

# Independence and interdependence in collective decision making: an agent-based model of nest-site choice by honeybee swarms

Christian List<sup>1,\*</sup>, Christian Elsholtz<sup>2</sup> and Thomas D. Seeley<sup>3</sup>

<sup>1</sup>*Department of Government, London School of Economics, London WC2A 2AE, UK*

<sup>2</sup>*Department of Mathematics, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK*

<sup>3</sup>*Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA*

Condorcet's jury theorem shows that when the members of a group have noisy but independent information about what is best for the group as a whole, majority decisions tend to outperform dictatorial ones. When voting is supplemented by communication, however, the resulting interdependencies between decision makers can strengthen or undermine this effect: they can facilitate information pooling, but also amplify errors. We consider an intriguing non-human case of independent information pooling combined with communication: the case of nest-site choice by honeybee (*Apis mellifera*) swarms. It is empirically well documented that when there are different nest sites that vary in quality, the bees usually choose the best one. We develop a new agent-based model of the bees' decision process and show that its remarkable reliability stems from a particular interplay of independence and interdependence between the bees.

**Keywords:** group decision making; honeybees; nest-site choice; Condorcet's jury theorem; information pooling; agent-based model

## 1. INTRODUCTION

Since the Marquis de Condorcet's work in the eighteenth century it is known that, when the members of a group have only noisy and partially reliable information about what is best for the group as whole, democratic decisions tend to outperform dictatorial ones. Condorcet showed that, if each member of a jury has an equal and independent chance better than random, but worse than perfect, of making a correct judgement on whether a defendant is guilty, the majority of jurors is more likely to be correct than each individual juror. Moreover, the probability of a correct majority judgement approaches certainty as the jury size increases. This result is a consequence of the law of large numbers: from many independent but noisy signals, majority voting can extract the information while filtering out the noise.

This insight, which has become known as 'Condorcet's jury theorem', has sparked a large body of social scientific work on the reliability of various decision procedures in juries, committees, legislatures, electorates and other settings (e.g. Grofman *et al.* 1983; Borland 1989; Austen-Smith & Banks 1996; List & Goodin 2001; List 2004). While the original theorem highlights the benefits of pooling independent information held by multiple individuals, a complexity arises in collective decisions when voting is supplemented by communication, as investigated by the theory of deliberative democracy (e.g. Elster 1986; Miller 1992; Knight & Johnson 1994; Dryzek & List 2003; Austen-Smith & Feddersen 2009). Communication can create interdependencies between

decision makers. On the one hand, these may facilitate information pooling and filtering (e.g. Luskin *et al.* 2002; Farrar *et al.* in press), but on the other hand, they may also lead to the amplification of certain errors, such as in fads and informational cascades, as briefly discussed at the end of this paper (e.g. Bikhchandani *et al.* 1992; Zuber *et al.* 1992; Sunstein 2002, 2006).

In this paper, we consider an intriguing non-human case of information pooling combined with communication: the case of nest-site choice by honeybee (*Apis mellifera*) swarms. We present a new theoretical model of the honeybees' collective decision process and investigate the role played by both information pooling and communication in it.

It is a long-standing empirical fact that, in late spring or early summer, a colony of honeybees that has reached a certain size tends to divide itself: the queen leaves with roughly two-thirds of the worker bees, and a daughter queen stays behind in the parental nest with the rest of the worker bees. How does the swarm that has left the colony find a new home? Empirical work by Lindauer (1955) and Seeley *et al.* (2006) have revealed a mechanism involving a 'search committee' of several hundred bees, the scouts, who fly out to inspect potential nest sites and then come back and perform waggle dances to advertise any good sites they have discovered. Initially, the scouts visit and inspect sites randomly, but once the dancing activity has built-up, they are more likely to visit and inspect sites advertised by others. Back at the swarm, each bee dances for the site she has inspected, with the duration of the dance depending on her perception of the site's quality: the better the site, the longer the dance. Thus, high-quality sites receive more advertisement and are visited by more scout bees, which in turn generate

\* Author for correspondence (c.list@lse.ac.uk).

One contribution of 11 to a Theme Issue 'Group decision making in humans and animals'.

even more dance activity for these sites. The process eventually leads to a ‘consensus’: the dancing and visiting concentrates on one popular site, and the swarm moves there. (The bees’ final decision to move appears to involve ‘quorum sensing’, as discussed by Seeley & Visscher 2003.) The striking empirical fact is that, when different possible nest sites vary in quality, the bees usually choose the best one (Seeley & Buhrman 2001).

While the empirical details of this process are well understood, the mechanisms underlying its striking reliability still lack a full explanation. Our model of the bees’ decision making is innovative in combining two features: first, it is *agent based*, in the sense that we explicitly model the individual behaviour of each scout as a simple stochastic process, and second and more importantly, it integrates insights from Condorcet’s jury theorem with those from the theory of deliberative democracy. Using computer simulations based on this model, we are able to predict that, under a wide range of parameter conditions, a consensus among the bees emerges for the best nest site with a high probability, even when the quality differences between sites are relatively small. Furthermore, we show that the remarkable reliability of the bees’ decision process stems from a particular interplay of *independence* and *interdependence* between the bees, as defined formally below.

Other mathematical models of nest-site choice by honeybees are a differential equation model by Britton et al. (2002), a matrix model by Myerscough (2003), another agent-based model by Passino & Seeley (2006), and a density-dependent Markov process model by Perdriau & Myerscough (2007). While shedding light on several important aspects of the bees’ decision process, none of these models exhibits both main characteristics of ours, i.e. being agent based and explicitly modelling the interplay between independence and interdependence. Moreover, our model is particularly parsimonious and makes very robust predictions. Since our computational results appear to be consistent with existing empirical findings about the bees, we suggest that our model adequately captures some key elements of the bees’ decision-making process.

The paper is structured as follows. After a formal exposition of our model, we state our two main hypotheses about the bees’ decision process. The first is, roughly, that this process is robustly reliable for a large class of parameter conditions; and the second that the presence of both independence and interdependence between individual bees is necessary and sufficient for the overall reliability. Methodologically, both hypotheses are formulated as hypotheses about our *model* of the bees rather than as hypotheses about the real world bees themselves; but to the extent that the model behaviour is consistent with the empirically observed behaviour of the bees, our hypotheses can be considered empirically adequate as well. To provide a computational test of our hypotheses, we finally report our computer simulations, followed by a brief concluding discussion.

## 2. MODEL

### (a) Basic ingredients of the model

There are  $n$  scout bees, labelled  $1, 2, \dots, n$ , who participate in the decision-making process, and there

are  $k$  potential nest sites, labelled  $1, 2, \dots, k$ , where each nest site  $j$  has an objective quality  $q_j \geq 0$ . We assume discrete time periods, labelled  $1, 2, 3, \dots$ , and explicitly model the behaviour of all  $n$  individual scout bees in each period.

At each time, a scout bee can be in one of two states: either she dances for one of the  $k$  potential nest sites or she does not dance for any site, which can mean that she has not yet found a site, she has flown out to search for sites, she is observing other bees, or she is resting. Formally, the state of bee  $i$  at time  $t$  is represented by a two-component vector  $x_{i,t} = (s_{i,t}, d_{i,t})$ , where

- $s_{i,t} \in \{0, 1, 2, \dots, k\}$  is the site for which bee  $i$  dances at time  $t$ , with  $s_{i,t} = 0$  meaning that she does not dance at time  $t$ , and
- $d_{i,t} \geq 0$  is the remaining duration of bee  $i$ ’s dance at time  $t$ .

We initialize the model by assuming there is no dancing activity at time 1, i.e. for all  $i$ ,  $x_{i,1} = (0, 0)$ .

### (b) How each bee changes her state from one time period to the next

As in any agent-based model, the state of bee  $i$  at time  $t+1$  depends on her own state at time  $t$  and the state of other bees at time  $t$ . We need to distinguish between two cases: either bee  $i$  does not dance for any site at time  $t$ , in which case she may or may not fly out and find a site to dance for at time  $t+1$ . Or she already dances for one of the sites at time  $t$ , in which case she continues her dance at time  $t+1$  unless its duration is over. We now discuss each case in turn.

*Case 2.1.* Bee  $i$  does not dance for any site at time  $t$  (i.e.  $s_{i,t} = 0$ ).

In this case, she has a certain probability of flying to one of the  $k$  sites and inspecting it. For each site  $j$ , we write  $p_{j,t+1}$  to denote the probability that the bee finds site  $j$  and dances for it at time  $t+1$ . Further,  $p_{0,t+1}$  denotes the probability that the bee remains at rest or finds no site, so that she does not dance at time  $t+1$ . Thus, the first component of the bee’s state at time  $t+1$ , namely  $s_{i,t+1}$ , takes the values  $1, 2, \dots, k$  (one of the sites) or  $0$  (no site) with probabilities  $p_{1,t+1}, p_{2,t+1}, \dots, p_{k,t+1}$  and  $p_{0,t+1}$ , respectively. By definition, these probabilities add up to 1.

How are the probabilities determined? The probability that a bee finds a given site depends on two factors: first, an *a priori* probability of how likely she is to find that site without any advertisement by other bees (this may depend on the site’s location, distance from the swarm, etc.) and second, the proportion of bees dancing for it. Formally, for each  $j$  (including the case  $j=0$  of no site), we define

$$p_{j,t+1} = (1 - \lambda)\pi_j + \lambda f_{j,t},$$

where  $\pi_j$  is the *a priori* probability of the  $j$ th site;  $f_{j,t}$  is the proportion of bees dancing for site  $j$  at time  $t$ ; and  $\lambda$  is the relevant weight, ranging between 0 and 1. The weight  $\lambda$  captures the amount of *interdependence* between the bees. If  $\lambda=0$ , each bee’s probabilities of finding the various sites remain the *a priori* probabilities, regardless of how many bees dance for them: this is the limiting case in which the bees do not influence each other at all through

communication. If  $\lambda = 1$ , by contrast, each bee's probabilities of finding the various sites are perfectly proportional to the numbers of bees dancing for them: this is the opposite limiting case in which the bees' dancing completely determines all bees' decisions to inspect the various sites.

It remains to define the second component of bee  $i$ 's state at time  $t + 1$ , her dance duration  $d_{i,t+1}$  if she has begun a dance for one of the  $k$  sites, say site  $j$ . (If she has found no site,  $d_{i,t+1}$  is set to zero.) Initially, we assume that  $d_{i,t+1}$  is always stochastically determined by the bee's independent assessment of site  $j$ 's true quality  $q_j$ . Later, we allow that there is a probability  $\mu \geq 0$  that  $d_{i,t+1}$  is unrelated to  $q_j$ , so as to capture the possibility that the bee's dance is prompted by mimicking other bees rather than by an inspection of site  $j$ . A value of  $\mu = 0$  represents the original case in which bees always independently assess a site's quality before dancing for it, while a value of  $\mu = 1$  represents the opposite case in which bees join dances solely based on the probability distribution  $(p_{1,t+1}, p_{2,t+1}, \dots, p_{k,t+1})$  over the  $k$  sites and thus—given a sufficiently large value of  $\lambda$ —based on mimicking the dances of others, without paying attention to any site's quality. Generally,

$$d_{i,t+1} = \begin{cases} q_j \exp(T_\sigma) & \text{with probability } 1 - \mu \\ & \text{('independent assessment')} \\ K \exp(T_\sigma) & \text{with probability } \mu \text{ ('mimicking')}, \end{cases}$$

where  $T_\sigma$  is a normally distributed random variable with mean 0 and standard deviation  $\sigma \geq 0$ , and  $K$  (relevant only in the case of mimicking) is some strictly positive constant. The parameter  $\sigma$  specifies the bee's *reliability*; a small value of  $\sigma$  corresponds to a high reliability, a large value to a low one. Under our definition, the bee's dance duration for any given site fluctuates around the numerical value of the site's true quality (setting aside the case of mimicking, where the dance duration fluctuates around the quality-independent constant  $K$ ). The bee's error is multiplicative, i.e. an overestimation of the site's quality by a factor of  $c > 0$ , i.e. the bee erroneously takes the site's quality to be  $c$  times its true quality—is as likely as an underestimation by the same factor, i.e. she takes the site's quality to be  $1/c$  times its true quality. Our results are robust to changes in the functional form of the error, e.g. we obtain similar results when the error takes an additive rather than multiplicative form.

*Case 2.2.* Bee  $i$  dances for one of the sites, say site  $j$ , at time  $t$  (i.e.  $s_{i,t} > 0$ ).

In this case, she continues to dance for the same site at time  $t + 1$  with the remaining dance time reduced by one period, unless that dance time is over; in the latter case, her state is reset to the state of no dancing. Formally,

$$x_{i,t+1} = \begin{cases} (s_{i,t}, d_{i,t} - 1) & \text{if } d_{i,t} > 1 \\ (0, 0) & \text{otherwise.} \end{cases}$$

**(c) When is a consensus reached?**

So far we have only modelled the behaviour of individual scout bees and have not yet explained what it means for a consensus to emerge among them. From

the states of the  $n$  bees at each time, we can determine the total number of bees dancing for each site at that time. Specifically, for each  $j$  (including the case  $j = 0$  of no site), the number of bees dancing for site  $j$  at time  $t$  is

$$n_{j,t} = |\{i : s_{i,t} = j\}|.$$

Now different criteria of consensus are conceivable. Generally, a consensus criterion can be understood as a mapping from the individual-level pattern of dance activity to a chosen nest site. According to the one such criterion, a consensus for a site  $j$  at a given time  $t$  would require that all the bees engaged in dance activity at time  $t$  support site  $j$ , i.e.  $n_{j,t} > 0$  while  $n_{h,t} = 0$  for all  $h \neq j$  with  $h \neq 0$ . However, as shown by Seeley & Visscher (2003), a consensus in this unanimitarian sense is not necessary, nor even generally sufficient, for the bees' selection of a nest site. Instead, the bees appear to make decisions by 'quorum', requiring merely 'sufficient' support for a site to be chosen.

This can be modelled in a number of different ways. For the present purposes, we focus on two illustrative criteria. According to the first and less demanding criterion—which is arguably too weak to capture the quorum requirement fully—site  $j$  is the winner at time  $t$  if it receives more support than any other site at  $t$ , i.e.  $n_{j,t} > n_{h,t}$  for any  $h \neq j$  with  $h \neq 0$ . According to the second and more demanding criterion, site  $j$  is the winner at time  $t$  if it meets a two-part condition: (i) it receives more than twice the amount of support received by the second most popular site (i.e.  $n_{j,t} > 2n_{h,t}$  for any  $h \neq j$  with  $h \neq 0$ ) and (ii) more than 20 per cent of the scout bees are engaged in dance activity at  $t$  (i.e.  $n_{0,t} < 0.8n$ ).

Our model would also allow the use of other consensus criteria, but these would yield broadly similar results about the bees' overall reliability. Differences between such criteria would become more significant in relation to speed-accuracy trade-offs, which are not the focus of this paper.

**3. HYPOTHESES**

Since our model is designed to represent the bees' empirically observed decision-making behaviour, the model should predict the reliability of the bees' decision process under empirically realistic assumptions. What do we mean by 'realistic'? It is reasonable to assume, first, that individual bees are neither very reliable nor completely unreliable, and second, that the bees' waggle dances have a significant but not exclusive influence on other bees' decisions to investigate potential nest sites. The first assumption corresponds to a non-extremal value of the bees' reliability parameter  $\sigma$ , and the second to a non-extremal value of the interdependence parameter  $\lambda$ . Initially, we assume no mimicking between the bees (i.e.  $\mu = 0$ ). We expect the following:

*Hypothesis 3.1.* Under a wide range of non-extremal parameter values of  $\sigma$  and  $\lambda$  (and  $\mu = 0$ ), the bees choose the best nest site.

Assuming this hypothesis turns out to be true—which is consistent with Seeley's empirical observations—we are also interested in explaining why this is the case. As



already indicated in the introduction, we suggest that two characteristics of the bees' decision process stand out. First, the bees are *independent* in that they individually inspect potential nest sites and dance to advertise them as a function of their individual quality assessments of these sites; they do not blindly join a dance for a nest site without having inspected the site themselves (i.e.  $\mu$  is 0 or low). We can express this in the language of probability theory by saying that, conditional on having identified a particular site, each bee's dance duration for that site is independent of other bees' dance durations for it. Second, the bees are *interdependent* in that they are more likely to inspect nest-sites advertised by others (i.e.  $\lambda$  is high). Expressed in probability-theoretic terms, the identification of a particular site by one bee is correlated with the identification of that site by others. We hypothesize that the reliability of the bees' decision process is driven by the interplay of these two characteristics:

*Hypothesis 3.2.* The bees' independence in assessing the various sites' quality and their interdependence through communication are both necessary and sufficient for the reliability of the bees' decision process.

Both hypotheses are deliberately stated informally here, but their operationalization will become clearer in the context of our computer simulations.

#### 4. COMPUTER SIMULATIONS

##### (a) Basic description

Implementing the model above as a MATHEMATICA program, we ran a number of computer simulations of the bees' nest-site choice under various parameter conditions. To ensure comparability across simulations, we fixed the number of scout bees at  $n=200$  and the number of potential nest sites at  $k=5$ . These assumptions are empirically motivated: there are usually several hundred scouts in a swarm, and there were typically five candidate nest sites in the experiments conducted by Seeley and others on Appledore Island, off the coast of Maine.

We also fixed the objective quality levels  $q_1, \dots, q_5$  of the five nest sites at 3, 5, 7, 9, 10, respectively, thus making it intuitively difficult for the bees to distinguish the two or three best nest sites. (Even when individual reliability is high, e.g.  $\sigma=0.2$ , the intervals in which individual quality assessments of the two best sites are likely to fall, namely  $[9 \exp(-0.2), 9 \exp(0.2)] = [7.37, 10.99]$  and  $[10 \exp(-0.2), 10 \exp(0.2)] = [8.19, 12.21]$ , overlap significantly. When individual reliability is lower, e.g.  $\sigma=1$ , the overlap between these intervals, now  $[3.31, 24.46]$  and  $[3.68, 27.18]$ , grows further.)

We further assumed that when a bee flies out randomly without following any other bees' advertisement for a site, she has a 25 per cent probability of finding some site, where the probability is equally distributed over the five sites (i.e.  $\pi_1 = \dots = \pi_5 = 5\%$  and  $\pi_0 = 75\%$ ). In all simulations, we calculated the bees' behaviour for 300 time periods, though a consensus, under both criteria introduced above, often emerged in less time. We verified that our findings are robust to changes in the choice of these fixed parameters.

Our first set of simulations was run to test hypothesis 3.1 by investigating the reliability of the bees' decision

process under a range of empirically motivated, non-extremal assumptions about individual bees' reliability ( $\sigma$ ) and their interdependence through signalling ( $\lambda$ ), in each case assuming no mimicking ( $\mu=0$ ). As reported below, our simulations broadly confirm hypothesis 3.1.

Our second set of simulations was designed to test hypothesis 3.2, focusing on the mechanisms underlying the reliability of the bees' decision process. To isolate the effects of independent assessments of the various sites' quality by the bees and communicative interdependence between them, we varied the parameters  $\mu$  and  $\sigma$  such that one of these two characteristics was completely or partially absent from the bees' decision making.

To model the full or partial absence of independence, we considered non-zero values of  $\mu$ , thereby allowing that a bee may join a dance for a site not on the basis of her independent assessment of its quality but merely as a result of mimicking other bees dancing for it (we set the relevant constant  $K$  equal to the maximal nest-site quality, but other values of  $K$  would yield similar results). Recall that our original case  $\mu=0$  meant that bees always independently assess a site's quality before dancing for it. By contrast, the higher the value of  $\mu$ , the less likely it is that a bee independently assesses a site's quality before dancing for it. In the limiting case  $\mu=1$ , bees join dances randomly, based on only the probability distribution over sites, without paying attention to any site's quality (i.e. the dance duration is determined by the site-quality-independent random variable  $K \exp(T_\sigma)$ , as defined above). Our simulation results reported below are consistent with hypothesis 3.2, showing that high values of  $\mu$  undermine the reliability of the bees' decision process, while low values support it.

To model the full or partial absence of interdependence between the bees, we varied the parameter  $\lambda$ . As already noted, a value of zero implies that each bee's probabilities of finding the various nest sites remain the *a priori* probabilities, regardless of other bees' dancing activity; a value of one implies that each bee's probabilities of finding those sites are perfectly proportional to the numbers of bees dancing for them; no other factor leads a bee to inspect any site. Here, too, our simulation results are consistent with hypothesis 3.2; low values of  $\lambda$  undermine the reliability of the bees' decision process while high values reinforce it. An exception arises for the limiting case  $\lambda=1$ , where the bees' probabilities of finding the different sites are given by the existing dance proportions for those sites. Here, there is not enough noise in the system for bees to discover any new sites not advertised by others. Small noisy deviations from perfect proportionality (i.e.  $\lambda < 1$ ) are necessary to permit the discovery of new sites.

##### (b) Results on hypothesis 3.1

Our first simulations capture what may be described as a best-case scenario: the reliability of bees in assessing sites is good ( $\sigma=0.2$ ), and their interdependence through communication is high ( $\lambda=0.8$ ). Figure 1 shows an illustrative simulation for these parameter values. The figure shows the number of bees engaged in dance activity for each of the five nest sites at each of the 300 time periods calculated. It is easy to see that

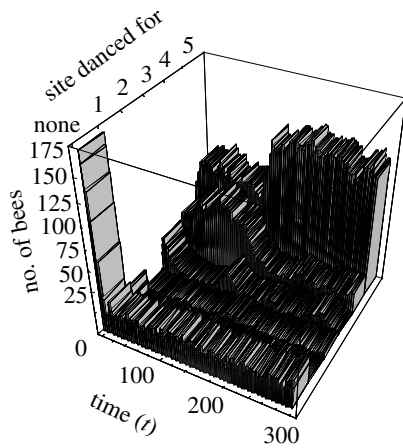


Figure 1. Illustrative simulations to test hypothesis 3.1. High reliability, high interdependence.

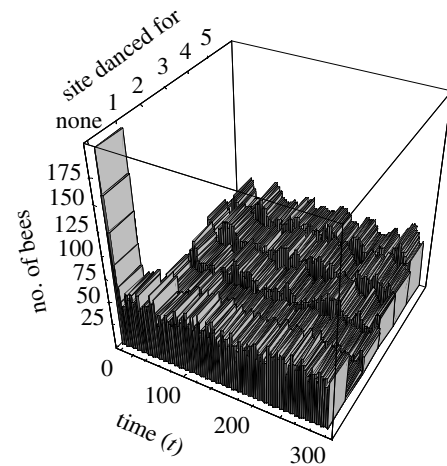


Figure 3. Illustrative simulations to test hypothesis 3.1. High reliability, low interdependence.

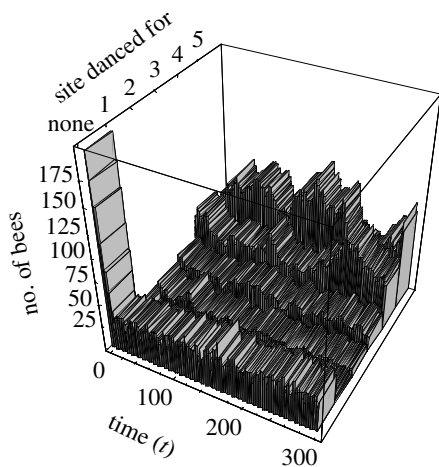


Figure 2. Illustrative simulations to test hypothesis 3.1. High reliability, medium interdependence.

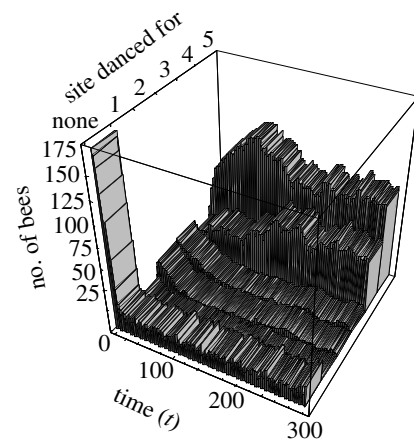


Figure 4. Illustrative simulations to test hypothesis 3.1. Low reliability, high interdependence.

after some initial amount of dance activity for other sites, the dance activity concentrates on the best site (site 5). To confirm that this pattern is not accidental, we repeated the simulation with the same parameter values 250 times. In each case, we determined the consensus winner using the two illustrative criteria introduced above, applied to the last time period of the simulation. Recall that according to the first and weaker criterion, a site wins if it receives more support than any other site; according to the second and stronger criterion, a site wins if it receives more than twice the amount of support received by the second most popular site and at least 20 per cent of the scout bees are engaged in dance activity. For the present parameter values ( $\lambda=0.8$  and  $\sigma=0.2$ ), the best nest-site emerged as the winner in nearly all cases, regardless of which criterion for a consensus was employed: Under the first criterion, the best site was chosen every time; under the second, it was chosen 246 times, while no site met the winner criterion in the remaining four cases.

In our next simulations, the interdependence between bees is reduced to a lower level ( $\lambda=0.5$ ), while the other parameter values remain as before. Figure 2 shows a representative simulation. While the best site (site 5) continues to receive the most support, there is also considerable dance activity for other sites, particularly the second best (site 4), throughout all time

periods. The consensus is less strong here. Again we repeated the simulation for the same parameter values 250 times. Under the less demanding criterion of consensus, the best nest-site emerged as the winner 226 times and the second best 22 times, with no winner in the remaining two cases; under the more demanding criterion, the best site won 104 times, with no winner in all other cases.

A further reduction in the interdependence between bees (to  $\lambda=0.2$ ) weakens the emergence of a consensus even more significantly, as shown in figure 3. In 250 repetitions, this effect is particularly evident when we employ the more demanding one of our two criteria for consensus. While under the weaker criterion the best site (site 5) still won 176 times (and the second best 63 times, the third best once and no winner 10 times), under the stronger criterion the best site won only 11 times and the second best once, with no consensus in the other 238 cases.

Having focused so far on the case in which bees are highly reliable in assessing nest sites, let us now introduce more noise into the bees' individual assessment of sites (setting  $\sigma=1$ ). Strikingly, if interdependence between bees is high (i.e.  $\lambda=0.8$ ), the overall pattern remains broadly the same as in the best-case scenario reported earlier. Figure 4 shows a sample calculation. In 250 repetitions of the simulation, the best site (site 5) emerged as the consensus choice, even under the stronger

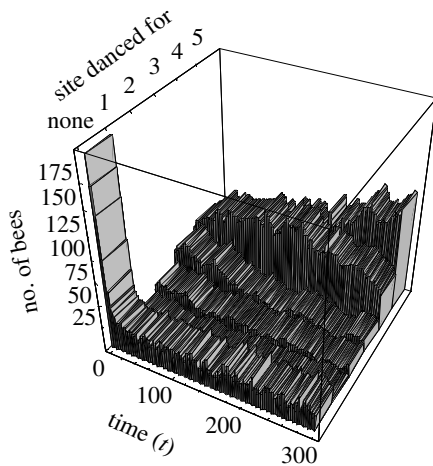


Figure 5. Illustrative simulations to test hypothesis 3.1. Low reliability, medium interdependence.

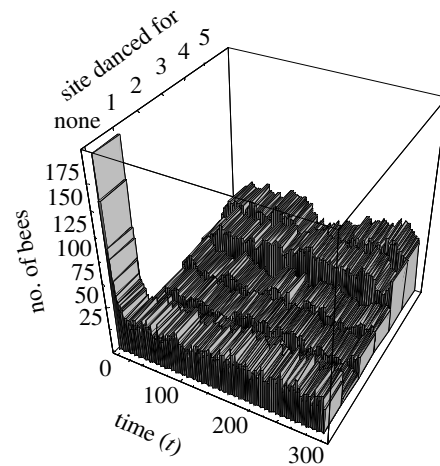


Figure 6. Illustrative simulations to test hypothesis 3.1. Low reliability, low interdependence.

criterion, 199 times and the second best site five times (site 4), with no consensus in the remaining 46 cases. Under the weaker criterion, the best site won 237 times, the second best 12 times, with no winner once.

Figures 5 and 6 show similar calculations for medium and low levels of interdependence (i.e.  $\lambda=0.5$  and  $\lambda=0.2$ , respectively) and essentially confirm the earlier results for higher individual reliability. In 250 repetitions of the simulations for a medium level of interdependence, the best site emerged as the winner under the strong criterion 94 times and the second best once, with no consensus in all other cases. (Under the weaker criterion, the effect is less pronounced: the best site won 220 times and the second best 28 times, with no winner twice.) When the level of interdependence was low, the best site won only seven times under the strong criterion, with no consensus in the other 243 cases. (Under the weaker criterion, the best site won 190 times, the second best 58 times and in the remaining two cases, no consensus emerged.)

Table 1 summarizes the frequencies of various consensus choices in 250 repetitions of the simulations.

### (c) Results on hypothesis 3.2

As indicated, we isolated the effects of independence and interdependence by running simulations for the special cases in which one or the other of these two characteristics was absent. Figure 7 shows the case in which bees independently assess sites and they are also relatively reliable ( $\sigma=0.2$ ), but there is no longer any interdependence between bees through communication ( $\lambda=0$ ). No clear consensus winner emerges. Figure 8 shows an illustrative case in which interdependence between bees is high ( $\lambda=0.8$ ), but they are no longer independent ( $\mu=1$ ); they all mimic the dances of other bees without independently verifying the sites' quality. In this example, after relatively little initial dance activity, a sudden cascade of support for site 2 emerges (the second worst site), which is reinforced by the bees' mimicking of others' dances. Equally, a cascade of support for another site could have randomly emerged.

More generally, we ran a large number of simulations with the level of interdependence ranging

from low ( $\lambda=0$ ) to high ( $\lambda=1$ ), keeping a high individual reliability and independence of bees ( $\sigma=0.2$  and  $\mu=0$ ). Figure 9 shows the proportion of wins for each of the five sites (in 250 simulations for each set of parameter values), for different levels of interdependence, where the winner is calculated using the more demanding criterion. The results are qualitatively similar under the less demanding criterion. The best site (site 5) consistently emerges as the winner only when the level of interdependence is above a certain threshold. (Recall our earlier remarks, in the basic description of the computer simulations, about the exceptional limiting case  $\lambda=1$ .)

Similarly, we ran a large number of simulations with the level of independence ranging from low ( $\mu=1$ ) to high ( $\mu=0$ ), keeping a high interdependence of bees and a high reliability in the event they do verify a site's quality ( $\lambda=0.8$  and  $\sigma=0.2$ ). Figure 10 shows the proportion of wins for each site (again in 250 simulations for each set of parameter values), for different levels of independence (displayed as  $1-\mu$ ). Again, we use the more demanding criterion of consensus; the results are qualitatively similar under the less demanding criterion. The best site (site 5) consistently emerges as the winner only when the level of independence is not too low.

## 5. DISCUSSION

We have developed an agent-based model of nest-site choice among honeybees. The model not only explicitly represents the behaviour of each individual bee as a simple stochastic process, but it also allows us to simulate the bees' decision-making behaviour under a wide variety of empirically motivated as well as hypothetical assumptions. The model predicts that, consistently with empirical observations by Seeley & Buhrman (2001), the bees manage to reach a consensus on the best nest site for a large range of parameter conditions, under both more and less demanding criteria of consensus. Moreover, the model shows that the remarkable reliability of the bees' decision-making process stems from the particular interplay of independence and interdependence between them. The bees are independent in assessing the quality of different nest sites on their



Table 1. Frequencies of various consensus choices in 250 replications of the simulations.

		high individual reliability ( $\sigma=0.2$ )		low individual reliability ( $\sigma=1$ )	
		strong consensus criterion	weak consensus criterion	strong consensus criterion	weak consensus criterion
high interdependence ( $\lambda=0.8$ )	1st best site	246 (98.4%)	250 (100%)	199 (79.6%)	237 (94.8%)
	2nd best site	0 (0%)	0 (0%)	5 (2%)	12 (4.8%)
	3rd best site	0 (0%)	0 (0%)	0 (0%)	0 (0%)
	none	4 (1.6%)	0 (0%)	46 (18.4%)	1 (0.4%)
medium interdependence ( $\lambda=0.5$ )	1st best site	104 (41.6%)	226 (90.4%)	94 (37.6%)	220 (88%)
	2nd best site	0 (0%)	22 (8.8%)	1 (0.4%)	28 (11.2%)
	3rd best site	0 (0%)	0 (0%)	0 (0%)	0 (0%)
	none	146 (58.4%)	2 (0.8%)	155 (62%)	2 (0.8%)
low interdependence ( $\lambda=0.2$ )	1st best site	11 (4.4%)	176 (70.4%)	7 (2.8%)	190 (76%)
	2nd best site	1 (0.4%)	63 (25.2%)	0 (0%)	58 (23.2%)
	3rd best site	0 (0%)	1 (0.4%)	0 (0%)	0 (0%)
	none	238 (95.2%)	10 (4%)	243 (97.2%)	2 (0.8%)

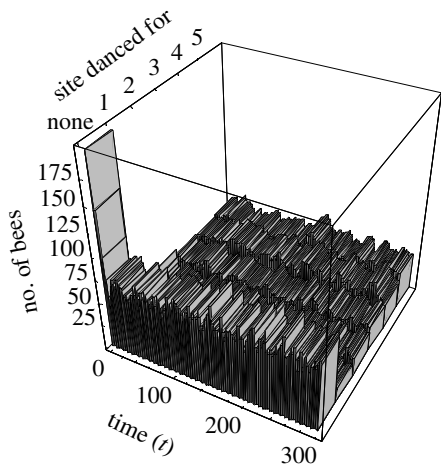


Figure 7. Illustrative simulations to test hypothesis 3.2. Independence without interdependence.

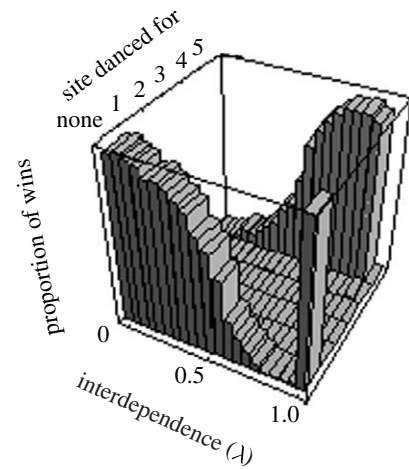


Figure 9. Sequences of simulations to test hypothesis 3.2. Interdependence ranging from low to high.

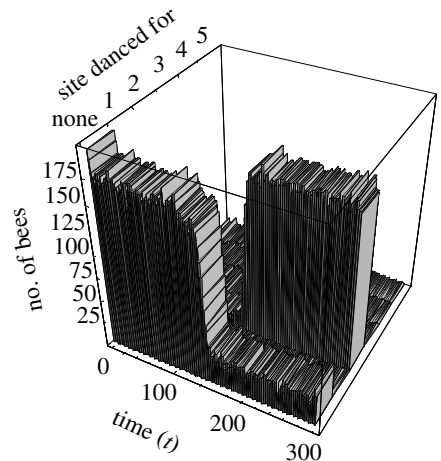


Figure 8. Illustrative simulations to test hypothesis 3.2. Interdependence without independence.

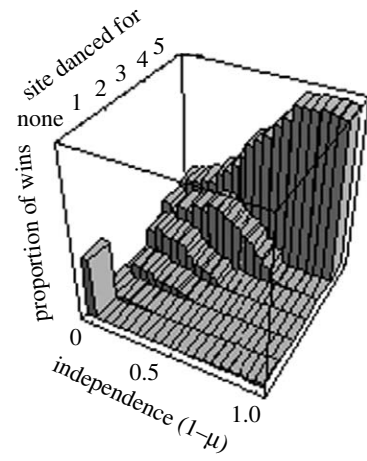


Figure 10. Sequences of simulations to test hypothesis 3.2. Independence ranging from low to high.

own, but interdependent in giving more attention to nest sites that are more strongly advertised by others.

Without interdependence, the rapid convergence of the bees' dances to a consensus would be undermined; there would not be a 'snowballing' of attention on the best nest site. Without independence, a consensus

would still emerge, but it would no longer robustly be on the best nest site; instead, many bees would end up dancing for nest sites that accidentally receive some initial support through random fluctuations. It is only when independence and interdependence are combined in the right way that the bees achieve their remarkable collective reliability.

To illustrate the importance of both independence and interdependence in collective decision making more generally, consider the human example of restaurant choice. If we walk into a street with many restaurants, knowing nothing about their quality, we may well pick whichever restaurant has the most diners, assuming that these people have chosen it for its quality. But if their reasoning was the same, we may all end up in the worst restaurant; if we do not, this is entirely accidental. This phenomenon is called an *informational cascade* (Bikhchandani *et al.* 1992). It is only if enough people choose a restaurant based on independently gathered information that such cascades can be avoided. Interdependence without independence can lead everyone to a bad decision. (Of course, in the restaurant case, additional complexities arise because differences in individual choices are due to not only different information but also different preferences; in the case of the bees, we have made the simplifying assumption that differences in individual choices are solely due to informational differences, presupposing that there is an objective quality standard for nest sites.)

Likewise, independence without interdependence can be suboptimal too. Imagine a world without any restaurant reviews or recommendations, where people only ever gather information about restaurants by wandering around the streets alone and checking out the restaurants they see. It can easily happen, then, that an outstanding but badly located restaurant may fail to get many customers because too few people stumble across it.

The bees' ingenuity lies in their avoidance of both of these problems. Nature has given them the right mix of independence and interdependence.

This paper is based on an unpublished manuscript of January 2005. We are grateful to Larissa Conrath, Kai Spiekermann and two anonymous referees for their helpful comments.

## REFERENCES

- Austen-Smith, D. & Banks, J. S. 1996 Information aggregation, rationality, and the Condorcet jury theorem. *Am. Pol. Sci. Rev.* **90**, 34–45. (doi:10.2307/2082796)
- Austen-Smith, D. & Feddersen, T. J. 2009 Information aggregation and communication in committees. *Phil. Trans. R. Soc. B* **364**, 763–769. (doi:10.1098/rstb.2008.0256)
- Bikhchandani, S., Hirshleifer, D. & Welch, I. 1992 A theory of fads, fashions, custom, and cultural change as informational cascades. *J. Pol. Econ.* **100**, 992–1026. (doi:10.1086/261849)
- Borland, P. J. 1989 Majority systems and the Condorcet jury theorem. *Statistician* **38**, 181–189. (doi:10.2307/2348873)
- Britton, N. F., Franks, N. R., Pratt, S. C. & Seeley, T. D. 2002 Deciding on a new home: how do honeybees agree? *Proc. R. Soc. Lond. B* **269**, 1383–1388. (doi:10.1098/rspb.2002.2001)
- Dryzek, J. & List, C. 2003 Social choice theory and deliberative democracy: a reconciliation. *Br. J. Pol. Sci.* **33**, 1–28. (doi:10.1017/S0007123403000012)
- Elster, J. 1986 The market and the forum. In *Foundations of social choice theory* (eds J. Elster & A. Hylland). pp. 103–132. Cambridge, UK: Cambridge University Press.
- Farrar, C., Fishkin, J. S., Green, D., List, C., Luskin, R. C. & Paluck, E. L. In press. Disaggregating deliberation's effects: an experiment within a deliberative poll. *Br. J. Pol. Sci.*
- Grofman, B., Owen, G. & Feld, S. L. 1983 Thirteen theorems in search of the truth. *Theory Decision* **15**, 261–278. (doi:10.1007/BF00125672)
- Knight, J. & Johnson, J. 1994 Aggregation and deliberation: on the possibility of democratic legitimacy. *Pol. Theory* **22**, 277–296. (doi:10.1177/0090591794022002004)
- Lindauer, M. 1955 Schwarmbienen auf Wohnungssuche. *Zeitschrift für vergleichende Physiologie* **37**, 263–324. (doi:10.1007/BF00303153)
- List, C. 2004 Democracy in animal groups: a political science perspective. *Trends Ecol. Evol.* **19**, 168–169. (doi:10.1016/j.tree.2004.02.004)
- List, C. & Goodin, R. E. 2001 Epistemic democracy: generalizing the Condorcet jury theorem. *J. Pol. Philos.* **9**, 277–306. (doi:10.1111/1467-9760.00128)
- Luskin, R. C., Fishkin, J. S. & Jowell, R. 2002 Considered opinions: deliberative polling in Britain. *Br. J. Pol. Sci.* **32**, 455–487. (doi:10.1017/S0007123402000194)
- Miller, D. 1992 Deliberative democracy and social choice. *Pol. Studies* **40**, 54–67. Special Issue.
- Myerscough, M. R. 2003 Dancing for a decision: a matrix model for nest-site choices by honeybees. *Proc. R. Soc. B* **270**, 577–582. (doi:10.1098/rspb.2002.2293)
- Passino, K. M. & Seeley, T. D. 2006 Modeling and analysis of nest-site selection by honey bee swarms. The speed and accuracy trade-off. *Behav. Ecol. Sociobiol.* **59**, 427–442. (doi:10.1007/s00265-005-0067-y)
- Perdriau, B. S. & Myerscough, M. R. 2007 Making good choices with variable information: a stochastic model for nest-site selection by honeybees. *Biol. Lett.* **3**, 140–143. (doi:10.1098/rsbl.2006.0599)
- Seeley, T. D. & Buhrman, S. C. 2001 Nest-site selection in honey bees: how well do swarms implement the 'best-of-N' decision rule? *Behav. Ecol. Sociobiol.* **49**, 416–427. (doi:10.1007/s002650000299)
- Seeley, T. D. & Visscher, P. K. 2003 Choosing a home: how the scouts in a honey bee swarm perceive the completion of their group decision making. *Behav. Ecol. Sociobiol.* **54**, 511–520. (doi:10.1007/s00265-003-0664-6)
- Seeley, T. D., Visscher, P. K. & Passino, K. M. 2006 Group decision making in honey bee swarms. *Am. Sci.* **94**, 220–229.
- Sunstein, C. R. 2002 The law of group polarization. *J. Pol. Philos.* **10**, 175–195. (doi:10.1111/1467-9760.00148)
- Sunstein, C. R. 2006 Deliberating groups versus prediction markets (or Hayek's challenge to Habermas). *Episteme* **3**, 192–213.
- Zuber, J. A., Crott, H. W. & Werner, J. 1992 Choice shift and group polarization: an analysis of the status of arguments and social decision schemes. *J. Pers. Soc. Psychol.* **62**, 50–61. (doi:10.1037/0022-3514.62.1.50)