HOW BEES CAN SURVIVE WHEN DISORIENTED

Abstract

Nest-site selection in honeybees is the process of individuating and choosing the next site where the colony will build their hive. This process is fundamental for their survival and it is a process involving hundreds of scout bees. Using an agent-based model, it is possible to simulate the bees' decision-making process when part of the population is disoriented and cannot perform the waggle dance to advertise a nest-site. Each bee has a probability to find a new nest depending on its own information and the information advertised by other bees, this information is affected by the degree of disorientation. Multiple scenarios have been simulated with various degrees of disorientation and a conservative definition of quorum. The results show that the decision-making process is robust to many degrees of disorientation. Interestingly, bees could benefit from a low degree of disorientation. This additional noise shifts the consensus towards the best site, improving the average final decision.

Introduction

It is known that finding a new nest is one of the most important choice an insect colony faces [1]. In many species, a colony invests a considerable amount of energy furnishing a nest, meaning that it would be costly to abandon a site should it turn out to be a poor one [2]. Many social insects have evolved complex mechanisms for finding new nests, evaluating them and choosing the best one [3]. These processes involve hundreds of individuals and are based on non-hierarchical distributed networks [4]. In this paper, the case of nest-site choice by honeybee (*Apis mellifera*) swarms has been considered. The process of swarming and nest selection for this species of honeybees is well understood [5][6]. Scout bees cluster near the home nest and begin searching for a suitable cavity in which to construct the new nest. Successful scouts report the location of the suitable sites by performing a dance on the surface of the cluster and thus can recruit followers to their discovery. Both the number of dances and the duration of such dances are correlated with the perceived quality of the nest [7]. This process leads to a 'consensus': the dancing and visiting bees concentrate on one popular site, and the colony moves there. The formation of a general decision involves 'quorum sensing' [3]. Given the importance of the dancing ritual in choosing a new nest, but also in foraging, it is important to understand what happens when bees are not able to communicate the correct information. It has been shown that, when honeybees are disoriented, they are still able to forage; though food-location information becomes more important when food sources are difficult to find [8]. It has never researched what happens to the decision process, during the period of scouting for a new nest, if part of the colony is disoriented. Thanks to an agent-based model it is possible to simulate the decision process in different scenarios. Starting from the model developed by List, Elsholtz and Seeley in [9] a new parameter has been introduced representing the proportion of correctly oriented bees. In [9], it is demonstrated that 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. This model assumes that bees cannot perfectly assess the quality of a nest and dances only partially influence the probability of finding a new site. The results are consistent with the empirical observation by Seeley & Buhrman [10]. The new model investigates how robust is the decision process with an additional assumption: not all the bees are correctly oriented and can advertise a new site. Other models of the decision process of honeybees have been developed using different approaches: a differential equation model by Britton et al. [11], a matrix model by Myerscough[12], another agent-based model by Passino & Seeley [13]. Britton et al. studied how swarms can make decisions even without any bees comparing the various possible home sites. Myerscough analysed the ability of swarm bees to produce unanimous decisions using the theory of Leslie matrices.

The new model has been used to test the effects of various degree of disorientation on both the ability to choose the best nest and the time required to reach a quorum. A fundamental problem faced by any decision-maker is finding a suitable compromise between swift decision and good ones [13]. This trade-off greatly depends on the definition of quorum and on the chosen time frame. It has been chosen to use a more conservative definition of quorum based on two different conditions. With a different definition of the quorum, results could change. In the following paragraph, it is described in details the model used and the experiments realized.

Methods

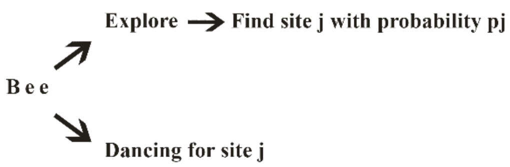
1.Model

The model is an agent-based model based on the model developed by List, Christian, Elsholtz, Christian, Seeley and Thomas [9]. This model simulates the bee's decision process based on the individual ability to find new nests and the ability to follow other bee's indications. The colony is composed of N bees, labelled 1,2…N, and k nests labelled 1,2…k, each one described by a quality q_j. Time is discrete, from 0 to *tmax*, where *tmax* is 300. At each time, the model simulates each scout bee. Bees can be in two states: either she dances for site j or she does not dance for any site, which can mean she is resting or watching another bee dancing. The state of each bee i at time t is formally described by the three-component vector $x_{i,t} = (s_{i,t}, d_{i,t}, o_{i,t})$, where

- $s_{i,t} \in \{0,1,2 \ldots k-1\}$ is the site for which the *i-th* bee is dancing for at time t, $s_{i,t} = 0$ means the bee is not dancing.
- $d_{i,t} \geq 0$ is the remaining duration of bee i's dance at time t.
- $o_{i,t} \in \{0,1\}$ oriented or disoriented dance (1 for the oriented dance)

Each vector is initialized at time t=0 as (0,0,*x*). Depending on the value of β, which represents the portion of correctly oriented bees, the value of *x* is initialized to 0 or 1. The percentage of 1 in the colony is equal to β.

At each time *t+1* the state of bee *i* is determined by the state of bee *i* at time *t* and by the state of all the other bees at time *t*. It is necessary to distinguish between to cases: in one case bee *i* is not dancing for any site and she may or may not fly out and find a new nest. Or she is already dancing for a site and continues till the duration is over.



Graph 1 Possible states for a bee.

Case 1: Bee *i* is not dancing for a site at time *t*, i.e. $s_{i,t} = 0$.

In this case, there is a certain probability that she flies out to one of the k nests and inspects it. For each nest j, $p_{j,t}$ denotes the probability of a bee of finding nest j at time *t* and dances for it at time *t+1*. In the case of $p_{0,t}$, this is the probability of remaining at the colony or not finding any nest. Thus, the first component of the vector $x_{i,t}$ takes values 0,2…k-1 with probability $p_{0,t}, p_{1,t} \ldots p_{k-1,t}$. By definition, the sum of all the probabilities is 1. Each of these probabilities is determined by two factors: an *a priori* probability that a bee finds that nest without any advertisement by other bees (this may depend on the nest's location, distance, etc.) and a second factor representing the proportion of bees that are correctly advertising a nest by dancing in the right direction.

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

- π_j represents the *a priori* probability of nest *j*
- $f_{j,t}$ represents the proportion of bees correctly dancing for nest *j* at time *t* (depends on β)
- λ represents is the relevant weight ranging from 0 to 1

The factor λ captures the amount of interdependence between bees. When $\lambda = 0$, each bee's probability of finding a nest depends only on the *a priori* probability, this is the limit case where bees do not influence each other through the "waggle dance". When $\lambda = 1$, each bee's probability of finding a new nest is proportional to the number of bees dancing in the right direction. The factor β represents the effect of being disoriented, a high value of β means that a high portion of the bees dancing is not correctly oriented. When $\beta = 1$, all the bees are correctly oriented and the probability $p_{j,t}$ depends on the bee's independent assessment and the bees' interdependence. When $\beta = 0$, the probability $p_{j,t}$ depends only on the bee's independent assessment, regarding the value of λ. The second component of $x_{i,t}$ is the dance duration for the chosen site *j*. This value is proportional to the nest quality q_j and depends on the bee's reliability σ.

$$d_{i,t+1} = q_j \exp{(T_\sigma)}$$

Where T_σ is a normally distributed random variable with mean 0 and standard deviation $\sigma \geq 0$. [1] shows that the bee's performance is robust to changes in the form of the error and to various value of σ.

Case 2: Bee *i* is dancing for nest *j* at time *t*, i.e. $s_{i,t} \neq 0$.

In this case, the bee continues to dance till the duration expires.

$$x_{i,t} = \begin{cases} (s_{i,t}, d_{i,t} - 1) \; if \; d_{i,t} > 1 \\ (0,0) \end{cases}$$

From the decisions of the single bees, a general consensus emerges among them. There exist different criteria of consensus, the definition used in this experiment is based on the notion of quorum. At each time *t* there are $n_{j,t}$ bees correctly dancing for site *j*, a quorum for nest *j* is reached when two conditions are met:

1. $n_{j,t} > 2n_{h,t}$ for any $h \neq j \; h \neq 0$
2. $n_0 < 0.8N$

Results can differ in relation to the definition of consensus. It has been chosen to use this definition to maintain a relationship with the work in [9], but other definitions are possible.

2.Hypothesis

The model simulates the bee's decision process under empirically realistic assumptions. Three key assumptions are made: first, each individual bee's reliability is not perfect, but is affected by an error.

Second, each individual bee's probability of finding a nest is influenced by other bee's waggle dance. Third, a portion of the colony can be disoriented and do not dance in the right direction.

Hypothesis 1

Honeybees can choose the best nest when part of the colony is disoriented.

Since bees rely on both their individual judgement and other bees' judgement, it is possible to reach a consensus for the best nest-site. The difficulty of the problem increases when bees are highly interdependent, i.e. the probability of finding a nest is correlated with the identification of the same site by other bees, and the portion of disoriented bee is high. In this case, many bees would not find the advertised site and would go back to the colony.

Hypothesis 2:

Hives with a higher portion of disoriented bee take longer to reach a quorum.

This hypothesis is based on the probability of finding a nest, which decreases with a high value of β. This decreases the probability of having the right number of bees dancing for a nest and increases the time needed to reach quorum.

3.Simulations

The model was implemented in Python. The number of bees was set to N=100 and the number of new nests to *k*=5. These assumptions are empirically motivated in [9][10]. The quality of the nest was fixed at $0, 1$,3,4,6,8. The model assumes a 10% probability of finding a nest and a 50 % probability of not finding any nest and returning to the home nest, without any influence by other bees. The time duration of the simulation was 300, to maintain a continuation with previous works [9].

The first simulation was a parameter sweep over β using value $\{0{,}0.2{,}0.4{,}0.6{,}0.8{,}1\}$, λ was fixed at a value of $\lambda = 0.8$. This test was repeated 100 times and the mean and variance for each value of β were recorded. The scenario depicted in the first simulation presents a high value of interdependence between bees. It is expected that increasing the number of oriented bees, the choice of the nest becomes easier, since there is a greater probability of finding the best nest. The probability of finding nest j is $p_{j,t} = 0.2\pi_j + 0.8f_{j,t}$. The intrinsic probability of finding nest *j* has a weight of only 20% on the overall probability. For $\beta = 1$, 80% of the overall probability depends on the portion of bees dancing for nest j. For $\beta < 1$, only a portion of the dancing bees are correctly advertising nest *j*. Since the sum of all the probabilities $p_{j,t}$ must be equal to 1, the probability $p_{0,t}$ increases with lower β. This happens because with a greater portion of disoriented bees there is a greater portion of bees that do not find any nest and come back to the home nest.

The second simulation was a parameter sweep over β using the previous values and fixing $\lambda = 0.2$. This test was repeated 100 times and the mean and variance for each value of β were recorded. The scenario depicted in the second simulation presents a low value of interdependence between bees. It is expected that the effect of β is less evident with respect to the previous scenario. The probability of finding nest j is $p_{j,t} = 0.8\pi_j + 0.2f_{j,t}$. The intrinsic probability of finding nest *j* has a weight of only 80% on the overall probability.

Results

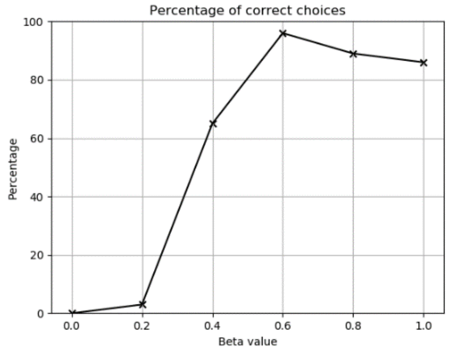


Figure 1 Result from first simulation. Parameter sweep over Beta with fixed value Lambda=0.8. Figure shows the percentage of correct choices.

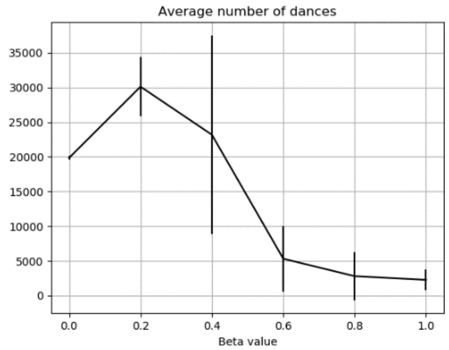


Figure 2 Result from first simulation. Parameter sweep over Beta with fixed value Lambda=0.8. Figure shows the average and standard deviation of the total number of dances.

The first simulation tested the influence of the parameter $\beta \in \{0, 0.2, 0.4, 0.6, 0.8, 1\}$ over the decision process. The λ parameter was set to a high value ($\lambda = 0.8$), which represents a high value of interdependence between bees. Every simulation calculated 300 times steps and was repeated 100 times. *Figure 1* shows the percentage of correct choices over 100 simulations. A simulation was recorded as successful when quorum was reached for nest *6*, the best one. Recall that quorum is reached when more than 20% of the bees are dancing and the best nest has more than twice the support of the second-best nest. The figure shows an increment of correct choices the higher β becomes. With value $\beta = 0$, the colony never reached quorum for the best site. For a value of $\beta = [0.4,1]$, the hive was able to reach quorum for the best site in more than 50% of the simulations. The highest percentage, 97%, was reached for $\beta = 0.6$. *Figure 2* shows the average total number and standard deviation of dances for each value of $\beta \in \{0, 0.2, 0.4, 0.6, 0.8, 1\}$. The total number of dances was $\sum_t L(k)$, where $L(k)$ is the number of dances as time *k*. For $\beta = 0$, the average value was 20000 (STD=200). For higher values of β, the mean number decreases from 30000 to 2700 with a maximum of 37000. *Figure 3* shows the average and standard deviation of the time needed to reach a quorum for each value of $\beta \in \{0, 0.2, 0.4, 0.6, 0.8, 1\}$. With value $\beta = 0$, the colony never reached consensus. For higher values of β, the mean time decreases from 290 to 20 time steps.

The second simulation tested the influence of the parameter $\beta \in \{0, 0.2, 0.4, 0.6, 0.8, 1\}$ over the decision process, when the interdependence between bees is low ($\lambda = 0.2$). *Figure 4* shows the percentage of correct choices over 100 simulations for each value of β. As for the previous simulation the are no correct choices for $\beta = 0$. The number of correct choices increases as β increases. The maximum value was reached for $\beta = 0.2$, with 50% of correct choices. *Figure 5* shows the average total number and standard deviation of dances for each value of $\beta \in \{0, 0.2, 0.4, 0.6, 0.8, 1\}$. For $\beta = 0$, the average value was 40000 (STD=100). For higher values of β, the mean number increases from 27000 to 37500 with a maximum of 50000. The standard deviation is high (25000) for all values of β. *Figure 6* shows the average and standard deviation of

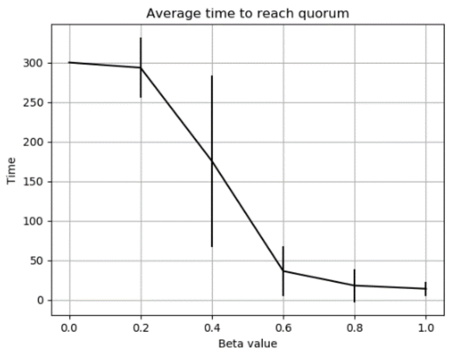


Figure 3 Result from first simulation. Parameter sweep over Beta with fixed value Lambda=0.8. Figure shows the average and standard deviation for the time needed to reach a quorum.

the time needed to reach a quorum for each value of $\beta \in \{0, 0.2, 0.4, 0.6, 0.8, 1\}$. With value $\beta = 0$, the colony never reached consensus. For higher values of β, the mean time increases from 200 to 250 time steps.

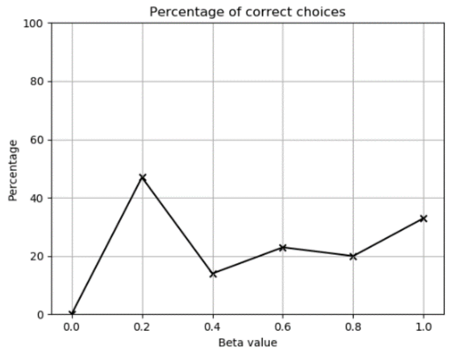


Figure 4 Result from second simulation. Parameter sweep over Beta with fixed value Lambda=0.2. Figure shows the percentage of correct choices.

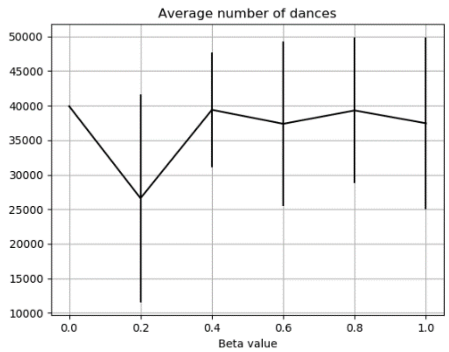


Figure 5 Result from second simulation. Parameter sweep over Beta with fixed value Lambda=0.2. Figure shows the average and standard deviation of the total number of dances.

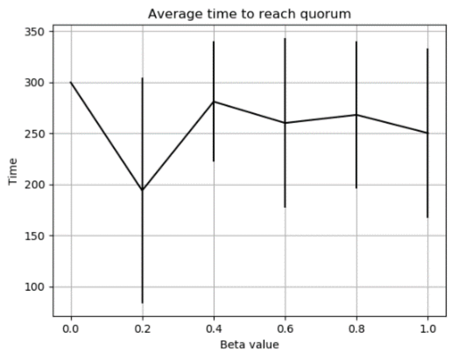


Figure 6 Result from second simulation. Parameter sweep over Beta with fixed value Lambda=0.2. Figure shows the average and standard deviation for the time needed to reach a quorum.

Discussion

The model developed in this paper is an agent-based model of the nest-site decision process in honeybees. This model simulates the behaviour of bees under empirically motivated assumptions. The model predictions are consistent with previous observations by [9][10], bees are able to reach a consensus on the best site for a large range of conditions. As shown in [9], colonies with a high level of interdependence perform better than colonies with lower levels since more attention is created on the best site and a cascade effect is formed. The model implemented in this paper introduces a new parameter representing the portion of bees correctly oriented during the dancing phase. This parameter was introduced to investigate the robustness of the decision-making process in challenging environments, where bees are not always able to use any point of reference to orient themself. Several studies have disrupted the honeybee waggle dance in order to assess the benefits it brings to colonies [14-16] during foraging, however fewer studies investigate its role during nesting. The model shows that colonies with a higher portion of oriented bees perform better, however it is interesting to note that the best choice is performed when part of the colony is disoriented. For both values of interdependence, the highest percentage of correct choices has been made when 40% and 80% of the colonies were disoriented, respectively for $\lambda = 0.8$ and $\lambda = 0.2$. The reason for this behaviour could lie in the fact that groups of individuals perform better choices on a harder problems, as the right balance between oriented and disoriented bees allows the colony to assess a wide range of information and therefore reach consensus on the best site more reliably. However, high values of β would lead to the problem being too difficult and undermine the efficiency of the decision process. Note how the average number of dances decreases with higher values of β (Fig. 2), the easier the problem becomes the smaller number of bees are needed to reach a quorum. This is also reflected with a lower time needed to reach a quorum (Fig.3). In the case of low interdependence, it is more difficult to note this behaviour since bees are less influenced by each other. The first hypothesis is confirmed by the results of the two experiments, bees are able to reliably choose the best nest among many possible choices, even under demanding criteria of consensus. Also the second hypothesis is confirmed by the first simulation, hives with a higher portion of disoriented bees take longer to reach a quorum. The reason for this behaviour follows the same logic previously explained. Looking at *Figure 6*, it is more difficult to tell whether the same behaviour appears. Due to the high variance, it is not possible to conclude whether the bees take longer to reach a consensus.

Conclusion

In conclusion, the aim of this paper was to investigate the decision-making process of honeybees when faced with a difficult task. Starting from the previous researches on the topic, a new agent-based model has been developed in order to investigate how bees are able to make the correct decision when part of the colony is disoriented and cannot advertise the visited site through the waggle dance. The results support the hypothesis that the bees' decision process is robust to various degrees of disorientation. The definition of quorum was strict, but it is not known what is the real definition used by honeybees. It would be interesting to perform an experiment with real bees to understand if the real definition is more, or less, strict than the one used in this model. Following the discoveries made by A. Dornhaus and L. Chittka [16] on the importance of the colony's habitat, it would be beneficial to investigates how important is the waggle dance in relation to the habitat. Moreover, different species of bees rely on the waggle dance in different ways when foraging [14], and it would be expected to be that same for nesting. The results from the previous experiments show that bees' decision process has evolved to benefit from bees' errors.

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