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Inaccurate and unverified information in decision making: a model for the nest site selection process of *Apis florea*

Timothy M. Schaerf[a,b,c,*], Mary R. Myerscough[b,c], James C. Makinson[a,c], Madeleine Beekman[a,c]

[a] *Behaviour and Genetics of Social Insects Laboratory, School of Biological Sciences, University of Sydney*
[b] *School of Mathematics and Statistics, University of Sydney*
[c] *Centre for Mathematical Biology, University of Sydney*

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We present an agent-based model for the nest site selection process of the open-nesting red dwarf honeybee, *Apis florea*. Our main aim was to determine how nest site requirements affect the bees' decision-making process. We either calculated our model parameters from experimental data or chose them so that our model would generate similar numbers of dancing bees and dance followers to those observed in real swarms with access to an abundance of suitable nest sites in all directions. We found that *A. florea* is less capable of making a collective decision on a new nest site when the area occupied by suitable sites is small compared to when suitable sites are abundant. Increasing the use of information regarding the location of potential nest sites or the accuracy of the information available enhanced the decision-making ability of *A. florea* when nest sites were scarce. We also found that swarm guidance might be hindered when suitable nest site areas are wide apart. We therefore examined two possible mechanisms for increasing directional agreement among dancers: mimicry of unverified dance information and self-regulation by inhibiting or changing dance behaviour based on observations of other dances. We show that, even at low levels, dance mimicry greatly enhances the ability of an *A. florea* swarm to make a decision and reduces the time to make a decision. However, in the presence of mimicry errors propagate through the swarm. Self-regulation had little or no effect, probably because of the overall low levels of dance activity present on the swarm at any given time. Our model results suggest that *A. florea*'s decision-making process allows swarms to locate a new nest site provided nest sites are abundant, even when they are of similar quality.

The decision of a group of animals to move as a collective from its current location to a new location can be one of the most important and, depending on the context, resource-intensive challenges that the group faces (Boinski & Garber 2000). There are many reasons why a group may move. The depletion of previously adequate food sources can lead colonies of the giant honeybee, *Apis dorsata* (Koeniger & Koeniger 1980) or army ants (Schneirla 1971) to move. The destruction or deterioration of an existing home will prompt established colonies of the red dwarf honeybee, *Apis florea* (Seeley et al. 1982) or the ant *Temnothorax albipennis* (Pratt et al. 2002) to abandon their old site and move elsewhere. Increased threat of predation and attack (Ward et al. 2008), seasonal migration (Berthold 1993) or an increase in colony size (Winston 1987) also result in group movements.

While on the move it is essential for the group to stay together. It is thus important that the group decides on the direction of travel prior to departure. The decision on the direction of travel can be achieved in various ways. In some species this is determined solely by a single individual while in others such a decision is reached in a more democratic way (Boinski & Garber 2000). When more than one individual is involved in deciding where to move to, these individuals must agree on a direction of travel prior to departure to avoid the group from breaking up. Often some form of quorum threshold is used so that sufficient individuals have approved the new location.

One of the best-studied decision-making processes with respect to group movement is nest site selection in social insects (reviewed in Visscher 2007). Nest site selection is a decentralized decision-making process where a homeless group of insects faces the challenge of identifying and selecting the best among multiple potential nest sites. There have been many empirical studies investigating the mechanisms of nest site selection (Lindauer 1955; Seeley & Morse 1978; Camazine et al. 1999; Seeley & Buhrman

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* Correspondence: T. M. Schaerf, Behaviour and Genetics of Social Insects Laboratory, School of Biological Sciences, Macleay Building A12, University of Sydney, Sydney, NSW 2006, Australia.
E-mail address: timothy.schaerf@sydney.edu.au (T. M. Schaerf).

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2001; Mallon et al. 2001; Pratt et al. 2002; Franks et al. 2003; Seeley & Visscher 2004; Stroemeyt et al. 2010), and these have been complemented by a raft of theoretical work (Britton et al. 2002; Myerscough 2003; Pratt et al. 2005; Passino & Seeley 2006; Janson et al. 2007; Perdriau & Myerscough 2007; List et al. 2009; Marshall et al. 2009; Nevai et al. 2010).

Previous work has suggested that the precision of the decision-making process with respect to the level of agreement achieved prior to the group's departure is dependent on the importance of locating a precise, particular site (Oldroyd et al. 2008; Makinson et al. 2011). When sites differ in their quality and are scarce, the group should deliberate until the best site possible has been located and decided on. If, on the other hand, sites of sufficient quality are abundant, a group does not need to invest heavily in the decision-making process. Here we investigate the decision-making process in *A. florea*. This species builds a single comb which is usually suspended from a tree branch. In its natural range, suitable nest sites are abundant and probably do not differ greatly in quality. Empirical work has shown that individuals involved in the decision-making process differ greatly in their preferred direction of travel prior to the group moving. This is in stark contrast to the cavity-nesting honeybee, *Apis mellifera*. Cavities of sufficient quality are scarce and the bees have been shown to depart only when the majority of individuals agree on where to move to (Camazine et al. 1999; Seeley & Buhrman 1999, 2001; Seeley 2003). Here we examine a model for the decision-making process of *A. florea*, which includes examining the potential consequences of having multiple sites being advertised at the time the decision to take flight is made.

In contrast to *A. florea*, the nest site selection process of *A. mellifera* is very sophisticated and well understood. The necessity for an *A. mellifera* colony to find a new home arises when the colony grows in size, usually during spring (Winston 1987). The colony's original queen and about two-thirds of her workers take flight from their old home and settle nearby in a temporary cluster, the reproductive swarm. A fraction of the workers (the scouts) then leave the swarm and explore the surrounding area in search of potential nest sites (Seeley et al. 1979). When a scout finds a potential nest site, it spends some time assessing its quality. If the site is of sufficient quality, the scout will inform other workers of its location via a waggle dance performed on the swarm. The waggle dance contains vectorial information about the site, and other bees on the cluster follow the dances and may be recruited to seek out the advertised site to assess it independently. If the recruits also determine that the site is of sufficient quality, they too will perform waggle dances for that site on their return to the swarm. In between bouts of dancing, scouts revisit the site for which they are dancing. Once the scouts detect that the number of bees at the site they are evaluating has passed the quorum threshold, they return to the cluster and start rousing the other bees to prepare them for flight (Seeley & Visscher 2003). The same scouts that were present to detect the quorum at the new nest site are also thought to be responsible for guiding the swarm to their new home (Beekman et al. 2006).

Swarms of *A. mellifera* are able to choose a nest site that best suits the colony's needs from many available potential sites (Seeley & Buhrman 2001). Site quality is dependent on the size of the cavity, its position and the size of its opening (Visscher 2007). High-quality sites are often scarce. Swarms in the open are vulnerable to inclement weather and cannot produce brood. Hence, the bees need to make a decision quickly, but not so quickly that they settle for a low-quality site. Fundamental to *A. mellifera*'s ability to select the best nest site are individual, independent assessments of nest site quality and dance decay. A scout's assessment of the quality of the site that it has visited is reflected by the number of waggle runs it performs on its initial return to the swarm. A scout that has found a high-quality site will generally perform more waggle runs on its first return than a scout that has found a lower-quality nest site (Seeley & Visscher 2008). On average the number of waggle runs performed by a scout decreases linearly on each return to the swarm (Seeley 2003; Seeley & Visscher 2008). Ultimately, every bee will stop dancing for a site regardless of the site's quality, although dancers for lower-quality sites tend to drop out more quickly than dancers for higher-quality sites. Such site quality-dependent dance decay ensures that low-quality sites will not be continually advertised by waggle dances and allows the swarm to select the best site even if this better site is discovered later in the decision-making process. Additionally, errors in the assessment of a site's quality by an individual are corrected by other scouts that visit the same site owing to independent assessment of site quality by each bee that visits a site. In general, the cessation of dancing as a consequence of dance decay helps to prevent stalemates in the decision-making process, especially when choices are being made between sites of similar quality. The nest site selection process in *A. mellifera* has evolved to deal with the very specific nesting requirements of the species and the importance of finding the best possible nest cavity. Studying the nest site selection process of other members of the *Apis* genus, especially those with different nesting requirements, may give clues to the evolutionary origins of the use of dance communication in nest site selection.

Apis florea and the closely related *Apis andreniformis* belong to the most basal clade of the *Apis* genus. The nesting biology of these species is significantly different to that of *A. mellifera*; suitable tree branches are abundant whereas cavities suitable for an *A. mellifera* colony are rare. Initial studies by Beekman et al. (2008) and Oldroyd et al. (2008) found that there are similarities between the nest site selection processes of *A. florea* and *A. mellifera*, but the processes differ in detail. Beekman et al. (2008) found that dances of *A. florea* scouts are imprecise with respect to distance and direction communicated. Oldroyd et al. (2008) found that up to 30 min before a swarm takes off there are still many sites being advertised by dancers. In contrast, *A. mellifera* dancers often reach near total consensus in the direction they are dancing for prior to take-off (Seeley & Buhrman 1999), even though the decision is quorum based rather than consensus based (Seeley & Visscher 2003).

Makinson et al. (2011) carried out a detailed study of the nest site selection process of five artificial swarms of *A. florea* in Thailand. In three of the swarms every dancer was uniquely marked as it performed its first dance, and in the two remaining swarms every bee in the swarm was individually marked. These experiments revealed important differences between *A. florea* and *A. mellifera*. First, most *A. florea* scouts tend to remain on the swarm once they start dancing for a particular location. This is in contrast to *A. mellifera* in which scouts consistently leave the swarm after each bout of dancing to revisit the site to which they are committed. In fact, leaving the swarm to revisit sites is a vital component of the decision-making process for *A. mellifera* as the quorum is measured at the new nest site. As *A. florea* scouts do not generally leave the swarm between bouts of dancing it is unlikely that they detect a quorum in the same way as *A. mellifera*. Second, there is no decay in the number of waggle runs performed by scouts between successive dance episodes. From the experiments of Makinson et al. (2011) there is evidence that dancers ultimately stop dancing for sites, although a few bees were extremely persistent, dancing repeatedly for many hours. It is not known whether there is any communication about the quality of potential nest sites via the dances of *A. florea* scouts, but given that most tree branches could be considered equally suitable, it is possible that no such information is encoded in a dance.

Here we describe a simple algorithmic agent-based model for nest site selection in *A. florea*. The model is similar to existing simulation models for nest site selection for *A. mellifera*, but it has been developed to emulate specific observed characteristics of *A. florea*. The core components of all existing models for nest site selection in *A. mellifera* are the positive feedback mechanism of recruitment by waggle dances and the presence of dance decay or dance cessation. The detail in which these mechanisms is treated varies from model to model. The most abstract approach is to make recruitment a function of both the number of bees already devoted to a site and site quality (Britton et al. 2002; Perdriau & Myerscough 2007; Marshall et al. 2009). Dance cessation is either dependent on site quality or occurs at a uniform rate for all sites in these models. A more detailed approach is to base the rate or probability of recruitment directly on the number of waggle runs performed for a site and make dance cessation a direct consequence of dance decay (Myerscough 2003; List et al. 2009). The most detailed approach focuses on the mechanics of the recruitment process, allowing individuals to follow dances, scout for nest sites independently and spend time assessing nest sites (Passino & Seeley 2006; Janson et al. 2007; Nevai et al. 2010). The tasks (states) adopted by bees and the transitions between these tasks are similar for all three models in the last category. Broadly, bees move from a resting state to an observer state where they seek to follow the dance of another bee on the swarm. Those that follow a dance use the dance information to help locate the advertised site. Bees that do not follow a dance explore independently. Any bee that finds a site will assess it and, provided it is of sufficient quality, return to the swarm and dance for the site. Bees return to their chosen site in between bouts of dancing to reassess site quality. A bee ceases its commitment to a site when it returns to the resting state. For reference, flow charts illustrating the individual states that model bees can adopt in the detailed individual-based models of Passino & Seeley (2006) and Janson et al. (2007) and the simpler individual-based model of List et al. (2009) are provided in Figs A1–A3, respectively, in Appendix 1. Equivalent states across the models are marked in the same colour. Our work extends the approach adopted by the most detailed models for *A. mellifera* by including species-specific behaviours of dance mimicry and continual monitoring of other bees' dances observed in *A. florea* and excluding reassessment of nest sites. *Apis florea*'s nesting biology requires that we take a different approach in modelling the spatial location of nest sites to that used in models of *A. mellifera*. An advantage of using an agent-based model is that it allows for explicit adjustment and tracking of individual behaviour while revealing emergent global properties of the underlying system. The probability-based nature of such a model also fits well with the variability seen in *A. florea* individuals.

Using the data of Makinson et al. (2011) we first see whether our model is capable of generating similar levels of on-swarm activity to that seen in real swarms, measured in terms of the number of dancers and dance followers. The experimental results derived from real swarms are characterized by a relatively high rate of dance following compared to the amount of dancing performed. We then use the model to study how accuracy in following directional information, the tendency to act on available information by seeking out advertised sites, and the presence and relative placement of multiple nesting regions affect the ability of the swarm collectively to choose a new nest. Finally, the model is used to explore potential mechanisms for building on-swarm dance activity and agreement among dancers by allowing bees the ability to mimic dances without independently assessing or visiting nest sites, or the ability to adjust their own behaviour based on the observed activity of other bees on the swarm.

AGENT-BASED MODEL

Our model emulates the behaviour of a swarm of *A. florea* described in Makinson et al. (2011) in which the dance following, dancing and flight activity of all bees was recorded. The model traces a fixed number of individual bees, N, that are actively involved in the decision-making process over a fixed set of equally spaced time steps. The behaviour of each bee follows the flow chart in Fig. 1.

According to Makinson et al. (2011) recruitment does not play as strong a role in nest site selection by *A. florea* as it does for *A. mellifera*. Only one-third of dancers were recruited to dance for a particular direction by another bee's dance in the fully marked swarms studied by Makinson et al. (2011). Recruitment was defined to occur if a bee danced within 30° of the average direction of the last dance it followed (see Table 2 of Makinson et al. 2011). This definition is based on the idea that since *A. florea* bees are inconsistent in the angle that they dance, dances within 30° of each other feasibly indicate the same nesting region. Approximately 69% of recruits in both fully marked swarms were observed to take flight in between following a dance and commencing a dance themselves. There was no flight activity between following and dancing for the other 31% of recruits. *Apis florea* dancers are often observed following the dances of other bees in between their own bouts of dancing (see Figure 1 of Makinson et al. 2011). By contrast,

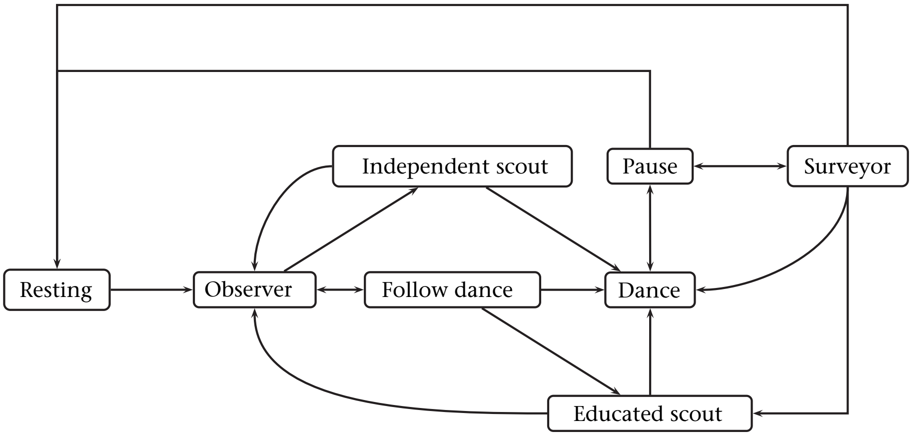

Figure 1. Flow chart of individual behaviour in our *A. florea* model. See text for further details of each of the states.

A. mellifera dancers do not engage in any additional dance following until they have completely finished dancing for a particular site (see for example Figure 6.9 of Seeley 2010). In spite of the low observed recruitment rates of *A. florea*, there is evidence that prior to take-off there is agreement among dancers on a general direction, as shown by the vectorial consensus analysis of Makinson et al. (2011).

In our model we have two mechanisms that allow a build-up in directional agreement among dancers prior to lift-off. The first mechanism is dance mimicry where dance followers mimic other bees' dances without leaving the swarm to examine an advertised site. The possible effects of mimicry among *A. mellifera* scouts have also been studied recently using an agent-based model (List et al. 2009). In particular, the potential hazards of mimicry are illustrated in their Figure 8 where its strong presence results in the simulated *A. mellifera* bees choosing the second worst of five available nest sites.

The second agreement-building mechanism allows dedicated dancers to observe the dances of other bees while still committed to a particular site. This is consistent with the observation that scouts in *A. florea* swarms frequently follow other bees' dances in between their own bouts of dancing. After observing a portion of the bees on the swarm, the model bees have the option of changing their own dance behaviour or of continuing to dance for their original site. This allows direct switching of allegiance between sites, a mechanism that was also examined in the differential equation model of Britton et al. (2002).

Figure 1 illustrates the role that each of the bees in our model can adopt and the transitions between these roles.

Initially the N bees that are involved in the decision-making process are at rest. For each time step of a simulation each resting bee has a constant probability, p_{observe}, of becoming an observer bee who actively looks for a dance to follow during the next time step.

Each observer bee randomly examines a fixed proportion of the other bees on the swarm, f_{search}. If a dancing bee is found during the observer's survey of the swarm there is a constant probability, p_{follow}, that the observer will follow the dancer for the remainder of the current time step. If an observer bee does not follow any dances then she will independently scout for a potential nest site during the next time step (Beekman et al. 2007).

If a bee follows a dance during one time step, she will perform one of three actions during the next time step. She will either attempt to find the site advertised by the dance or start dancing for the site without visiting it or return to the process of observing the bees on the swarm described above. The probability of attempting to visit a site advertised by a dance is p_{visit}, the probability of dancing for a site immediately is p_{mimic} (such that $p_{\mathrm{visit}} + p_{\mathrm{mimic}} \leq 1$) and the probability of returning to the observer state is $1 - p_{\mathrm{mimic}} - p_{\mathrm{visit}}$.

We describe viable nesting regions by an angular range. Two parameters relate to the quality of the individual sites within the region: p^i_{start} and p^i_{cease}. These parameters describe the probability of starting or ceasing dancing for region i. Each nesting region represents an environment with suitable nest sites everywhere. A bee attempting to find a site advertised by a dance leaves the swarm at an angle determined by a normally distributed random variable with a mean equal to the angle of the dance followed and a standard deviation of θ°. A bee attempting to find a potential nest site by independent scouting leaves the swarm at a random angle uniformly distributed between 0° and 360°. If a bee discovers a potential nest site by flying into nesting region i then the probability that she will return to the swarm at the next time step and dance for that site is p^i_{start}. Bees that do not find a site, or that do find a site and decide not to dance for it, return to the swarm as observers for the next time step.

A bee dancing for a site in region i pauses from dancing with a fixed probability, p_{pause}, while still remaining committed to that site. We assume that there is some inaccuracy in the waggle dance of each bee. A bee that has visited a site will dance precisely in the direction of the site in the first time step after her return to the swarm. A bee that dances for a site without visiting it will initially dance at the same angle as the dance that she followed in simulations where mimicked dance information is transferred precisely, or at a normally distributed random angle with mean equal to that of the dance followed and standard deviation Ψ° in simulations where mimicked dance information is replicated inaccurately. If the bee continues to dance for a site for more than one time step, her dance angle will change to an angle that is a normally distributed random variable with mean equal to the angle danced at the previous time step and standard deviation ϕ°. Variation in dance angle across different bouts of dancing is a common feature of the dances produced by *A. florea* scouts; see for example Figure 5 of Makinson et al. (2011).

A paused dancer can either cease dancing with probability p^i_{cease}, resume dancing for the direction for which she was originally dancing with probability p_{resume}, become a surveyor of the activity of other bees on the swarm with probability p_{survey} or remain paused with probability $1 - p^i_{\mathrm{cease}} - p_{\mathrm{resume}} - p_{\mathrm{survey}}$ during the following time step.

A bee in the surveyor state searches a random fraction of the bees on the swarm, f_{survey}, for dancers. If she finds dancers she compares the angle for which they are dancing with the angle for which she was previously dancing. Bees that are dancing within 30° of the angle that the surveyor is still committed to are counted as dancing in the same direction as the surveyor; bees that are dancing at an angle that differs by more than 30° from the surveyor's dance are counted as dancing in a different direction. This is consistent with the analysis comparing following and dancing angles performed by Makinson et al. (2011). The number of dances in the same direction, n_{agree}, the number of dances in a different direction, n_{disagree} and the total number of dances observed $n_{\mathrm{total}} = n_{\mathrm{agree}} + n_{\mathrm{disagree}}$ are noted by the surveyor. The surveyor can then change her own dancing behaviour based on her observations of the other dancers. The probability of changing her behaviour is determined by the fraction of bees that she observed dancing in a direction different to the direction to which she is currently committed, $f_{\mathrm{disagree}} = n_{\mathrm{disagree}}/n_{\mathrm{total}}$. A surveyor can lose commitment for her current direction and become an educated scout for a different direction randomly chosen from the dances she observed with probability $f_{\mathrm{disagree}} p_{\mathrm{visit'}}$. A surveyor can spontaneously mimic a dance in a randomly chosen observed direction that is different from her own with probability $f_{\mathrm{disagree}} p_{\mathrm{mimic'}}$. A surveyor may also cease dancing completely based on her observations of other dancers on the swarm; the probability of ceasing dancing based on another bee's dance is $f_{\mathrm{disagree}} p_{\mathrm{inhibited}}$. If a surveyor does not seek out an advertised site, spontaneously mimic another dance or cease dancing completely then she will return to the paused state with probability $1 - f_{\mathrm{disagree}} p_{\mathrm{visit'}} - f_{\mathrm{disagree}} p_{\mathrm{mimic'}} - f_{\mathrm{disagree}} p_{\mathrm{inhibited}}$.

Table 1 summarizes the parameters used by the model and their functions. We implemented the individual-based model in MATLAB (MathWorks, Natick, MA, U.S.A.).

We need to implement some form of stopping criteria to determine when the decision-making process is concluded. We propose two stopping criteria. We perform all our simulations for a fixed number of time steps and then apply both stopping criteria in turn to the same data set and find when the criterion of each test is first met.

The first stopping test is based on activity on the swarm. If the number of bees dancing during a time step is greater than or equal to some threshold value, then a quorum has been reached. The second stopping test is based on both swarm activity and the

Table 1
List of parameters used in the agent-based model

Parameter	Description
N	Total number of bees
p_{observe}	Probability of a resting bee becoming an observer
p_{follow}	Probability of following an observed dancing bee
p_{visit}	Probability of seeking an advertised site
p_{mimic}	Probability of mimicking a followed dance
p^i_{start}	Probability of dancing for a site in region i
p^i_{cease}	Probability of ceasing dancing for a site in region i
p_{pause}	Probability of a dancing bee pausing
p_{resume}	Probability of a paused bee resuming dancing
p_{survey}	Probability of a paused bee becoming a surveyor
$p_{\text{visit}'}$	Probability of a surveyor becoming an educated scout
$p_{\text{mimic}'}$	Probability of a surveyor mimicking a dance
p_{inhibit}	Probability of a surveyor resting
f_{search}	Fraction of the bees on the swarm surveyed by observer bees
f_{survey}	Fraction of the swarm surveyed
f_{disagree}	Fraction of dancers that disagree with surveyor
n_{agree}	Number of bees agreeing on dance direction with a surveyor
n_{disagree}	Number of bees disagreeing on dance direction with a surveyor
n_{total}	Total number of dancers observed by a surveyor
θ°	Standard deviation of the angle flown by educated scouts
ϕ°	Standard deviation of the angle danced
Ψ°	Standard deviation of the angle danced by a mimic

All probabilities are associated with the actions of individual bees. See text for further detail.

directions of dances. Makinson et al.'s (2011) analysis suggested that there may be some form of agreement between dancers prior to take-off, which they quantified with a consensus vector. A consensus vector is formed by constructing unit vectors in the direction danced by each bee and then adding all the unit vectors together. If the magnitude of the consensus vector passes a threshold, then vectorial consensus has been reached. The direction of the consensus vector gives the average direction indicated by dances. We make the assumption that all the scouts that were dancing prior to lift-off attempt to guide the swarm, and the consequence is that the direction of the swarm's flight is the same as the consensus vector.

NUMERICAL EXPERIMENTS

We used our model to examine the influence that species-specific behaviours and the relative location of nest sites have on nest site selection by *A. florea*. First, we tuned parameters that could not be estimated directly from available data to emulate swarm activity observed in real bees (in the section What Parameters give Realistic Results?). Tuning was performed with a suitable nesting region filling the entire angular domain. We then restricted the suitable nesting region to a single arc of angular extent 100° and analysed the model swarm's ability to make a decision when the tendency to act on dance information, p_{visit}, and the accuracy of information use, θ°, were adjusted (see Frequency and Accuracy of Dance Information Use). Next, we examined the effect that spatial separation between two suitable nesting regions had on decision making (see Can *A. florea* Choose between Two Regions of Equal Size?). Finally, we examined how dance mimicry and continual monitoring of dance activity by surveyor bees can affect decision making (see the sections What are the Effects of Mimicry on Speed and Accuracy?, Self-inhibition and Direct Switching *and* Consensus-building Mechanisms with Two Nesting Regions). We performed 1000 replicates for each set of parameters in each experiment. This number was chosen so that a relatively large number of simulations could be performed without the time required to complete the entire study becoming prohibitive. A brief discussion of the accuracy of simulation results as a function of the number of replicates for each parameter set is provided in Appendix 2.

We used the experimental data from swarm 5 in Makinson et al. (2011), which was a fully marked swarm, to estimate p_{visit}, p^i_{cease} and θ°. The other fully marked swarm, swarm 4, was exceptionally small and atypically inactive compared to the other four experimental swarms, making it a less reliable source for parameter estimation.

In swarm 5 there were 1590 instances of following, 365 of which were followed by flight activity. We therefore estimated the probability of seeking an advertised site after following as $p_{\text{visit}} = (365/1590) \approx 0.23$.

To estimate the probability of dance cessation, p^i_{cease}, we counted the dance episodes performed throughout swarm 5's decision-making process and then looked for cases where a bee performed an activity other than dance after completing a dance episode. Dance episodes were identified here as any period of continuously producing a waggle dance without any form of break such as taking flight, following another bee's dance or walking to another location on the swarm. There were 233 separate dance episodes recorded for swarm 5, 72 of which were followed by another activity other than dancing. Our estimate for p^i_{cease} is $p^i_{\text{cease}} = (72/233) \approx 0.3$. This estimate for p^i_{cease} is likely to be an underestimate as it does not include cases where bees performed a dance and then were not recorded as performing another activity for several hours or more, but it is sufficient for the numerical experiments detailed here.

To estimate θ° we extracted all instances of dancing that were preceded by a bee following another bee's dance. We calculated the angular differences between the average angle of the dances followed and the dances subsequently performed by each bee. Figure 2 contains a histogram of the difference between following and dance angles. The sample standard deviation of the data set is 52.7401°; however the data are unlikely to come from a normally distributed process (two-sided Shapiro–Wilks test: $P = 0.039$). In particular, the data have much taller central peaks than normally distributed data. The shape of the graph suggests that it may contain data from bees that did make use of dance information (in the central region) and those that did not (those with a very large angular difference between following and dancing). However, we have no method of distinguishing between bees that inaccurately use information that they

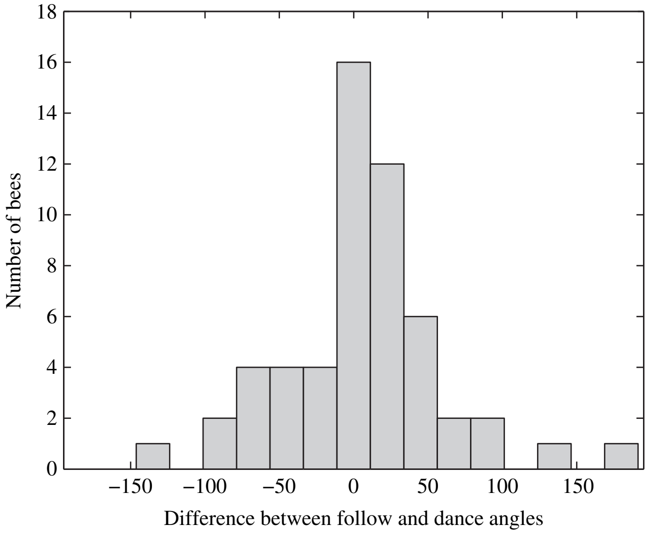

Figure 2. The difference between the average angle of dances followed and the average angles of the dances performed subsequently by members of swarm 5 from the experiments of (Makinson et al. 2011).

Table 2
Magnitude and time intervals of maximum vectorial consensus for 15 min intervals for the five swarms studied by Makinson et al. (2011)

Swarm	Maximum vectorial consensus	Interval before take-off (min)
1	16.8892	45–30
2	11.6389	15–0
3	8.4377	30–15
4	2.7468	45–30
5	8.0596	15–0

have acquired from waggle dances and those that are simply disregarding waggle dances that they have followed. As a result we cannot filter the data to retain only the comparisons between following and dance angles for bees that genuinely tried to use dance information that they observed. Although the experimental data are not normally distributed, for the sake of simplicity we have retained the use of normally distributed random variables to determine dance and flight angles. For our simulations we set $\theta^\circ = 50^\circ$, close to the observed sample standard deviation.

Each time step of our numerical experiments is equivalent to 15 min of activity with all simulations being run for 40 time steps, which is equivalent to 10 h (approximately the period of time a swarm is active during 1 day) of on-swarm activity. Both stopping tests detailed in the Agent-based model section were used to determine whether a quorum or vectorial consensus was reached at some time during the 40 time steps, and if so, at what time. All model bees started in the resting state at time 0 unless otherwise stated. The first bees that become observers will not be able to find a dance to follow and thus become independent scouts. Independent scouts that find and like a nesting region will thus become the swarm's first dancers.

To estimate a threshold for vectorial consensus sufficient for a swarm to take-off, we examined vectorial consensus plots generated at 15 min intervals up to the time of take-off for all five swarms of Makinson et al. (2011). The peak magnitude of the consensus vector and the corresponding 15 min interval for which the peak occurred are recorded in Table 2. Four of the five swarms achieved a peak vectorial consensus magnitude greater than eight units. The swarm that did not surpass the eight-unit mark was the unusually inactive swarm 4. Therefore we chose a threshold of eight units to determine whether a swarm will take flight according to vectorial consensus. We also set the threshold for a successful on-swarm quorum to eight bees. In general it is easier for our model bees to reach a quorum-based decision than it is to reach a vectorial consensus-based decision.

What Parameters give Realistic Results?

By adjusting the parameters p_{observe}, p^i_{start}, p_{follow}, p_{pause}, p_{resume} and f_{search} we sought to emulate the on-swarm activity of swarm 5 studied by Makinson et al. (2011). All other parameters were held constant based on experimentally derived values ($p_{\text{visit}} = 0.23$, $p^i_{\text{cease}} = 0.3$, $\theta^\circ = 50^\circ$). We worked with a model swarm of size $N = 2700$, close to the size of swarm 5. We presented our model swarm with a single nesting region encompassing the entire available angular range from 0° to 360°. This simulated the environment in which the experiments of Makinson et al. (2011) were performed where there was an abundance of equally viable nesting sites in all directions. We performed 100 replicates for each set of parameter values.

Swarm 5's on-swarm behaviour was characterized by a large number of individuals following dances (572 followers in total) and a comparatively smaller number of bees that actually danced (32 in total). The fraction of instances of dance following that ultimately led to dancing at a closely related angle (within 30°) was very small. Furthermore, the data of Makinson et al. (2011) indicate that for swarm 5 approximately 34% of the bees that danced were recruited by following another bee's dance and that the other 66% became dancers because of other stimuli, probably independently scouting for sites.

We found that by setting $p_{\text{observe}} = 0.007$, $p^i_{\text{start}} = 0.01$, $p_{\text{follow}} = 0.6$, $p_{\text{pause}} = 0.3$, $p_{\text{resume}} = 0.3$ and $f_{\text{search}} = 0.35$, we produced a swarm that on average had 34.67% dancers that were recruited (sample standard deviation, 9.85%), 38.57 dancers in total (sample standard deviation, 5.3772) and 634.58 dance followers (sample standard deviation, 23.98). For the tuning experiments to determine the above parameters we set $p_{\text{mimic}} = 0$ and $p_{\text{survey}} = 0$. A very small arbitrary amount of noise was imposed on the dance direction of individuals from one time step to the next by setting $\phi^\circ = 3^\circ$. The parameter values used for all subsequent numerical experiments are listed in Table 3, including those derived from the tuning described in this section. Details of the sensitivity

Table 3
List of parameter values used in the agent-based model for numerical experiments described in the text

Parameter	Single region		Two regions/Mimicry	Surveyor		
	Variable p_{visit}	Variable θ°		Variable $p_{\text{visit}'}$	Variable $p_{\text{mimic}'}$	Variable p_{inhibit}
N	2700	2700	2700	2700	2700	2700
p_{observe}	0.007	0.007	0.007	0.007	0.007	0.007
p_{follow}	0.6	0.6	0.6	0.6	0.6	0.6
p_{visit}	**0 to 1.0**	0.23	0.23	0.23	0.23	0.23
p_{mimic}	0	0	**0/0.001 to 0.1**	0	0	0
p^i_{start}	0.01	0.01	0.01	0.01	0.01	0.01
p^i_{cease}	0.3	0.3	0.3	0.3	0.3	0.3
p_{pause}	0.3	0.3	0.3	0.3	0.3	0.3
p_{resume}	0.3	0.3	0.3	0.3	0.3	0.3
p_{survey}	0	0	0	0.4	0.4	0.4
$p_{\text{visit}'}$	0	0	0	**0 to 1.0**	0	0
$p_{\text{mimic}'}$	0	0	0	0	**0 to 1.0**	0
p_{inhibit}	0	0	0	0	0	**0 to 1.0**
f_{search}	0.35	0.35	0.35	0.35	0.35	0.35
f_{survey}	—	—	—	0.35	0.35	0.35
θ°	50°	**0° to 90°**	50°	50°	50°	50°
ϕ°	3°	3°	3°	3°	3°	3°
Ψ°	—	—	**—/0° or 50°**	—	50°	—

The parameters that vary within each set of simulations are shown in bold.

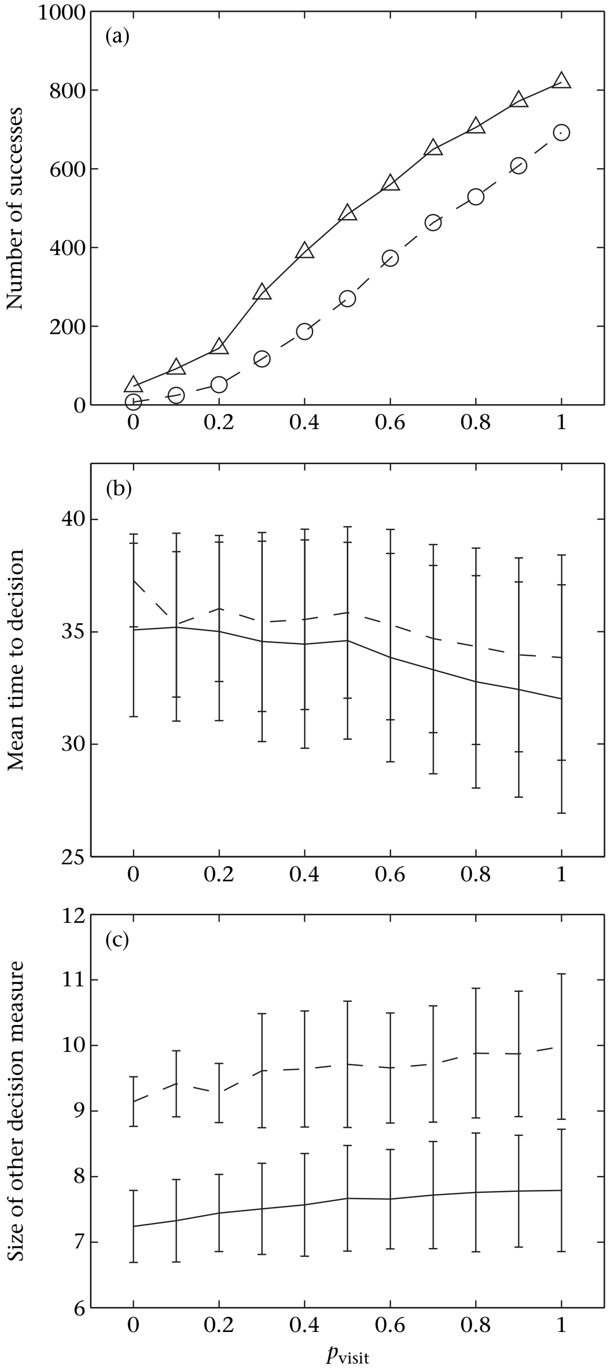

Figure 3. Results for single nesting region simulations in which the tendency to act on dance information, p_{visit}, was adjusted. All other parameters were the same as those provided in Table 3. 1000 simulations were performed for each value of p_{visit}, with 11 000 simulations performed in total. (a) Number of times that the swarm successfully decided to take flight according to the quorum stopping test (solid line, with discrete data points plotted as triangles) or the vectorial consensus stopping test (dashed line, with discrete data points plotted as circles). (b) Mean time to the quorum (solid line) and vectorial consensus (dashed line) decisions being made. (c) Mean magnitude of the consensus vector at the time of quorum (solid line) and mean number of bees dancing at the time of vectorial consensus (dashed line). In (b) and (c) means are given ± 1 SD. Means and standard deviations were calculated using results from all 1000 simulations for each set of parameter values.

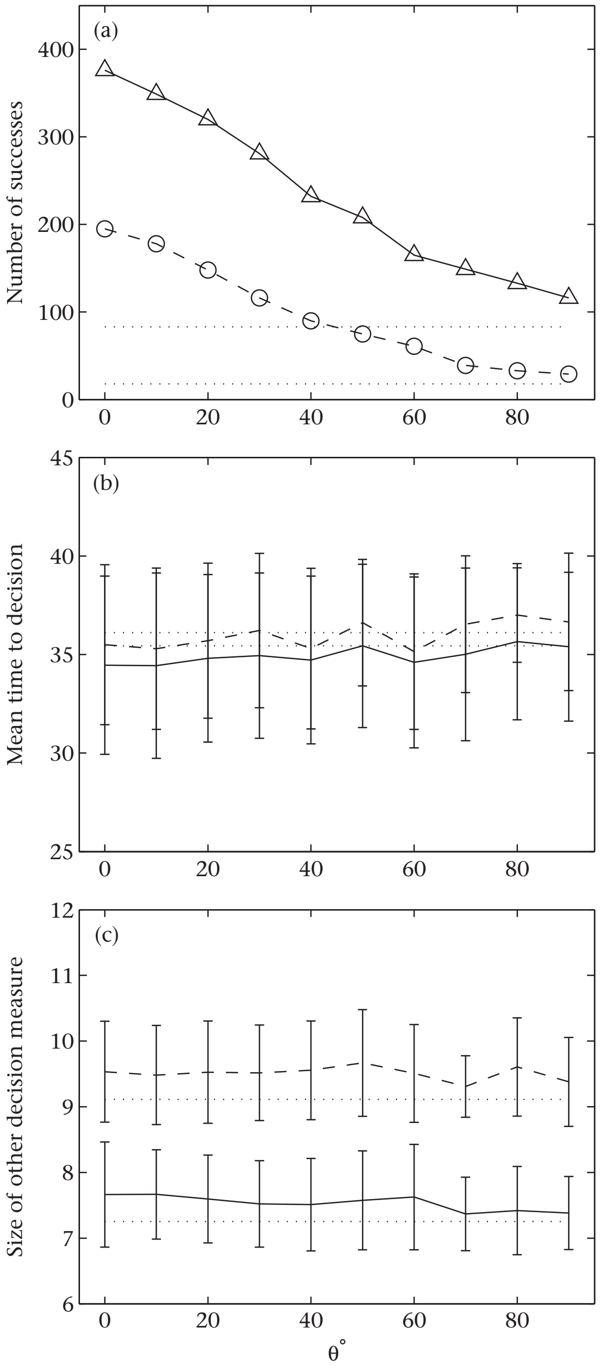

Figure 4. Results for single nesting region simulations in which the accuracy in using dance information, θ° was adjusted. All other parameters were the same as those provided in Table 3. 1000 simulations were performed for each value of θ°, with 11 000 simulations performed in total. (a) Number of times that the swarm successfully decided to take flight according to the quorum stopping test (solid line, with discrete data points plotted as triangles) or the vectorial consensus stopping test (dashed line, with discrete data points plotted as circles). (b) Mean time to the quorum (solid line) and vectorial consensus (dashed line) decisions being made. (c) Mean magnitude of the consensus vector at the time of quorum (solid line) and mean number of bees dancing at the time of vectorial consensus (dashed line). In (b) and (c) means are given ± 1 SD. The dotted lines that appear in all of the diagrams correspond to the set of results where bees that followed a dance and then sought out the advertised site fly in a random direction uniformly distributed between 0° and 360°. Note that an increase in θ° indicates a decrease in the accuracy of dance information use. Means and standard deviations were calculated using results from all 1000 simulations for each set of parameter values.

of the model to small variations in the tuned parameters around the values in Table 3 are provided in Appendix 3.

The values of the experimental and tuning-based parameters given in Table 3 describe a model swarm that is made up of individuals that are reluctant to seek out advertised sites, inaccurate in using dance information, disinclined to dance for a site even if they manage to find it and unlikely to persist in dancing for a site for an extended period of time. In the following sections we scrutinize the capacity of such a swarm to make a decision when nesting options are restricted to only certain surrounding sectors.

Frequency and Accuracy of Dance Information Use

Here we examine the ability of a swarm to make a decision when the available nest sites are confined to a single arc of trees that cover an angular range of 100°. The viable nesting region always lies between the bearings of −30° and 70°. We adjusted the tendency of individuals to seek out sites based on dances that they have followed, p_{visit}, and their accuracy in using dance information, $\theta°$, independently. All other parameters were kept constant in each set of simulations at the values in Table 3. The parameter p_{visit} ranged between 0 and 1.0 in increments of 0.1 and $\theta°$ ranged between 10° and 90° in increments of 10°. We also performed sets of simulations in which bees that followed a dance searched in precisely the direction indicated by the dance (that is, with $\theta^{\circ} = 0^{\circ}$) and in which the direction that a bee flies after following a dance is uniformly randomly distributed between 0° and 360°. The last case corresponds to bees not making use of any directional information contained in a waggle dance, and effectively acting as independent scouts. We identified all the swarms that were successful in passing either, or both, of the quorum and vectorial consensus thresholds and the time at which they first passed these thresholds (measured in time steps rather than minutes). For every successful quorum-based decision we measured the magnitude of the consensus vector at the time of quorum, and for every successful vectorial consensus-based decision we measured the number of bees dancing at the time of consensus, to compare the relative magnitudes of the two decision measures. The single nesting region simulation results are plotted in Figs 3 and 4. In these figures a 'success' is simply having passed one of the two stopping tests.

In general, increasing p_{visit} or decreasing $\theta°$ increased the ability of the swarm to reach a decision (Figs 3a, 4a). The consensus vector always pointed within the nesting region when either quorum or vectorial consensus was reached, so that the model predicts that the swarm will always set off towards a site within the nesting region once the decision to take-off has been made. Unsurprisingly, the number of quorum-based successful decisions exceeded the number of vectorial consensus-based successful decisions (Figs 3a, 4a). Forming a vectorial consensus is more difficult because it requires not only sufficient dancing bees but also good agreement among the angles danced. The time to reach quorum is consistently lower than the time to reach vectorial consensus (Figs 3b, 4b). The

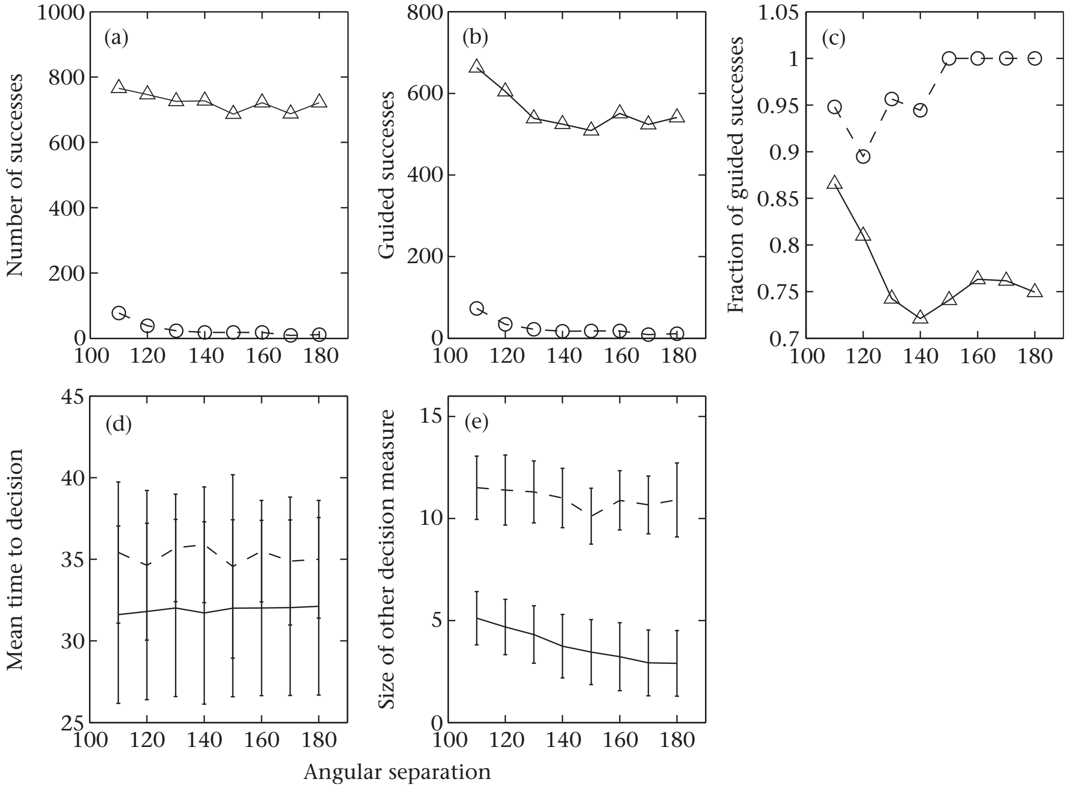

Figure 5. Results for two nest site simulations in which model bees were presented with two nest sites of equal quality and equal angular range. 1000 simulations were performed for each placement of nesting regions, with 8000 simulations in total performed for this set of experiments. (a) Number of times that the swarm successfully decided to take flight according to the quorum stopping test (solid line, with discrete data points plotted as triangles) or the vectorial consensus stopping test (dashed line, with discrete data points plotted as circles). (b) Number of times the swarm reached a nest site using the quorum stopping test (solid line, with discrete data points plotted as triangles) or the vectorial consensus stopping test (dashed line, with discrete data points plotted as circles). (c) Proportion of successful decisions that resulted in guided successes for the quorum (solid line, with discrete data points plotted as triangles) and vectorial consensus (dashed line, with discrete data points plotted as circles) models. (d) Mean time to the quorum (solid line) and vectorial consensus (dashed line) decisions being made. (e) Mean magnitude of the consensus vector at the time of quorum (solid line) and mean number of bees dancing at the time of vectorial consensus (dashed line). In (d) and (e) means are shown ± 1 SD. The horizontal axis for all the diagrams corresponds to the angular separation between the two possible nesting regions. Means and standard deviations were calculated using results from all 1000 simulations for each set of parameter values.

number of bees dancing at the time of vectorial consensus usually exceeds the quorum threshold of eight and the consensus vector is often below the threshold value at the time of quorum (Figs 3c, 4c). These two results are consistent with the additional complexity involved in forming a vectorial consensus. Adjusting p_{visit} or θ° does not drastically alter the mean time to make a decision, but higher values of p_{visit} (which correspond to a greater tendency to act on dance information) tend to correspond to a slightly decreased decision time (Figs 3b, 4b). Using parameter values identical to those obtained from tuning and experimental data ($p_{\text{visit}} = 0.23$, $\theta^\circ = 50^\circ$) resulted in the swarm making 208 of 1000 successful decisions in a mean time of 35.44 time steps according to the quorum-based stopping test (20.8% success rate) and 75 of 1000 successful decisions in a mean time of 36.61 time steps according to the vectorial consensus-based stopping test (7.5% success rate). In contrast, when a much larger nesting region was presented (which filled the entire 360° range during the tuning experiments) 99 of 100 quorum-based decisions were successful in a mean time of 25.24 time steps (99% success rate) and four of 100 vectorial consensus decisions were successful in a mean time of 36 time steps (4% success rate). The low success rates in meeting either the quorum or vectorial consensus thresholds suggests that our model bees have a limited capacity to make a decision and that another mechanism other than the rate of recruitment, which is observed to be low, is required for the swarm to succeed in making a group decision within the course of a day.

Can A. florea *Choose between Two Regions of Equal Size?*

We next presented our bees with two equally attractive nesting regions ($p^1_{\text{start}} = p^2_{\text{start}} = 0.01$ and $p^1_{\text{cease}} = p^2_{\text{cease}} = 0.3$) of equal angular extent. Each nesting region corresponded to an arc of trees filling an angular range of 100°. The first region always filled the angular range from a bearing of −30° to a bearing of 70° (centred about a bearing of 20°). The position of the second region was adjusted by changing the angular separation between its centre and the centre of the first region. Angular separation between the two nesting region centres was adjusted between 110° and 180° in increments of 10°. These angular differences were always measured anticlockwise relative to the centre of the first region located at a bearing of 20°. As before, all simulations were performed for 40 time steps. The parameter values are given in Table 3. It was not as likely that the consensus vector would always point inside one of the suitable nesting regions as it was for the single nesting region simulations. If the vector points outside one of the nesting regions, then the swarm will not find a nest site after it has taken off, if we assume that it is guided by the dancers that rely only on dance angle information for direction. Hence, we measured the number of times that the consensus vector points inside a suitable nesting region. The swarm achieved a 'guided success' if it made a decision to take-off, and the consensus vector pointed within one of the two nesting regions.

Figure 5 plots the results of the two nesting region experiments. With the greater range of suitable nest sites, the ability of the swarm to make a decision to take-off according to the quorum-based stopping test is mostly higher than for the single nest site experiments (Fig. 5a). The ability of the swarm to make a decision to take flight based on vectorial consensus is generally poor, and it declines as the angular separation between the centres of the two nesting regions increases (Fig. 5a). This is because the contributions to the consensus vector from bees dancing in directions that are separated by close to 180° will almost completely cancel each other out. The fraction of quorum-based decisions that result in a guided

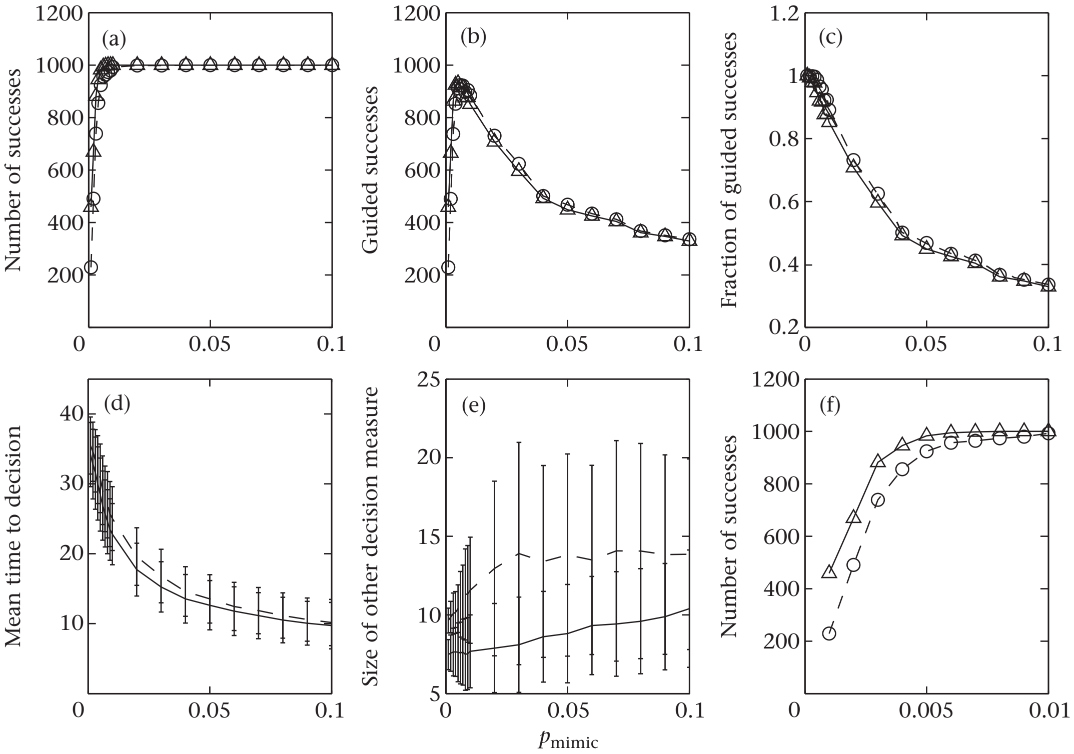

Figure 6. Results for mimicry simulations in which mimics initially dance at exactly the same angle as that of the dancer that they followed. All but one bee started in the resting state for these simulations. The lone bee not resting was initially set to dance at a bearing of 200°, which is an angular difference of 180° to the suitable nesting region. 1000 simulations were performed for each value of p_{mimic}, with 19 000 simulations performed in total. The horizontal axes all correspond to p_{mimic} and the vertical axes all represent identical quantities to those in (a) to (e) of Fig. 5. (f) Detail of the sloped region of (a) over a subset of the values of p_{mimic} that were used. Means and standard deviations were calculated using results from all 1000 simulations for each set of parameter values.

success diminishes as the angular separation between the nesting regions widens, dropping from over 85% to approximately 75% as the separation increases from 110° to 140° (Fig. 5c). The fraction of vectorial consensus decisions that result in guided success is continually high, always remaining above 89% (Fig. 5c). Overall, a decision to take flight is more likely to be made when it is based solely on the number of bees dancing on the swarm, but the swarm is more likely to be guided in a wrong direction, especially if the separation between the two available nesting regions is large. The decision time for either stopping criterion is not greatly affected by the angular separation of the nesting regions (Fig. 5d).

There is a downward trend in the magnitude of vectorial consensus at the time of quorum, as the angular separation between the nesting regions increases. Again this can be attributed to the effective cancellation of contributions to the consensus vector from bees that dance in opposite directions (Fig. 5e).

What are the Effects of Mimicry on Speed and Accuracy?

Here we examine the effects of varying the probability of directly mimicking dances, p_{mimic}, from 0.001 to 0.01 in increments of 0.001 and from 0.01 to 0.1 in increments of 0.01.

We presented the bees with a single nesting region identical to that used for the single nesting region simulations in the section Frequency and Accuracy of Dance Information Use with an angular range of 100° confined between the bearings of −30° and 70°. We allowed the mimicry of dances to occur in two different ways. In the first case, if a bee decided to mimic the dance of a bee that it had just followed then it would start to dance at exactly the same angle as that of the dance followed. This means that there was more accuracy in the transmission of mimicked dancing when bees did not leave the swarm than when a bee sought out a site before returning to the swarm to dance (which is controlled by θ° in our model). In the second case, we forced mimics to be just as imprecise in perpetuating angular information as bees that independently verified the presence of a nest site by setting $\Psi^{\circ} = 50^{\circ}$. All other parameter values were identical to those used for the two nesting region simulations (see Table 3).

We performed four sets of mimicry calculations. The first two sets of simulations studied the propagation of an error through the system when mimicry is performed with either total precision in the first set or the imprecision defined by Ψ°. The initial condition for the first two sets of simulations had all but one of the 2700 bees in the swarm starting in the resting state. To start an error in the system, we set the remaining bee to dance at a bearing of 200° at the start of each simulation, which is an angular difference of 180° to the centre of the only suitable nesting area. The third and fourth sets of simulations were initialized with all bees in the resting state, the same as the one and two nesting region experiments of previous sections. Mimicry was performed with total precision in the third set and imprecisely in the fourth set.

Figure 6 illustrates the results of the sets of simulations in which mimics initially danced at exactly the same angle as the dancer that they followed and one bee initially danced in an erroneous direction. The effects of mimicry on the ability of the swarm to make a decision to take flight, based on either the quorum or vectorial consensus stopping tests, were dramatic. There was a 100% success rate in making a decision by either measure for values of p_{mimic} of 0.04 and above (Fig. 6a), and the

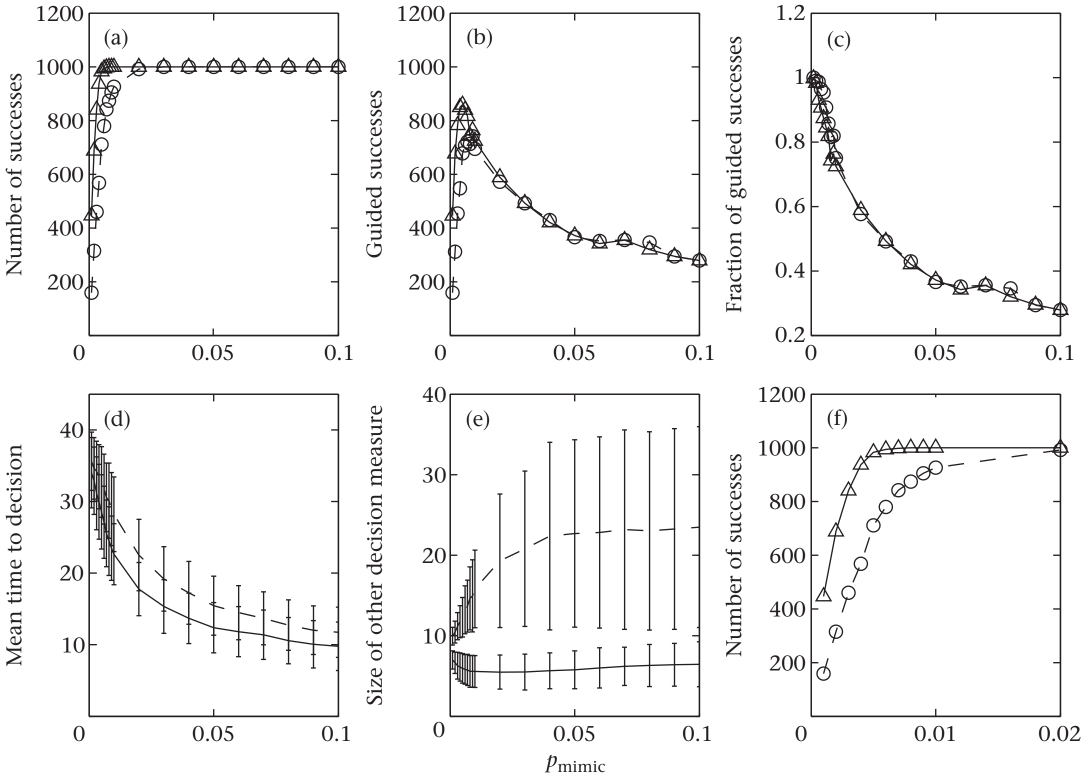

Figure 7. Results for mimicry simulations in which mimics initially dance at a random angle which is normally distributed, has mean equal to that of the dance being mimicked and standard deviation $\Psi^{\circ} = 50^{\circ}$. All but one bee started in the resting state for these simulations. The lone bee not resting was initially set to dance at a bearing of 200°, which is an angular difference of 180° to the suitable nesting region. 1000 simulations were performed for each value of p_{mimic}, with 19 000 simulations performed in total. The horizontal axes all correspond to p_{mimic} and the vertical axes all represent identical quantities to those in (a) to (e) of Figs 5 and 6. (f) Detail of the sloped region of (a) over a subset of the values of p_{mimic} that were used. Means and standard deviations were calculated using results from all 1000 simulations for each set of parameter values.

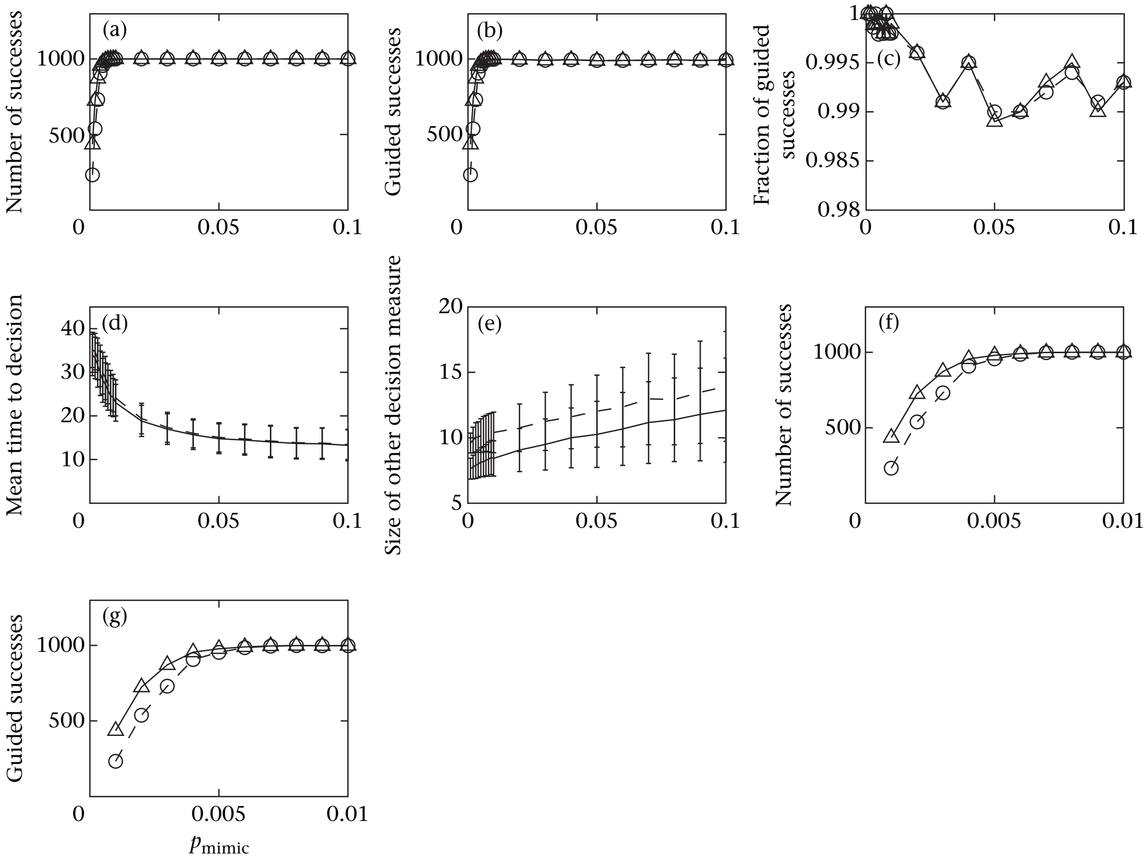

Figure 8. Results for mimicry simulations in which mimics initially dance at exactly the same angle as that of the dancer that they followed. All bees started in the resting state for these simulations. 1000 simulations were performed for each value of p_{mimic}, with 19 000 simulations performed in total. The horizontal axes all correspond to p_{mimic} and the vertical axes all represent identical quantities to those in (a) to (e) of Figs 5–7. (f) and (g) Detail of the sloped regions of (a) and (b), respectively, over a subset of the values of p_{mimic} that were used. Means and standard deviations were calculated using results from all 1000 simulations for each set of parameter values.

time to make the decision by both measures was vastly reduced in comparison to the previous one and two nesting region simulations (Fig. 6d). However, in a proportion of cases the swarm was not guided to a suitable nest site. For $p_{\text{mimic}} = 0.04$, less than 51% of the swarms would have been guided to somewhere within the only suitable nesting region (Fig. 6c). Similar results can be seen in Fig. 7 where mimics initially danced at random angles centred about the angle of the dance that they followed and one of the swarm initially danced in an erroneous direction. Up to 43% of the swarms with $p_{\text{mimic}} = 0.04$ would have landed somewhere within the suitable nesting area (Fig. 7c).

The lack of independent verification of nest sites associated with mimicry means that a very bad error, such as that produced by our bee initially dancing at an angle of 200°, has the potential to propagate and amplify in our system. In the absence of the initial, very wrong, dancer our model bees perform much better when they are allowed to mimic other bees' dances, as illustrated in Figs 8 and 9. The success rate of making a decision by passing the quorum and vectorial consensus thresholds was 100% for values of p_{mimic} equal to 0.009 and above when precise mimicry is employed (see Fig. 8a). For $p_{\text{mimic}} \geq 0.009$ with precise mimicry, 98.9% or more of the swarms would have been guided to somewhere inside the suitable nesting region (Fig. 8c). When mimics were as inaccurate in using dance information as educated scouts, values of p_{mimic} of 0.009 or higher resulted in 100% success in passing the quorum threshold; values of $p_{\text{mimic}} \geq 0.05$ resulted in 100% of the model swarms making a decision according to the vectorial consensus threshold (see Fig. 9a). More than 70% of the swarms with imprecise mimicry would have flown somewhere within the suitable nesting region after taking flight (Fig. 9c). As with the mimicry experiments that utilized an initially erroneous dancer, mimicry reduced the amount of time required to make a decision when there was no initial error (Figs 8d, 9d).

Self-inhibition and Direct Switching

Does the presence of surveyor bees enhance the model swarm's capacities to reach vectorial consensus? We presented our bees with a single nesting region which occupied the same region as for the single nesting region experiments in the sections Frequency and Accuracy of Dance Use and What are the Effects of Mimicry on Speed and Accuracy? The parameters associated with the quality of the region were set as $p^i_{\text{start}} = 0.01$ and $p^i_{\text{cease}} = 0.3$. We set the probability of individual bees making the transition from the paused state to the surveyor state as $p_{\text{survey}} = 0.4$ so that paused bees will always move out of the paused state in the next time step of a simulation. (Since $p_{\text{resume}} = 0.3$ and $p^i_{\text{cease}} = 0.3$, it follows that the probability of remaining in the paused state $1 - p_{\text{resume}} - p^i_{\text{cease}} - p_{\text{survey}} = 0$.) Only one of the potential changes in behaviour was available to swarm surveyors in each of the three sets of experiments that we performed.

In the first set of experiments we examined the effect of self-inhibitory behaviour among surveyors by setting $p_{\text{visit}'} = 0$, $p_{\text{mimic}'} = 0$ and varying p_{inhibit} between 0 and 1 in steps of 0.1. The presence of self-inhibition had little effect on the ability of the swarm to make a consensus-based decision although at higher

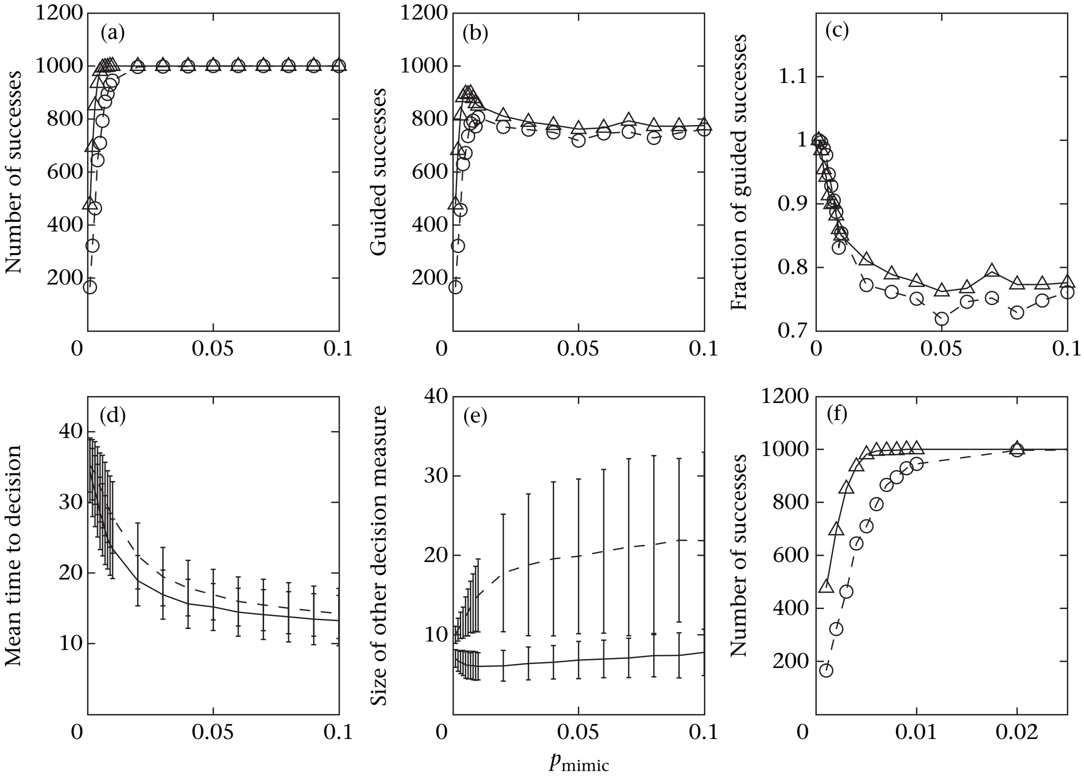

Figure 9. Results for mimicry simulations in which mimics initially dance at a random angle which is normally distributed, has mean equal to that of the dance being mimicked and standard deviation $\Psi^{\circ} = 50^{\circ}$. All bees started in the resting state for these simulations. 1000 simulations were performed for each value of p_{mimic}, with 19 000 simulations performed in total. The horizontal axes all correspond to p_{mimic} and the vertical axes all represent identical quantities to those in (a) to (e) of Figs 5–8. (f) Detail of the sloped region of (a) over a subset of the values of p_{mimic} that were used. Means and standard deviations were calculated using results from all 1000 simulations for each set of parameter values.

levels it seemed to affect the ability to reach quorum-based decisions (see Fig. 10a). One reason why the presence of inhibition had little effect was that generally there are very few bees dancing at any given time step. If one or two bees remove themselves from dancing, then the length of the consensus vector will not necessarily increase because of the removal of some dissent, but the small number of bees dedicated to any site will be reduced by a relatively large portion. There is also likely to be a reduction in the number of bees dancing and the magnitude of the consensus vector, as surveyors are not actively involved in advertising their sites while they are watching other bees on the swarm.

In the next set of experiments we examined the effect of allowing bees the possibility of switching their allegiance to another advertised direction by setting $p_{\text{inhibit}} = 0$, $p_{\text{mimic}'} = 0$ and varying $p_{\text{visit}'}$ between 0 and 1 in steps of 0.1. Again, the main effect was a reduction in the ability of the swarm to make a quorum-based decision without any improvement in the ability to make a vectorial consensus-based decision (see Fig. 11a). This result is expected as the parameters currently used in our model make it difficult to generate educated dancers. Given the high level of inaccuracy with which bees utilize dance information, it is not certain whether they will even find the suitable nesting region, and then, if they do find it, the probability that they will come back and dance for it is very small. Many of the bees that are encouraged to inspect a nest site other than the one that they are currently devoted to end up returning to the observer state rather then being re-recruited to dance for a new site.

In the final set of surveyor-related experiments, we observed the effects of allowing only our surveyors the ability to mimic other bees' dances. For these experiments we set $p_{\text{inhibit}} = 0$, $p_{\text{visit}'} = 0$ and varied $p_{\text{mimic}'}$ between 0 and 1 in steps of 0.1. The general trend of the results is that as $p_{\text{mimic}'}$ increases, the ability of the swarm to make quorum-based decisions increases and there also seems to be some improvement in the ability of the swarm to make a consensus-based decision (see Fig. 12a). The average time to pass the threshold of either decision-making measure is not affected by variations in $p_{\text{mimic}'}$ (Fig. 12b).

Consensus-building Mechanisms with Two Nesting Regions

The ability of our model swarm to make a decision in the presence of two nesting regions of equal quality is low when the decision to take flight is based on vectorial consensus (see Can *A. florea* Choose between Two Regions of Equal Size?). When the suitable nesting region filled the entire 360° of the domain, the ability of the swarm to make a vectorial consensus-based decision was also very poor. Here we briefly revisit the two-region experiments to see whether either mimicry or self-inhibition by surveyors can improve the ability of the swarm to make a decision. We performed three experiments with the centres of the nesting regions separated by 170°, which was the angular separation that resulted in the lowest number of successful vectorial consensus-based decisions originally (only nine). We ran 1000 simulations for each set or parameters used. In the first experiment we set $p_{\text{mimic}} = 0.007$ while keeping all other parameter values the same as those listed for the two-region experiments in Table 3. The number of vectorial consensus-based decisions rose to 670, 503 of which indicated a direction inside one of the nesting regions. In the second experiment we allowed bees the ability to become surveyors by setting $p_{\text{survey}} = 0.4$, and allowed surveyors the ability to remove themselves from the decision-making process by setting

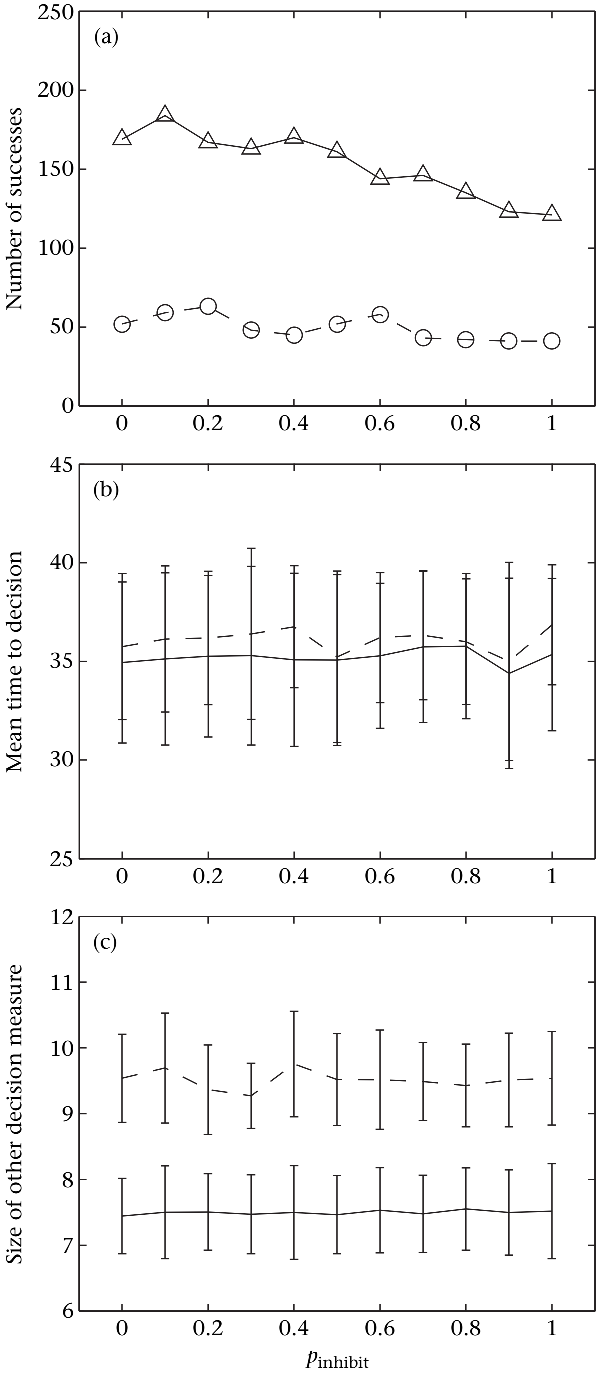

Figure 10. Results for single nesting region simulations in which the tendency for surveyor bees to inhibit their own behaviour after observing other bees on the swarm, p_{inhibit}, was adjusted. All other parameters were the same as those provided in Table 3. 1000 simulations were performed for each value of p_{inhibit}, with 11 000 simulations performed in total. (a) Number of times that the swarm successfully decided to take flight according to the quorum stopping test (solid line, with discrete data points plotted as triangles) or the vectorial consensus stopping test (dashed line, with discrete data points plotted as circles). (b) Mean time to the quorum (solid line) and vectorial consensus (dashed line) decisions being made. (c) Mean magnitude of the consensus vector at the time of quorum (solid line) and mean number of bees dancing at the time of vectorial consensus (dashed line). In (b) and (c) means are given ± 1 SD. Means and standard deviations were calculated using results from all 1000 simulations for each set of parameter values.

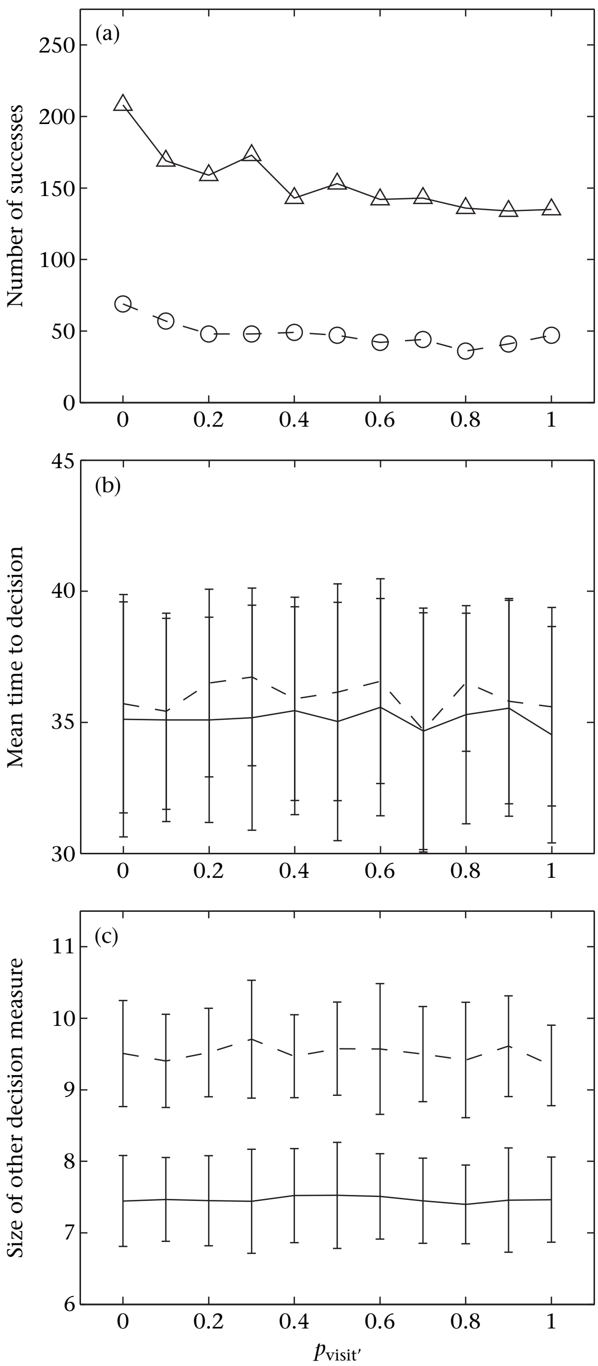

Figure 11. Results for single nesting region simulations in which the tendency for surveyor bees to seek out sites advertised by other dancers on the swarm, $p_{\text{visit}'}$, was adjusted. All other parameters were the same as those provided in Table 3. 1000 simulations were performed for each value of $p_{\text{visit}'}$, with 11 000 simulations performed in total. (a) Number of times that the swarm successfully decided to take flight according to the quorum stopping test (solid line, with discrete data points plotted as triangles) or the vectorial consensus stopping test (dashed line, with discrete data points plotted as circles). (b) Mean time to the quorum (solid line) and vectorial consensus (dashed line) decisions being made. (c) Mean magnitude of the consensus vector at the time of quorum (solid line) and mean number of bees dancing at the time of vectorial consensus (dashed line). In (b) and (c) means are given ± 1 SD. Means and standard deviations were calculated using results from all 1000 simulations for each set of parameter values.

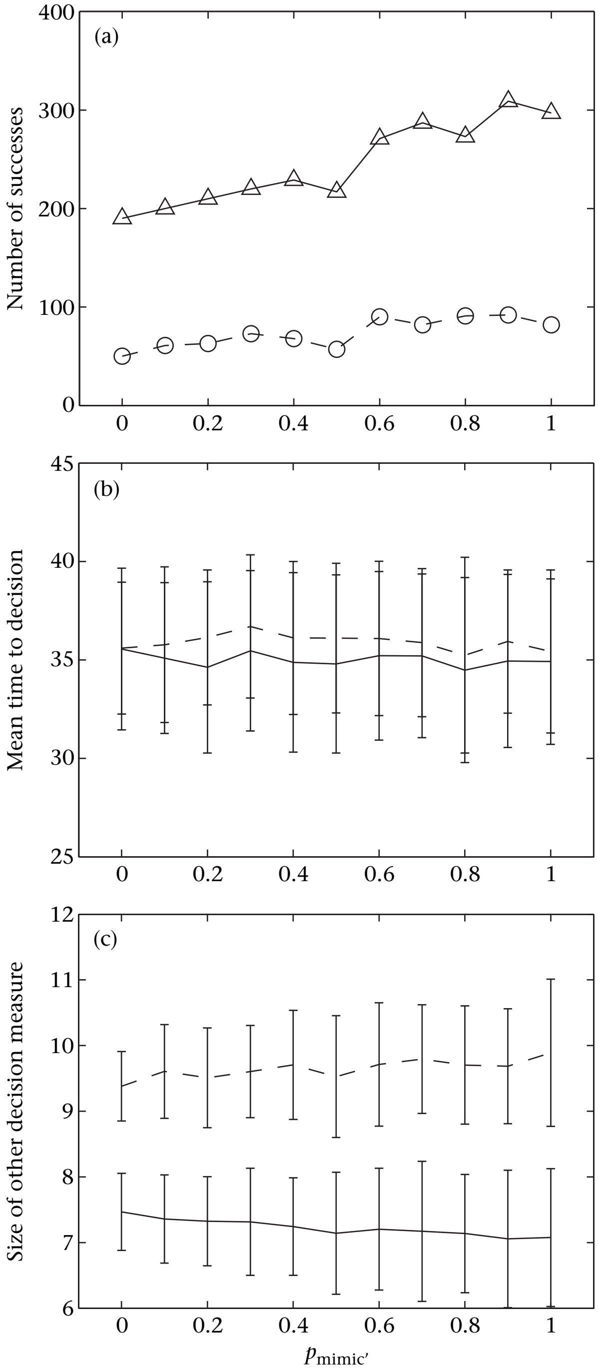

Figure 12. Results for single nesting region simulations in which the tendency for surveyor bees to mimic dances produced by other dancers on the swarm, $p_{\text{mimic}'}$, was adjusted. All other parameters were the same as those provided in Table 3. 1000 simulations were performed for each value of $p_{\text{mimic}'}$, with 11 000 simulations performed in total. (a) Number of times that the swarm successfully decided to take flight according to the quorum stopping test (solid line, with discrete data points plotted as triangles) or the vectorial consensus stopping test (dashed line, with discrete data points plotted as circles). (b) Mean time to the quorum (solid line) and vectorial consensus (dashed line) decisions being made. (c) Mean magnitude of the consensus vector at the time of quorum (solid line) and mean number of bees dancing at the time of vectorial consensus (dashed line). In (b) and (c) means are given ± 1 SD. Means and standard deviations were calculated using results from all 1000 simulations for each set of parameter values.

$p_{\text{inhibit}} = 0.1$. There were 18 of 1000 successful vectorial consensus-based decisions for the swarms with self-inhibiting surveyors, all of which indicated a direction inside one of the nesting regions. Finally, we again allowed for surveyor bees by setting $p_{\text{survey}} = 0.4$ but this time allowed the surveyors the ability to mimic observed dances with $p_{\text{mimic}'} = 0.9$. The surveyor-mimics achieved 47 successful vectorial consensus-based decisions, 45 of which indicated somewhere within the suitable nesting regions.

DISCUSSION

Our simulations suggest that the availability and distribution of suitable nest sites has an important effect on the ability of swarms of *A. florea* to make a decision during the nest site selection process. When placed in an environment in which nesting options are restricted, a model swarm of *A. florea* will find it more difficult to make a collective decision based on an on-swarm quorum but less difficult to make a decision based on vectorial consensus (see Frequency and Accuracy of Dance Information Use). This difficulty in making a decision can be associated with inaccuracy in using dance information and the low tendency of individuals to make use of information from observed dances. When model bees used dance information more accurately or more frequently they were more capable of making a decision. This was due to a greater number of bees flying into the range of the suitable nesting region, either because individuals had a greater tendency to act on information and take flight or because they were more accurate and therefore more likely to find an advertised site. Ultimately a large number of bees flying into the suitable nesting region by either mechanism results in a higher overall probability of the swarm producing dancers than if only a small number of bees found the nesting region.

Both our single and two nesting region experiments show that it is not necessary for *A. florea* to distinguish between the quality of individual tree branches in regions of foliage or to distinguish between the quality of multiple regions of foliage to make a decision. However, some form of agreement about the general direction of travel is important. If the threshold for the swarm to take-off is based solely on the number of dancers on the swarm it is possible that the swarm could be guided in an incorrect direction. As shown in our two nesting region experiments, a decision based on both the number of dancers and some form of directional agreement results in a higher probability of the swarm finding a site once they have taken flight (see Can *A. florea* Choose between Two Regions of Equal Size?, Fig. 5). The observations of Makinson et al. (2011) support the idea that both a threshold number of dancers and some directional agreement are formed in real swarms of *A. florea*.

Although it is not yet known whether real *A. florea* bees distinguish between the quality of different nest sites, it is at least important for individuals to verify the existence of suitable sites in a particular direction. This is illustrated by our simulations with mimicry in which an initial erroneous dancer is included. In these simulations the quality of decisions about which direction the swarm should fly diminished with an increasing probability that individuals would mimic dances, and thus not independently check advertised sites (see What are the Effects of Mimicry on Speed and Accuracy?, Figs 6, 7). When there was no initial error, swarms that included mimics were highly successful in making a decision by either stopping criterion (Figs 8, 9). The precision of dance mimicry also had an effect on the swarm's direction of flight. Swarms that contained precise mimics had a 99% or higher probability of flying to somewhere inside the suitable nesting region, but those with inaccurate mimics arrived in the suitable nesting region less than 72% of the time. If mimicry does occur in real swarms it is probably at relatively low levels, but even at low levels it can potentially have a powerful effect. There is potential to include effects of mimicry in analytical models, such as the differential equation model of Britton et al. (2002) by the addition of an extra recruitment term at a rate proportional to the number of bees already committed to a site, but with a rate constant that is independent of the quality of the site. The same modification could be made to the model of Marshall et al. (2009) and mimicry could be incorporated into the model of Nevai et al. (2010) by allowing bees to flow directly from the observer state to the assessor state.

Mimicry is a recruitment-based mechanism for increasing activity and agreement among members of a swarm. The observed rates of recruitment within *A. florea* swarms are relatively low but swarms reach a general agreement about direction prior to take-off. The underlying mechanism of the bee's perception that this agreement has been reached is not known. We examined two potential mechanisms where dancing bees adjust their own behaviour after observing the dance behaviour of other bees on the swarm, either by inhibiting their own dances or by switching allegiance to a direction advertised by another bee (Self-inhibition and Direct Switching, Figs 10–12). Although the effects of self-inhibition seemed to be small, it is possible that such a mechanism could play a more prominent role in removing dissent when there are many bees dancing on the swarm. Switching allegiance via mimicry did improve our swarms' overall decision-making ability.

There are still many unanswered questions regarding the nest site selection process of *A. florea*. It is assumed that *A. florea* dancers have visited potential nest sites prior to dancing, but there is no explicit evidence for this. *Apis florea* exhibits a high degree of variability when dancing for forage or a new home (Beekman et al. 2008), and this could be interpreted as an inability to communicate accurately via the dance language. It could be that *A. florea* has no need for the greater precision that is observed in *A. mellifera*, given an abundance of nest sites, so that it suffices if dancers describe regions rather than precise points in their dances. Our simulations suggest that if the area of available nest sites is restricted, then a swarm will find it more difficult to make a decision based on the overall number of dancers but will be more capable of making a decision that takes into account the directions that dancers advertise (see Frequency and Accuracy of Dance Information Use). Observing the nest site selection process of real swarms of *A. florea* with restricted nesting options will shed light on whether or not they do find decision making more difficult in those circumstances. It would also be of interest to compare the variability of dance angles produced by individual bees in environments with limited nesting options versus those in environments with a wealth of nesting options.

Our results support the hypothesis (Makinson et al. 2011) that the nest site selection process in honeybees has been shaped by the species' nest site requirements. While *A. mellifera* requires cavities with specific characteristics that may be difficult to locate, an *A. florea* swarm can choose from a large number of sites that are more or less equal in quality. The presence or absence of near-consensus on the direction in which the swarm needs to fly can have a profound effect on swarm guidance. When the swarm needs to move to a specific location, agreement prior to lift-off seems essential for successful guidance. However, if the exact location is of lesser importance, a swarm can achieve an 'in-flight' collective agreement and settle for the average direction advertised by all scouts prior to lift-off (Diwold et al. 2011). This suggests that the decision-making process in *A. florea* could continue into the swarm's flight and that the earlier on-swarm nest site selection process acts as a means of sampling the environment to locate regions with many nesting opportunities.

Previous studies of collective movement (Couzin et al. 2005) show that if the main desired outcome is for the group to remain intact as it moves, that outcome can be met even with some dissent among individuals about a preferred direction of travel. However, when the direction of travel is decided while on the move, successful guidance is possible only if the group does not need to move to a specific location. If the exact location is vital, groups should initiate movement only once the specific direction of travel has been agreed on. There is evidence in *Macaca tonkeana* and *A. mellifera* of mechanisms that remove dissenting votes or dances in a group's predeparture period, which can be related both to the need to retain group cohesion and the desire to travel to an exact location. In *M. tonkeana* the decision to move is based on the total number of votes that are cast by group members passing a threshold, and the ultimate direction of movement is the direction that receives the most votes. However, after the decision, and before the group moves, all members of the group that were voting for a losing direction either give up voting any further, or they adjust their vote to agree with the winning direction. Only when dissent is removed from the group do they actually move (Sueur et al. 2010). Such expiration of dissent is also evident in *A. mellifera*, where it has been frequently observed that in the period just prior to lift-off only one nest site is advertised by the remaining dancers (Seeley & Buhrman 1999; Seeley 2003). The apparent consensus among *A. mellifera* dancers predeparture may be the result of dance decay causing dancers for less favourable sites to drop out of the decision-making process more quickly. *Apis florea* swarms, however, continue to advertise multiple sites predeparture (Makinson et al. 2011). This advertisement of multiple sites implies that the goal of an *A. florea* swarm may be not to choose a specific location, but rather to create enough informed individuals to retain group cohesion during flight. Our results suggest that, provided areas that contain suitable sites are abundant, a group does not need to agree completely before departure and can still decide on the exact location while en route. It is thus plausible that the decision-making process of *A. florea* may be mainly aimed at coordinating a time of lift-off and agreeing on a general direction without the concerns of choosing the best of all available sites.

Acknowledgments

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Appendix 1

Flow Charts of Other Agent-based Models

Figures A1–A3 contain flow charts showing the connection between states for individual agents in the models of Passino & Seeley (2006), Janson et al. (2007) and List et al. (2009), respectively.

Appendix 2

Convergence of Results

In choosing the number of simulations to be performed for each data point we sought to balance the reliability/accuracy of our results against the amount of time required to perform our numerical experiments. For reference, the time to complete 1000 simulations (the number of simulations that we ultimately performed for one set of parameter values) was approximately 1 h. To examine the effect that the number of simulations could have on our results we performed the numerical experiment where p_{visit} was varied (described in Frequency and accuracy of dance information use) with 10, 100, 1000 and 10 000 iterates per parameter set. The proportion of successful decisions made according to the quorum and vectorial consensus stopping tests is illustrated in Fig. A4. The most variable output came from the sets of simulations with 10 iterates per set of parameter values (black lines), where the proportion of successes oscillated across different values of p_{visit}. The underlying increase in the proportion of successful decisions as p_{visit} increases was already readily apparent with 100 iterates per set of parameter values (red), with the results from 1000 simulations (blue) and 10 000 simulations (green) per parameter set most closely matching each other. Ultimately it would have been sufficient to perform only 100 simulations per set of parameter values to determine the underlying trends of the system as different parameters were varied. However, we opted to seek more accurate results using 1000 simulations per set of parameters. For reference, Passino & Seeley (2006) performed 100 simulations per set of parameters in their agent-based model study of nest site selection by *A. mellifera*.

Appendix 3

Sensitivity to Adjustment of Parameters

The parameter values for p_{observe}, p^{i}_{start}, p_{follow}, p_{pause}, p_{resume} and f_{search} were determined by a preliminary series of tuning experiments in which we sought to generate the same proportion of recruited dancers as those seen in a real *A. florea* swarm as well as similar numbers of dancers and followers. Here we examine the sensitivity of the proportion of recruited dancers, the total number of dancers and the total number of followers to small changes in the tuned parameters centred around the values that we ultimately used for our main numerical experiments. The set-up for the sensitivity analysis simulations was identical to the tuning experiments discussed in What Parameters give Realistic Results? We performed 100 simulations per set of parameter values. Figure A5 illustrates the effect of varying each of the tuned parameters on the proportion of dancers who were successfully recruited to dance by another bee's dance. Figure A6 illustrates the effect of varying each of the tuned parameters in turn on the total number of dancers, and Fig. A7 illustrates the effects of varying the tuned parameters on the total number of followers. Dashed horizontal lines in each of the figures represent the values of each quantity seen in swarm 5 of the study of Makinson et al. (2011). For each figure, all tuned parameter values are identical to those listed in Table 3 with the exception of one parameter that was varied in each panel.

In general, increasing any of the tuned parameters, with the exception of p_{pause}, increases the proportion of dancers that were recruited by following another bee's dance (Fig. A5a–e, c–f). Lower values of p_{pause} correspond to a lower probability for individuals to move out of the dancing state, and hence longer periods of dances being advertised. This lengthened period of advertising means that there is a greater chance of dances being followed, and ultimately other bees being recruited for the viable nesting region which occupies the full 360° range in these simulations (Fig. A5d).

The effect of varying each of the tuned parameters on the total number of dancers is complex with the cause of some of the underlying trends not being immediately obvious (see Fig. A6). However understanding the results in Fig. A6 gives deeper insight into how our model works when there is a suitable nesting region in all directions. In general, increasing the probability of becoming active, or of dancing upon discovering a nest site, increases the overall number of dancers (Fig. A6a, b). Increasing the probability of following a dancer found on the swarm actually decreases the total number of dancers in the nesting region in all directions (Fig. A6c). At first this result seems counterintuitive, but it is internally consistent with the model. Model bees that follow dances return to the observer state for the next time step, whereas bees that do not follow a dance, or do not find a dance to follow, decide to scout independently. Independent scouts are guaranteed to find the nesting region, so a greater number of independent scouts ultimately leads to a greater number of dancers. On the other hand, there is only a 23% chance of a dance follower leaving the swarm (since $p_{\text{visit}} = 0.23$ for tuning simulations), so increased dance following restricts the number of bees that find the nesting region, and that become dancers. Increasing the probability of entering the paused state, p_{pause}, and therefore no longer actively attempting to recruit other bees increases the average number of dancers seen in model swarms (Fig. A6d). This is because a smaller proportion of dancers will remain to be followed as p_{pause} increases, resulting in a greater number of independent scouts, which in turn leads to more dancers. The average number of dancers decreases when either the probability of dancing, p_{resume}, or the proportion of swarm bees examined in search of a dance, f_{search}, is increased (Fig. A6e, f). This decrease occurs because both p_{resume} and f_{search} influence the probability of finding a dance to follow. Increasing either parameter will increase the probability of dance following, and thus decrease the number of independent scouts. The decrease in independent scouts restricts the number of bees that discover the nesting region and ultimately results in fewer bees dancing. The probability for dancing for a site has the strongest effect on the average total number of dancers (Fig. A6b), with variation in other parameters generally keeping the mean total dancers in the range of 35 to 45 bees.

In general the only tuned parameter that has a substantial effect on the number of followers is the probability of a resting bee becoming actively involved in the decision-making process, p_{observe} (Fig. A7a). A greater number of observers translates to a greater number of potential followers. The other parameters do not influence a bee's behaviour until after it has attempted to find a dance to follow, with the exception of f_{search}.

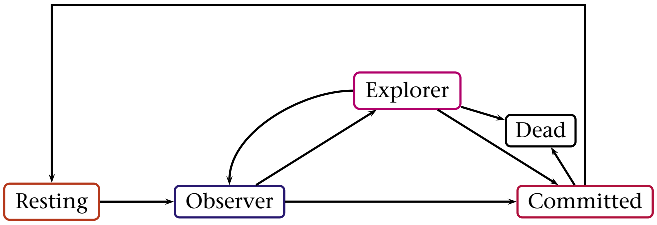

Figure A1. Flow chart showing the connection between states in the individual-based model of Passino & Seeley (2006).

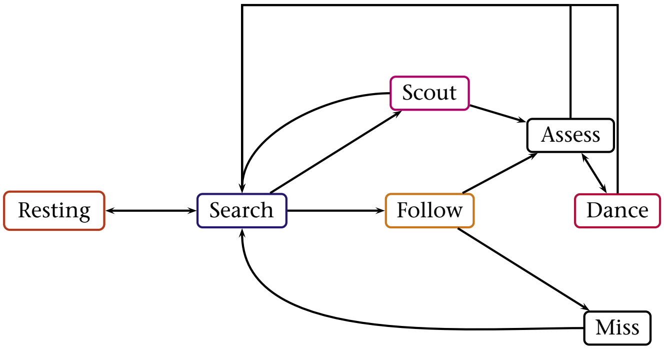

Figure A2. Flow chart showing the connection between states in the individual-based model of Janson et al. (2007).

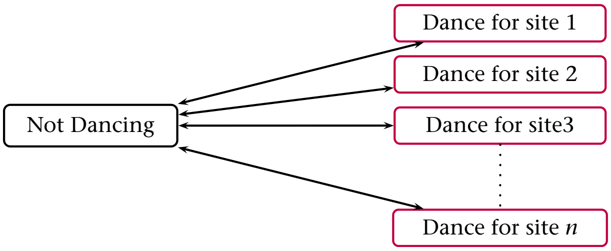

Figure A3. Flow chart showing the connection between states in the individual-based model of List et al. (2009).

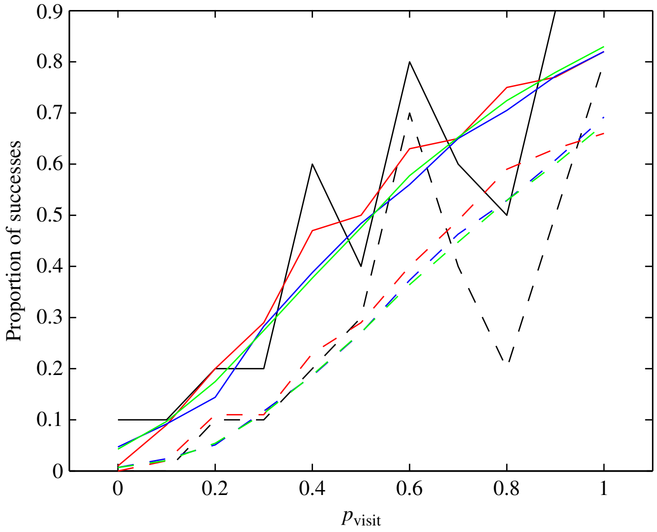

Figure A4. The proportion of successful decisions made according to the vectorial consensus (dashed lines) and quorum (solid lines) stopping tests across sets of 10 (black), 100 (red), 1000 (blue) and 10 000 (green) simulations as a function of p_{visit}.

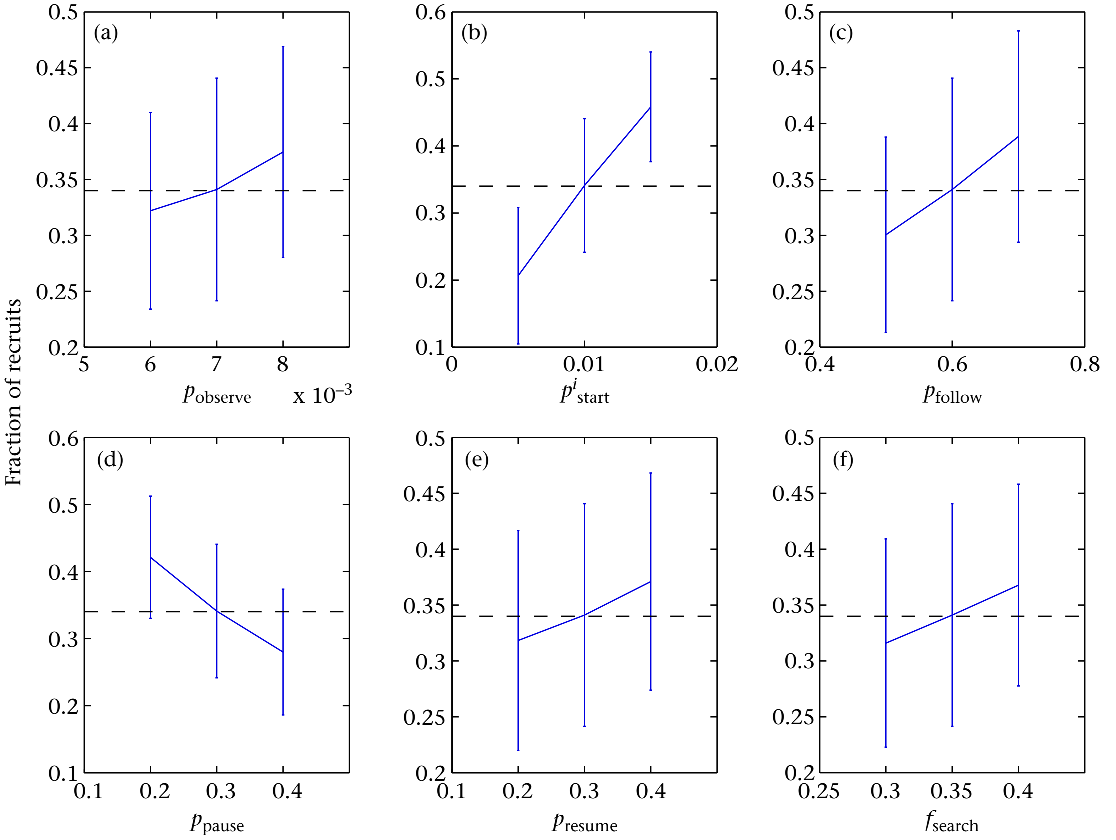

Figure A5. The effects of small variations in tuned parameters on the mean fraction of dancers recruited by another bee's dance across 100 simulations. Means are given ± 1 SD. The horizontal dashed line represents the fraction of recruited dancers observed in swarm 5 of Makinson et al. (2011). See Table 1 for a description of each parameter.

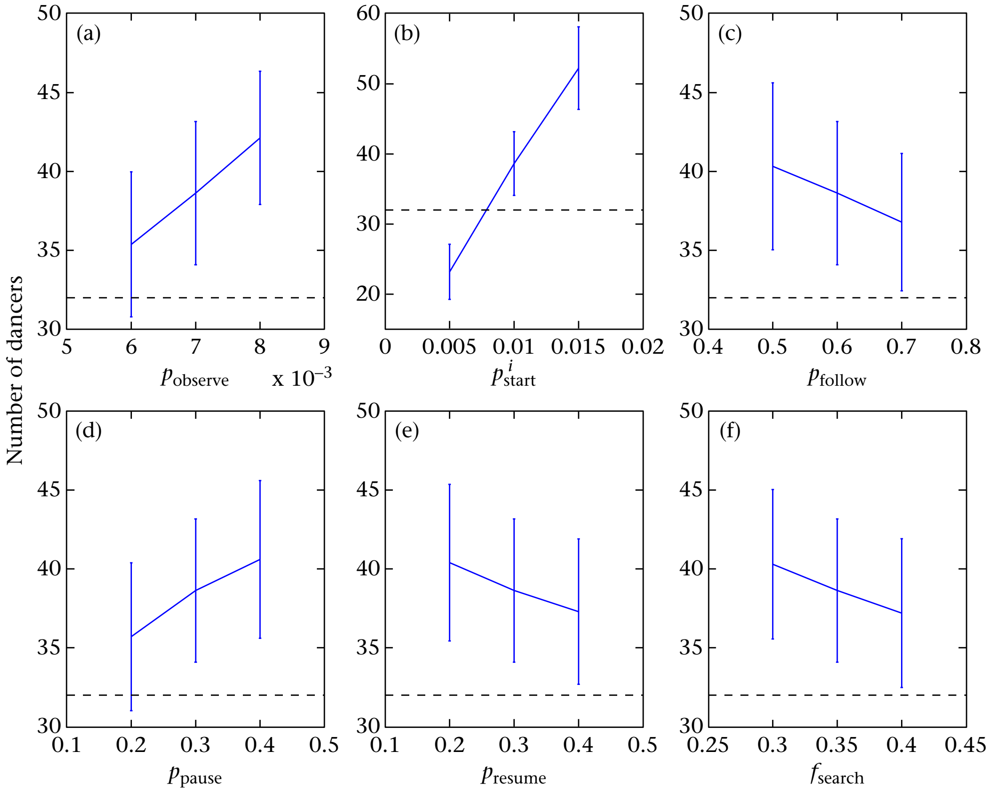

Figure A6. The effects of small variations in tuned parameters on the mean number of unique dancers across 100 simulations. Means are given ± 1 SD. The horizontal dashed line represents the number of dancers observed in swarm 5 of Makinson et al. (2011). See Table 1 for a description of each parameter.

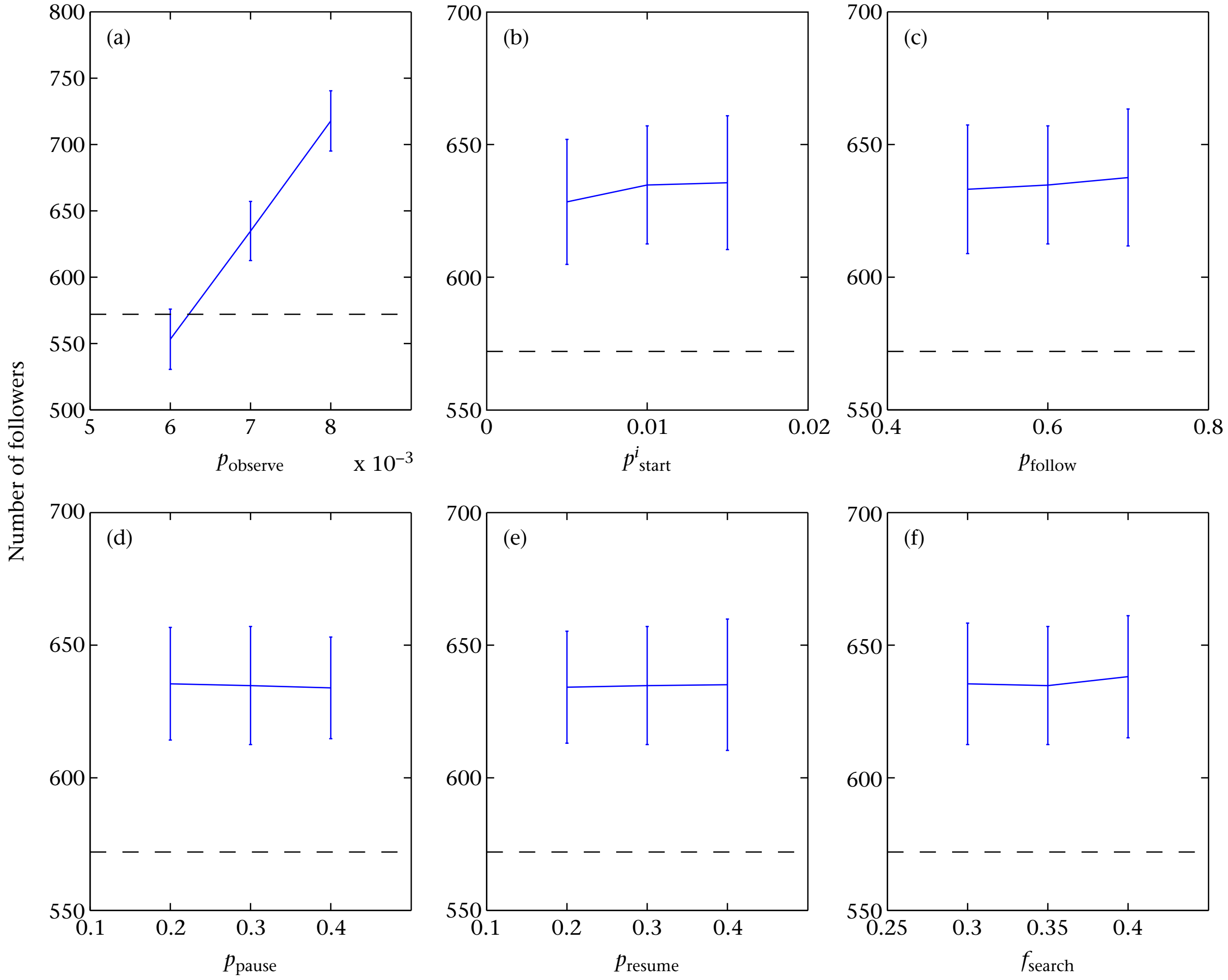

Figure A7. The effects of small variations in tuned parameters on the mean number of dance followers across 100 simulations. Means are given ± 1 SD. The horizontal dashed line represents the number of followers observed in swarm 5 of Makinson et al. (2011). See Table 1 for a description of each parameter.