm cluster) using a stochastic version of the "survival of the fittest" idea from evolutionary algorithms, giving each nest site a certain level of quality ("fitness"). We will also include in our model certain behaviors of individual bees, most critically their decisions about how strongly to dance for a nest site and whether to explore for or be recruited to a nest site.

A fundamental problem faced by any decision maker is finding a suitable compromise between swift decisions and good ones. If an animal, or a group, has to make a quick decision, it is apt to make a poor decision for lack of time to look broadly and deeply at its options (Franks et al. 2002). Assuming that a honeybee swarm experiences a speed-accuracy trade-off in choosing a nest site, we wondered whether the behavioral parameters of the bees have been tuned by natural selection so that a swarm minimizes its chances of choosing a poor site while incurring low time/energy costs while making its choice. One candidate parameter is the quorum threshold of swarm bees. Two previous studies have shown that the way the scout bees in a swarm know when they have chosen their future home site is by sensing a quorum, i.e., by noting when one of the potential nest sites under consideration is being visited by a sufficiently large number (10–20) of bees (Seeley and Visscher 2003, 2004b). Another candidate parameter is the dance decay rate of swarm bees. Several studies have reported that scout bees dance less and less strongly as they make sequential dances for a given nest site (Lindauer 1955; Beering 2001; Seeley 2003). A third candidate param-

eter is the tendency of swarm bees to find nest sites by exploring vs being recruited. The former process is how a swarm finds possible nest sites, and the latter lies at the heart of how a swarm chooses among the possible sites. It seemed a priori that all three parameters—quorum threshold, decay rate, and exploration tendency—could strongly affect the outcome and the timing of a swarm's decision making. To explore these possibilities, we used our model to create "pseudomutant" swarms, ones with different values of these three parameters, and studied how increasing or reducing each one affects the speed and accuracy of a swarm's selection of a nest site.

Model of nest-site selection

We model the nest-site selection process that occurs on the cluster and the concurrent quorum-sensing at the nest sites. We defer the study of other characteristics like heating, buzz-running, liftoff, and connections to "in-transit" swarming to future studies. Key references on nest-site selection include the early work of Seeley (1982) and the work of Camazine et al. (1999). However, the studies of Seeley and Buhman (1999, 2001), with subsequent results of Seeley (2003), form the basis for our model of the "on-cluster" portion of the nest-site selection process. The work of Seeley and Visscher (2003, 2004b) allows us to specify the quorum-sensing portion of the model and integrate it with the on-cluster portion. In the next section, the experimental data from these studies will be used to check the model's validity.

Table 1 summarizes the notation used in the development of the model.

Landscape of nest-site quality

Suppose that a bee is represented by $\theta \in \mathbb{R}^2$ which is its position in two-dimensional space. We will assume that there are a fixed number of B scouts, and bee i will be named θ^i so that we represent it by its location. The cluster is at $[0,0]^1$. We use a two-dimensional map to represent the spatial distribution of nest sites. During nest-site selection, scouts sample a "nest-site quality landscape," which we think of as a spatial distribution of the potential nest sites with encoded information on nest-site quality.

The nest-site quality landscape is denoted by $J(\theta)$, $\theta \in \mathbb{R}^2$. To represent a nest site at location θ , we assume that there is one small "cell" (peak) at position θ of height N^j that is proportional to the quality of site j . We consider a "perfect" nest site to be represented by $N^j=1$ and a completely unacceptable one as $N^j=0$. Hence, no two nest sites are at the same location, and we can model the spatial distribution of sites.

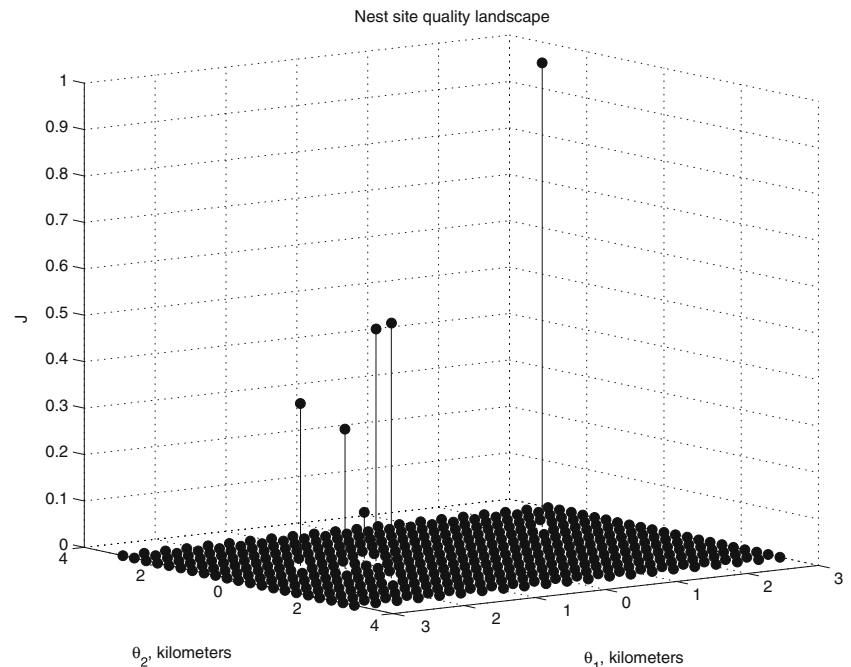
We assume that the nest-site selection process takes place in a square region with 6 km per side. We sample every 0.3 km so that there will be 21 partitions on each dimension for a total of $21^2=441$ values to define the nest-

Table 1 Notations used in the development of the model

Variable	Description
θ^i	Location of bee i
B	Number of scouts
J	Nest-site quality landscape
N^j	Quality parameter of nest site j
k	Index of expedition
$B_c(k)$	Number of committed scouts
$B_u(k)$	Number of uncommitted scouts
$B_o(k)$	Number of scouts seeking to observe dances
$B_r(k)$	Number of bees that rest on the cluster
$B_e(k)$	Number of bees that explore
$S^i(k)$	Nest-site quality assessment by i^{th} bee
$w^i(k)$	Noise due to errors in quality assessment
ε_t	Quality/dance threshold
p_d	Probability of death on expedition
$B_d(k)$	Number of bees that die at step k
$B_{dt}(k)$	Total number died by step k
k_j^i	Step that bee i discovered site j
$L^i(k)$	Dance strength of bee i at step k
$L^{ij}(k)$	Dance strength of bee i at step k for site j
γ	Initial dance strength for best site
ε_s	Dance decay rate
p_m	Probability of becoming an observer
ε_q	Quorum threshold
$L_t(k)$	Total number of dances at step k
$p_e(k)$	Probability observer becomes explorer
σ	Tendency to dance parameter
$p_r(k)$	Probability recruited by bee i
T_a	Agreement time

site quality landscape. We will assume that $B=100$ based on the results of Seeley and Buhrman (1999). This number of scouts will, on average, sample most of the landscape after a few hours if they are all dedicated to random sampling (as we assume explorers are). However, since some scouts may find sites and become dedicated to them, it can take longer on average to sample all locations. In some situations, all locations will never be sampled, but that depends on the dynamics of the selection process. With the choices here, once in a while, a site will not be found during the entire nest-site selection process. Since in our model the choice of the landscape is dependent on B , the model is only valid for a range of values around $B=100$. However, if other significantly different ranges are of interest, the model can be adjusted. Furthermore, note that we present the landscape as having the spatial features to provide intuition; however, the key feature is that there are unknown sites of various qualities that have a nonzero probability of being discovered.

Nest-site locations, which we uniformly distribute across the domain, are initially unknown to the scouts. Nest-site selection can then be thought of as trying to find a single maximum point on the nest-site landscape. One example of a nest-site landscape is shown in Fig. 1. Here, we have a number of potential nest sites of varying quality, but only one that is perfect. We will assume that the quality of a nest site is constant during the nest-site selection process. Below, however, we will assume that bees sample the nest-site landscape function with some noise; hence, two bees that visit the same site will have different assessments of its quality.

Fig. 1 Example nest-site quality landscape

Bee roles and expeditions

Let k be the index of the nest-site expedition, and assume that all the scouts go out at one time and return with their nest-site quality assessments at one time (an asynchronous model with randomly spaced arrivals and departures will behave in a qualitatively similar manner). Our convention is that at time $k=0$, no expeditions have occurred; at time $k=1$, one has occurred; and so on. Step $k=0$ represents the time when the cluster is first formed. All scouts, $i=1,2,\dots,B$, have $\theta^i(0)=[0,0]^T$ so that initially they are on the cluster. We assume that each nest-site expedition takes 30 min and that the whole selection process takes at most 32 h, so that, at most, 64 expeditions are taken (we ignore effects of weather and the number of days that the selection process might span). If in a simulation of the nest-site selection process it takes longer than 32 h, we simply call that case a failure and discard the results. As shown later, it is relatively rare for the process to fail to make a choice.

Of the B scouts involved in nest-site selection, we assume that there are $B_c(k)$ “committed scouts” (ones that advertise for a nest site and repeatedly return to that site). Initially, $B_c(0)=0$ since no sites have been found. We assume that there are $B_u(k)=B_o(k)+B_r(k)$ “uncommitted scouts” with $B_o(k)$ that observe the dances of committed scouts on the cluster and $B_r(k)$ that rest on the cluster. Initially, $B_r(0)=B_o(0)=0$. We assume that there are $B_e(k)$ “nest-site explorers”¹ that are not dedicated to a nest site, but go on expeditions to search for nest sites. Initially, $B_e(0)=B$ since all bees will go explore to start out.

We ignore the specific path used by the nest-site explorers to find nest sites. A bee that explores for nest sites simply samples the nest-site landscape once on its expedition and thus computes the value of $J(\theta(k))$, which represents its combined overall assessment of nest-site quality for a site at $\theta(k)$ during expedition k . Let the nest-site quality assessment by the i^{th} committed scout or nest-site explorer be

$$S^i(k) = \begin{cases} J(\theta^i(k)) + w^i(k) & \text{if } J(\theta^i(k)) + w^i(k) > \varepsilon_t \\ 0 & \text{if } J(\theta^i(k)) + w^i(k) \leq \varepsilon_t \end{cases}$$

where $w^i(k)$ is noise due to errors made in the scout assessing a nest site. Here, we let $w^i(k)$ be uniformly distributed on $(-0.1, 0.1)$ (to represent up to a $\pm 10\%$ error in nest-site assessment). The ε_t value sets a lower threshold on an acceptable site. Here, $\varepsilon_t=0.2$. We take $S_i(k)=0$ for the observers and resting scouts at step $k \geq 0$. Hence, it is assumed that each scout has an internal yardstick for nest-site quality and the noise can represent either inaccuracies in this yardstick or assessment errors.

¹ Often, in the literature such “explorers” are referred to as “scouts.” Here, we call all bees actively involved in the nest-site selection process “scouts,” as this is how they are often referred to in experimental studies. Consequently, nest-site scouts can explore, observe dances, rest, and be committed or uncommitted to a nest site.

To be consistent with empirical studies, we assume that during the nest-site selection process, at most 10% of the scouts that act as committed scouts or nest-site explorers die, but that bees on the cluster do not. Hence, during each of the at most 64 expeditions over the 32-h period, there is a probability $p_d = 0.1/64$ that each bee that goes on an expedition will die. We let the number of bees that die at step k be $B_d(k)$ and the total number that die by step k , including at step k , be $B_{dt}(k)$.

Next, we must specify the locations where all the scouts will go on their expeditions. Uncommitted scouts that are currently resting stay on the cluster. The $B_o(k)$ uncommitted scouts that are observers either explore or get recruited to a site. The locations for the $B_e(k)$ nest-site explorers to look for a nest site at the next step are simply defined by placing them randomly on the nest-site landscape with a uniform distribution. We assume that recruited scouts go exactly to the nest site they were recruited to and committed scouts go back to the same site they last visited (unless they stopped dancing for that site and thus become uncommitted and then typically rest).

Dance strength determination

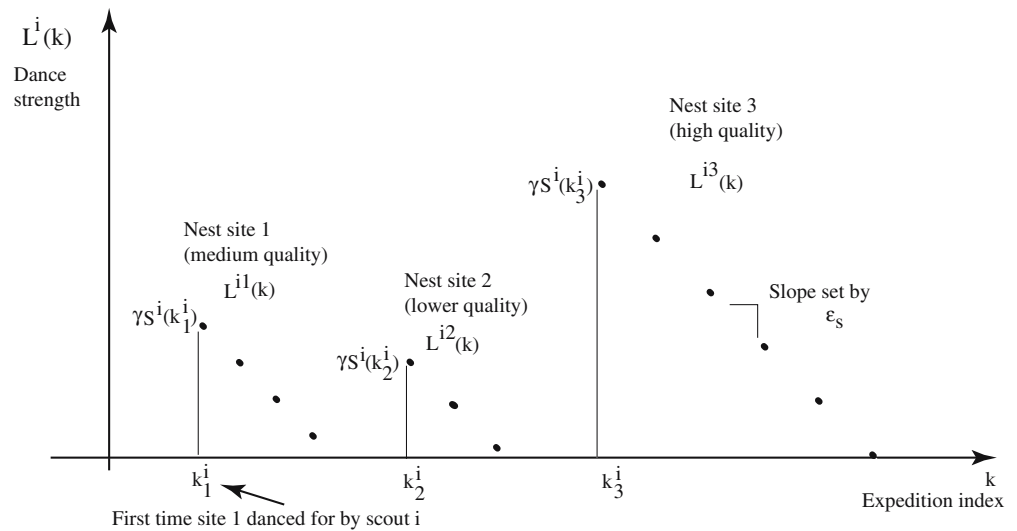
Let $k_j^i \geq 1$ be the time index of the expedition that nest-site explorer i first finds and assesses the quality of nest site j (i.e., the first time it computes N^j and remembers the nest-site location $\theta^i(k)$). Assume, for the discussion below, that bee i is a recruiter. Let $L^i(k)$ be the strength of the i^{th} committed scout’s (or nest-site explorer’s) dance for a nest site at time k . We assume that $L^i(k)$ is composed of a sequence of elementary functions $L^{ij}(k)$ that represent how the i^{th} committed scout or nest-site explorer will dance for the j^{th} site after the k^{th} expedition. Let

$$L^{ij}(k) = \begin{cases} \max\left\{(\gamma S^i(k_j^i) - \varepsilon_s(k - k_j^i)), 0\right\} & \text{if } S^i(k_j^i) > \varepsilon_t \\ 0 & \text{if } S^i(k_j^i) \leq \varepsilon_t \end{cases}$$

for $k \geq k_j^i$. This way, the committed scout or nest-site explorer’s dance strength is dictated by its initial assessment, and then the dance strength decreases over time provided that nest-site quality remains constant. The overall “duration” of the dance, i.e., the number of expeditions it will continue to dance for a nest site, is different from the dance “strength” $L^i(k)$ for a nest site in between expeditions.

The $\varepsilon_t > 0$ parameter sets a threshold for site quality before there will be any dancing for a site. The factor $\gamma > 0$ is a parameter that represents the proportionality between nest-site quality and initial dance strength the first time that the committed scout dances for the site. Based on the experimental results in Seeley (2003), we choose $\gamma=150$ waggle runs. The value of $\varepsilon_s > 0$ is a parameter used to represent the decrease in dance strength between successive

Fig. 2 Example sequence of nest-site recruitment dances by nest-site explorer i . She advertises three different sites. Each dot represents a dance on the cluster of a certain strength in between expeditions



expeditions, and based on the experiments in Seeley (2003), we know that $\epsilon_s=15$ waggle runs per nest-site visit; however, we will study in simulation the effect of changing this value.

An example sequence of dances is shown in Fig. 2. There, nest-site explorer i finds nest site 1 and dances for it over a number of expeditions but then eventually stops dancing and remains quiet (rests) on the cluster for a while. Later, it follows a dance to site 2, but since it was of lower quality, it stops dancing for it sooner than it had stopped dancing for site 1. Later on, it follows a dance to nest site 3 and finds it a high-quality site, so it dances for it more strongly and over more expeditions.

The shape of the functions used (e.g., the slopes) is chosen to reflect the experimental findings in Seeley and Buhrman (1999) and Seeley (2003). However, it is important to note that it is not the shape of the function that matters in the decision-making process, but that the area under each shape is proportional to the site quality since this represents how strong a scout's vote is for a site (this will be clarified in our simulations below). This feature seems to add a type of robustness to the decision-making process. We know that bees do not precisely decrease their number of waggle runs to achieve a perfectly linear decrease; it is only linear on average (Seeley and Buhrman 1999; Seeley 2003). It is the integral of the $L^{ij}(k)$ curve by bee i for site j over the time period while it advertises for site j that represents the bee's overall assessment of the site. If the shape of the curve changes, but the integral remains the same, the overall number of recruits will on average be the same (using the formulas below), so that the outcome of the decision-making process is not affected. It is, however, critical to the process that the number of expeditions over which a bee dances is limited. If it were not, then there would be no "expiration of dissent" (Seeley 2003), and ultimately, agreement would sometimes not be reached. Our simulations in "Effect of dance decrease rate" will validate this.

Resting and switching nest-site allegiance

Next, our model must account for the fact that relatively few bees switch from dancing for one site to another. To do this, we let $p_m \in [0, 1]$ denote the probability that a bee that just finished dancing for a site, or is resting, will become an uncommitted observer. Here, we will in simulation adjust p_m to match what is found experimentally in Seeley and Buhrman (1999, 2001) in terms of frequency of switching allegiance. In particular, we found that a value of $p_m=0.25$ resulted in an appropriate distribution in terms of the number of switches in allegiance (e.g., in most simulations, fewer than 10% of the bees dance for two sites). Bees that decide to dance for another site become uncommitted scouts that may follow a dance. Bees that decide not to dance remain bees that "rest" on the cluster (we do consider them to be a type of uncommitted bee since at each step there is the probability p_m that they will become "active" uncommitted scouts in the sense that they may stop resting and observe and follow a dance). This then defines how the number of resting bees $B_r(k)$ changes with time.

Quorum sensing at nest site, piping at cluster, and liftoff signal

We assume that there is a threshold for the number of bees at a nest site that must be reached before scouts returning from that nest site will pipe at the cluster [piping is an acoustic signal that scouts produce to stimulate the nonscouts to warm their flight muscles in preparation for the joint liftoff and flight to the new nest site (Seeley and Tautz 2001)]. We let $\epsilon_q > 0$ denote this quorum threshold and, based on the experiments by Seeley and Visscher (2003, 2004b), let $\epsilon_q=20$ bees. We will, however, vary this parameter in our simulations to study its effect.

If a bee visits a nest site where there are fewer than ϵ_q other scouts from their cluster, upon returning to the

cluster, the bee will not pipe, but may recruit. If a bee visits a nest site and there are greater than ε_q bees there, then upon returning to the cluster, the bee will both pipe and may also recruit.

If there is a level of piping at the cluster coming from more than ε_q bees, it is assumed that the bees lift off. Upon lift off, it could be that one or more nest sites had more than ε_q scout visitors; however, as in nature, this will be relatively rare in our simulations. In this case, we assume that there is a “split decision” that is resolved via the bees returning to the cluster to resolve the dispute (Lindauer 1955, 1961).

Explorer allocation and scout recruitment

To model the allocation of nest-site explorers and the recruitment of scouts to nest sites, we need to model how the $B_c(k)$, $B_o(k)$, and $B_e(k)$ values change over time. In defining these, we assume that $B_r(k)$ and $B_d(k)$ are already defined, in the manner discussed above, at step k . If at step k , $L^i(k)=0$, and the bee is not resting, then bee i is an uncommitted scout. For such a bee:

1. It could be that it explored on the last expedition and found nothing. In this case, it becomes an observer bee and may explore again or be recruited to a nest site.
2. It could be that it was committed to a nest site during the last expedition, but it stopped dancing for it. In this case, if it does not rest (as defined above), it may get recruited to a nest site or explore.

Each of these cases results in adjustments to the numbers of bees in the various roles as we define next.

Modeling the cluster dance floor is complicated by a lack of understanding of how explorers are allocated in the nest-site selection process. The problem is that while the recruitment process to nest sites via waggle runs is relatively well-understood, it is not known why a bee chooses to be recruited rather than to explore (and vice-versa). Here, we assume that an uncommitted bee on the cluster (one that is not resting, but is actively seeking to get involved in the process), searches for dances to follow, and if it does not find one after some length of time, it gives up and goes exploring. That is, we assume the bee uses the wait-time to find a dancer as a cue about whether it should explore. Verification of this awaits experimental study. However, it is well known that in social foraging, a bee uses the wait-time to get unloaded in order to estimate hive nectar influx and thus knows how other foragers are doing, so that it can decide whether to dance and for how long. And there is some evidence (Seeley 1983) that a forager decides to explore for a new food source, rather than get recruited to one, based on how long it searches to find a dancer advertising a food source. Hence, it seems plausible that the bees could use such a wait-time cue in nest-site selection also. In both the nest-site selection and social foraging cases, the wait-time to find a dancer cue explains several features of distributed honeybee decision making found in

nature. First, in nest-site selection, it will lead to a two-phase search-agreement process. In the beginning, when there are few dances, wait-times are long and many bees explore. As sites are found, more bees dance and thus recruit so that fewer bees explore. Second, in foraging for nectar, when nectar intake is low, there will be less dancing and thus more exploring in order to find new sources.

A characteristic that would certainly impact the delays in finding dancers is that there are only so many bees that can observe the dancing at any one time (due to physical constraints that lead to only a limited number of observers for each dancer). Such physical constraints lead to a limited number of recruits and impose natural delays in any observer bee getting recruited. It seems logical that if the bee is delayed too much, it will decide simply to go find a site on its own.

To model explorer allocation based on wait-time cues, we assume that the wait-time is inversely proportional to the bees’ tendency to be recruited to a nest site (i.e., if there is a long wait-time, it tends to go exploring). Considering the social foraging process (Seeley 1995), the wait-time is assumed to be proportional to the total number of waggle runs on the cluster. The more bees that are dancing strongly on the cluster, the more likely it is that an observer bee will quickly find a dancer to follow. Let

$$L_t(k) = \sum_{i=1}^{B_c(k)} L^i(k)$$

be the total number of waggle runs on the cluster at step k . We take the $B_o(k)$ observer bees and, for each one with probability $p_e(k)$, we make it an explorer. We choose

$$p_e(k) = \exp\left(-\frac{1}{2} \frac{L_t^2(k)}{\sigma^2}\right) \quad (1)$$

Notice that if $L_t(k)=0$, there is no dancing on the cluster so that $p_e(k)=1$ and all the observer bees will explore (e.g., $L_t(0)=0$ so initially, all observer bees will choose to explore). If $L_t(k)$ is low, the observer bees are less likely to find a dancer and thus will not get recruited to a nest site. They will, in a sense, be “recruited to explore” by the lack of the presence of any dance. As $L_t(k)$ increases, they become less likely to explore and, as discussed below, will be more likely to find a dancer and get recruited to a nest site. Here, we choose $\sigma=4,000$, so that if there are a total of 5,000 waggle runs at some point, there is less than a 50% chance that an uncommitted scout that is observing dances (not resting) will explore. We will show in simulation that this choice of σ produces patterns of choice behavior for the nest-site selection process that closely correspond to experiments.

The explorer allocation process is concurrent with the recruitment of observer bees to nest sites. Observer bees are recruited to nest sites with probability $1-p_e(k)$ by taking any observer bee that did not go explore and having

it be recruited. To model the actual scout recruitment process, we view $L^i(k)$ as the “fitness” of the nest site that the i^{th} bee visited during expedition k . Then, the probability that an observer bee will follow the dance of bee i is defined to be

$$p_i(k) = \frac{L^i(k)}{\sum_{i=1}^{B_c(k)} L^i(k)}. \quad (2)$$

In this manner, bees that dance stronger will tend to recruit more scouts to their site. Using these operations, we can define $B_c(k)$ and $B_c(k)$ and this completes the model.

Model validation

In this section, we will simulate the model in order to validate its behavior. We use the parameter values defined in “[Model of nest-site selection](#).” Of course, the nest-site selection process is stochastic; here, we provide plots for a “typical run” for these parameter values. In the next section, we provide Monte Carlo simulations to evaluate average nest-site selection behavior and error rates (including for the case where the parameters of this section are used).

At the outset, it is important to discuss the issue of errors in reaching agreement and how we view the crescendo and liftoff of the swarm. We assume that the crescendo, and thus agreement, is represented by a surge in the number of bees visiting a site and a corresponding surge in the number of bees advertising for that site. We assume that once the nest-site quorum threshold is achieved, before the next expedition there will be worker piping, heating, and then lift off, but do not explicitly model these characteristics. We simply terminate the process after the quorum is reached and before the next expedition.

With this approach, it is possible to have what we call “failures” for two reasons: (1) a failure to agree before 32 h, and for this case, we simply discard the results and restart; and (2) a failure to agree on one site, and in this case, there may be two or more sites that achieve a quorum threshold simultaneously. For case (2), we record that this occurred and then discard the results and start over. It makes sense to do this since in nature, if there is simultaneous agreement on more than one site, then there is an aerial tug-of-war and the process restarts. Hence, in any case, there is one site ultimately chosen, and our simulations represent this. We do, however, record the numbers of the two types of failures since these data are instructive for tuning the parameters of the model to represent what is found in experiments (this will be shown in the next section).

Here, we assume that for all our simulations there are six nest sites (for ease of plotting). Table 2 shows the nest-site quality N^i for each of the sites. Case 1 refers to all simulations except in “[Effect of nest-site quality landscape](#),” where we study case 2. In both cases, a successful nest-site selection results in the choice of site six. The data for case 1 are plotted in Fig. 1.

Table 2 Nest-site qualities

Site, $i=$	Symbol	N^i (case 1)	N^i (case 2)
1	▷	0.1	0.5
2	△	0.3	0.6
3	◇	0.35	0.7
4	□	0.5	0.8
5	◦	0.55	0.9
6	*	1	1

Pattern of scout nest-site visits and cross inhibition

First, consider Fig. 3, where we show the number of bees visiting each of the six sites over the entire process. Note that bees find every one of the sites in this case and even the unacceptable site ($N^1 < \varepsilon_t = 0.2$) is visited several times. As expected, there are generally more bees visiting higher-quality sites. Note that some sites are found by the scouts, but are later “lost” and then found again. This is due to the decrease in the dancing and the persistency of the explorers that results in them rediscovering the site.

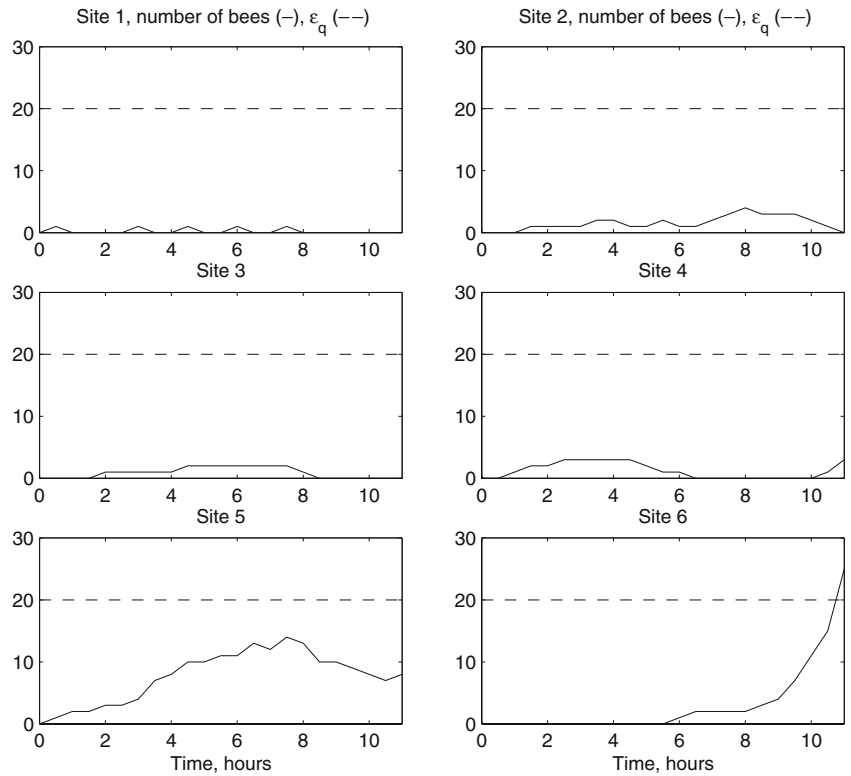
Due to the rates of recruitment based on nest-site quality, there is a crescendo for nest site 6, so it is selected since it was the first to go over the quorum threshold of $\varepsilon_q = 20$. Simultaneously, there is a type of “cross inhibition” that has been seen experimentally in studies by Seeley and Buhrman (1999, 2001), where as site 6 begins to dominate the process, it inhibits the dancing for some other sites (e.g., sites 2 and 5) and the numbers of bees visiting them decreases.

Bee roles and dancing patterns

Figure 4 shows the numbers of bees in various roles during the process, and the total amount of dancing. The numbers of committed scouts rises and the number of uncommitted scouts falls as expected. The number of scouts allocated to exploration results in a significant amount of searching early in the process, and less at the end. The number of resting bees, ones that rest after dancing for some site, rises and then falls sometimes when bees reenter the process. The number of bees that die rises as expected. The total amount of dancing shows a crescendo, as expected.

Next, Fig. 5 shows the average and standard deviation of $L^i(k)$ at each step. Furthermore, the “*” at the top of each plot indicates that some bee is visiting the site at that step (shown simply to indicate when sites are discovered or visited). The pattern of dancing across the sites is as one would expect given Fig. 3. The ceasing of the dancing results in abandonment of lower-quality sites, and for the lowest-quality site, although it is found, it is not danced for. The lower right plot for site 6 shows an interesting characteristic. Well before the crescendo occurs, the average dance strength is actually decreasing for a time period. Why? This is due to the ceasing of dancing, even for the chosen site. As the bees abandon other sites, more bees are dancing for the chosen site, so that the amount of dancing by each individual bee can decrease since other bees are

Fig. 3 Number of bees visiting each of six nest sites



joining in on the agreement for the chosen site, so that overall, the crescendo is achieved.

Pattern of dances and events leading to agreement

In Fig. 6, we show the sequence of dances by each bee over the entire process. Here, each horizontal line is used to identify the sequence of dances and events for each of the

$B=100$ bees. Here, we see an overall pattern of dancing that illustrates the crescendo since there are many more symbols near the end that correspond to the perfect site (in particular, consider the last step, and count the number of “*” symbols on the vertical axis on the right), but some bees do not join in since they are resting or have died. Dances for better sites tend to be longer in duration.

To study these sequences more carefully, consider Fig. 7, where we plot the dance strength sequences for bees $i=37$,

Fig. 4 Number of bees allocated to each task, and the total amount of dancing (*bottom plot*). Note that the number of bees seeking to observe dances (B_o) and the number of explorers (B_e) both start out at 100 bees. This is because, initially, there are no dances to follow; hence all the bees seeking to observe dances go exploring instead

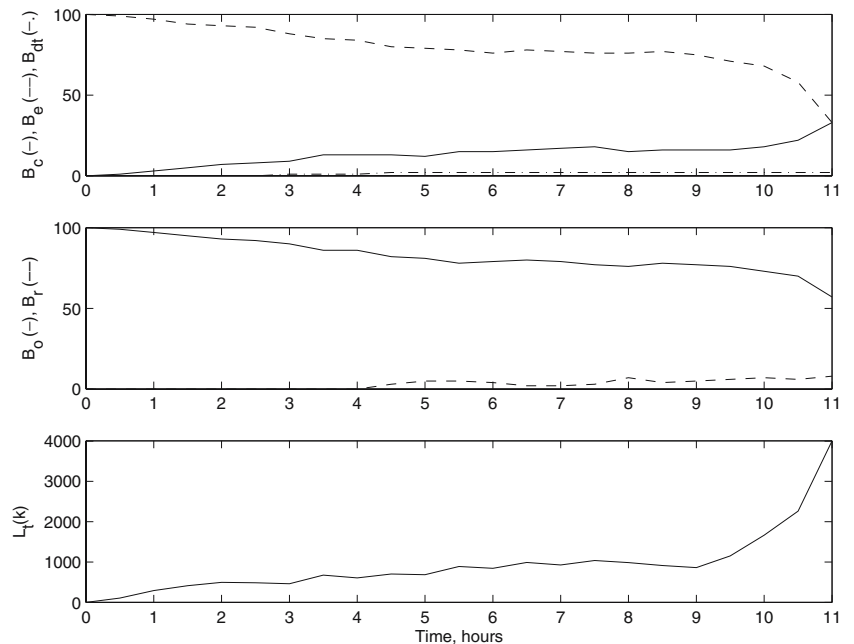
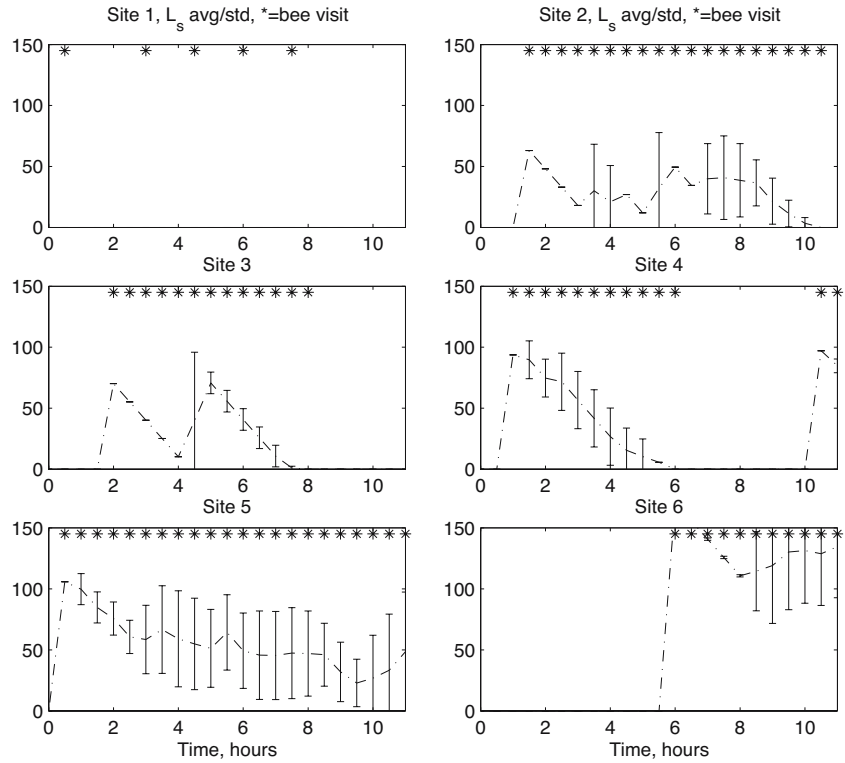


Fig. 5 Average and standard deviation of $L'(k)$ over i for each k (bars), and “*” indicates that some bee is visiting the site, for each site



51, 60. Bee 60 found a relatively low-quality site midway through the process, performed a sequence of dances for it, then rested until the end of the process. Bee 51 starting dancing for a moderate-quality site, danced for it for a

while, and then joined the crescendo near the end. Bee 37 started dancing for the best site midway through the process and was still dancing for it while the crescendo occurred.

Fig. 6 Sequence of dances and events for a sample nest-site selection process. A “+” is used to indicate that the bee died at expedition k . An “x” is used to indicate that the bee ceased dancing for a nest site. The symbols from Table 2 represent dances for the six different nest sites

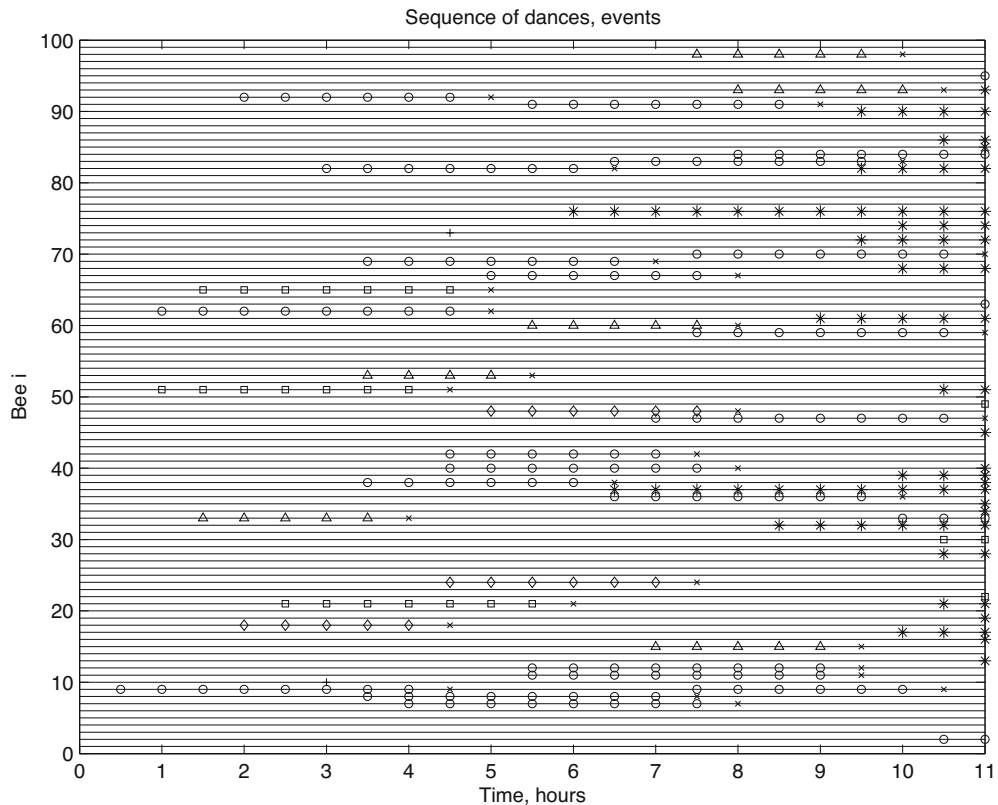
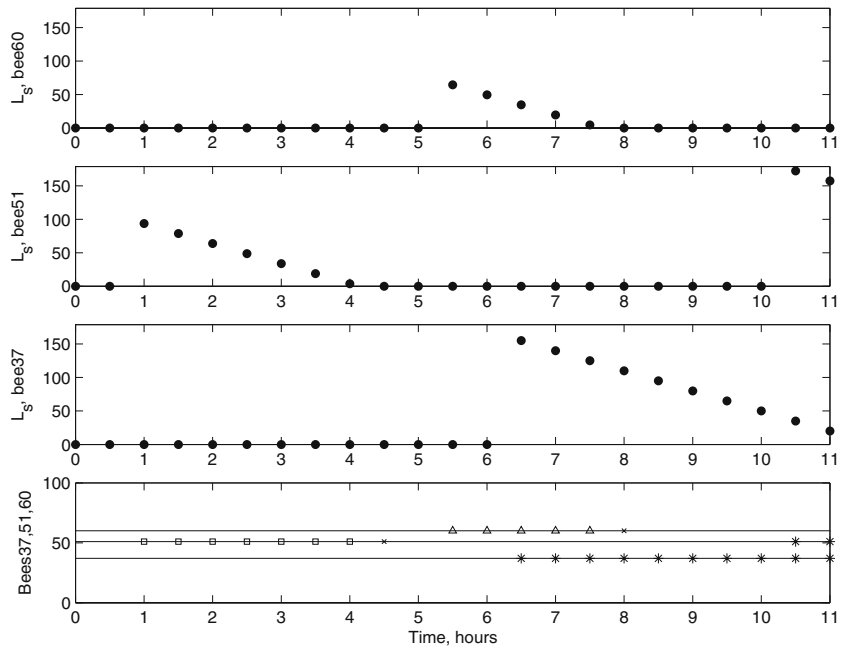


Fig. 7 Dance strengths and sequence of events for three bees. The meanings of the symbols in the bottom plot are the same as in Fig. 6. Note that with the noise w^i that represents inaccuracies in nest-site assessment, the initial dance strengths can vary (e.g., when bee 37 finds the perfect site, it dances about 150 waggle runs, but when bee 51 finds the perfect site near the end of the process, it dances with a strength greater than $\gamma N^6 = 150(1) = 150$ since $S^6 > N^6 = 1$ due to w^6). Clearly, this variation will affect the strengths of all subsequent dances for a site, and when the bee will cease to dance for the site



Allegiance-switching frequency

In Fig. 8, the distribution of the number of sites visited is shown. For this case, 40% of the bees were explorers but did not dance for any site, 51% danced for one site, and 9% danced for two sites. Hence, few bees switch “allegiance” from one site to another. The agreement emerges via a competitive process of scouts advertising sites, but not forever insisting on staying dedicated to any site, as reported by Seeley and Buhrman (1999).

Effects of behavioral parameters on choice speed and accuracy

Here, we run a Monte Carlo simulation to determine the effects of three parameters in the model on the speed and accuracy of nest-site choice. To do this, we run $N_{sim}=100$ simulations where a single site is chosen,² and we do this for each parameter value and compute the following values:

Average time to agree: Let T_a denote the time that the bees agree on a nest site, which is defined by the time after bees have returned to the cluster after having sensed more than ϵ_q bees at a nest site. We compute the average T_a value for N_{sim} simulations. We also compute the standard deviation of the T_a values.

Average total amount of dancing: For a particular nest-site selection process, $L_t(k)$ is the total number of waggle runs at step k , and we let $\Sigma L_t(k)$ denote the total number of waggle runs that occurred by the end of the process. We compute the average of $\Sigma L_t(k)$ for N_{sim} simulations.

² We ran cases for $N_{sim} > 100$ but obtained the same qualitative results since by $N_{sim}=100$, the averages we computed had converged. Standard deviations shown in subsequent plots are for the data from $N_{sim}=100$ simulations in all cases.

Percent correct and other decisions: We compute the percentage of the N_{sim} cases where the correct decision was reached, and we compute the percentage of the cases where one of the inferior sites was chosen.

Number of split decisions and failures: We run the simulation so that a decision on only one site is reached N_{sim} times. We call the cases where there is a split decision (e.g., where the quorum threshold is reached at the same time for two or more sites), or when there is no decision by the end of 32 h, “failures.” We compute the number of failures of each of the two types.

The parameters we consider are the quorum threshold ϵ_q , the slope of the decrease in dancing by a committed scout ϵ_s , and the tendency to explore rather than be recruited σ . We show how varying these parameters in a range around those used in “[Model validation](#)” will affect the speed,

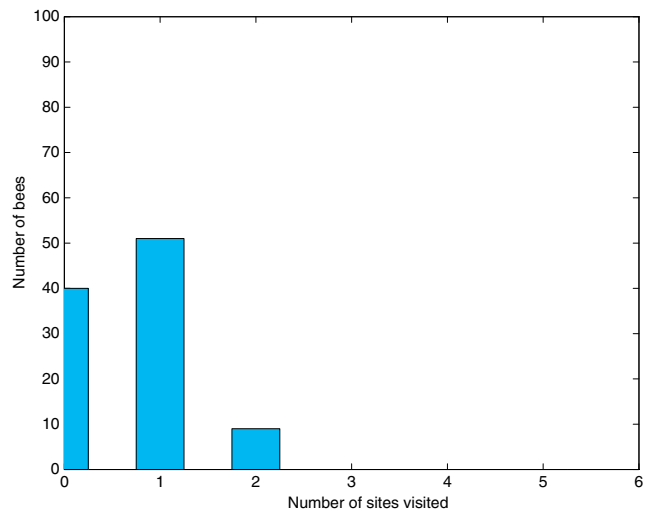


Fig. 8 Distribution of the number of sites visited

number of waggle runs needed, and accuracy of the decision-making process.

Effect of quorum threshold size

Here, we let $\varepsilon_s=15$ and $\sigma=4,000$, the values used in “[Model validation](#),” and we study the effect of varying ε_q , the quorum threshold. In particular, we perform N_{sim} nest-site selection processes that reach agreement for values $\varepsilon_q \in \{5, 10, 15, 20, 25, 30, 35\}$. The results are shown in Fig. 9. As ε_q increases, there needs to be more bees to achieve the quorum and it takes longer to get more bees recruited, so the average time to come to agreement goes up. After around $\varepsilon_q=15$, however, the curve in the upper left plot levels off somewhat. This is due to the high recruitment rates that can be achieved above that level by the positive feedback effect from recruitment to a site. Notice too that as ε_q increases, the average total number of waggle runs increases almost linearly since generally more dancing needs to be done to assemble more bees at a nest site to achieve a higher quorum threshold.

Next, consider the effects on accuracy of the decision-making process. First, notice that as ε_q increases, the percentage of correct choices does also since higher values of ε_q imply that more bees agreed on the best site. The lower right plot shows the number of split decisions and number of cases where there was no decision after 32 h. Notice that the number of split decisions is greatest for low ε_q values; this is due to quick agreement by assembling only a few bees at a site. It is more likely that simultaneous agreement on more than one site occurs if agreement requires only a few bees at a site. As ε_q goes up, the number of split decisions goes down. For most values of ε_q there

are only a few (or no) cases where the scouts fail by not agreeing before 32 h.

The key feature to notice is the relationship between all four plots in Fig. 9. With respect to the average time to agree and average total number of dances to agree, a lower value of ε_q is better since it reduces both of these and thus provides faster agreement with lower overall energy expended by the group of scouts to achieve that agreement. The amount of energy is low due both to the lower number of waggle runs needed to achieve agreement and to the short amount of time needed to reach agreement. At the same time, however, a low value of ε_q results in many more errors in choosing the best site and more split decisions (i.e., accuracy suffers). The best value of ε_q is an intermediate one (of approximately 15–25 bees) where a relatively fast agreement can take place, without too much dancing, and there is a low error percentage and few failures.

Effect of dance decrease rate

Here, we let $\varepsilon_q=20$ and $\sigma=4,000$, the values used in “[Model validation](#),” and study the effect of varying ε_s , the rate of decrease in dancing. In particular, we perform N_{sim} nest-site selection processes that reach agreement for values $\varepsilon_s \in \{5, 10, 15, 20, 25, 30, 35\}$. Small values of ε_s test the effect of elimination of “expiration of dissent” (Seeley 2003). The results are shown in Fig. 10. Notice that as ε_s increases, bees cease dancing faster, and the average time to come to agreement goes up. This is due to it being more difficult for a quorum to be reached since recruitment is not sustained long enough to build up bees at a single nest site. Hence, in a sense, the bees are more timid in advertising sites, and this makes the whole process

Fig. 9 Effect of ε_q on speed, number of waggle runs, percentage of correct decisions, and number of failures

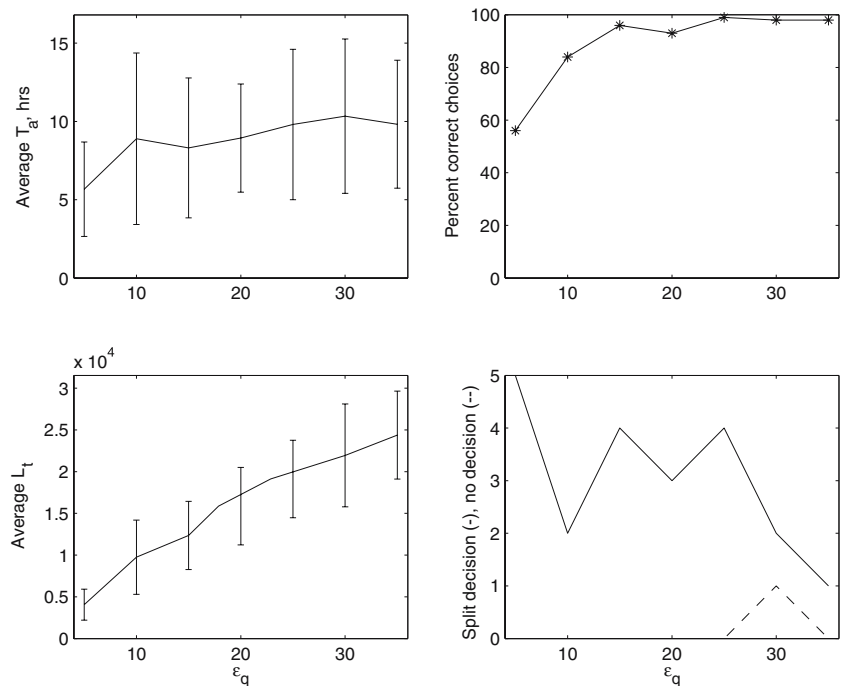
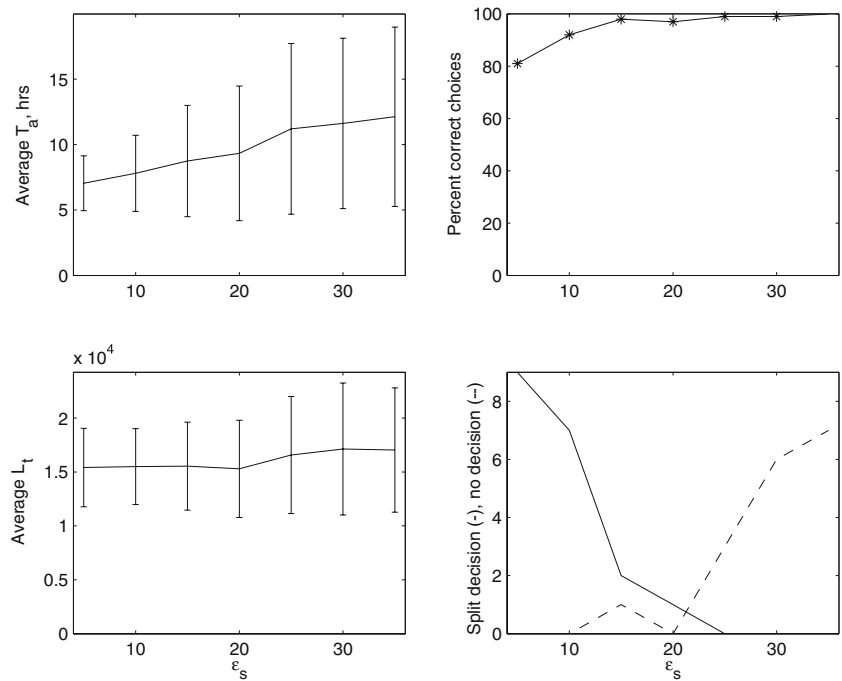


Fig. 10 Effect of ε_s on speed, number of waggle runs, percentage of correct decisions, and number of failures



sluggish. This sluggishness also raises slightly the overall amount of dancing that must be done to achieve consensus.

As ε_s increases, the percentage of correct choices does also. This is because when ε_s is too low, the bees persistently advertise too long. This strengthens the positive feedback for poor sites to such a level that the group cannot make good distinctions of relative quality between sites, which leads to errors. This is why “expiration of dissent” is important. The lower right plot shows the number of split decisions and number of cases where there was no decision after 32 h. Notice that the number of split decisions is greatest for low ε_s values; this is due to the slow decrease in dancing for these values so that many sites are danced for, and it is more likely that simultaneous agreement on more than one nest site is achieved. As ε_s goes up, the number of split decisions goes down; however, the number of cases where there is no decision goes up. This is due to there never being a sustained advertisement for any site, so that a build up of bees at a site is not as likely to be achieved, and a quorum is never reached.

Again, the key feature to notice is the relationship between all the four plots. Regarding the average time to agree and average total number of dances to agree, a lower value of ε_s is better since it reduces both of these. It results in these reductions because if ε_s is lower, then there is enough recruitment to achieve a quorum quickly. At the same time, however, a low value of ε_s results in more errors in choosing the best site and more split decisions (i.e., accuracy suffers). The best value of ε_s is an intermediate one (approximately 15–20) where a relatively fast agreement can take place, without too much dancing, and where acceptable choice error percentage, number of split decisions, and number of agreement failures are achieved.

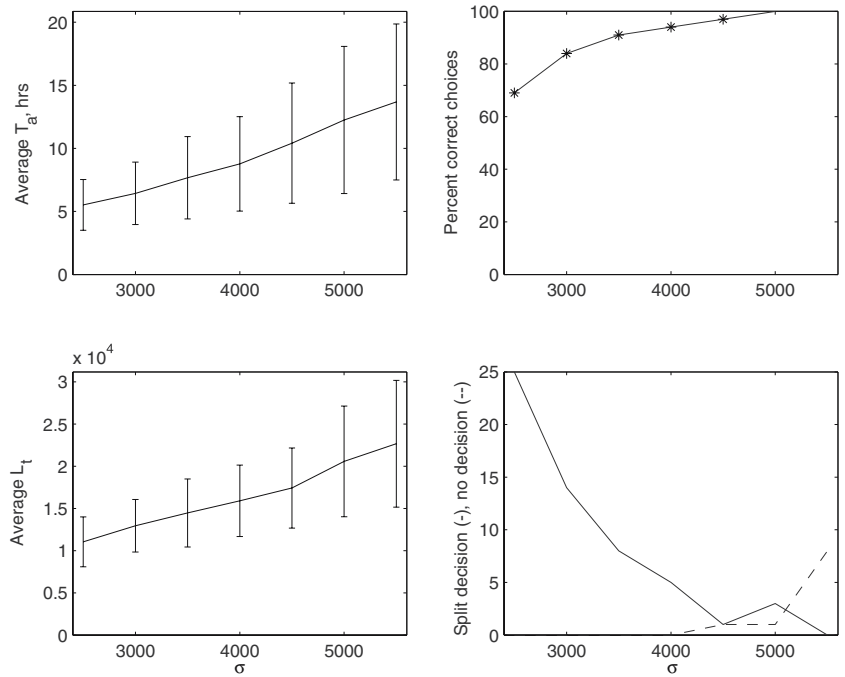
Effect of tendency to explore

Here, we let $\varepsilon_q=20$ and $\varepsilon_s=15$, the values used in “[Model validation](#),” and study the effect of varying σ , the tendency to explore. In particular, we perform N_{sim} nest-site selection processes that reach agreement for values $\sigma \in \{2,500, 3,000, 3,500, 4,000, 4,500, 5,000, 5,500\}$. The results are shown in Fig. 11. Notice that as the tendency to explore increases (i.e., σ increases), the average time to come to agreement goes up. This is because the bees have a higher tendency to explore rather than be recruited, so it takes longer to build consensus for a nest site. Likewise, increasing σ increases the average total number of waggle runs needed to reach agreement since more dancing needs to be done to get enough recruits to reach consensus.

As σ increases, the percentage of correct choices does also since the best site is more likely to be found. The lower right plot shows the number of split decisions and number of cases where there was no decision after 32 h. Notice that the number of split decisions is greatest for low σ values; this is due to there being a low tendency to explore and a corresponding high tendency to be recruited that results in fast buildup of recruits at a nest site and fast decisions but frequent split decisions. As the tendency to explore goes up, the number of split decisions goes down; however, the number of cases where there is no decision goes up. This is due to an over-tendency of bees to explore so that they never get recruited and a quorum is never reached.

The key feature to notice, once again, is the relationship between all four plots. In terms of the average time to agree and average number of dances to agree, a lower value of σ is better since it reduces both. It results in these reductions because if σ is lower, then there is less tendency to explore,

Fig. 11 Effect of σ on speed, number of waggle runs, percentage of correct decisions, and number of failures

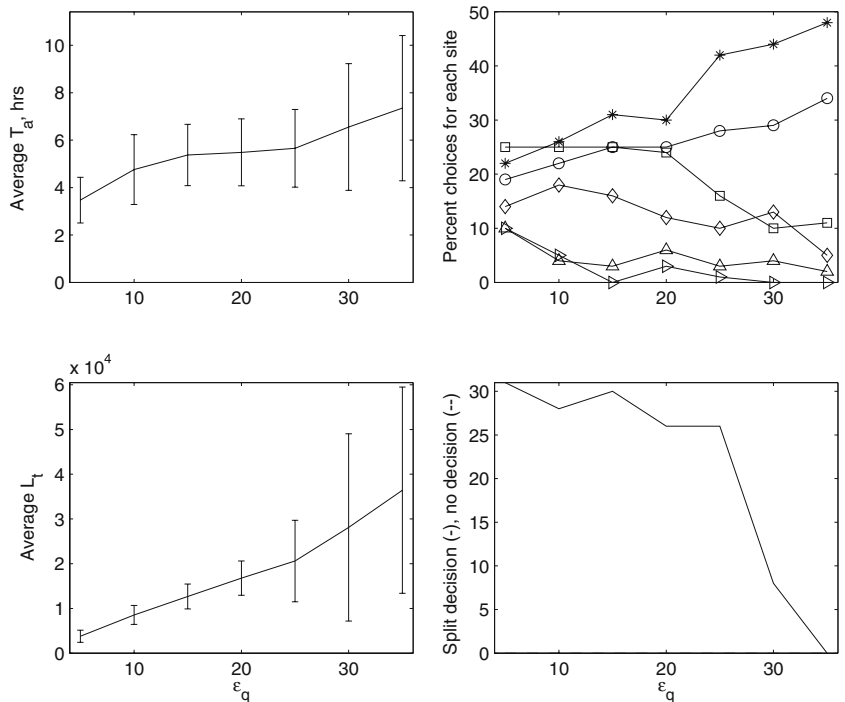


and this makes the positive feedback on the recruitment process stronger so that agreement occurs faster. At the same time, however, a low value of σ results in more errors in choosing the best site and more split decisions (i.e., accuracy suffers). The best value of σ is an intermediate one (approximately 3,500–5,000) where a relatively fast agreement can take place, without too much dancing, and where an acceptable choice error percentage and number of failures are achieved.

Finally, note that the simulation case discussed in the model validation study ([Model validation](#)) was performed

after doing the Monte Carlo runs in this section. This ensured that we had an appropriate value for σ since, unlike for ε_s and ε_q , there are no experimental studies that have sought to identify the value for σ . The value of this study is in fact significantly increased due to our ability to use the mathematical model and simulations to examine the role of σ . We feel that these simulations are suggesting a new idea that deserves experimental study. The idea is that it is the tendency to explore that is regulating the positive feedback element of the recruitment process, and this ensures that a fast and relatively error-free agreement is reached.

Fig. 12 Effect of ε_q on speed, number of waggle runs, percentage of correct decisions, and number of failures. Landscape with sites of quality shown for case 2 in Table 2 and symbols from that table define the data in the upper right plot



Effect of nest-site quality landscape

Next, we briefly discuss how the results change when there is a nest-site quality landscape with site qualities of 1, 0.9, 0.8, 0.7, 0.6, and 0.5 (case 2 in Table 2), i.e., with less variance in quality among the six sites. In the interest of brevity, we consider only the effects of quorum threshold size since results for dance decrease rate and tendency to explore are qualitatively similar. We use all the same parameters as in “Effect of quorum threshold size.” The results are shown in Fig. 12.

First, compare the average time to agree in Fig. 12 to the corresponding plot in Fig. 9. The average time to agree is generally shorter for this nest-site quality landscape (i.e., case 2) since there are more good sites to choose from. At the same time, the total number of dances is comparable for the two cases. Next, in the upper right plot in Fig. 12, we see a clear indication of a proportional relationship between the quality of a site and how often that site is chosen. Notice that for each value of ε_q , there is generally an ordering of the plotted data, with the percent of choices for each nest site generally proportional to nest-site quality. There are more errors in distinguishing between two sites that are close in quality (Fig. 12), but fewer when the difference in the quality of the sites is greater (Fig. 9). The nest-site selection process amplifies the distinctions in quality between multiple sites, but is constrained in how accurately it can do this by noise in site quality assessment, other stochastic elements in the nest-site selection process (e.g., resting/observing and explore/get-recruited decisions), and the time-constrained nature of the process. Next, notice that in Fig. 12, there are no failures to agree, although there are sites close in quality. In this case, the bees find high-quality sites relatively quickly, vigorously advertise them, but due to dance decay, they manage to have either a split or unanimous decision. Finally, note that the number of split decisions for this nest-site quality landscape is high relative to Figs. 9, 10, and 11. This is also due to the inability of the group to distinguish between sites of similar quality. Overall, we again see that an intermediate value of ε_q , 15–25, appears to simultaneously minimize errors and time/energy costs.

Discussion

The principal significance of this paper is that it provides evidence that the behavior of the scout bees in a honeybee swarm has been tuned by natural selection to create a social decision-making process that balances the competing demands for speed and accuracy. This trade-off between speed and accuracy has been demonstrated empirically in studies of individuals (humans, Osman et al. 2000; bees, Chittka et al. 2003) and of groups (ants, Franks et al. 2003), so there is no doubt that decision makers are often confronted with the problem of finding a suitable compromise between speedy decisions and accurate ones. If an individual or a group must make a swift decision, then it will be prone to making a poor decision because it cannot

sample the options sufficiently broadly or because it cannot deliberate on its options sufficiently deeply, or both (Franks et al. 2002). What is less clear, however, is how decision-making processes are tuned to achieve a favorable balance between the competing goals of speed and accuracy.

In their reports on the quorum-sensing aspect of the nest-site selection process in honeybees, Seeley and Visscher (2003, 2004b) have suggested that quorum size is one parameter of this decision-making process that has been tuned by natural selection to provide a balance between speed (favored by a small quorum) and accuracy (favored by a large quorum). With respect to speed, they proposed that the use of a quorum to determine when to begin preparing the swarm for liftoff means that preparations for liftoff can begin as soon as enough bees have approved one of the potential sites, even if others are still scouting other sites. And with respect to accuracy, they proposed that the quorum requirement promotes accuracy because the scouts should not initiate liftoff preparations until a sizable number of them have all judged that a site is desirable. These verbal arguments are supported by the results of this modeling study, for when the quorum threshold in the model was varied, and everything else in the decision-making process was held constant, the model makes it clear that a low quorum yields relatively rapid but often inaccurate decisions and that a high quorum produces slower but more accurate decisions. It is noteworthy that the model’s prediction of the quorum size that achieves a good balance between speed and accuracy, some 15–20 bees, essentially matches the empirical finding that scout bees initiate liftoff preparations when the number of bees at one of the sites has reached 10–20 bees (Seeley and Visscher 2003). Moreover, we show that for this range of ε_q values, the swarm’s choice error rate decreases as the differential site qualities increase. Decision-making performance is best when it matters the most. An analogous phenomenon exists in hoarding gray jays, where simultaneous choice errors decrease as the rate of availability of choices decreases since then choice errors are costly (Waite and Field 2000; Waite 2002).

The tuning of quorum size to achieve an adaptive balance between choosing quickly and correctly may prove to be a common phenomenon in groups that use quorum sensing as part of their decision-making process. It also occurs as part of the nest-site selection by the ant *Leptothorax albipennis* (Mallon et al. 2001; Pratt et al. 2002). In this ant, as in honeybees, the decision-making process is based on competitive recruitment to the various possible nest sites. At first, this competitive recruitment proceeds rather slowly, by means of a tandem-running process, although the recruitment is faster for better sites. Later on, once a quorum of ants has assembled at one of the sites, the ants from this site begin to rapidly recruit other ants by carrying them there, and this usually brings the vast majority of the ants to this site, the colony’s future home. Dornhaus and Franks (2003) and Franks et al. (2003) discovered that the ants adjust the threshold quorum size for initiating rapid recruitment (carrying) in relation to the environmental conditions. Under harsh conditions, they

use a low quorum threshold, which speeds up the colony's decision making but also causes it to make more errors, whereas under benign conditions, they use a high quorum threshold and perform their decision making more slowly but with fewer errors.

One of the more curious features of bee behavior that underlies the decision-making process of honeybee swarms is the way that a scout reduces the strength of her dancing for any given prospective nest site over repeated visits to the site. Specifically, each time a scout visits a potential nest site and then returns to the swarm cluster to advertise the site, she produces fewer waggle runs and so advertises her site less strongly. It has long seemed clear that this decay in dancing fosters the consensus building among the dancing scout bees by ensuring that bees do not persist in advertising inferior sites (Lindauer 1955; Camazine et al. 1999; Seeley and Buhrman 1999; Beering 2001). What has not been obvious heretofore is just how critical the rate of decrease in dancing is to the success of the decision-making process. The results shown in Fig. 10 indicate that as this rate climbs to levels higher than what is observed in nature (15 waggle runs per nest-site visit), the time needed to reach a decision steadily increases. This occurs because if the bees were to let their recruitment signals (dances) decay too quickly, then it would become difficult for the bees to reach a quorum at any one site. Our results also show that if the dance decay rate were to be lower than what is observed in nature, then an even greater problem would arise: the decision making would tend to fail altogether as split decisions would become increasingly common. These failures would arise because if the bees would not let their dances fade, then the recruitment signals for even the second-rate sites would remain strong and a quorum would be reached quickly at more than just the top-ranked site. Again, it is noteworthy that our model's prediction of the dance decrease rate that balances speed and accuracy tradeoffs, 15–20 waggle runs per nest-site visit, essentially matches the empirical finding that, on average, scout bees shorten their dances by 15 waggle runs per visit to a nest site (Seeley 2003).

The third parameter of the nest-site selection process that we have considered is the tendency of scout bees to follow dances and so be recruited to a potential nest site vs the tendency to explore independently for a potential nest site. We have assumed in our model that an uncommitted scout bee searches for dances to follow and that if she does not find one after some length of time, then she gives up searching for a dance and goes exploring for a nest site. Mathematically, we adjusted the probability that an uncommitted scout bee will explore, at a given level of dancing, by assigning a value to the parameter σ in Eq. 1. As σ increases, the probability of exploring increases. We found that the tendency of a scout bee to explore vs be recruited strongly affects the bees' process of social decision-making. Increasing this tendency is predicted to decrease the speed of the decision making, by weakening the positive feedback (i.e., dancers beget dancers) that lies at the heart of the decision-making process. Increasing the tendency to explore is also predicted to increase the

accuracy of the decision making, although at very high levels, there is an increase in the number of cases where no decision is reached, probably because a high tendency to explore, and thus a low tendency to be recruited, means that a quorum at a site is not likely to be achieved. Our model suggests that it will be important for future empirical studies to examine how the allocation of scout bees to exploration affects the recruitment to nest sites because it now seems clear that getting the right balance between exploration and recruitment is essential for achieving high performance in the social choice of a nest site.

Future work could also examine the impact of significantly changing the value of B (which would require modifications to the model). This number is curiously low, only about 2–5% of the bees in a swarm (Gilley 1998; Seeley and Buhrman 1999). Is B kept low simply for energy conservation, i.e., to minimize the number of bees involved in the energetically costly task of scouting, or do speed–accuracy considerations also influence its value?

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