

Agent-based modelling of nest site selection by bees and ants

by

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Abstract

In this study we develop an agent-based time discrete model to show how honeybees and ants are able to choose the best site available under different circumstances. We focus on the agent-based model introduced by Christian List, Christian Elsholtz and Thomas Seeley in their paper: *Independence and interdependence in collective decision making: an agent-based model of nest-site choice by honeybee swarms. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 364(1518):755-762, 2009.* In that paper, the authors model the nest site selection of honeybees using an agent model and study the affect of advertising and reliability in nest site selection of honeybees. We extend the model and run it for honeybees to show that being closed-minded reduces the accuracy of the final result. We then modify the model and apply it to two different species of ants. We study how changing different parameters such as colony size, threshold, advertising and reliability can affect the final consensus accuracy. We finally compare results from our mathematical simulations to that of lab experiments and discuss the similarities and differences between the two insect species.

Keywords: Group decision making; agent-based model; social insects; nest-site selection; consensus; threshold; advertising; reliability; honeybees; ants.

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Four years ago I wrote a letter to SFU as part of my application to the master degree program hoping and praying that I get accepted in graduate school. I wrote about how I've always been fascinated by mathematics hoping that one day I would make my own contribution to the field. I never thought that one day I would be writing this as part of the thesis.

Today is the day I can finally say I did it. I have achieved one of the most important goals in my life; I pursued a master's degree. Although getting to this point has been one of the hardest things I have done, I had a lot of fun doing it and I'm glad I went through with it. I've learned a lot about myself in the process, what drives me, what motivates me and what makes me push myself to the limit.

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Chapter 1

Introduction

1.1 Motivation and overview

Group decision making is a very important process in animal behavior. Animals and social insects make decisions on daily basis about where to feed, rest and live. To name a few examples, birds decide on communal routes when migrating from one place to another to maximize their survival probability of the journey [45, 40, 1]. Bats use group decision-making to decide on communal roosts [19, 18]. Bees use group decision to decide on where to forage [36]. Wasps, bees and ants collectively decide on a new home on which the survival of the colony depends [4, 39, 28, 5, 35]. These decisions are important because they directly affect the survival of the different animal species and colonies.

Group decision making in social insects involves sharing information between individuals and voting on one option from multiple choices. Even though each insect makes an individual choice and might not be fully informed when making that choice, the group decision tends to be better than the individual decision. Nest site selection in social insects is one of the important processes that has been studied and modeled mathematically using different models. For example nest site selection in honeybees has been modeled using differential equations [2]. The authors adapted a classical model of disease and information spreading to model how bees decide on a new site and change their opinion from one site to another until the entire colony reaches a decision. It has also been modeled using a population matrix (also named as Leslie matrix) [25]. This model explains how bees find the best site available by observing the dynamics of the dancing activity and its evolution from one time step to another. Furthermore, nest site selection in honeybees has been studied using a stochastic model in [27]. The authors study how robust is the nest-site selection process to random events. Their model predicts that bees choose more reliably when the two sites are of low quality than when both sites are of high quality. It also predicts that the delay in

finding the second site has more effect on the final choice when both sites are of high quality.

Agent models are in particular a powerful tool for modeling and understanding group decision making processes. Their power relies in the ability to model individual behavior based on given rules and interactions between the individuals to predict the overall colony behavior. Agent models have been successfully used when enough data is available to estimate the needed parameters; for example, in [29] the authors develop an agent-based model of nest site choice by *Temnothorax albipennis* ants. To estimate the model's parameters, they use extensive data collected from hundreds of individual ants from several colonies over multiple experiments in a laboratory setting. Models of bees' foraging and house hunting are other examples of agent-based models done in [36, 21]. Similarly, the parameters used in these models were estimated using extensive experiments with individually marked bees.

In this study we develop an agent-based model to show how bees and ants are able to choose the best site available under different circumstances. In the following sections of the introduction we provide the biological background on nest selection by bees and ants and then elaborate on existing mathematical models, as well as on the contributions of the present thesis.

1.2 Nest site selection in honeybees - *Apis mellifera*

Honeybees are social insects that live in colonies. They are highly organized and participate in a variety of complex tasks such as finding a new hive, building a hive and collecting food. A honeybees colony consists of one queen and several thousands of workers. The worker bees are responsible for building the hive, collecting food, and many other tasks that are directly related to the survival of the colony. In late spring and early summer, when a new queen is born in the colony, the old queen takes two-thirds of the worker bees with her and leaves the hive to settle in a nearby place [21]. Several hundred worker bees fly out to search for a potential new hive and report back to the group on the quality, distance and location of the potential site using a communication method called the waggle dance. Each waggle dance consists of a series of dance circuits. Each dance circuit consists of a waggle run and a return run. The duration of the waggle run depends on the distance to the nest site. The duration of the return run depends on the quality of the nest site. As the nest site quality increases the duration of the run increases. The angle of the run indicates the direction to the food source or nest site. For more details on how a waggle dance is used as a communication method between honeybees refer to [34].

Honeybees evaluate the quality of a site based on many characteristics including the size of the hive, the entrance area and the amount of light it receives. Honeybees prefer hives

Nest-site property	Preference	Reference(s)
Nest height from ground	5 m > 1 m	[37]
Nest exposure/visibility	Visible > Hidden	[37]
Distance from parent nest	Beyond 300 m	[37]
Entrance area	12.5 cm ² > 75 cm ²	[37]
Entrance location	Bottom > Top	[37]
Entrance direction	Southward > Northward	[37, 16, 17]
Cavity volume	10 liters < 40 liters > 100 liters	[37]
Previous occupancy	Previously used > New	[32, 44]
Nasanov pheromone	With pheromone > Without pheromone	[20, 33]
Cavity dryness	Damp sawdust = Dry	[37]
Cavity soundness	Walls with holes = Sounds walls	[37]

Table 1.1: Site preference for bees. Different experiments show that bees prefer medium size hives with small entrance area located at the bottom of the nest cavity facing southward.

with the following characteristics: the entrance is of small area, facing southwards, and is located at the bottom of the nest cavity; the nest itself is of medium size; and the nest is situated at a medium height. For a full list of nest sites properties that have been tested in various papers see Table 1.1 [43].

The nest hunting in bees starts with the exploration phase where bees fly out searching for a new hive. When a bee finds a new potential site she assesses the site based on the attributes in Table 1.1 then flies back to the swarm to advertise this site using the waggle dance. Consequently, other bees in the swarm can fly to the new site and do their own assessment. Within the swarm each bee dances for the site she assesses; the duration of the dance depends on her perception of the site quality. The better the site quality the longer the dance duration. As a result of this advertising method, hives with better quality get longer advertising periods and therefore more bees will assess these hives and dance for it. After several days of searching, debating and evaluating the potential sites, this process leads to a consensus wherein some critical number of bees dance for one particular site, which then causes the swarm to initiate a move [38]. In other words, migration starts when enough scout bees, but not all, have approved the potential site. It is important to note that the colony is able to determine the best site available with high accuracy even though not all bees see all potential sites and therefore there is little to no comparison happening.

In the mathematical model introduced in Chapter 2 we represent the above process by a vector, x , that shows the state of bee i at time t . The vector x shows which site bee i is dancing for and the remaining duration of the dance. In the exploration phase $x = (0, 0)$. We represent the different attributes of a site by a single quality parameter. A high quality implies a highly desirable site. We change the state of bee i from one time step to another

based on the state of bee i and the state of other bees at the previous time step. We use an advertising parameter to determine how much weight to put on advertising compared to individual assessment of the site. Furthermore, we use a quorum threshold as our stopping criterion where only some bees, not all, need to approve the potential site before moving to the migration phase. We present the entire model in detail in Chapter 2.

1.3 Nest site selection in ants

Similar to honeybees, ants are also social insects that live in colonies and participate in a voting process when choosing a new nest. Ants can reliably choose a high quality site over a low quality one with great accuracy [29, 31, 9, 10, 5]. In this study we look into two different species of ants: *Temnothorax albipennis* (*T. albipennis*) and *Myrmecina nipponica* (*M. nipponica*).

T. albipennis is a species of small ants. The colony consists of one queen and several hundred of workers. They live in rock crevices and rubble and they are sometimes referred to as rock ants. The size of their colony is usually around 100-500 ants. *T. albipennis* ants prefer dark sites with high cavity, spacious floor area and a small entrance [13, 22]. They also prefer sites with grit particles over dead conspecifics [12]. Table 1.2 shows the summary of preferred site characteristics for *T. albipennis* [43]. *M. nipponica* is another species of ants that we will look into. They live in small colonies in mosses, fern roots and decaying logs on the forest floor. *M. nipponica* colonies consist of one queen and tens of workers. They are found in small colonies of 40 ants or less. Table 1.3 shows the summary of preferred site characteristics for *M. nipponica*.

Ants' migration process from one site to another consists of four phases: exploration, assessment, canvassing and commitment [29, 5]. Each phase represents a different level of commitment to the site. In the exploration phase ants search for new nest sites until they find one. When ants find a new potential nest the assessment phase starts. In this phase the ant assesses the site based on the properties they prefer. The assessment duration is inversely proportional to the quality of the site. When the quality of the site is low the duration of the assessment is long. When the assessment phase is over ants will either accept the new nest site and move to canvassing phase or reject it because it does not meet their needs. In the canvassing phase *T. albipennis* and *M. nipponica* advertise the site to other ants to get more support; however, the advertising method for each species is different and therefore will be discussed separately.

In the mathematical model discussed in Chapter 4 we use a vector, x , to represent these phases. The vector x has three parameters. The first parameter shows the site ant i is

Nest-site property	Preference	Reference(s)
Cavity height	1.6 mm > 0.8 mm	[13]
Cavity floor area	912 mm ² > 456 mm ²	[22, 24]
Cavity entrance width	2 mm > 4 mm	[13]
Cavity illumination	Dark > Light	[13]
Presence of dead ants	Grit particles > Dead conspecifics	[12]

Table 1.2: Site preference for *T. albipennis* ants. Different experiments show that ants prefer dark sites with high cavity, spacious floor area and a small entrance.

Nest-site property	Preference	Reference(s)
Moisture	Wet > Dry	[6]
Cavity illumination	Dark > Light	[6]
Cavity entrance width	Narrow > Wide	[6]
Social information	Existing pheromone trails > Non existing	[6]

Table 1.3: Site preference for *M. nipponica* ants. Different experiments show that ants prefer wet, dark sites. Also when given a choice between equivalent nests *M. nipponica* chooses the nest that has pre-established pheromone trails.

assessing. The second parameter shows the remaining duration of that assessment, the third parameter shows the site ant i is canvassing for. The exploration phase is represented by setting $x = (0, 0, 0)$ since in this phase an ant is still searching for a nest and has not found one yet. Furthermore, as shown in [30] ant colonies are able to choose a high quality site with high accuracy without having to compare all available sites. We model this by assigning each site a quality value. Ants vary their assessment duration based on the site’s quality without comparing it to other sites. In our model we only compare site qualities in the case that an ant is canvassing for one site and accidentally finds another one. We choose to not model the commitment phase mathematically because in this phase ants migrate from one site to another. It does not change the consensus criteria or the winning site. It is only used to move brood and food to the new site. Finally we model the decision to accept or reject a site using probabilities that are based on the quality of the site. High quality sites have a high probability of being accepted and advertised.

T. albipennis ants use a mechanism called tandem runs in the canvassing phase. In this phase the ants travel back to their old nest to find other ants and physically push them to the new nest to make their own assessment. The higher the quality of the site, the larger the number of tandem runs it receives which leads to more ants assessing and canvassing to it. On the other hand, *M. nipponica* use chemicals instead of tandem runs to advertise the new potential nest. If *M. nipponica* like the new site and want to advertise it they lay pheromone trails on the way back to their original site creating a chemical path between

these two sites which makes it easy for other ants to follow that path and make their own assessment. If they reject the new nest they don't advertise it, so they don't lay pheromone trails on the way back to their original site. The more desirable the site, the more ants visit this site; therefore, the stronger the pheromone trail is on the path to that site. The stronger the pheromone trails the more ants it attracts. In our mathematical model we use a parameter to represent how much weight to put on advertising and how much weight to put on individual assessment of the site. We don't differentiate between various types of advertising such as waggle dances, canvassing or pheromone trails. We are only concerned about whether there is advertising or not.

When the number of ants assessing a certain site reaches a threshold, the ants enter the commitment phase. In this phase *T. albipennis* ants start transporting their mates and brood items from the old nest to the new nest. *T. albipennis* carry other ants in addition to brood items to the new nest to speed up the transportation process while *M. nipponica* only transport brood items. All other ants in *M. nipponica* species move to the new nest themselves by following the chemical trail. As previously mentioned we don't model the commitment phase in our mathematical model. We use quorum threshold as our stopping criteria. This threshold depends on the size of the colony. We base the value of the threshold on lab experiments done in various papers. For full details on the nest site selection process of these two species see [29, 5] for *T. albipennis* and *M. nipponica* respectively. Full details on setting up our mathematical model are presented in Chapter 4

Note that we will refer to *T. albipennis* species as trail ants and *M. nipponica* species as chemical ants for simplicity when comparing simulations and results in all future chapters of this study.

1.4 Related mathematical models

Bees and ants nest site selection has been modeled mathematically using various approaches. We summarize some of these approaches in this section and discuss their advantages and disadvantages. We then introduce our model and compare it to other approaches and list some of the advantages of our approach.

Nest site selection in honeybees has been modeled using differential equations in [2]. The authors adapt a classical mathematical model of disease and information spreading to model how bees choose a new site given multiple options with different qualities. This model focuses on the dancing bees and how dancing changes from one site to another. The advantage of this model is its simplicity. It can be used to study how the decision making process changes depending on when the high quality site is introduced to the model. It is

also used to study whether the colony is able to switch its attention to a new better site even when it is found later in the decision making process. Since the authors model dancing behavior instead of individuals, it is rather difficult to study how individual decisions affect the overall results. For example it is difficult to adapt the model to study the decision making process if the quality of the site is dependent on the bee evaluating the quality. It is also difficult to study how individual errors in evaluation the site's quality affects the overall consensus result.

In [25] the author studies nest site selection in bees using a population matrix. Similar to [2], she focuses on the dancing behavior and models the dancing decay and propagation through the swarm. The author bases her model on the observation that the number of waggle runs in a scout's dance decreases after each successive visit to the nest site and ceases after a certain number of visits. The model represents a highly simplified version of swarm decision making by modeling the dancing behavior and how it changes. The author shows that bees are able to choose the high quality site with high accuracy. However, the model assumes that there are no random events. It also assumes that dances occur synchronously. In real life these assumptions are inaccurate since most of the time the high quality site is found later in the decision making process and not all dances happen at the same time.

In [21] the authors model the nest site selection for honeybees using an agent model. The model is used to show how each bee makes a decision based on her own assessment of the site in addition to observing other bees around her. In [21] the colony's decision is not modeled explicitly, it is rather a result of individual decisions combined together. As a result it can be easily adapted and used to study random events and investigate how these events affect the colony's decision. One of the disadvantages of [21] is that it does not model the revisiting feature documented in [34] where bees revisit sites and the number of waggle runs in a scout's dance decreases after each successive visit until it stops.

Ant nest site selection has also been modeled mathematically using an agent model. In [29] the authors model both the final consensus result in addition to the time taken in each phase of the decision making process. The transition from one state to another is modeled using probabilities. The model set up is complicated and contains many states and transitions which in turn needs many estimated parameters to define how each ant changes her position from one state to another. The advantage of this model is that it predicts the time and consensus accuracy for trail ants accurately in most cases (see [29] for exceptions where the model fails to predict the observed behavior). However, its disadvantage relies in how specialized the model is. It can not be easily applied to other species of ants such as chemical ants and it also can not be simply adapted and used for bees.

In this study we use the model introduced in [21] and modify it by adding the revisiting feature to study how it affects the final decision making. Due to the simplicity of this model and how it can easily be adapted to study random events we decide to modify it to model the decision making process in ants. We study different random events and parameters such as introducing the high quality site late in the decision making process or making the high quality site hard to find. We also study how different advertising and reliability parameters affect the final decision. The advantage of our model compared to [21] is the addition of the revisiting feature. We discuss this feature in detail in future chapters and discuss how it affects the final decision. The advantage of our model compared to [29] is the fewer parameters that we need to estimate since we are only interested in modeling the consensus accuracy instead of the state of each ant at each time step. Our agent model also uses a much more simplified set up compared to [29] and fewer transitions between different phases of the recruitment process. In our model we are only interested in the final consensus accuracy and do not study the time taken in each phase of the recruitment process therefore we do not need to track the state of each ant at each time step. Another advantage of our study is that we use a general model that is easily adapted to both bees and ants. We study the effect of various random events (see details in Chapter 5) and how each event changes the consensus accuracy whereas all previous papers we discussed focus on either bees or ants, but not both, and only study one or two scenarios.

In Chapter 2 we summarize the mathematical model introduced in [21] and modify it by adding the revisiting feature. In Chapter 3 we discuss the effect of our modifications, in particular the changes in the final consensus accuracy for bee colonies, as compared to the results observed in [21]. We then modify the model further and adapt it to study the decision making process in ant colonies in Chapter 4. In Chapter 5 we present seven different simulations. In each simulation we vary one parameter while keeping the rest constant to study how varying this parameter affects the consensus accuracy. We finish Chapter 5 by presenting a summary of all the parameters we studied and how they affect the final results. We also compare our results to experimental data. In Chapter 6 we discuss the similarities and differences in group decision making by bees, ants and humans and finally present our conclusions for this work in Chapter 7.

Chapter 2

Modeling nest site selection in honeybees

2.1 Summary of the agent model in [21]

In this section we will summarize the mathematical model introduced in [21]. This model is a time discrete agent model that describes how bees reach a consensus when choosing a new hive. The model uses discrete time periods, labelled $t = 1, 2, \dots, T$, and models the behavior of all scout bees individually in each time period. There are N scout bees, labelled $i = 1, 2, \dots, N$, who participate in the decision making process and K potential hive sites, labelled $1, 2, \dots, K$, each potential site $\alpha \in \{1, 2, \dots, K\}$ has an objective quality $q_\alpha \geq 0$. A site with high objective quality is more desirable than a site with low objective quality. We let q_α be a value in $\{0, 1, 2, \dots, 10\}$.

At each time period t , bee i can either be dancing for a potential site α , or not dancing for any site. If bee i is dancing for a site then she is actively advertising and voting for it. If she is not dancing for any site then she is at rest, observing other bees, or she is still searching for a site. We denote the site bee i dances for at time t by $s_{i,t} \in \{0, 1, 2, \dots, K\}$. If $s_{i,t} = 0$ bee i does not find a site to dance for at time t . The duration of the dance increases with the quality of the site; the higher the quality of site α , the longer bee i dances for it. We use $d_{i,t} \geq 0$ to denote the remaining duration of bee i 's dance at time t .

Let the state of bee i at time t be a vector $x_{i,t} = (s_{i,t}, d_{i,t})$. The vector $x_{i,t}$ shows the site bee i is dancing for and the remaining duration of the dance at time t . We initialize the model by setting $x_{i,1} = (0, 0)$ for all i which means that at time 1 there is no dancing activity and no scout bee is voting for any site.

We now need to define how each bee changes her state from one time period to another. At time $t + 1$, the state of bee i namely $x_{i,t+1} = (s_{i,t+1}, d_{i,t+1})$ changes depending on its own state and the state of all other bees in the previous time period t . There are two cases to be considered: case 1) bee i is not dancing for any site at time t therefore $x_{i,t} = (0, 0)$ and case 2) bee i is dancing for site α at time t so $x_{i,t} = (\alpha, d_{i,t})$. We discuss each case separately.

Case 1: The state of bee i at time t is $x_{i,t} = (0, 0)$ which means that bee i is not dancing for any site at time t .

In this case bee i has a certain probability of finding one of the potential K sites and dancing for it at time $t + 1$. Bee i could either find the site independently without any advertising from other bees, or find it through advertising by other bees. We let $p_{\alpha,t+1}$ be the combined dependent and independent probability of finding site α at time $t + 1$. We also let $p_{0,t+1}$ be the probability that bee i remains at rest or does not find a site and therefore does not advertise for any site at time $t + 1$. At time $t + 1$ the first component of $x_{i,t+1}$ namely $s_{i,t+1}$ takes the value of one of the potential K sites: $(1, 2, \dots, K)$ with probability $p_{1,t+1}, \dots, p_{K,t+1}$ respectively or $s_{i,t+1} = 0$ with probability $p_{0,t+1}$ which means that bee i does not find a site to dance for at time $t + 1$. The probability $p_{\alpha,t+1}$ is calculated based on two factors:

- i. The probability of bee i finding site α independently without the help of other bees. In other words, the likelihood that bee i finds site α on her own. We let π_{α} be the probability that bee i finds site α independently without the help of other bees. It is important to emphasize that π_{α} does not depend on bee i , it only depends on how hard it is to find site α based on its location and distance from the original nest site.
- ii. The probability of finding site α through advertisement from other bees. In this case, the probability is proportional to the number of bees dancing for site α . We let $f_{\alpha,t}$ be the proportion of bees dancing for site α at time t . Mathematically,

$$f_{\alpha,t} = n_{\alpha,t}/N,$$

where $\alpha = \{0, 1, 2, \dots, K\}$ and $n_{\alpha,t}$ denote the number of bees dancing for site α at time t . When the number of bees dancing for a site increases, the probability that other bees find and evaluate this site will also increase.

The probability $p_{\alpha,t+1}$ can be represented mathematically using the above two factors as follows,

$$p_{\alpha,t+1} = (1 - \lambda)\pi_{\alpha} + \lambda f_{\alpha,t}, \tag{2.1}$$

where $\alpha = \{0, 1, 2, \dots, K\}$ and $p_{\alpha,t+1}$ is the combined independent searching and advertising probability of finding site α at time $t + 1$. The probability π_{α} is a constant value between 0 and 1 that is independent of time. The parameter λ is a weight parameter between 0

and 1 used to determine how much weight to put on advertising. Setting $\lambda = 0$ means that all bees find the new site on their own and there is no communication between the bees. Similarly setting $\lambda = 1$ means that all bees find the new site through advertising and cannot find the potential sites individually.

Note that the sum of $p_{\alpha,t+1}$ for all available sites including not finding a site equals to 1 as shown below:

$$\begin{aligned}
\sum_{\alpha=0}^K p_{\alpha,t+1} &= \sum_{\alpha=0}^K (1-\lambda)\pi_{\alpha} + \sum_{\alpha=0}^K \lambda f_{\alpha,t} \\
&= (1-\lambda) \sum_{\alpha=0}^K \pi_{\alpha} + \lambda \sum_{\alpha=0}^K n_{\alpha,t}/N \\
&= (1-\lambda)(1) + \lambda(1) \\
&= 1
\end{aligned} \tag{2.2}$$

We still need to define how the second component, $d_{i,t+1}$, of bee i 's state at time $t + 1$ is calculated. If bee i does not find a site at time $t + 1$ then she will not dance at time $t + 1$ so we let $d_{i,t+1} = 0$. Initially we assume that the duration of the dance $d_{i,t+1}$ is determined by bee i 's independent assessment of the quality of the site she finds. In later simulations we may allow the duration $d_{i,t+1}$ to be independent of the quality, so as to capture the possibility that the bee's dance is initiated by mimicking what other bees are doing rather than the independent assessment of the quality of the site. We denote the mimicking probability by $\mu \geq 0$. The value of μ is chosen to be a constant value between 0 and 1. The parameter $\mu = 0$ means that bees will always assess the quality of the site before dancing for it. The parameter $\mu = 1$ means that bees will join dances randomly without paying attention to the quality of the site. Mathematically if bee i finds site α at time $t + 1$ then we calculate the dancing duration as follows:

$$d_{i,t+1} = \begin{cases} q_{\alpha} \exp(V_{\sigma}) & \text{with probability } 1 - \mu \text{ (independent assessment)} \\ C \exp(V_{\sigma}) & \text{with probability } \mu \text{ (mimicking),} \end{cases} \tag{*}$$

where V_{σ} is a normally distributed random variable with mean 0 and standard deviation σ . The parameter σ is a positive constant between 0 and 1 that specifies how reliable the bees are in assessing the quality of a site. A small value of σ corresponds to a high reliability. Under this definition the dance duration $d_{i,t+1}$ will fluctuate around the objective quality of the site with probability $1 - \mu$ and it will fluctuate around a constant C with probability μ . The parameter C is a positive constant that is only used in the mimicking case. In this model we let C equal the maximum nest site quality, 10, however other values of C will yield similar results.

To clarify this with an example, if we take a site with quality 10, use a high reliability parameter $\sigma = 0.2$ and assume a one standard deviation range for V_σ then we get a duration result in the range $[10 \exp(-0.2), 10 \exp(0.2)] = [8.19, 12.21]$ when using the independent assessment case $q_\alpha \exp(V_\sigma)$. Since we used a high reliability parameter in this example we notice that the assessment result is close to the objective quality 10 of the site bee i is assessing. On the other hand if we use a low reliability parameter $\sigma = 1$ then the duration will fall in the range $[3.68, 27.18]$ which is a big fluctuation around the objective quality 10. In the case of mimicking, the duration of the dance will fall in the range $[8.19, 12.21]$ when $\sigma = 0.2$ regardless of the quality of the site that bee i is assessing.

Case 2: The state of bee i at time t is $x_{i,t} = (\alpha, d_{i,t})$ which means that bee i has found site α and she is dancing for it at time t .

In this case at time $t + 1$ we need to check the remaining duration of the dance $d_{i,t}$ at time t . If the remaining duration of the dance is still positive then we reduce it by 1. Otherwise we set the state $x_{i,t+1}$ of bee i back to $(0, 0)$. Mathematically $x_{i,t+1}$ is calculated as follows:

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

meaning that bee i will keep voting and advertising for site α until the remaining dance duration is zero. Each time period the dance duration is reduced by 1 until it reaches zero. At the end of the dancing duration, the state of bee i goes back to $(0, 0)$ and bee i is now ready again to visit, evaluate and advertise other sites.

The above two cases conclude the discussion of how bee i changes her state from one time period to another. Now we discuss how to stop the voting process and declare one of the sites as the winning site. For a site α to be the winner it needs to have sufficient support from all the dancing bees involved in the decision making process. Furthermore, the voting process is over when site α has the majority of the vote. In [21] the authors consider two different stopping criteria to declare a winning site. The first criterion is a strict one where site α receives more than twice the amount of support received by the second most popular site, and more than 20 percent of the scout bees are engaged in dance activity at time t . The second (weaker) stopping criterion is where site α receives more support than any other site at time t .

The model described in this section allows us to use different stopping criteria for choosing a winning site which gives a similar consensus, but a different speed-accuracy trade off outcome. For example if we increase the stopping criteria to require more scout bees to agree on the winning site then the voting process will take a longer time to finish, but the

result will be more accurate. Since the focus of this study is not to balance the trade-off between speed versus accuracy we refer the reader to [26] for more details on this subject. In [26] the authors discuss how evolution in honeybees has settled on a value for threshold and dance decay that results in a balanced speed and accuracy outcome, which minimizes the time needed to achieve consensus and maximizes the probability that the best site is chosen.

2.2 Setting up the mathematical model

2.2.1 Our extension and modifications

We add two new features to the model introduced in the previous section:

1. One of the behaviors discussed in [34] but not included in the model in [21] is that some bees decide to permanently exit the voting process and no longer participate in it. It is not clear why the bees simply stop dancing for a site. However, one of the theories that was mentioned in [34] is that they simply lose their enthusiasm and decide to exit the voting process after voting for a site for many times and not getting enough support for it from other bees.

To represent these bees in our mathematical model we add another possible value to the parameter $s_{i,t}$, namely $s_{i,t} = K + 1$ and its corresponding probability p_{exit} . This state means that bee i has decided to exit the voting process and no longer dances for any site. The difference between this value and $s_{i,t} = 0$ is that bees with site $s_{i,t} = 0$ are not dancing at time t but can re-enter the voting process at any other time period while the value $s_{i,t} = K + 1$ means that bee i is not dancing at time t and will not re-enter the voting process at any future time period. We add a small probability, p_{exit} , to the model; hence, at any time period bee i has a certain probability of exiting the voting process and never entering it again. The advantage of this addition is that the voting process has to reach an end. The longer the voting process takes the more bees decide to exit the voting process. While in theory a simulation of the model discussed in [21] could go on forever, our addition to the model insures that it does not.

Mathematically, our new definition of $s_{i,t}$ is $s_{i,t} \in \{0, 1, 2, \dots, K, K + 1\}$. Sites 1 to K are our potential sites for which bee i dances for at time t . The value $s_{i,t} = 0$ means bee i does not find a site to dance for at time t but it is still looking for a site and can re-enter the voting process. The value $s_{i,t} = K + 1$ means bee i does not find a site to dance for at time t and will no longer participate in the voting process.

There are now 3 cases we need to discuss regarding how bee i changes her state from time t to $t + 1$:

Case 1 in Section 2.1 is modified as follows: In this case we add one step before continuing the process as discussed in Section 2.1. Bee i has a certain probability p_{exit} of exiting the voting process permanently $x_{i,t} = (K + 1, 0)$. If bee i does not exit the voting process permanently then we follow case 1 discussed in the previous section. Mathematically;

$$x_{i,t+1} = \begin{cases} (K + 1, 0) & \text{with probability } p_{exit} \\ \text{(follow case 1 discussed in Section 2.1)} & \text{with probability } 1 - p_{exit}, \end{cases}$$

in summary, if bee i exits the voting process we set $x_{i,t+1} = (K + 1, 0)$ otherwise we follow the discussion in case 1 Section 2.1 to determine what the state of bee i is. Note that all bees have the same probability of exiting the voting process meaning that p_{exit} does not depend on bee i .

Case 2 of Section 2.1 stays the same and does not need to be modified.

Case 3: We need to add a new case to handle the state of bee i at time t when bees decide to exit the voting process. The state of bee i at time t is $x_{i,t} = (K + 1, 0)$. In this case at time $t + 1$ the state of bee i stays as $(K + 1, 0)$.

2. The second addition is adding a revisiting feature. Based on experiments in [34], Seeley found that bees revisit and advertise a nest site multiple times. However, each time a bee revisits a nest site the duration of the dance decreases. He found that the drop in dance strength per consecutive trip appears to be a constant regardless of the nest site quality and the number of times a bee revisits a nest site. In those experiments the number of dance circuits in a first trip varied between 91 to 22 while the drop in dance circuits was 15 dance circuits per revisit. For full details on those experiments see Figure 6.10 of [34]. In our model we represent this behavior as follows: given that bee i does not exit the voting process, she has a certain probability $p_{revisit}$ of flying back to revisit the previously visited site and voting for it again. For each consecutive visit the voting duration is reduced by a constant d_{drop} . In this case assuming that the last visited site is α then $s_{i,t+1}$ is calculated as follows:

$$s_{i,t+1} = \begin{cases} \alpha & \text{with probability } p_{revisit} \\ \text{(follow case 1 discussed in Section 2.1)} & \text{with probability } 1 - p_{revisit}, \end{cases}$$

and $d_{i,t+t}$ is calculated as follows for both cases

$$d_{i,t+1} = (\star) - (Md_{drop}),$$

where d_{drop} represents the drop in the voting duration and M is the number of consecutive visits to site α . We set $M = 0$ when a bee visits a nest site for the first time which equals our original equation (\star) discussed in the previous section. We set $d_{drop} = 2$ in all our simulations. Sections 2.2.2 and 2.2.3 shows the full list of parameters and a flowchart of the full model including our extensions.

2.2.2 List of parameters

Parameter	Definition
t	Time index
N	Total number of scout bees
K	Number of potential hives
q_α	Objective quality of site α
$s_{i,t}$	The site bee i dances for at time t
$d_{i,t}$	The remaining duration of bee i 's dance at time t
$x_{i,t}$	The state of bee i at time t
$p_{\alpha,t}$	The probability of finding site α at time t
$p_{0,t}$	The probability that a bee remains at rest or does not find a hive
π_α	The probability that a bee finds site α independently
$f_{\alpha,t}$	Proportion of bees dancing for site α at time t
$n_{\alpha,t}$	The number of bees dancing for site α at time t
λ	Parameter used to determine how much weight to put on advertising
μ	Mimicking probability
V_σ	Normally distributed variable with mean 0 and standard deviation σ
σ	Reliability of bee's in assessing the quality of a site
C	Maximum nest site quality available in a simulation
p_{exit}	Probability of exiting the voting process
$p_{revisit}$	Probability of revisiting a site that was visited in the previous time step
d_{drop}	Drop in the voting duration
M	Number of consecutive visits

Table 2.1: List of parameters for the bee nest site selection model.

2.2.3 Flowchart of the full model

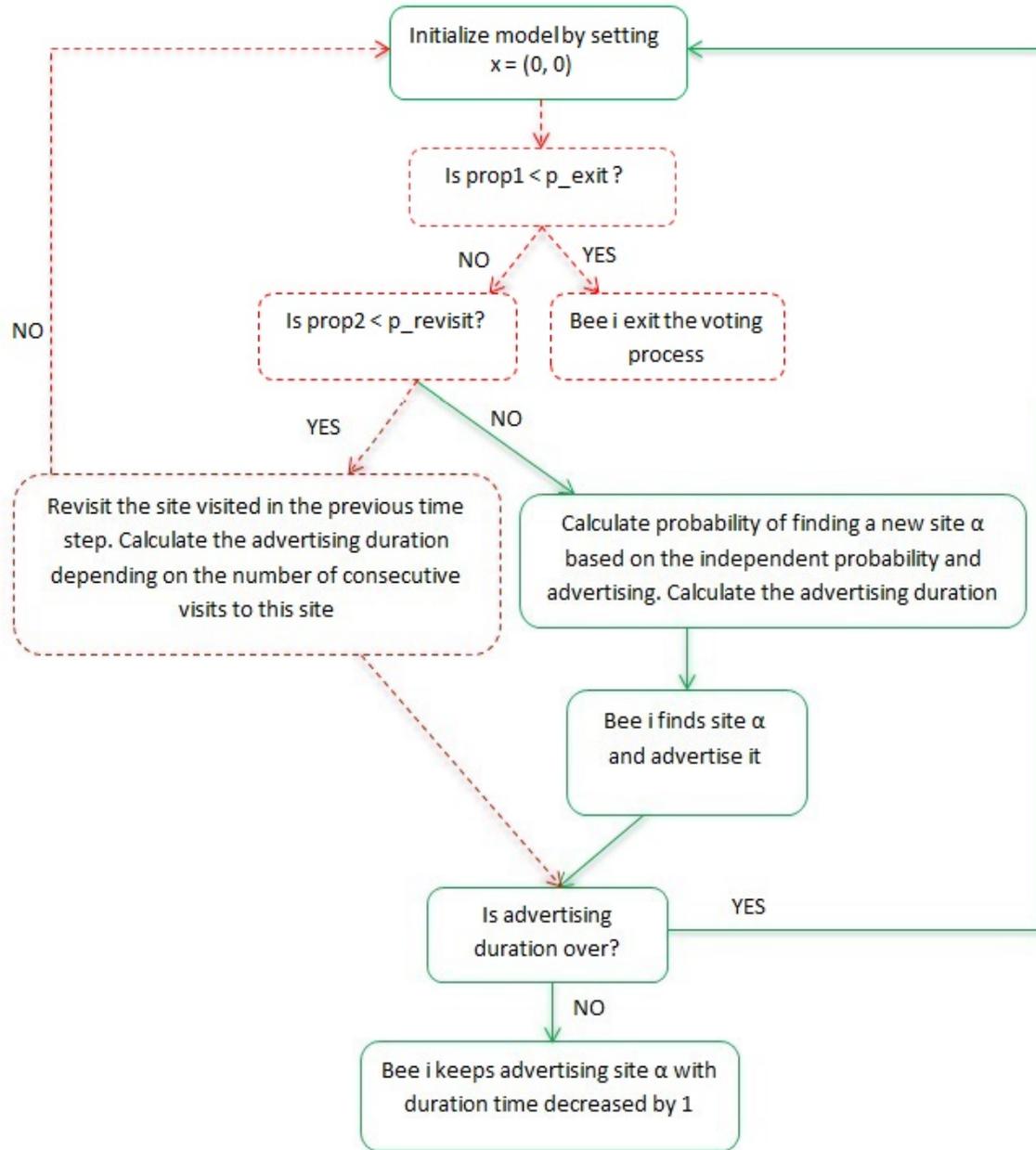


Figure 2.1: Flowchart of the full honeybee model. The green (solid) part of the flowchart shows the original model introduced in [21] while the red (dotted) part shows our modifications.

Chapter 3

Honeybee experiments and simulations

3.1 Introduction and summary of simulations

In this section we compare the results of different simulations to find how certain changes in parameters affect the final consensus and time. In Simulation 1 we run the model introduced in [21], (our code with p_{exit} and $p_{revisit}$ set to zero), and we also run our model using two different values of revisiting probability $p_{revisit} = 0.4$ and 0.8 . We run each case 100 times and graph the average result of all the runs. In Simulation 2 we introduce a stricter stopping criteria forcing the bees to spend more time deciding which hive to choose before declaring a winning site. In the second simulation we expect the stricter threshold to take more time compared to the first simulation but to give a better consensus result. We use the same values for $p_{revisit}$ as in Simulation 1 and we run each case 100 times. Finally we present some graphs to compare the results from Simulations 1 and 2. Table 3.1 shows the full list of initial values we use in both simulations. We choose to use the same values used in [21] with the exception of the stopping criteria which will be disused for each simulation separately. We set $p_{revisit}$ to 0, 0.4 and 0.8 to investigate if more revisiting probability gives better consensus results.

Parameter	Value in Simulation 1 and 2
T	300
N	200
K	5
q_α	{3, 5, 7, 9, 10}
$p_{0,t}$	0.75
π_α	0.05
λ	0.8
μ	0
σ	0.2
C	10
p_{exit}	0, 0.0001
$p_{revisit}$	0, 0.4, 0.8
d_{drop}	2

Table 3.1: List of parameter values used for the bee nest site selection model in Simulation 1 and 2.

3.2 Simulations

3.2.1 Simulation 1 - With or without revisiting?

In this simulation we run the model with p_{exit} and $p_{revisit}$ set to zero. We also run the model using two different values of revisiting probability $p_{revisit} = 0.4$ and 0.8 and $p_{exit} = 0.0001$. We run the models a total of 300 times; 100 times using the original model with no revisiting or exit features, 100 times using our modification with $p_{revisit} = 0.4$ and $p_{exit} = 0.0001$ and 100 times with $p_{revisit} = 0.8$ and $p_{exit} = 0.0001$. We record the average number of correct consensus for each case (a correct consensus is defined as the percentage of time the bee colony chooses the highest quality site over the other available sites in the simulation). We also record the average time needed to reach consensus. We set our stopping criteria in this simulation as follows: A site α is declared a winner when it receives more than twice the amount of support received as the second most popular site, more than 20 percent of the scout bees are engaged in dance activity at time t , and finally $t > 20$ to give bees enough time to find all available sites.

In this simulation we get 88% correct consensus when using the model introduced in [21] compared to 84% and 83% using our model with 0.4 and 0.8 revisiting probability respectively. The results show a better consensus when there is no revisiting feature. See ($t > 20$) in Figure 3.2. We also find that adding the revisiting feature results in more time

for the colony to reach consensus compared to the model in [21]. The higher the revisiting probability, the more time needed to reach consensus. See ($t > 20$) in Figure 3.3.

3.2.2 Simulation 2 - Restricted consensus criterion

In this simulation we run the same 3 cases used above (no revisiting, 0.4 revisiting probability and 0.8 revisiting probability) using a stricter stopping criterion. In this simulation a site α is declared a winner when it receives more than twice the amount of support received by the second most popular site, more than 20 percent of the scout bees are engaged in dance activity at time t and finally $t > 30$. Adding another extra 10 time steps before declaring a winner allows bees to spend more time advertising and assessing sites. In our model this time also results in more revisiting trips. Using a stricter stopping criterion in the model introduced in [21] results in a better consensus results as expected (93% compared to 88% in Simulation 1) since bees in this case have more time to assess and advertise and decide on a site.

This result is consistent with time versus reliability studies done in different papers where if a colony has more time to choose a site they tend to choose the better site more often compared to a colony that does not have a lot of time. For example a colony that has its original site destroyed and must find one immediately, will settle for a lower quality site compared to a colony that chooses to leave its original site and has more time to find the best site available. However, our model with the revisiting feature seems to give similar results whether we use a loose or a strict stopping criterion. Our first thought was that this contradicts our theory in that adding a stricter stopping criterion should result in a better consensus; however, it actually supports it. We have two factors playing against each other in our model:

1. In our model we have the revisiting feature which, as we found in Simulation 1, results in a lower consensus accuracy compared to the model introduced in [21]. Adding more time allows more revisiting to happen; therefore, resulting in less consensus accuracy compared to Simulation 1.
2. Adding a stricter stopping criterion results in a better consensus. This is confirmed by comparing the consensus accuracy without revisiting feature in Simulations 1 and Simulation 2.

This is the reason why our model with the revisiting feature gives a consensus value in Simulation 2 that is similar to Simulation 1. In Simulation 2 the accurate consensus value is (85% and 82%) when the revisiting probabilities are 0.4 and 0.8 respectively compared to (84% and 83%) in Simulation 1. We find that adding a revisiting feature requires more time to reach consensus compared to not having a revisiting feature. We also find that adding a stricter stopping criterion in Simulation 2 requires more time compared to having a loose stopping criterion in Simulation 1 for all cases. See Figure 3.2 and 3.3 for full results of

Simulations 1 and 2.

In addition to Figures 3.2 and 3.3 that show the full results for all our simulations we also add a couple of examples (Figure 3.1) to show how a single simulation looks. These two plots show how the number of bees voting for each site changes from one time step to another until the colony reaches the quorum threshold.

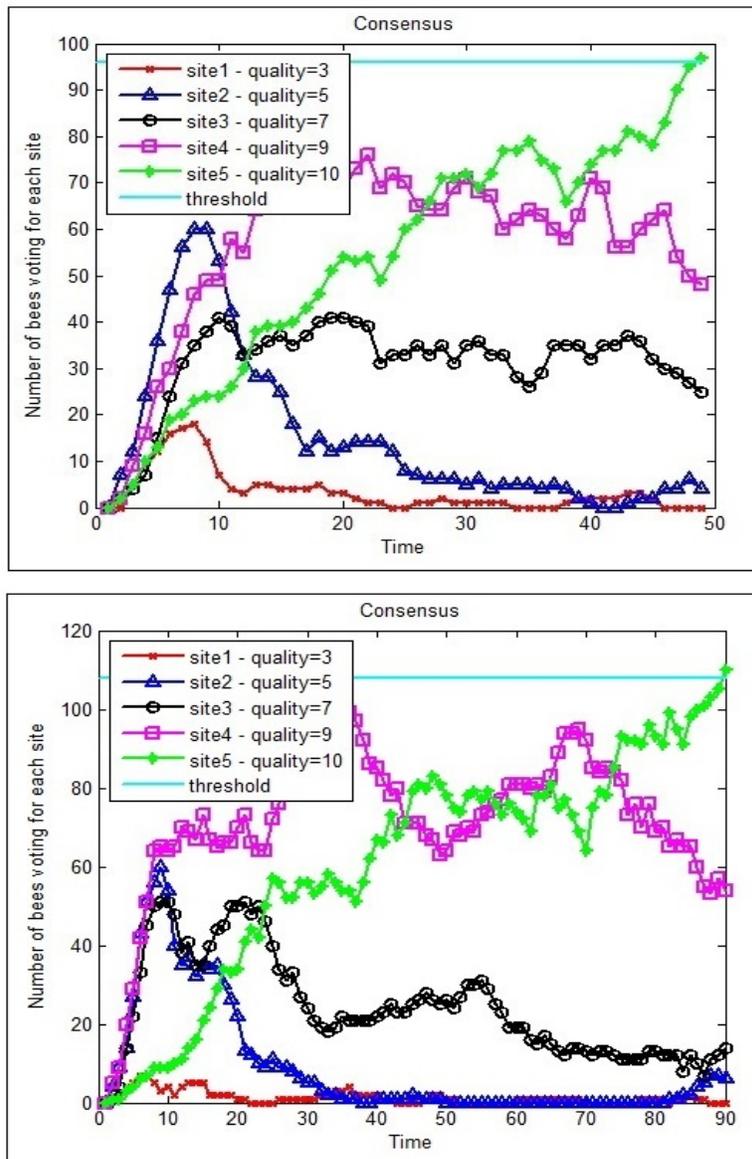


Figure 3.1: Honeybee model single simulation. The Examples show how the number of bees dancing for each site changes from one time step to another until the colony reaches the quorum threshold.

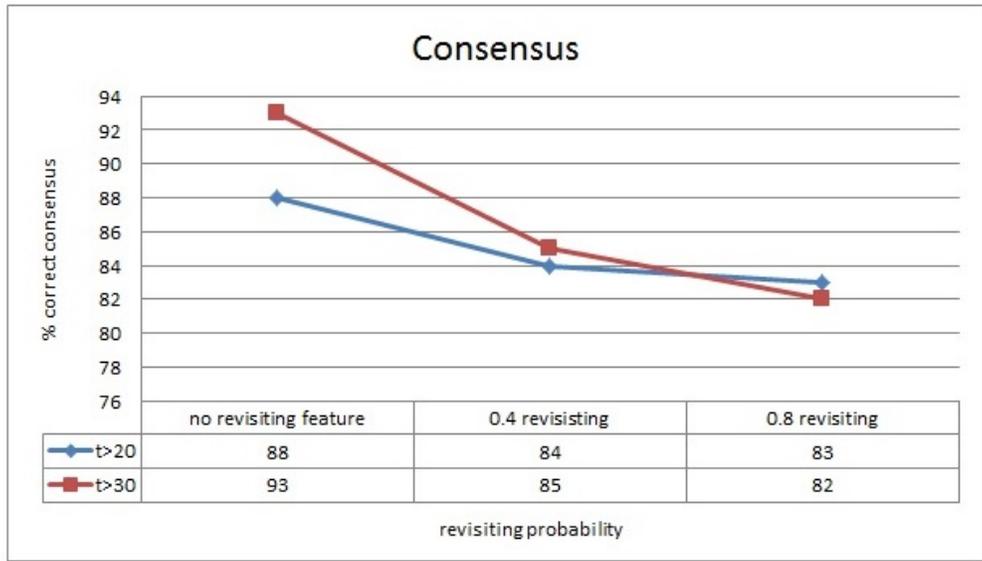


Figure 3.2: Percentage of correct consensus vs probability of revisiting for honeybees. The higher the revisiting probability is, the less percentage of correct consensus we get. Comparing the results of Simulation 1 to Simulation 2 shows that in the case where we do not have revisiting we get better consensus results when the consensus criteria is stricter. On the other hand the stricter criteria does not affect the final result when revisiting probability is 0.4 or 0.8.



Figure 3.3: Total time needed to reach consensus vs probability of revisiting for honeybees. The higher the revisiting probability is, the more time is needed to reach consensus. Comparing the results of Simulation 1 to Simulation 2 shows colonies using stricter consensus criteria need more time to reach consensus.

3.3 Summary of simulations

Bee colonies are extremely good at choosing a high quality site over a low quality site in different circumstances. In this chapter we looked into two factors that affect the site choice: how strict the stopping criterion is and how strongly bees get attached to a site they visit. Using a strict consensus criterion in the model introduced in [21] results in a better consensus outcome but takes more time to reach consensus. Using our model with the revisiting feature we notice that in both simulations we got a worse consensus result compared to [21]. We believe that this is because bees get attached to the site they find, so instead of trying to find better sites they use that time to revisit the same site repeatedly.

In a way this behavior is similar to how human group decision making works. Both human beings and honeybees can be stubborn about their initial opinion; however, there is a huge difference in the behavior of human beings and honeybees. Human beings can be stubborn about their opinion and not willing to change it unless they find another better option; sometimes even then we refuse to change our opinion due to ego, politics and other reasons. Honeybees behave differently in that they automatically and willingly stop supporting a position if they do not get enough support from other bees. They decide to exit the voting process leaving the decision to other members of the colony which helps in getting a better outcome in a faster time period. They are also willing to change their support from one position to another a lot easier than humans do when finding a better side to support.

Going back to our model: although, our results show when bees get attached to a site they visit the correct consensus result drops, it drops only by 5% or 10% when using a loose or a strict stopping criterion respectively. The bees eventually stop dancing or switch their opinion which helps the colony reach a correct decision with high accuracy despite the disadvantage of some bees being attached to certain sites they visit.

Since bees do revisit previously found sites, it is possible that it is because evolution showed that this is beneficial for the species. One might wonder whether this is a correct implementation of this feature given that it results in a lower correct consensus percentage. We emphasize that even though the revisiting feature lowers the consensus rate, it increases the time needed to reach consensus as shown in Figure 3.2. This might just be the extra time the colony needs to find another better site to migrate to. We remind the reader that the survival of the colony does not only depend on the accuracy of the consensus result, but also depends on finding the correct balance between time and accuracy.

Chapter 4

Modeling nest site selection in ants

4.1 Setting up the mathematical model

We modify the mathematical model introduced in [21] and apply it to two different ant species. In this model we have N worker ants, labelled $i = 1, 2, \dots, N$, who participate in the decision making process and K potential nest sites, labelled $1, 2, \dots, K$, where each nest $\alpha \in \{1, 2, \dots, K\}$ has an objective quality $q_\alpha \geq 0$. A site with high objective quality is more desirable than a site with low objective quality. We denote the dimensionless quality of site α by \bar{q}_α . To make a quality \bar{q} dimensionless and between 0 and 1 we divide it by the highest site quality available in a simulation. For example if we only have 2 sites in a simulation with $q \in \{5, 10\}$ then the dimensionless quality $\bar{q} \in \{0.5, 1\}$. At each time period t ant i can be assessing a potential site α , canvassing for a potential site α , or at rest.

The state of ant i at time t denoted by $x_{i,t}$ can be represented by 3 parameters: the nest ant i is assessing at time t denoted by $s_{i,t}$, the remaining duration of the assessment time of ant i at time t before she moves to the canvassing phase denoted by $d_{i,t}$, and finally the site ant i is actively advertising at time t denoted by $w_{i,t}$. Similar to our model in Chapter 2 $s_{i,t} \in \{0, 1, 2, \dots, K\}$. If $s_{i,t} = 0$ ant i does not find a site to assess at time t . Also $w_{i,t} \in \{0, 1, 2, \dots, K\}$. If $w_{i,t} = 0$ ant i does not find a site to canvas to at time t .

The main difference between this model and our previous model in Chapter 2 is that the vector $x_{i,t} = (s_{i,t}, d_{i,t}, w_{i,t})$ which represents the state of ant i at time t has 3 parameters instead of 2. It shows which site ant i is assessing, the remaining duration of the assessment time and finally which site she is canvassing for. Note that an ant cannot be in 2 phases at the same time. You must have both $s_{i,t}, w_{i,t} \geq 0$ but $s_{i,t}w_{i,t} = 0$. Another difference is the duration value here is different from the duration value in the bee model. In the bee model the duration parameter represents the duration of the advertisement. In the ants model the duration parameter represents the assessment duration. It shows the time spent

on assessing the site before moving to the canvassing phase. Based on experiments done in [29] the assessment duration is inversely related to the quality of the site. This relationship between site quality and assessment duration ensures faster population growth at the better nests. Therefore in the mathematical model presented in this chapter, the lower the quality of the site the more time ant i spends in the assessment phase before she moves to the canvassing phase.

We initialize the model by letting $x_{i,1} = (0, 0, 0)$ for all i which means that at time 1 there is no assessment or canvassing activities. Similar to the bee model the state of ant i at time $t + 1$ depends on her own state and the state of all other ants at time t . There are 3 cases to consider in this model. We discuss each case separately.

Case 1: The state of ant i at time t is $x_{i,t} = (0, 0, 0)$ which means that ant i is not in the assessment or canvassing phase at time t .

In this case, ant i has a certain probability of finding one of the K potential nest sites and entering the assessment phase at time $t + 1$. Ant i could either find the site independently without any advertising by other ants or by the help of other ants that are in canvassing phase. We let $p_{\alpha,t+1}$ be the combined dependent and independent probability of finding site α at time $t + 1$. We also let $p_{0,t+1}$ be the probability that ant i remains at rest or does not find a site and therefore does not enter the assessment phase for any site at time $t + 1$. At time $t + 1$ the first component of $x_{i,t+1}$ namely $s_{i,t+1}$ takes the value of one of the potential K sites: $1, 2, \dots, K$ with probability $p_{1,t+1}, \dots, p_{K,t+1}$ respectively or $s_{i,t+1} = 0$ with probability $p_{0,t+1}$ which means that ant i is not in canvassing phase at time $t + 1$. The probability $p_{\alpha,t+1}$ can be represented mathematically using the same two factors (i and ii) discussed in Chapter 2 Case 1 as follows:

$$p_{\alpha,t+1} = (1 - \lambda)\pi_{\alpha} + \lambda f_{\alpha,t},$$

which is the same equation as (2.1) used in Chapter 2. The parameter π_{α} is the probability that ant i finds site α independently without the help of other ants and $f_{\alpha,t}$ is the proportion of ants canvassing for site α at time t .

The second component, $d_{i,t+1}$, of ant i 's state at time $t + 1$ is determined by ant i 's independent assessment of the quality of the site she finds. If ant i does not find a site at time $t + 1$ then she will not assess anything at time $t + 1$ so $d_{i,t+1} = 0$. If she finds site α , then $d_{i,t+1}$ is calculated based on the quality of the site ant i finds with probability $1 - \mu$ or based on a constant C with probability μ . The parameter C is a positive constant which equals the highest site quality value available in a simulation. In our model $d_{i,t+1}$ is

determined as follows:

$$d_{i,t+1} = \begin{cases} M - (D\bar{q}_\alpha \exp(V_\sigma)) & \text{with probability } 1 - \mu \\ M - (DC \exp(V_\sigma)) & \text{with probability } \mu, \end{cases}$$

where M is a constant used to get a decreasing duration depending on the site quality so that the higher the site quality the smaller the assessment duration. We use the parameter D to scale the dimensionless quality to be between 1 and 10. We let $D = 10$ and $M = 30$ in all our simulations unless mentioned otherwise. The parameter V_σ is a normally distributed random variable with mean 0 and standard deviation σ . The parameter σ specifies the ant's assessment reliability. A small value of σ corresponds to a high ant reliability. The probability μ is a constant between 0 and 1 used to capture the possibility that the ant's assessment duration of the site is dependent on the wrong quality C instead of the real site quality q_α . Even though our model allows the addition of this feature we set $\mu = 0$ in all our simulations to be able to accurately compare different results without worrying about wrong assessment durations.

Finally the third component of ant i 's state at $t + 1$ namely $w_{i,t+1}$ is set to zero in this case since ant i cannot be in two phases at the same time. It cannot be assessing one nest while canvassing another. Also ants cannot enter canvassing phase for a site before assessing it.

Case 2: The state of ant i at time t is $x_{i,t} = (\alpha, d_{i,t}, 0)$ which means that ant i has found site α and she is assessing it at time t .

In this case at time $t + 1$ we need to check the remaining assessment duration, $d_{i,t}$, at time t . If the remaining duration of the assessment is positive, ant i continues to assess the same site at time $t + 1$ with the remaining assessment time reduced by one period. If the assessment duration is over, ant i will either enter the canvassing phase to get more support for the site or reject the site because it is not of sufficient quality. Formally,

$$x_{i,t+1} = \begin{cases} (s_{i,t}, d_{i,t} - 1, 0) & \text{if } d_{i,t} \geq 1 \\ (0, 0, s_{i,t}) & \text{if } d_{i,t} < 1 \text{ with probability } 1 - p_{\alpha, reject} \\ (0, 0, 0) & \text{if } d_{i,t} < 1 \text{ with probability } p_{\alpha, reject}, \end{cases}$$

where $p_{\alpha, reject}$ is the probability of rejecting site α . It is calculated based on ant i 's assessment of the quality of the current site she is assessing compared to other available sites. Mathematically,

$$p_{\alpha, reject} = \min[1, \max_\gamma [\bar{q}_\gamma \exp(V_\sigma)] - \bar{q}_\alpha \exp(V_\sigma) + 0.1],$$

where $\gamma \in \{1, 2, \dots, K\}$. In other words we evaluate the term: $\bar{q}_\gamma \exp(V_\sigma)$ for all available K sites in a simulation then use the maximum value in the above equation. The higher the quality of the site being assessed, q_α , the smaller the probability that it gets rejected, $p_{\alpha, reject}$. Therefore, ants assessing a high quality site have a higher probability to enter the canvassing phase for this site compared to ants assessing a low quality site.

Case 3: The state of ant i at time t is $x_{i,t} = (0, 0, \alpha)$ which means that ant i has found site α and she is in canvassing phase at time t .

In this case ant i has already assessed site α and decided that it is good enough so she entered the canvassing phase to get more support for it. While ant i is in the process of getting support for site α it can stumble upon another site. Ant i can get lost or it can get pushed by another ant to a new site β . Site β can in fact be the same site as α to resemble the scenario that ant i gets lost and finds site α using another path or gets canvassed to site α using another path. In these cases ant i does not know that this site is the same site she was already canvassing and therefore treats it as a new site. When ant i finds site β she needs to make a decision on whether to abandon site α and start assessing site β or stick to site α and keep getting support for it. We model this using probabilities similar to Case 1 as follows: ant i has a certain probability of getting lost and finding one of the K sites on her own. For each site β we write π_β to denote the probability that ant i finds site β on her own at time $t + 1$. Furthermore, π_0 denotes the probability that ant i does not get lost at time $t + 1$ and therefore keeps getting support for the old site α . Mathematically,

$$\pi_0 + \sum_{\beta} \pi_\beta = 1.$$

Ant i can also find a new site via advertising from other ants who are in canvassing phase. The probability for finding site β in $t + 1$ while ant i is in canvassing phase is $p_{\beta,t+1}$ which is a combination of the probability of finding the new site independently and finding it via advertising. Mathematically we use the same probability equation 2.1 used in Case 1:

$$p_{\beta,t+1} = (1 - \lambda)\pi_\beta + \lambda f_{\beta,t},$$

where $p_{\beta,t+1}$ is the probability of finding site β at time $t + 1$. The value λ is a weight parameter between 0 and 1, we use it to determine how much weight to put on advertising. Setting $\lambda = 0$ means that all ants find the new site on their own and there is no canvassing being done between the ants. The parameter $f_{\beta,t}$ is the proportion of ants in canvassing phase for site β at time t . The sum of $p_{\beta,t+1}$ for all available sites including not finding a site equals to 1 as shown equation 2.2.

When ant i finds a new site, β , while canvassing to another site it checks the perceived quality, $\bar{q}_\beta \exp(V_\sigma)$, of the new site. If the perceived quality of the new nest is higher than the perceived quality of the old site, ant i abandons the old site and enters the assessment phase for the new site. Otherwise; it goes back to the old site and keeps getting support for it. So assuming ant i is currently canvassing to site α and it stumbles upon a new site β the following mathematical equation determines its state at $t + 1$:

$$x_{i,t+1} = \begin{cases} (0, 0, \alpha) & \text{if } \bar{q}_\alpha \exp(V_\sigma) \geq \bar{q}_\beta \exp(V_\sigma) \\ (\beta, d_{i,t+1}, 0) & \text{otherwise,} \end{cases}$$

where $d_{i,t+1}$ is calculated the same way as previously discussed:

$$d_{i,t+1} = \begin{cases} M - (D\bar{q}_\beta \exp(V_\sigma)) & \text{with probability } 1 - \mu \\ M - (DC \exp(V_\sigma)) & \text{with probability } \mu. \end{cases}$$

In summary if the perceived quality, $\bar{q}_\alpha \exp(V_\sigma)$, of site α is higher or equal to the new perceived quality of site β , then ant i stays canvassing to site α . The state of ant i at time $t + 1$ equals to its state at time t . If the perceived quality of site α is less than site β then ant i 's state at time $t + 1$ changes. Ant i abandons site α and starts assessing site β with the duration of the assessment determined by the quality of site β .

Now that we have discussed the transition from time t to $t + 1$ what's left is to determine the stopping criteria for the model and declare one of the potential nest sites as the winner. We choose to implement this step by setting a threshold for the stopping criteria that matches the threshold observed in experiments. When ants reach this threshold we stop the process and record the winning site. It is important to note here that even though we stop the model when the threshold is reached, in real life the process moves to a new phase called the commitment phase. We choose to not implement the commitment phase since in this phase ants migrate the entire colony from the old nest to the new one. Therefore, this phase does not change the winning site. Figure 4.1 shows the flowchart of the assessment and canvassing phases for house hunting model for ants.

4.1.1 List of parameters

Parameter	Definition
t	Time index
N_c	Colony size
N	Total number of worker ants
K	Number of potential sites
q_α	Objective quality of site α
\bar{q}_α	Dimensionless quality of site α
$s_{i,t}$	The site ant i assess at time t
$w_{i,t}$	The site ant i canvas for at time t
$d_{i,t}$	The remaining duration of ant i 's assessment at time t
$x_{i,t}$	The state of ant i at time t
$p_{\alpha,t}$	Probability of finding site α at time t
$p_{0,t}$	Probability that an ant remains at rest or does not find a nest
π_α	Probability that an ant finds site α independently
$f_{\alpha,t}$	Proportion of ants advertising site α at time t
λ	Parameter used to determine how much weight to put on advertising
μ	Mimicking probability
V_σ	Normally distributed variable with mean 0 and standard deviation σ
σ	Reliability of ants in assessing the quality of a site
C	Maximum nest site quality available in a simulation
M	Constant used to get a decreasing duration depending on the site quality
D	Parameter used to scale \bar{q}_α to be between 1 and 10
$p_{\alpha,reject}$	Probability of rejecting a site after it has been assessed

Table 4.1: List of parameters for the ant nest site selection model.

4.1.2 Flowchart to show the full model for ants

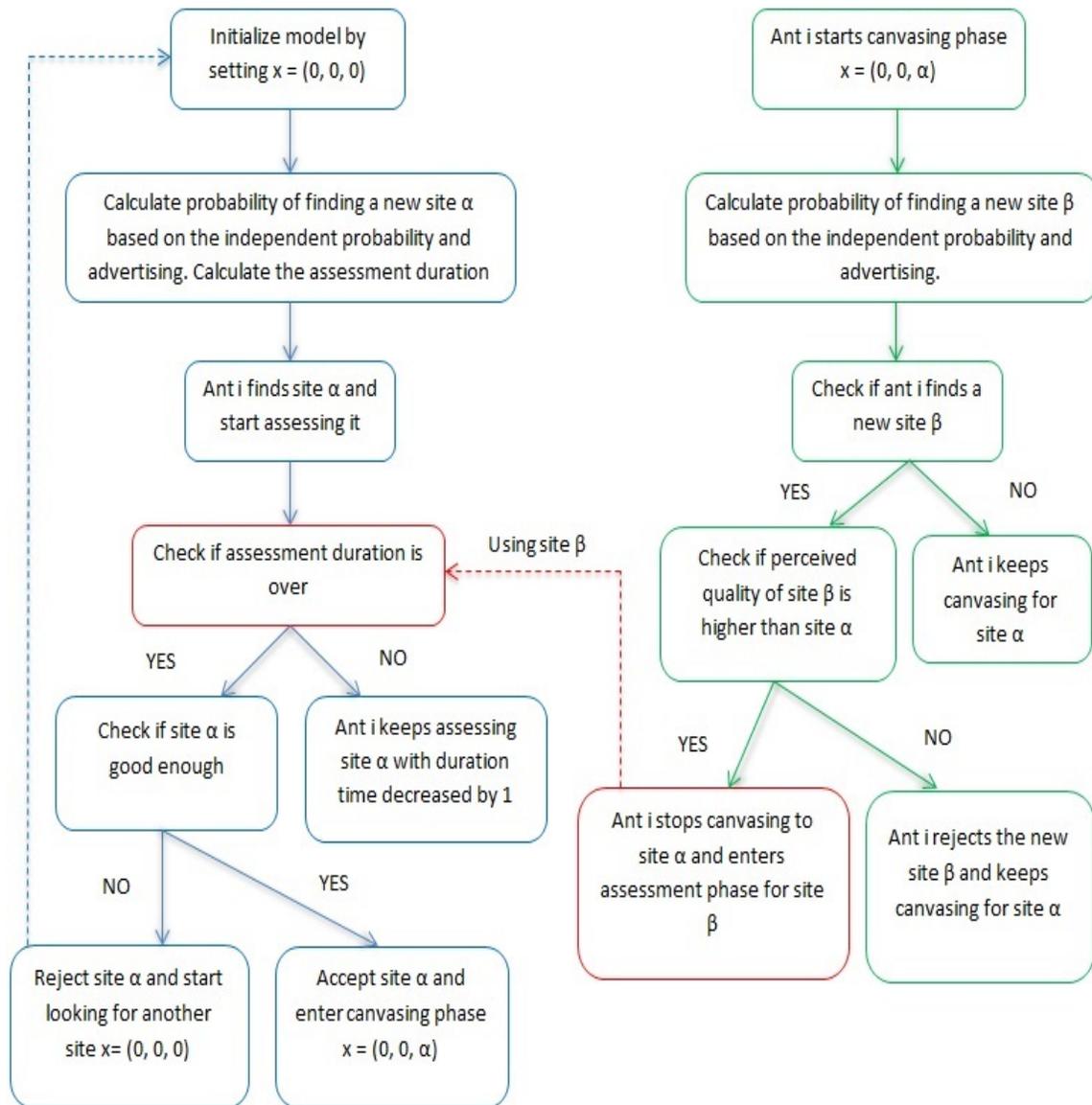


Figure 4.1: Flowchart of the ant model from the starting point at time zero until ants reach a consensus. The left part of the flowchart shows the assessment phase while the right part of the flowchart shows the canvassing phase.

Chapter 5

Ant experiments and simulations

5.1 Introduction and summary of simulations

In this chapter we perform different simulations and compare their results to biological experiments. In Simulation 0 we run our model using different values of reliability and advertising. We find the best combination of these values that results in the highest consensus percentage for the high quality site. We repeat the runs 200 times for each combination and graph the average result of all runs. In Simulations 1-6 we vary a certain parameter while keeping the rest constant. We study how the change in that parameter affects the behavior of the colony. These runs are repeated 100 times each. The result shown in the graphs is the average of these 100 runs. The same 100 simulations are run using 3 different values of advertising: high, medium and low corresponding to $\lambda = 0.8, 0.4$ and 0.2 respectively.

We also run the simulations using different colony sizes, N_c : 20, 40, 80, 200, 500 for chemical ants and 40, 100, 250, 500, 1000 for trail ants. We used different sizes of colonies for chemical ants vs trail ants since chemical colonies are usually smaller than trail colonies in nature. Chemical ant colonies have an average size of less than 40 ants compared to 100-500 for trail ant colonies as discussed in [5]. It is for that reason we choose to run our simulations using smaller sizes for chemical ants compared to trail ants. Not all ants in the colony participate in the decision making process i.e. $N < N_c$. We choose the number of worker ants, N , to be $\text{round}(0.52N_c)$ for chemical ants and $\text{round}(14.7+0.4N_c)$ for trail ants based on the estimates found in multiple lab experiments in [5] and [29] respectively. We also set the quorum threshold to be $0.714 + 0.248N$ for chemical ants and $0.9521 + 0.0141N$ for trail ants based on lab experiments in [5] and [10] respectively.

Unless mentioned otherwise, in all simulations we set the parameter $\mu = 0$. We also set $D = 10$, $M = 30$ and $T = 500$. For a full list of parameters and values used in our

simulations in this chapter see Tables 5.1 and 5.2. Note that all Figures for Simulations 1-6 are combined and presented at the end of the chapter.

Parameter	Simulation 0	Simulation 1	Simulation 2	Simulation 3
N_c	40	20, 40, 80, 200, 500	20, 40, 80, 200, 500	20, 40, 80, 200, 500
N	round(0.52 N_c)	round(0.52 N_c)	round(0.52 N_c)	round(0.52 N_c)
T	500	500	500	500
K	5	2	2	2
q_α	[0 3 5 7 9 10]	[0 5 10]	[0 10 10]	[0 5 10]
π_α	[0.75 0.05 0.05 0.05 0.05 0.05]	[0.9 0.05 0.05]	[0.9 0.09 0.01]	[0.9 0.09 0.01]
λ	0.2, 0.4, 0.6, 0.8	0.2, 0.4, 0.8	0.2, 0.4, 0.8	0.2, 0.4, 0.8
σ	0.2, 0.4, 0.6, 0.8, 1	0.2	0.2	0.2
μ	0	0	0	0
M	30	30	30	30
D	10	10	10	10
Threshold	0.714+(0.248 N)	0.714+(0.248 N)	0.714+(0.248 N)	0.714+(0.248 N)
Delay	N/A	N/A	N/A	N/A

Parameter	Simulation 4	Simulation 5	Simulation 6
N_c	20, 40, 80, 200, 500	20, 40, 80, 200, 500	20, 40, 80, 200, 500
N	round(0.52 N_c)	round(0.52 N_c)	round(0.52 N_c)
T	500	500	500
K	3	3	3
q_α	[0 5 7 10]	[0 5 7 10]	[0 5 7 10]
π_α	[0.85 0.05 0.05 0.05]	[0.85 0.05 0.05 0.05]	[0.85 0.05 0.05 0.05]
λ	0.2, 0.4, 0.8	0.2, 0.4, 0.8	0.2, 0.4, 0.8
σ	0.2	0.2	0.2
μ	0	0	0
M	30	30	30
D	10	10	10
Threshold	0.714+(0.248 N)	0.714+(0.248 N)	0.714+(0.248 N)
Delay	1/4 avg time Simulation 1	1/2 avg time Simulation 1	3/4 avg time Simulation 1

Table 5.1: Various parameters used in each simulation for chemical ants.

Parameter	Simulation 0	Simulation 1	Simulation 2	Simulation 3
N_c	400	40, 100, 250, 500, 1000	40, 100, 250, 500, 1000	40, 100, 250, 500, 1000
N	round(14.7+0.4 N_c)	round(14.7+0.4 N_c)	round(14.7+0.4 N_c)	round(14.7+0.4 N_c)
T	500	500	500	500
K	5	2	2	2
q_α	[0 3 5 7 9 10]	[0 5 10]	[0 10 10]	[0 5 10]
π_α	[0.75 0.05 0.05 0.05 0.05 0.05]	[0.9 0.05 0.05]	[0.9 0.09 0.01]	[0.9 0.09 0.01]
λ	0 .2, 0.4, 0.6, 0.8	0.2, 0.4, 0.8	0.2, 0.4, 0.8	0.2, 0.4, 0.8
σ	0.2, 0.4, 0.6, 0.8, 1	0.2	0.2	0.2
μ	0	0	0	0
M	30	30	30	30
D	10	10	10	10
Threshold	0.9521+(0.0141 N)	0.9521+(0.0141 N)	0.9521+(0.0141 N)	0.9521+(0.0141 N)
Delay	N/A	N/A	N/A	N/A

Parameter	Simulation 4	Simulation 5	Simulation 6
N_c	40, 100, 250, 500, 1000	40, 100, 250, 500, 1000	40, 100, 250, 500, 1000
N	round(14.7+0.4 N_c)	round(14.7+0.4 N_c)	round(14.7+0.4 N_c)
T	500	500	500
K	3	3	3
q_α	[0 5 7 10]	[0 5 7 10]	[0 5 7 10]
π_α	[0.85 0.05 0.05 0.05]	[0.85 0.05 0.05 0.05]	[0.85 0.05 0.05 0.05]
λ	0.2, 0.4, 0.8	0.2, 0.4, 0.8	0.2, 0.4, 0.8
σ	0.2	0.2	0.2
μ	0	0	0
M	30	30	30
D	10	10	10
Threshold	0.9521+(0.0141 N)	0.9521+(0.0141 N)	0.9521+(0.0141 N)
Delay	1/4 avg time Simulation 1	1/2 avg time Simulation 1	3/4 avg time Simulation 1

Table 5.2: Various parameters used in each simulation for trail ants.

5.2 Simulations

5.2.1 Simulation 0 - Advertising and reliability

We start by running the model using different values of advertising and reliability to find the best combination of these values. The best combination is defined as the combination of advertising and reliability that results in the highest consensus percentage corresponding to the high quality site. We repeat the runs 200 times for each combination and graph the average result of all the runs. For chemical ants we use a colony size, N_c , of 40 which has the following number of worker ants, $\text{round}(N = 0.52N_c)$ and a quorum threshold equals $0.714 + 0.248N$ [5]. For trail ants we use a colony size of 400 which has the following number of worker ants, $\text{round}(N = 14.7 + 0.4N_c)$ [29] and a quorum threshold of $0.9521 + 0.0141N$ [10]. It is worth noting that the percentage of chemical ants involved in the decision making is relatively high compared to bees and trail ants. Chemical ant colonies also have a relatively large quorum threshold compared to trail ants.

In this simulation we introduce 5 sites where each has a different quality 3, 5, 7, 9, 10 and all have the same probability of being found, 0.05. We test the following values for advertising $\lambda = 0, 0.2, 0.4, 0.6, 0.8$ and the following values of reliability $\sigma = 0.2, 0.4, 0.6, 0.8, 1.0$. We record the average correct percentage of consensus for each combination over 200 runs. For the full list of parameters used in this simulation see the first column entitled Simulation 0 of Tables 5.1 and 5.2 for chemical and trail ants respectively.

Tables 5.3 and 5.4 show the average percentage for correct consensus over 200 runs for chemical and trail ants using different values of advertising and reliability. For chemical ants we notice that the higher the reliability the better the consensus. Setting the value of the advertising constant and varying reliability we find that we get better consensus results when reliability is $\sigma = 0.2$. In the case of advertising, when we set the reliability as a constant we see the best consensus value when advertising is $\lambda = 0.4$. We also notice that advertising is not very important when ants' reliability is high; however, when ants reliability is low, advertising is important to reach better consensus. For example when reliability is low, $\sigma = 1$ (low reliability corresponds to a large value of σ), no advertising gives 30% correct consensus; however, 0.4 advertising gives 74% correct consensus which is a 44 percentage point improvement. On the other hand, when reliability is high, $\sigma = 0.2$, no advertising gives 85.5% correct consensus; however, 0.4 advertising gives 89.5% correct consensus which is only a 4 percentage point improvement. Figure 5.1 shows the full results.

Varying the reliability parameter in trail ants results in similar behavior to chemical ants where higher reliability leads to a better consensus. See Figure 5.2. However, the advertising parameter affects trail colonies differently. For high reliability, 0.2, we see a similar

		low advertising		λ		high advertising
		0	0.2	0.4	0.6	0.8
high reliability	0.2	85.5	86.5	89.5	83	83.5
	0.4	85.5	85.5	83.5	77.5	75.5
σ	0.6	77.5	81.5	85.5	78	73.5
	0.8	55	75.5	80.5	76	68
low reliability	1	30	60	74	75	65

Table 5.3: Chemical Ant Results - average percentage of correct consensus over 200 runs for different values of advertising and reliability.

		low advertising		λ		high advertising
		0	0.2	0.4	0.6	0.8
high reliability	0.2	79.5	77	80.5	73	68.5
	0.4	76.5	76	76	68	66
σ	0.6	73.5	67.5	67	67.5	64.5
	0.8	69.5	66.5	65.5	64	66
low reliability	1	66	67	58.5	65	64.5

Table 5.4: Trail Ant Results - average percentage of correct consensus over 200 runs for different values of advertising and reliability.

behavior to chemical ants where the best consensus results are observed when advertising is around 0.4; however, when reliability is low ($\sigma = 0.6, 0.8$ and 1) the best consensus values are observed when there is little to no advertising at all. This is counter-intuitive and very interesting observation. We believe that this result is due to the large size of this colony combined with the low quorum threshold and the low reliability parameter. This combination of parameters results in early mistakes when evaluating the site's quality (as a result of low reliability) which gets spread around quickly (as a result of the large colony size). Due to the low quorum threshold for this colony, advertising does not have enough time to fix this mistake. It actually makes the mistake worse by advertising the wrong quality site that is found early in the search process. This makes the overall colony consensus result worse. In other words, for low reliability simulations mistakes get advertised and spread quickly due to the large colony size. Since the quorum threshold in this case is a lot smaller than the threshold for chemical ants, the colony does not have enough time to recover from the mistakes and ends up choosing the wrong site more often. For these simulations the trail colony is better off choosing and evaluating the sites individually with no advertising.

Based on the results found in this simulation we choose to set $\lambda = 0.2, 0.4$ and 0.8 and $\sigma = 0.2$ in all subsequent simulations.

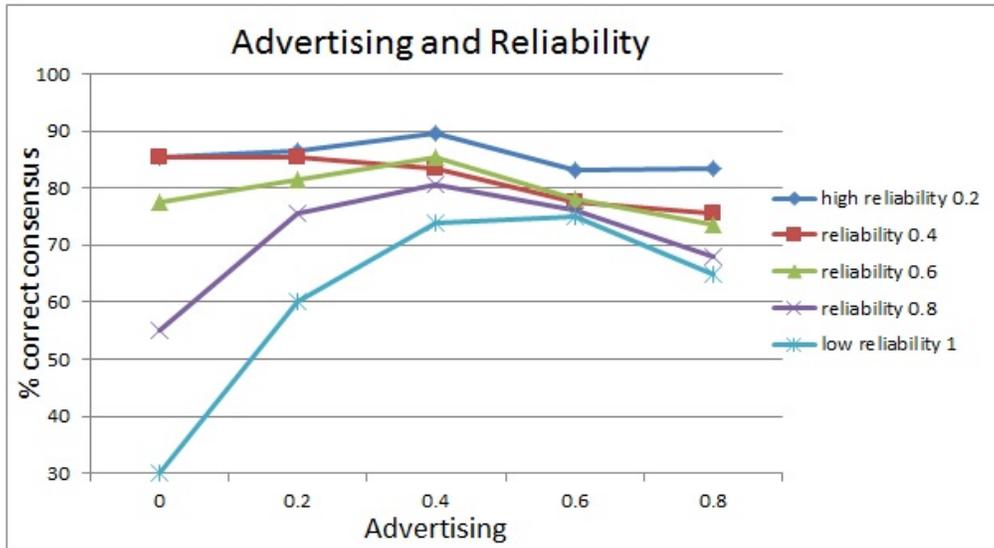


Figure 5.1: Percentage of correct consensus vs advertising parameter λ for 5 different values of reliability for chemical ants. Runs with high reliability parameter do better than low reliability. The optimal advertising parameter in this case is somewhere in the middle around 0.4.

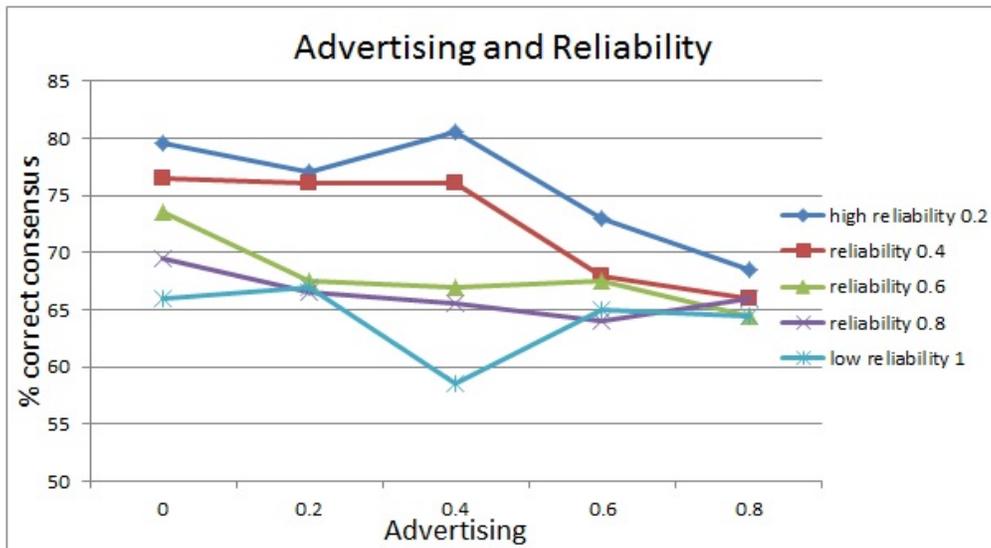


Figure 5.2: Percentage of correct consensus vs advertising parameter λ for 5 different values of reliability for trail ants. Runs with high reliability parameter do better than low reliability. The optimal advertising parameter in this case is somewhere in the middle around 0.4 when reliability is high: (0.2 and 0.4) and 0 when reliability is medium or low: (0.6, 0.8 and 1).

5.2.2 Simulation 1 - Two sites; different qualities

According to biological experiments, if ant colonies are given a choice between a high quality site and a low quality site the colony chooses the high quality site with great accuracy [29, 31, 9, 10, 5]. To test our model in this scenario we only introduce 2 sites in this simulation, one site has high quality, 10, and the other site has low quality, 5. Both sites have the same probability of being found 0.05. We run the simulation with different colony sizes and different advertising values to study how advertising and colony size affects the overall result. For chemical ants we run the simulation for colony sizes: 20, 40, 80, 200 and 500. For each size we run the simulation 300 times: 100 times with high advertising parameter ($\lambda = 0.8$), 100 times with medium advertising parameter ($\lambda = 0.4$), and 100 times with low advertising parameter ($\lambda = 0.2$). We calculate the average for each set of 100 runs and graph the final results. We repeat the same runs for trail ants using the following colony sizes: 40, 100, 250, 500, 1000. For a full list of parameters and values used in this simulation see the second column, Simulation 1, in Table 5.1 and 5.2 for chemical and trail ants respectively.

In all the runs chemical and trail ants choose the higher quality site with 96 – 100% accuracy. If we compare results over different colony sizes we find that bigger colony sizes give slightly better consensus results compared to smaller colonies. Since the difference in consensus accuracy in these simulations is small (maximum of 4%) we conclude that all colonies do extremely well regardless of colony size similar to what is observed in [8, 10]. We leave the discussion behind these small differences to be explained in future simulations when it is more significant. For full results of this simulation see the first graph entitled Simulation 1 in Figure 5.3 for chemical ants and Figure 5.5 for trail ants.

Figure 5.9 is another way of viewing the results. It shows the distribution of how many runs resulted in a correct consensus (consensus towards the highest quality site), how many runs resulted in a split between two sites where both sites reach the threshold at the same time period and how many runs failed to reach the correct consensus. In [11] when 18 trail ant colonies were given a choice between good and poor sites, all 18 colonies migrated to the good site and there was no split noticed. Similarly in [5] colonies migrated from their original site to a high quality one without any splits. In our simulation, we notice similar behavior to lab experiments. There were only 2 splits noticed out of the total number of 600 simulations in this scenario for both chemical and trail ants. For example in Figure 5.9 the first bar shows that out of 100 runs using high advertising parameter, 0.8, and small colony size, 40, we have 96 runs resulted in a correct consensus, 0 runs resulted in a split and 4 runs resulted in the wrong consensus. We only show the bar graphs for trail ants since there are no splits observed for chemical ants in any of our simulations in this chapter.

The advertising value also results in a slightly different overall colony choice in this scenario. Chemical ant colonies that use medium advertising do slightly better than other colonies while trail colonies that use no advertising do slightly better than other colonies. Again since the difference is small (maximum of 4%) we can conclude that all runs, regardless of advertising value, are able to find the best site with high accuracy. This result is expected since the choice between the high and low quality sites is obvious (quality is 5 versus 10) and all ants are highly reliable, $\sigma = 0.2$. In the next simulations our choice will not be so obvious and varying the advertising parameter will actually make a bigger difference in the end result.

Another observation is that larger colonies find the high quality site faster than smaller colonies and therefore reach consensus faster. See Simulation 1 in Figure 5.4 for chemical ants and Figure 5.6 for trail ants. Figure 5.4 shows that chemical ants using high advertising parameter take an average of 59 time periods to reach consensus when colony size is 20 versus 48 time periods when colony size is 500. This is because larger colonies have more scouts to search for new sites and therefore find them faster which matches observations in [10]. We also find that when we keep the colony size constant simulations with high advertising parameter take longer time to finish compared to simulations with low advertising parameter. For example in Figure 5.4 when colony size is 20 we need 59 time periods to reach consensus when using high advertising parameter. However, we only need 43 time periods when using a medium or low advertising parameter.

5.2.3 Simulation 2 - Two sites; same quality; one is harder to find than the other

In this simulation we have 2 sites with the same high quality, 10, but one of them is 9 times easier to find than the other one. The probabilities of finding site 1 and site 2 are 0.01 and 0.09 respectively. In this case the different probabilities could mean that it is physically harder to find one site over another or one site is further away from the other one and therefore harder to find. We run this simulation for both chemical ants and trail ants for the same sizes and advertising parameters used in Simulation 1. See Tables 5.1 and 5.2 for the full list of parameters and values used in Simulation 2.

Shown in Figures 5.3 and 5.5 ants pick the site that is easier to find with 94 – 100% accuracy regardless of colony size and advertising parameter. This shows that when site quality is the same, colonies prefer sites that are closer to their original nest. The advantage of this choice is to minimize the exposure time and the migration time from the original site to the new one. This result matches results found in [11] where 15 colonies were forced to migrate to a new site after their original site was destroyed. Given two sites with identical quality: 14 out of the 15 colonies migrated to the near site and only one colony migrated

to the far away site resulting in a 93.3% accuracy in picking the closer site.

Figures 5.4 and 5.6 show that runs with high advertising parameter need more time to reach consensus compared to runs with low advertising parameters for both chemical and trail ants. The results also show that bigger colonies need less time to reach consensus compared to smaller colonies. Since bigger colonies can deploy more worker ants and are able to find all the available sites faster [10]. We also notice that there was no split in the decision making process for chemical ants while sometimes trail ants split and did not reach a consensus towards a site. See Figure 5.10 for trail ants which shows the number of splits, fails and correct consensus for different values of advertising and colony sizes.

5.2.4 Simulation 3 - Two sites; the far high quality one is hard to find

In this simulation we use two sites, one with high quality and the other one with low quality: 10 and 5 respectively. We let the high quality site be 9 times harder to find than the low quality site. The probability of finding the high quality site is 0.01 while the probability of finding the low quality site is 0.09. Similar to Simulation 2 the different probabilities could mean that it is physically harder to find one site versus another or one site is further away from the other one and therefore harder to find. This simulation is intended to evaluate whether ants in our mathematical model can choose a far better site over a nearby but poor quality one. We repeat this simulation using the same values of advertising and colony sizes used in previous simulations. For a full list of parameters and values used in this simulation see Table 5.1 and 5.2 for chemical and trail ants respectively.

In lab experiments ant colonies actively choose the better site even though it is further away [31, 11]. In an experiment done in [31] four out of nine colonies chose the better site that was located further away. Three colonies chose the nearby but poor quality site and two colonies split between the far and near sites resulting in 44.4% accuracy. In similar lab experiments performed in [11] ant colonies migrated to the better far away site even when it was 2, 3 or 9 times further away from the poor site. Eighteen colonies were forced to migrate to a new site given 24 hours. When the poor site was only 30 cm away from the original site, and the good site was 30, 60 or 90 cm away from the original site all 18 colonies migrated to the good further away site. In the case where the good site was 285 cm away from the original site, 16 out of 18 colonies emigrated to the good further away site giving a high 88.9% accuracy. In the above experiments ant colonies actively choose the better site even though it is further away. However, the number of colonies that actually choose the site located further away varied in different experiment from 44.4% to 88.9% to 100% depending on how far the high quality site is compared to the low quality site. In this simulation we claim that varying the distance between the new and old sites, in addition to varying the advertising parameter gives similar results to those observed in above lab

experiments.

The results of our mathematical simulations for both chemical and trail colonies are similar to those of lab experiments. Ants in our mathematical simulations actively choose the higher quality site even though it is further away from the original site. The change of site quality from 10 in Simulation 2 to 5 in Simulation 3 resulted in more colonies choosing the more distant site which supports our claim mentioned above. We discuss the details for chemical ants results separately from trail ants results in this case since the behavior for these colonies is different.

Chemical ants: when we keep the size of the colony constant we notice that simulations with high advertising parameter perform better than those with low advertising parameter. For example in Figure 5.3 when the colony size is 40 we get 67% correct consensus using high advertising parameter compared to 32% correct consensus using a low advertising parameter. In this scenario the low quality site gets found earlier than the high quality site because it is easier to find. An error in this model is magnified when it gets advertised and spread around quickly. However, since the quorum threshold is higher for chemical ants, they can in fact recover from the errors and choose the high quality site as long as the advertising parameter is high enough. In other words the higher the advertising parameter the better chance the colony has to recover from early voting mistakes and the better the overall colony decision is.

Keeping the advertising parameter constant and varying the size of the colony shows that bigger colonies do a better job in finding the best choice compared to smaller colonies. Looking at Figure 5.3 again shows that for high advertising parameter when colony size is 20 we get 45% correct consensus compared to 100% when colony size is 500. This result is consistent with the observation in [8] which states that bigger colonies can deploy more scouts and therefore find the high quality site faster and start advertising for it earlier. Early advertising for the high quality site results in a better choice accuracy.

Another observation is that simulations with high advertising parameter takes longer time to reach consensus compared to low advertising parameter. See Figure 5.4. This is consistent with experiments done in [41, 14] where we notice a trade off between speed and accuracy or speed and cohesion. More advertising gives better results but takes longer. In nature ant colonies might prefer accuracy over speed or vice versa depending on the situation. For example if the colony's site gets suddenly destroyed then the colony may prefer speed over accuracy. On the other hand, if a colony is looking to improve its existing site then they may prefer accuracy and cohesion over speed. Finally there was no colony splitting observed in any of our simulations in this case. Ant colonies either chose the distant high quality site or nearby low quality one which matches results observed in [7]. This

supports the theory that higher thresholds in chemical ant colonies may mitigate colony splitting.

Trail ants: When we keep the size of the colony constant we notice that simulations with low advertising parameter do better than those with high advertising parameter which is unintuitive and does not match results for chemical ant colonies. For example in Figure 5.5 we see that when colony size is 500 high advertising parameter results in 32% correct accuracy; however, a low advertising parameter results in 89% accuracy. Even though this is counter-intuitive it actually matches our theory in that a high threshold is needed for advertising to be effective since it takes more time. In this case, similar to chemical ants, the low quality site gets found earlier than the high quality site because it is easier to find. Higher advertising parameters result in advertising the wrong sites found earlier in the decision making process. Since the quorum threshold is lower for trail ants the colony does not have enough time to recover from the errors and therefore reaches a consensus towards the low quality site. In other words, the higher the advertising parameter the less chance the colony has to recover from early voting mistakes since the ants end up advertising the wrong site and reaching the threshold fast.

For medium and low advertising parameters bigger colonies do a better job in finding the best site compared to smaller colonies. This result matches the claim in [8] stating that "In a more complex environment, or when nest sites are farther away, small colonies may be at a greater disadvantage when it comes to discovering nests". Even though the authors did not test that theory in their paper our model predicts the same result. For example in Figure 5.5 using low advertising parameter simulations with colony size 40 results in 35% correct consensus compared to 98% correct consensus when colony size is 1000. For simulations using a high advertising parameter the correct consensus has a small improvement of 10% when we increase the size of the colony from 40 to 500 but it drops from 32% to 18% when we change the colony size from 500 to 1000. The reason behind this is that the bigger the colony size the more scouts go around searching for sites and the higher the probability of finding the high quality site as discussed before. Therefore with bigger colonies we see higher consensus percentage towards the best site. The same goes for chemical and trail ants; however, for the colony size of 1000 the combination of the small threshold and the very large colony size results in spreading the mistakes faster than other cases due to the high number of workers in large colonies. This causes the observed drop in consensus accuracy.

Simulations with high advertising parameter take longer time to reach consensus compared to low advertising parameter. See Figure 5.6. One difference we notice between chemical and trail ant colonies is the time chemical colonies take to reach consensus is more

than double what trail ants need. This is because chemical colonies have higher threshold so more advertising activities happen in these colonies and more time is needed for consensus to occur. In addition, chemical colonies need more time to reach their threshold simply because the quorum threshold for chemical ants is higher than trail ants [7]. Furthermore, trail colonies are bigger than chemical colonies which implies that trail colonies have more workers and can search and find potential nests faster as previously discusses. Another time related observation is when colony size gets bigger the time to reach consensus for trail ants is reduced. For trail ants big colonies combined with low thresholds result in more scouts searching and finding nests faster and reaching consensus faster. Therefore trail ants need less time to reach consensus when increasing the colony sizes.

Finally we notice that bigger colonies have a greater tendency to split than smaller colonies. For simulations using sizes 40, 100, 250, 500, 1000 we run each simulation 300 times per colony size: 100 with low advertising parameter, 100 with medium advertising parameter and 100 with high advertising parameter. Out of 300 run for each colony size the overall number of splits per colony size were: 6, 13, 17, 22, 15 respectively. Split percentages for each combination of colony size and advertising parameter are shown in Figure 5.11. Lab experiments found that bigger colonies have greater tendency to split [10] because bigger colonies have more scouts and tend to find more of the available nests faster than smaller colonies. This supports the increase of number of splits from 6 to 17 to 22 when increasing the size from 40 to 250 to 500 ants. However, large colonies use larger thresholds than smaller colonies to make collective decisions which may help reduce splitting by larger colonies [10]. This explains the drop from 22 to 15 splits when increasing the colony size from 500 to 1000.

5.2.5 Simulation 4 - Adding a small delay

In this simulation we start the model by introducing two sites each with a 0.05 probability of being found one with low quality, 5, and one with medium quality, 7. After some time of running the simulation and allowing ants to visit and evaluate each of these two sites we add a new site with a higher quality, 10, with the same probability, 0.05, of being found. We let the time delay before we add the high quality site be approximately a quarter of the average time needed to reach consensus in Simulation 1 for each colony size. For chemical ants of colony sizes 20, 40, 80, 200, 500, the time delay is 13, 11, 11, 10, 10 time steps respectively. For trail ants of colony sizes 40, 100, 250, 500, 1000, the time delay is 7, 6, 6, 6, 6 respectively. Note that the time delays are rounded up to the closest integer. For a full list of parameters and values used in this simulation see Simulation 4 in Tables 5.1 and 5.2 for chemical and trail ants.

The purpose of this simulation is to mimic what happens in nature since most colonies do not find the high quality sites first. We study whether colonies can switch their attention to the highest quality site even though it is found late in the process. Based on lab experiments done in various papers such as [11, 31, 9] ant colonies can in fact switch to a better site. Ant colonies can reach a consensus towards the high quality site even though it is often found after multiple poor quality sites. This is done by increasing assessment time for poor quality sites [29]. Furthermore, when the high quality site is found later in the decision making process colonies start emigrating simultaneously to both sites [11] then redirect all traffic to the better one.

The results of our simulations for both chemical and trail colonies are similar to those of lab experiments. Ants in our simulations actively switch to the better site even though it is found after the poor sites. One difference between chemical and trail colonies is that chemical colonies have higher correct consensus rate compared to trail colonies. Chemical colonies have a 77% to 100% success rate compared to 0% to 36% for trail ants. We discuss the results for each colony separately.

Chemical ants: Simulations with medium advertising parameter do better than those with high and low advertising parameter when colony size is 20 and 40. For example when colony size is 20 Figure 5.3 shows simulations with medium advertising parameter have a 88% accuracy rate compared to 79% for simulations using a low advertising parameter. The Figure also shows that all simulations choose the high quality site with a 100% accuracy when colonies are large: 200 and 500. This is consistent with the explanation mentioned in previous simulations where the low quality site gets found earlier than the high quality site. An error in this model is magnified when it gets advertised and spread around quickly. Because the threshold is high for chemical ants they can recover from errors and reach a consensus towards a high quality site even though it is found later in the decision making process. The higher the advertising parameter the more chance the colony has to recover from early voting mistakes and the better the overall colony decision making result is. In this case medium advertising parameter provides a better advertising balance between delaying the decision making process enough time for the better site to be found and not advertising the wrong site fast enough before the high quality site is introduced to the model.

Similar to Simulation 3, when we keep the advertising parameter constant, bigger colonies do a better job in finding the best site compared to smaller colonies. This is because bigger colonies can deploy more scouts and therefore find the high quality site faster [8]. Early advertising for the right site results in a better accuracy when choosing the site. Furthermore, simulations with high advertising parameter take longer time to reach consensus compared to simulation with low advertising parameter. This can be

explained by the same speed versus consistency trade off reasoning used in Simulation 3. See Figure 5.4. Also similar to Simulation 3 there was no colony splitting observed in any simulations for this scenario. Ant colonies either chose the distant high quality site or the nearby low quality site which matches results observed in [7]. This again supports the theory that higher thresholds in chemical ant colonies may mitigate against colony splitting.

Trail ants: We notice that simulations with high advertising parameter do better than those with medium to low advertising parameter. Simulations with high advertising parameter have a 7% to 36% success rate compared to 0% to 10% for medium advertising and 0% to 11% for low advertising. See Figure 5.5. Increasing the advertising parameter in this case seems to delay the decision making process long enough for the higher quality site to be found and advertised. This results in a better success rate for simulations with high advertising parameter compared to low and medium advertising parameters. Another observation is that trail ants have a lower success rate compared to chemical ants. This is because their threshold is low so they do not have enough time to recover from mistakes like chemical ant colonies do, which results in a lower success rate compared to chemical ants.

Keeping the advertising parameter constant, smaller colonies do a better job in finding the best site compared to bigger colonies. This is because bigger colonies can deploy more scouts and therefore find all available sites faster [8] and advertise it earlier. In this simulation the early finding and advertising of the two available sites causes the colony to reach consensus on one of these sites before the high quality site is introduced into the simulation.

Simulations with high advertising parameter take longer time to reach consensus compared to those with low advertising parameter. This can be explained by the same speed versus consistency trade off reasoning used in Simulation 3 [41, 14]. For example in Figure 5.6 when colony size is 40, simulations with high advertising parameter need 32 time periods to reach consensus while simulations with low advertising parameter need 27 time periods.

Finally similar to simulation 3 we notice that bigger colonies have greater tendency to split than smaller colonies. See Figure 5.12. For simulations using sizes: 40, 100, 250, 500, 1000 the overall number of splits per colony size were: 13, 14, 18, 19, 19 respectively. The increase in splits from 13 to 19 when increasing the colony size from 40 to 500 is because bigger colonies have greater tendency to split [10]. Since bigger colonies have more scouts and tend to find more of the available nests faster than smaller colonies. However, large colonies use larger thresholds than smaller colonies to make collective decisions which may help reduce splitting by larger colonies [10]. This explains the no change in the 19 splits observed when changing colony size from 500 to 1000.

Note that we used different time delays for each colony size as discussed in the beginning of this section. Therefore, we will not compare the time taken to reach consensus for different scenarios in this simulation. The different time delay for each size definitely affects the results and we may not conclude that the time difference is due to the change in colony size. Having said that, we have included Figures 5.4 and 5.6 with the rest of the simulations for visibility of this data.

5.2.6 Simulation 5 - Adding a large delay

We introduce a larger time delay in Simulation 5 compared to Simulation 4 and we keep all other parameters the same. In Simulation 5 the time delay is chosen to be approximately half the average time needed to reach consensus in Simulation 1. For chemical ants the time delay is 25, 21, 21, 20, 20 time steps for each colony size: 20, 40, 80, 200, 500, respectively. For trail ants the time delay is 13, 12, 12, 11, 11 for colony size: 40, 100, 250, 500, 1000 respectively. For a full list of parameters and values used in this simulation see Simulation 5 in Tables 5.1 and 5.2 for chemical and trail ants.

We expect the results of this simulation to be similar to Simulation 4. This implies that if colonies with high advertising parameter did better than colonies with low advertising in Simulation 4 we expect a similar outcome in Simulation 5. However, since we introduced a longer time delay we also expect the success rate to be lower than Simulation 4 since more colonies will reach consensus before the high quality site is introduced to the model. In experiments done in [11], ant colonies did a better job in choosing the best site when the high quality site was found earlier. Ant colonies had a higher accuracy rate when the high quality site was 2 or 3 times further away from an in-the-way low quality site compared to when it was 9 times further away. In other words, the further away the high quality site is, the longer ants take to find it which results in a lower consensus rate since the colony reaches consensus before finding the high quality site.

Chemical ants: The results of our mathematical simulations match our expectations. Keeping the size of the colony constant, we notice that simulations with medium advertising perform better than those with high and low advertising parameter. Medium advertising provides a better advertising balance between delaying the decision making process enough time for the better site to be found and not advertising the wrong site fast enough before the new site is introduced to the model. The success rate in this case is 60% to 100% compared to 77% to 100% for the same case in Simulation 4. See Figure 5.3 for full results.

Keeping the advertising parameter constant, bigger colonies do a better job in finding the best site compared to smaller colonies. See Figure 5.4. Simulations with high advertising parameter take a longer time to reach consensus compared to low advertising parameter.

Also there was no colony splitting observed in Simulation 5 like all previous simulations done using chemical ants [7].

Trail ants: Keeping the size of the colony constant, we notice that simulations with high advertising do better than those with medium and low advertising parameter. Simulations with high advertising parameter have a range of 0% to 11% success rate compared to a range of 0% to 2% for medium advertising and 0% for low advertising. The overall success rate for this simulation is in the 0% to 11% range compared to 0% to 36% in Simulation 4. This is because the time delay introduced in this simulation is double the time delay in Simulation 1. Therefore many colonies reach consensus towards the available sites before the new one is introduced to the model. It is important to note that even though the consensus accuracy is 0% to 8% for the purpose of this simulation, experiments done in [9] found that in a similar setting where the low quality site gets found earlier, the colony migrates and settles in the low quality site similar to what we found in our simulations. However, colonies will migrate again to the new higher quality site when it gets found. Furthermore, in this simulation, we expect the colony to find the high quality site and migrate to it if we allow the simulation to keep going and don't stop it when the threshold is reached for the nearby poor quality site. See Figure 5.5 for full results. Note that in this scenario colonies that do not use advertising are never able to choose the best available site.

Keeping the advertising parameter constant, smaller colonies do a better job in finding the best site compared to bigger colonies. Also as shown in Figure 5.6 simulations with high advertising parameter take longer time to reach consensus compared to low advertising parameter. The overall number of splits per colony size are 2, 2, 1, 0, 0. Many colonies reached consensus before finding the high quality site which explains why we have less splits in this simulation compared to Simulation 4. See Figure 5.13 for the distribution of success runs, failed runs and splits per colony size and advertising parameter.

Doubling the delay time from Simulation 4 to Simulation 5 seems to affect the trail ant colonies much more than chemical ants. The consensus accuracy dropped from 77%-100% range to 60%-100% in chemical ants while the drop was from 0%-36% to 0%-11% for trail ants. This drastic drop might seem strange but it is consistent with our findings from previous simulations. This drop in trail ants is directly related to the small threshold in this colony in addition to the large colony size. As mentioned previously, large colonies can deploy more scout ants to explore all available sites more quickly [8]. Since the quorum threshold is low, trail ants reach consensus towards the available sites fast, before the new high quality site is introduced to the simulation. In chemical ant colonies, the colony size is smaller and the quorum threshold is higher. This implies that we have less worker ants searching for nests and a higher quorum threshold to reach. Which means that chemical

ants need more time to reach consensus. This extra time allows us to introduce the new better site before the colony reaches consensus and gives the colony enough time to redirect their attention to the new better site giving a much higher consensus accuracy compared to trail ants.

5.2.7 Simulation 6 - Switching site quality

We start this simulation by introducing two sites to the model. One site has a high quality, 10, and the other site has a poor quality, 5, each with a 0.05 probability of being found. After running the model for a few time steps we switch the quality of the sites such that the high quality site, 10, changes to poor quality, 5, and the poor quality site changes to high quality. The purpose of this simulation is to find out if the colonies are able to change their opinion of a site after assessing and recruiting to it. In nature this resembles a scenario where a site was determined to be good and then something happened (like a flood) that changed the quality of that site and renders it poor quality.

We choose the switch time to be $3/4$ the average time it takes colonies to reach consensus in Simulation 1. For chemical ants the time switch is 37, 30, 29, 29, 28 for colony sizes 20, 40, 80, 200, 500 respectively. For trail ants it is 19, 18, 18, 17, 17 time periods for colony of sizes: 40, 100, 250, 500, 1000. For example if we are running the simulation for a chemical colony of size 20 then we start it by introducing site 1 with quality 10 and site 2 with quality 5. After 37 time steps if the colony has not reached a consensus yet we switch the quality of site 1 to 5 and site 2 to 10. For the purpose of this simulation, success rate is calculated as follows: in our above example if the colony chooses site 2 after 39 time steps then this choice is considered a correct consensus. Any choice made before the switching is done is considered a fail for the purpose of this simulation since the decision was made too early and did not allow the switch to happen.

We find that ant colonies are able to change its direction and redirect recruiting to the better site when switching the site quality. For chemical ants keeping the size of the colony constant, we notice that simulations with high advertising do better than those with low advertising parameter. Simulations with high advertising parameter have range of 72% to 100% success rate compared to 54% to 95% range success rate for low advertising. See Figure 5.3. Keeping the advertising parameter constant, bigger colonies do a better job in finding the best site compared to smaller colonies which match what's observed in [8]. Simulations with high advertising parameter takes longer time to reach consensus compared to low advertising parameter. See Figure 5.4. In addition, there was no colony splitting observed in all our simulations for this case [7].

For trail ants keeping the size of the colony constant, we notice that simulations with high advertising do better than those with medium and low advertising parameter. Simulations with high advertising parameter have a range of 6% to 64% success rate compared to a range of 0% to 33% for medium advertising and 0% to 18% for low advertising. Keeping the advertising parameter constant, smaller colonies do a better job in finding the best site compared to bigger colonies. See Figure 5.5. One interesting finding, in particular is the sharp drop in the success rate for high advertising when increasing the colony size from 40 to 1000. This is because larger colonies have more scouts and can find all available sites faster [8] which in this simulation results in a lower accurate consensus result since the colony reaches a consensus early before we switch the site's quality. Simulations with high advertising parameter take longer time to reach consensus compared to low advertising parameter. See Figure 5.6 for full results. As shown in Figure 5.14 the overall number of splits per colony size were: 15, 16, 12, 4, 9. Since we have more fails (a consensus towards a low quality site) for larger colonies compared to smaller once we see less splits for larger colonies compared to smaller once.

The main difference between chemical and trail ants in Simulations 4, 5 and 6 is that the accuracy of the consensus rate increases when colony size increases for chemical ants, while it decreases for trail ants. Although we don't have lab experiments to support this observation, we believe that it is consistent with results in Simulations 1, 2 and 3. The scenarios in simulations 4-6 are similar, we are essentially delaying the introduction of the new better site. Trail ants have a smaller threshold and a larger colony size compared to chemical ants [5]. Large colonies can deploy more scout ants and find available sites faster [8]. Since the quorum threshold is low, trail ants reach consensus towards the available sites rapidly, before the new site is introduced to the simulation or before the site switch occurs while chemical ants need more time to reach consensus due to their smaller size and higher threshold. This extra time allows us to introduce the new higher quality site before the colony reaches consensus. This gives the colony enough time to redirect their attention to the new higher quality site which results in the observed behavior in Simulations 4, 5 and 6 in Figures 5.3 and 5.5.

5.3 Summary of simulations

Ant colonies are extremely good at choosing a high quality site over a low quality one in different situations and scenarios. There are many factors that affect the choice accuracy some of these factors are colony size, threshold, advertising and reliability of the ants. Another important factor is the scenario or situation the colony faces. Different scenarios require ant colonies to adapt and change these parameters to get the best outcome. In this section we discuss some of our main findings and compare them to what is observed in different

papers. We also summarize all our observations in Table 5.5.

We found that when colonies are given a simple choice between a high and a low quality site the colony chose the high quality site with 96%-100% accuracy. Furthermore, when colonies are given a choice between a far away high quality site and a nearby site with the same quality colonies chose the nearby site with 94%-100% accuracy. Results from our simulations matches lab experiences. Many studies found that in a simple scenario where ants are given a choice between a high quality site and a low quality site the colony is able to choose the high quality site with great accuracy. For example in [22] 14 colonies were given a choice between a high quality site and another low quality one; 11 out of 14 colonies choose the high quality site over the low quality one. In a second experiment with a similar setting and different site attributes 14 out of 14 colonies choose the high quality site. In [11] when 18 colonies were given a choice between good and poor sites all 18 colonies migrated to the good site. In the same paper the authors also found that when keeping the quality of the site constant colonies choose a nearby site over a far away site. Fifteen colonies were forced to migrate to a new site after their original nest was destroyed. Given two sites with identical quality, 14 out of the 15 colonies migrated to the nearby site and only one colony migrated to the far away site.

In [8] the authors found that large colonies have more potential scouts and therefore they are able to find potential nests faster than small colonies. In [10] the authors also found that larger colonies took less time than smaller colonies to find the good nest. Given a simple scenario where a colony have to choose between a high and a low quality site both above studies found that colony size does not affect the choice accuracy. All colonies behave the same and are able to find the high quality site even though smaller colonies take more time to find it. Results from Simulation 1 and 2 matches results of these two studies. However, our results predict that colony size will in fact make a difference when the high quality site is introduced to the simulation later in the decision making process. Our model predicts that the choice accuracy for trail ants will decrease when colony size increases because larger colonies have more scouts and will find available sites faster and migrate to it before the high quality site is introduced to the simulation. On the other hand, chemical ants accuracy increases when colony size increase because chemical ant colonies are smaller and use higher quorum thresholds so they need more time to find and reach consensus towards available sites. As previously discussed this extra time allows us to introduce the new higher quality site before the colony reaches consensus which gives the colony enough time to switch its attention to the new high quality site.

Another main result is how advertising affects the decision outcome. In [21] the authors show that honeybees get better consensus result when advertising is high. Going into our

ant simulations we expected to see similar results since we used the model introduced in [21] and extended it for ant colonies. However, we were surprised to get different results; our model predicts that given a highly reliable colony and a choice between 5 sites colonies perform better when using medium advertising parameter. We find that for advertising to work effectively we need a higher threshold to allow enough time for the colony to advertise the high quality site and recover from early mistakes made by advertising the first site found (which in most cases is not the highest quality one). Our model predicts that high advertising does not always give better consensus results. Sometimes low or medium advertising are a better choice given the scenario a colony is facing and the reliability of the colony.

Some simulations for chemical ants with colony size 40 yield a non monotonic behavior compared to other colony sizes. Simulations for size 40 yield a lower accuracy compared to what we expect and a much shorter time to reach consensus than expected. What's intriguing is that chemical ants are usually found in nature in groups of less than 40 as mention in [5]. This leads us to believe that the optimal decision for this colony size is not necessarily that which maximizes accuracy. Other criteria such as speed, cohesion or reward rate may be more relevant in the animal decision making which is what was observed in [42]. To prove whether this is accurate we think more lab experiments around the colony size 40 might show some interesting behavior that is different from other colony sizes for chemical ants.

One final note we think is worth mentioning here is that the time index used in our model is fictional. It is not related in any way to the real time taken for colonies in lab experiments. We did not investigate the time ratio between different phases of recruitment (searching, assessment and advertising). In this study we are only interested in the colony's decision as a whole; we don't keep track of the state of each ant at each time step so it is extremely difficult for us to make any conclusions regarding time ratio of different phases or compare our time to experiments time. We believe that modifying our model to actually use real time that is similar to the time observed in lab experiments and studying the trends and behavior would be a very interesting problem to look into for future work.

We summarize all our observations and results in Table 5.5. We left the reference field empty in the case that we did not find references to either confirm or deny our observations. We believe that those cases are nice scenarios and can easily be duplicated in a lab setting by scientists in the experimental biology field. Those lab experiments can then be used to identify whether our model predictions are accurate or not.

Results	Simulations	References
<p>1. Reliability: Colonies with high reliability get better consensus accuracy compared to colonies with low reliability.</p>	B 0	[21]
<p>2. Colony size: Colonies have high consensus accuracy regardless of colony size when the two sites are found at approximately the same time and have noticeably different quality.</p> <p>Given a delay in finding the high quality site: larger colonies get better consensus accuracy when colonies have high quorum threshold.</p> <p>Given a delay in finding the high quality site: larger colonies get worse consensus accuracy when colonies have low quorum threshold.</p>	<p>B 1, 2</p> <p>CA 4-6</p> <p>TA 4-6</p>	[8, 10]
<p>3. Quality versus distance: When keeping the distance from the new sites to the original site constant, colonies chose the high quality site with great accuracy.</p> <p>When keeping the quality of the site constant, colonies prefer near by sites over far away site.</p> <p>When varying quality and distance such that the high quality site is further way from the original nest than the low quality site colonies prefer the far away high quality site over the nearby low quality one.</p>	<p>B 1</p> <p>B 2</p> <p>B 3</p>	<p>[5, 11, 22]</p> <p>[11, 31]</p> <p>[11, 31]</p>
<p>4. Latency in finding the high quality site: The larger the delay in finding the high quality site, the less the consensus accuracy of the colony.</p>	B 4, 5	[11]
<p>5. Threshold: Colonies using higher quorum thresholds require more time to reach consensus but are more accurate and are associated with less colony splitting.</p>	B 1-6	[7, 14]

<p>6. Splits:</p> <p>In some scenarios trail ant colonies split between the high quality site and another low quality one and did not reach a consensus.</p>	TA 2-6	[10, 31]
<p>We did not notice any splits for chemical ant colonies. They always reached a consensus.</p>	CA 1-6	[5, 7]
<p>Colonies have an extremely small split percentage when the two sites are found at approximately the same time and have noticeably different quality.</p>	B 1	[5, 10, 11]
<p>7. Advertising:</p> <p>medium advertising gives better consensus accuracy when the colony is reliable and the sites are found at approximately the same time.</p>	B 0	
<p>Low to no advertising gives better consensus accuracy when the colony is not reliable, the threshold is small and the sites are found at approximately the same time.</p>	TA 0	
<p>Colonies using high to medium adverting perform better when there is a delay in finding the high quality site.</p>	B 4-6	
<p>Colonies using higher advertising parameter need more time to reach consensus.</p>	B 1-6	

Table 5.5: Summary of all results from all simulations for both chemical and trail ants. Simulations and References columns show the simulation number and the reference that supports our results. In the case that we did not find references to support our results we left that entry empty. CA: chemical ant simulations. TA: trail ant simulations. B: both chemical and trail ant simulations.

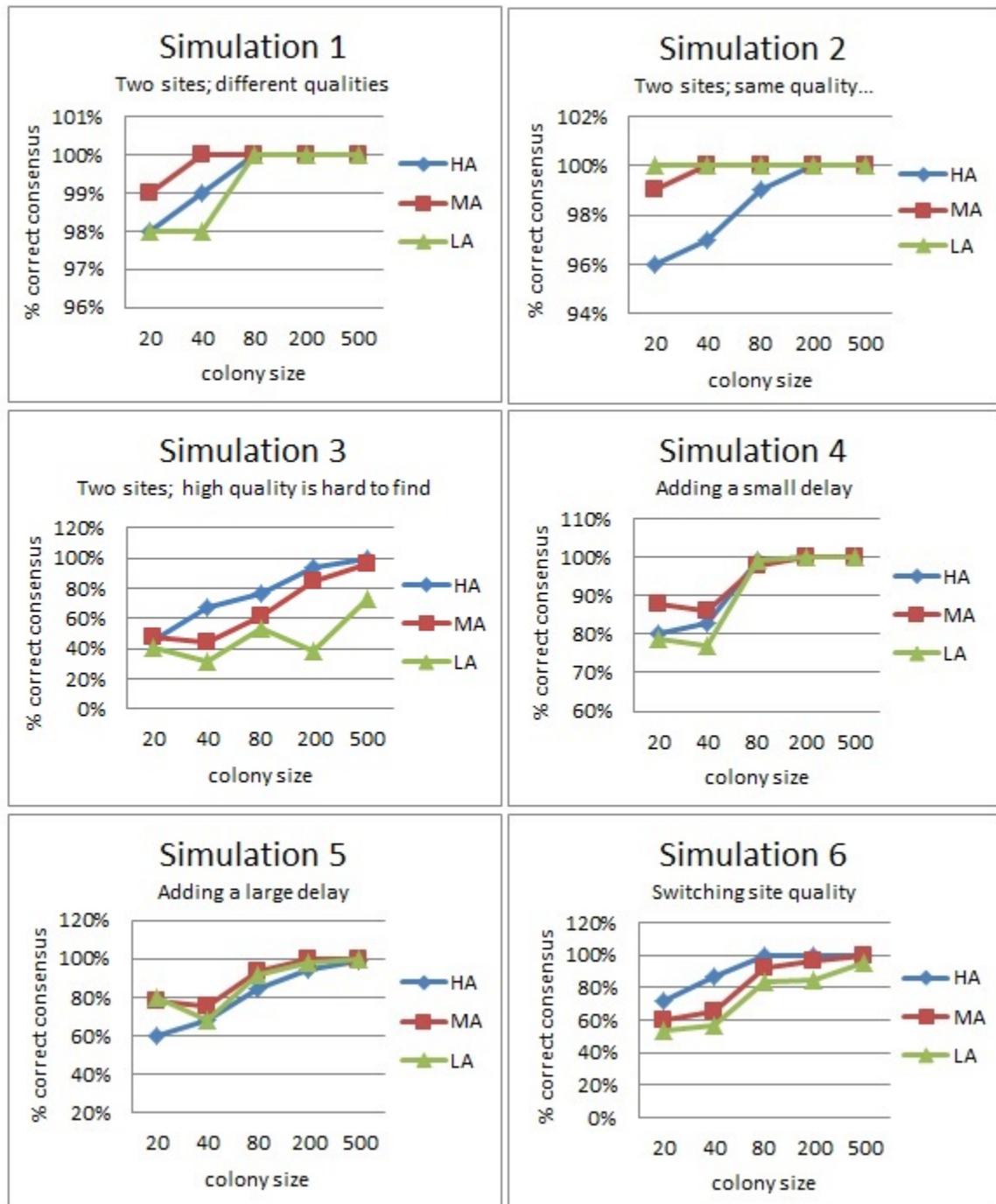


Figure 5.3: Percentage of correct consensus vs colony size for 3 different values of advertising for Simulations 1-6 using chemical ants. For example in Simulation 1 when using low advertising parameter (0.2) we have 98% correct consensus when colony size is 20 and 40 and a 100% correct consensus when colony size is 80, 200 and 500. HA: high advertising, MA: medium advertising, LA: low advertising.

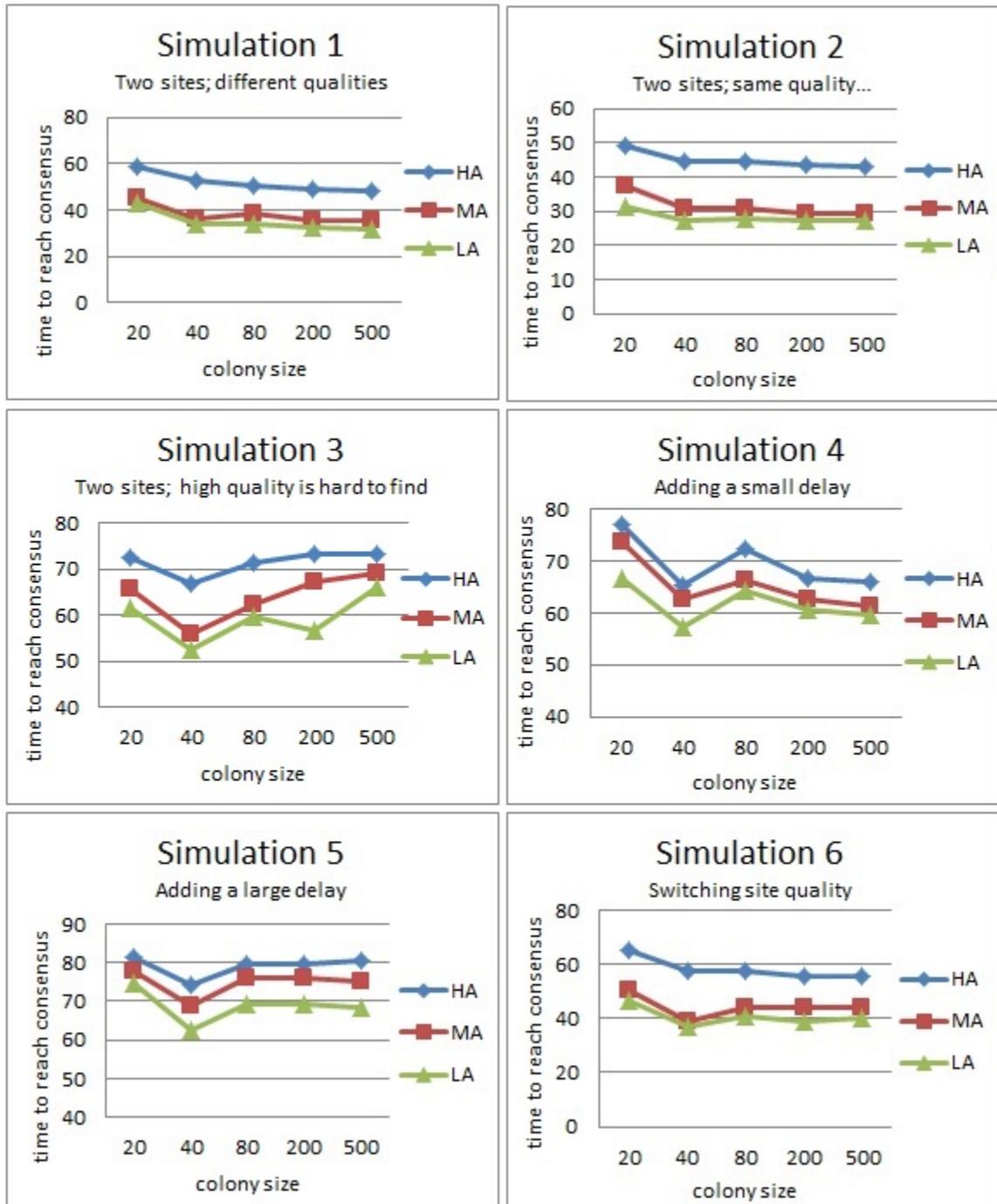


Figure 5.4: Time needed to reach consensus vs colony size for 3 different values of advertising for Simulations 1-6 using chemical ants. For example in Simulation 1 runs with high advertising (0.8) take longer to reach consensus compared to medium (0.4) and low advertising (0.2), also bigger colonies take less time to reach consensus. HA: high advertising, MA: medium advertising, LA: low advertising.

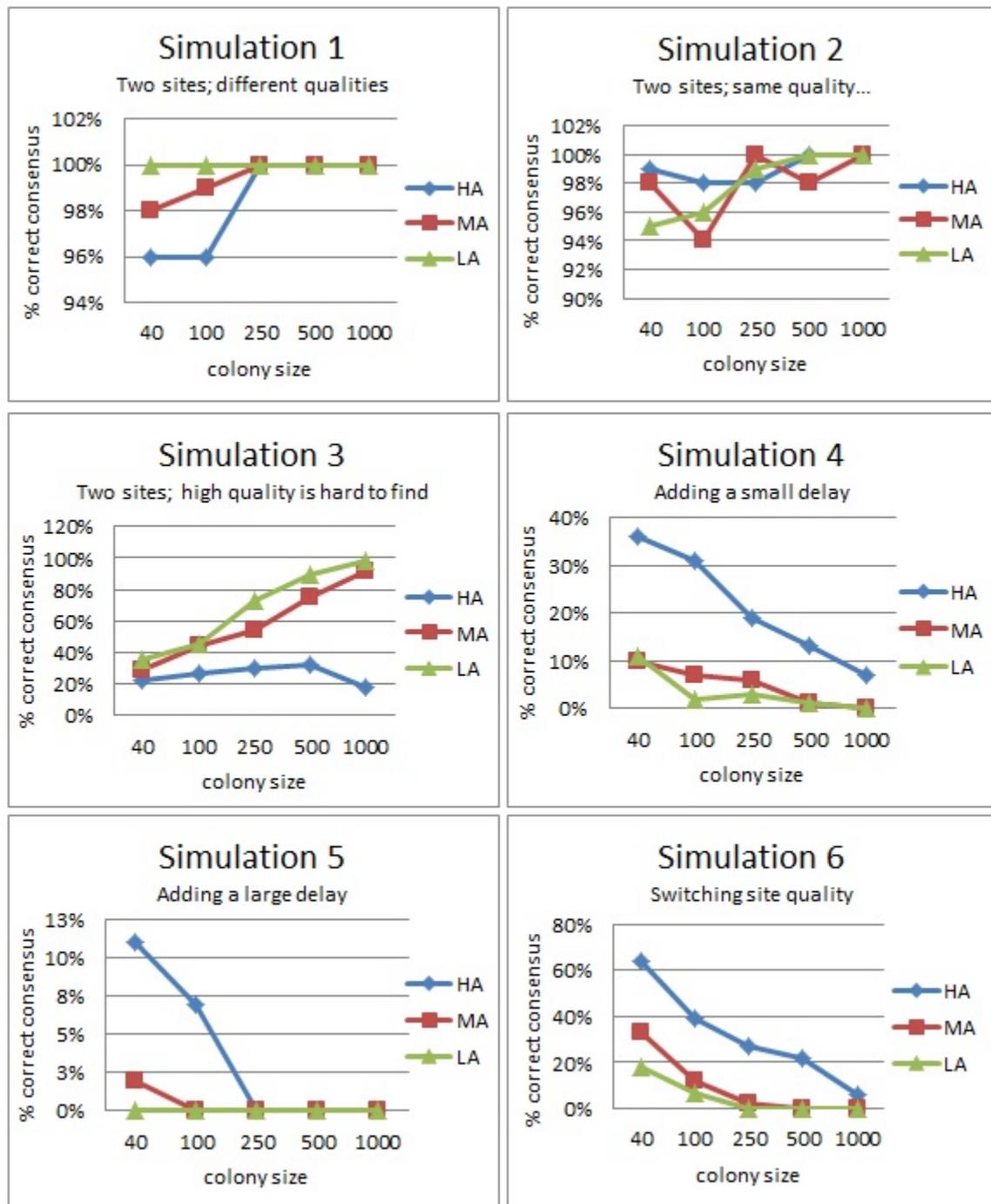


Figure 5.5: Percentage of correct consensus vs colony size for 3 different values of advertising for Simulations 1-6 using trail ants. For example in Simulation 1 we have 100% correct consensus when using low (0.2) advertising parameters regardless of colony size but when using medium (0.4) or a high (0.8) advertising parameters the percentage of correct consensus varies between 96% to 100% correct consensus depending on the colony size used. HA: high advertising, MA: medium advertising, LA: low advertising.

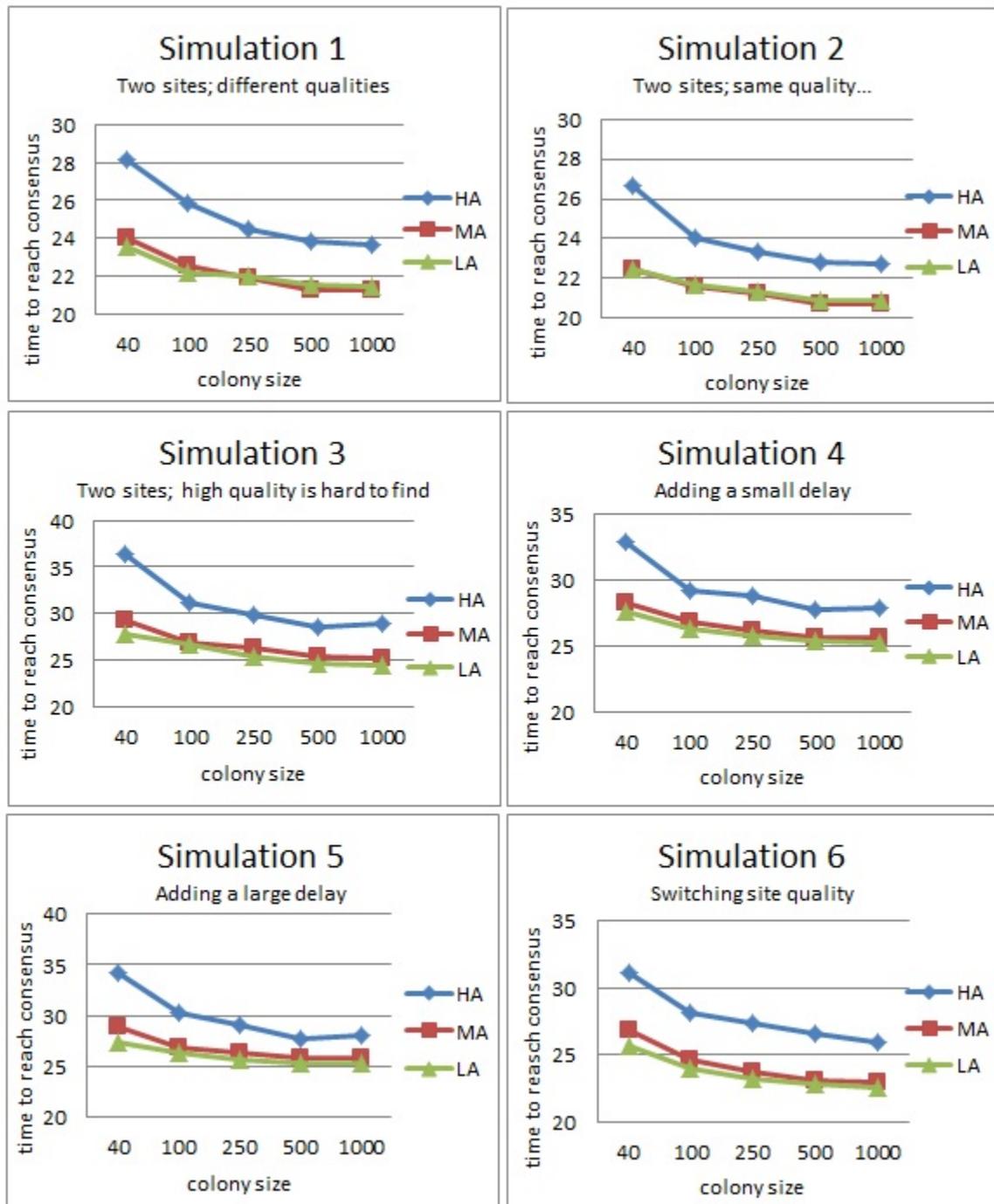


Figure 5.6: Time needed to reach consensus vs colony size for 3 different values of advertising for Simulations 1-6 using trail ants. For example in Simulation 1 runs with high advertising (0.8) take longer to reach consensus compared to medium (0.4) and low advertising (0.2), also bigger colonies take less time to reach consensus. HA: high advertising, MA: medium advertising, LA: low advertising.

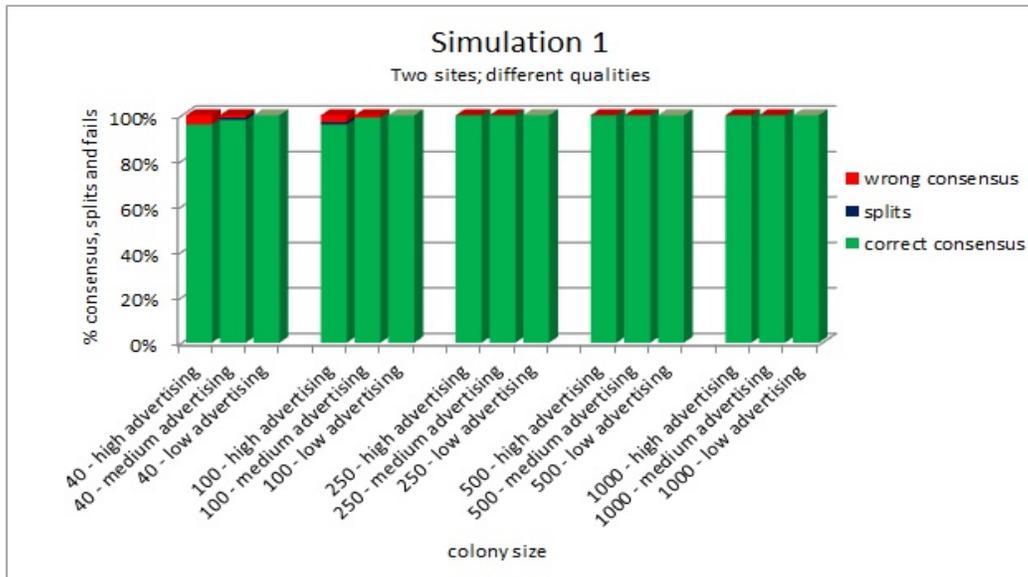


Figure 5.7: Percentage of correct consensus, fails and splits vs colony size and advertising parameter for trail ants in Simulation 1. For example the first bar shows that out of 100 runs using high advertising parameter (0.8) and small colony size (40) we have 96 runs resulted in a correct consensus, 0 runs resulted in a split and 4 runs resulted in a wrong consensus.

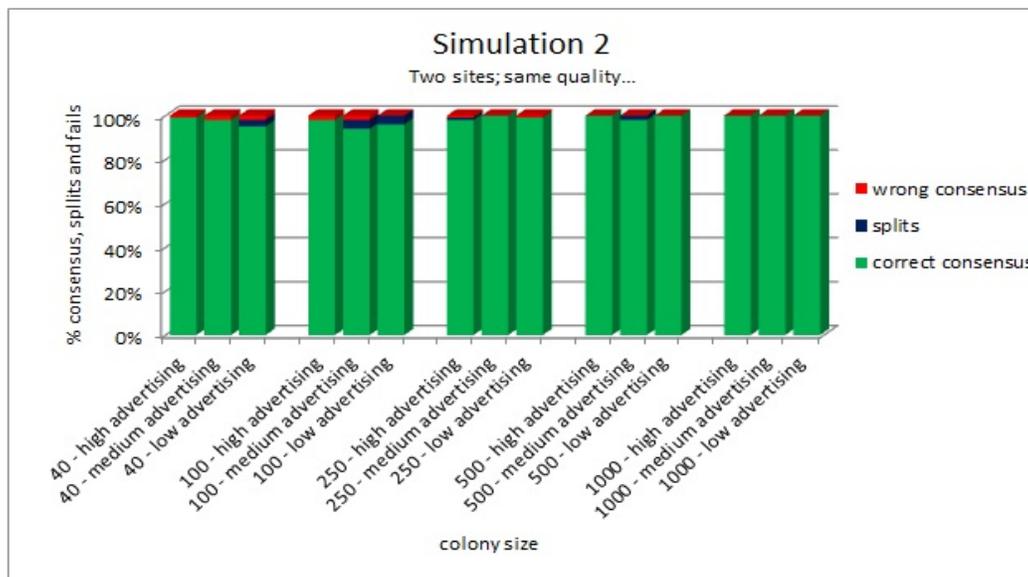


Figure 5.8: Percentage of correct consensus, fails and splits vs colony size and advertising parameter for trail ants in Simulation 2. For example the first bar shows that out of 100 runs using high advertising parameter (0.8) and small colony size (40) we have 99 runs resulted in a correct consensus, 0 runs resulted in a split and 1 runs resulted in a wrong consensus.

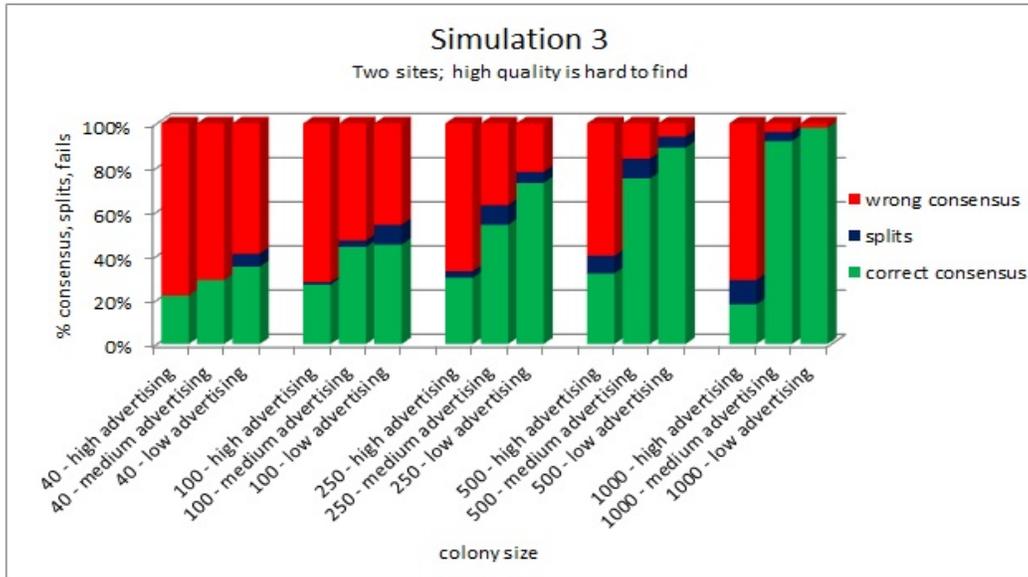


Figure 5.9: Percentage of correct consensus, fails and splits vs colony size and advertising parameter for trail ants in Simulation 3. For example the first bar shows that out of 100 runs using high advertising parameter (0.8) and small colony size (40) we have 22 runs resulted in a correct consensus, 0 runs resulted in a split and 78 runs resulted in a wrong consensus.

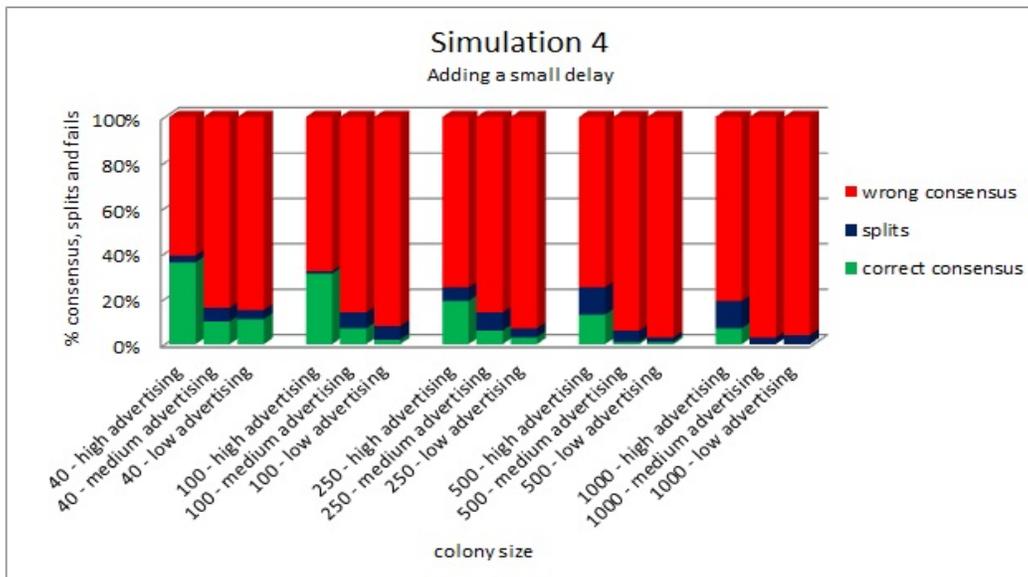


Figure 5.10: Percentage of correct consensus, fails and splits vs colony size and advertising parameter for trail ants in Simulation 4. For example the first bar shows that out of 100 runs using high advertising parameter (0.8) and small colony size (40) we have 36 runs resulted in a correct consensus, 3 run resulted in a split and 61 runs resulted in a wrong consensus.

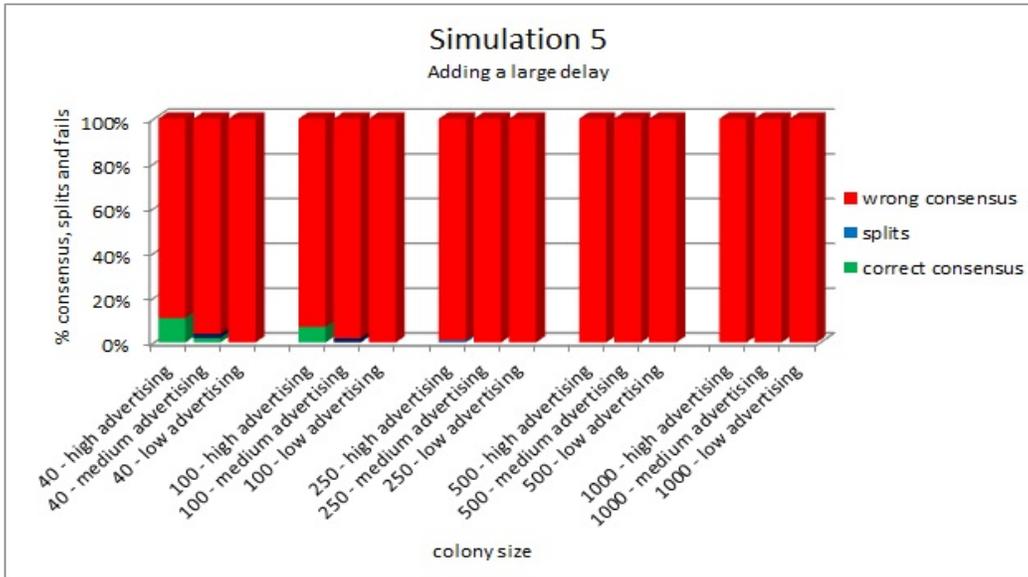


Figure 5.11: Percentage of correct consensus, fails and splits vs colony size and advertising parameter for trail ants in Simulation 5. For example the first bar shows that out of 100 runs using high advertising parameter (0.8) and small colony size (40) we have 11 runs resulted in a correct consensus, 0 runs resulted in a split and 89 runs resulted in a wrong consensus.

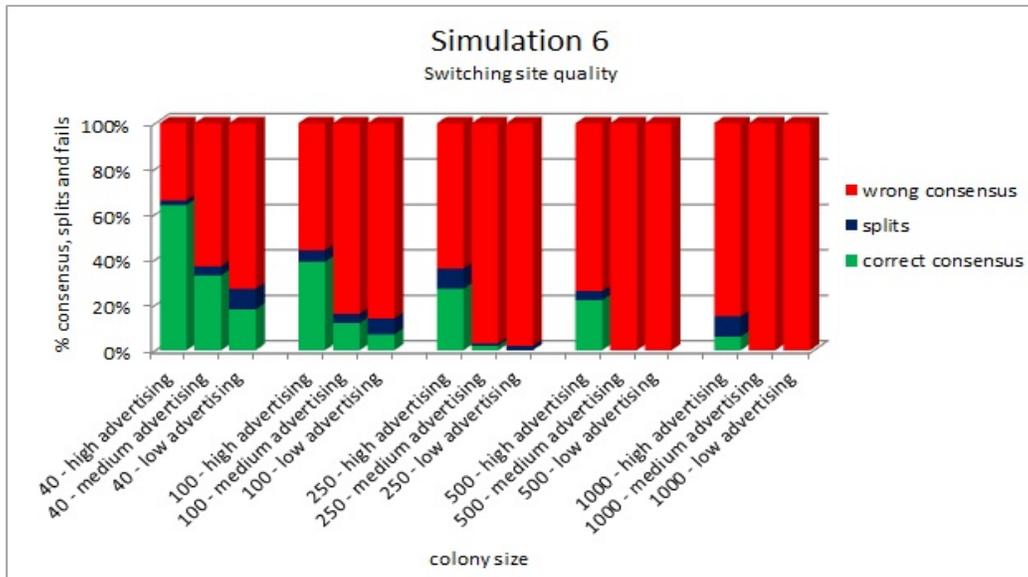


Figure 5.12: Percentage of correct consensus, fails and splits vs colony size and advertising parameter for trail ants in Simulation 6. For example the first bar shows that out of 100 runs using high advertising parameter (0.8) and small colony size (40) we have 64 runs resulted in a correct consensus, 2 runs resulted in a split and 34 runs resulted in a wrong consensus.

Chapter 6

Discussion

6.1 Group decision-making in honeybees and ants

In both honeybee and ant colonies, individuals make decisions based on the information available to them. Combined together, these individual decisions result in a colony's decision. In this section we discuss the similarities and differences in the decision making process between honeybees and ants.

Both ants and bees employ a multi-step process to show their commitment to a chosen site. In honeybees, workers visit the site in the exploration phase then advertise the location, distance and desirability of the site to the rest of the colony in the advertising phase. In the final step the colony votes for one of the available sites and reaches a consensus. This leads the whole colony to move from the advertising and debate phase to the migration phase of the process. Ants also have four phases to show their commitment to the site: exploration, assessment, canvassing and commitment phase. Each phase was discussed in detail in Chapter 1. Each phase of the decision-making process for bees and ants show a higher commitment to the site. The similar structure of the site selection process in this case is the main reason we decided to extend the honeybee's model and use it for ants.

All colonies are able to communicate with each other and advertise a certain choice. Honeybees use the waggle dance, trail ants use tandem runs while chemical ants use pheromone trails to cast their vote. The communication method used by honeybees and chemical ants is clearly more sophisticated than that used by trail ants. This might explain why the threshold is lower in trail ants compared to chemical ants and bees. It can also explain why in some cases trail ants are better off relying on their own assessment versus advertising to reach a better consensus outcome. In our research, the model introduced in [21] was easily extended from honeybees to ants because it does not differentiate between the advertising methods. It is only concerned about whether there is advertising or not. It is for this reason

we can only use our model to discuss the accurate consensus outcome and compare that for different colonies. However, we cannot use it to compare the time to reach consensus for different colonies since we don't take into consideration that different advertising methods take different time duration.

Regarding advertising, different simulations show that when the colonies' individual decisions are not reliable, advertising is highly important to reach a more accurate outcome. In [21] the authors show that for honeybees higher advertising gives a better consensus outcome. In our extended model we show that higher advertising does not always imply better consensus outcome. Even though this is true for most cases, in some scenarios the colony reaches a better results when there is medium amount of advertising. In other scenarios colonies are better off using little to no advertising at all. We also show that in addition to advertising and reliability there are other factors that affect the outcome such as the size of the colony, the quorum threshold and the scenario itself. For example ant colonies that use the same advertising and reliability parameters have a different consensus accuracy when the quality of the sites are different. They also have a different consensus accuracy based on when the high quality site is found. The sooner the high quality site is found in the decision making process the better the outcome. See Chapter 5 for details.

Both honeybees and ants are democratic colonies that use a quorum threshold to reach consensus. Our numerical results show that we don't need the entire colony or even all workers to cast a vote to reach an accurate consensus. Both colonies are able to choose the best available site using a quorum threshold where only a small percentage of the colony needs to be involved in the decision making process. Another observation is that both ants and honeybees are able to make highly reliable decisions without having to visit all available sites. which implies that these colonies assess a site based on its characteristics not based on how it compares against another site.

Finally we notice more splits in trail ant colonies compared to honeybees and chemical ants. When ant colonies split the colony start migrating to multiple sites then eventually direct the movement to one site. On the other hand, Thomas Seeley noticed that when bees split, the groups start migrating to different sites but the queen refuses to follow either one which leads both groups to come back to the swarm and not migrate anywhere.

It is due to these similarities in addition to the simplicity of [21] that we were able to extend the model and apply it to ant colonies. Furthermore, we were able to obtain numerical results that are similar to those obtain in different lab experiments.

6.2 Group decision-making in human and social insects

Humans live in a highly sophisticated environment where many decisions are made by groups. Group decisions in humans vary from small decisions that affect a small group of people to big decisions that affect the country or planet we live in. For example a group of people can decide on which restaurant to go to or which movie to watch. On the other hand, a group of people needs to decide on which president to vote for or which side to support regarding the global warming debate. It might not be very obvious but many animal colonies including social insects also live in a sophisticated environment. They need to make decisions that affect the survival of the colony. Even though there are many similarities between human and social insects decision making process, see [3] for details. We choose to focus on the differences instead. We discuss four main differences in this section: 1. Communication 2. Advertising 3. Optimality concept and 4. Stubbornness.

1. Communication: Even though both humans and insects use advertising to get more support to their choice the communication method is very different. In insects communicating between individual is simple and done by signals or certain acts such as the waggle dance in bees or canvassing in ants. In humans the communication method is extremely sophisticated. Humans can present arguments and proofs to support their point of view. The existence of a communication language in humans allows us to not only cast a vote for one of the available options but also rank all options available. It allows us to discuss the reasoning behind our decision. It also allows us to exchange information, arguments and hypotheses for each choice before casting our vote. See [3] for more details on this difference.

2. Advertising: Both humans and insects advertise their choice to get more support for it. One difference in advertising is the individual advertising a choice. In our mathematical models each ant and each bee had exactly the same advertising weight. In another words, if ant 1 advertised site α and ant 2 advertised site α the advertising weight is the same for both ants. It is advertising that matters not the individual doing the advertising. Similarly if ant 1 voted for site α and ant 2 voted for site α both votes count and affect the threshold equally. With the existence of celebrities, social media and big organizations that drive our day to day lives, this process is very different in humans compared to insects. In humans there are influential individuals or celebrities that easily influence a group of people. When one of these influential individuals makes a choice it is weighted higher than other non influential individuals since it will affect the opinion of many of their followers. In [15] the author discusses this phenomenon in details and studies human decision making in different scenarios such as the presence or absence of advertising and influential individuals. It shows how different weight of advertising in individuals can affect the decision making process for

humans compared to social insects.

3. Optimality concept: In group decision making humans and insects individually vote for one choice among many others to reach an optimal decision. In insects that optimal decision is clear. It is directly related to the survival of their colony; therefore, all individuals vote or act according to the colonies best interest. This is very different for humans. As individuals we act to maximize our benefit or the payoffs we expect to attain according to our beliefs, point of view, political parties or many other personal factors. This changes the definition of an 'optimal choice' for humans compared to insects which changes the outcome of our choice. To summarize this point, insects vote to benefit the group while humans vote to benefit themselves. In our model this criterion is shown by assigning an absolute quality value for each site. If this was a model used for human choice selection then the quality for each site would be related to the individual assessment of that site. See [3] for more details on this difference.

4. Stubbornness: I think this criteria can be effectively described by Max Planck's quote regarding social process: "A new scientific truth does not triumph by convincing its opponents and making them see the light, but rather because its opponents eventually die, and a new generation grows up that is familiar with it". This is how stubborn and closed minded humans can be. When a human being decides to vote for a certain outcome, it is extremely hard to get them to change their opinion. On the other hand, insects will vote for a certain outcome and as seen in our simulations in Chapter 3 honeybees, like humans, can also be stubborn; however, after a certain amount of time they automatically choose to exit the debate and let other honeybees make a decision. The willingness of honeybees and ants to change their opinion helps these colonies reach a better decision compared to humans.

Chapter 7

Concluding remarks

In this research we use the model introduced in [21] for honeybees and extend it to be used for ants. There are some studies in the natural sciences that discuss the similarities and differences between humans, bees and ants decision making process such as [23, 3]; however, to my knowledge this is the first mathematical study that applies the same agent model with minor modifications to both ants and bees. We believe this is the first agent-based model that can be easily extended to many social insects and used to show how advertising, reliability, quorum threshold and colony size affect the consensus result of the colony. We also believe that using some numerical optimization methods, this model can be used to find the optimal values of these parameters which result in the highest consensus accuracy for different scenarios of colony migration.

Our key finding in this research is that advertising does not always give a better outcome. In some cases as discussed in trail ants, given a highly reliable colony, it is better for individuals to make decisions on their own without advertising. Especially when there is not enough time for advertising to be affective.

We also show in Chapter 3 that honeybees can get attached to a certain choice which results in a worse consensus accuracy. We show that bees are easily willing to switch their support to another site or simply stop advertising a site when they don't get enough support. This helps the colony reach an accurate decision. In Chapter 5 we run our modified model for ant colonies using different scenarios. We find that similar to lab experiments, colony size, threshold, advertising and reliability affect the accuracy of the outcome.

We believe that this is the first mathematical model that studies how changing colony size, threshold, advertising and reliability affects the accuracy of the outcome. This study gives an insight into why many lab experiments perform the same experiment but get different results. We believe that the reason for the different results is that ant colonies

used in different experiments may be using a different advertising or reliability parameters. They may have different sizes and use different thresholds. Also a minor change in the scenario itself or the time the high quality site is found may result in a different outcome. We hope this work can help people understand how complicated choosing a new home is for social insects and how minor changes in different parameters can affect the final decision.

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