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Agent-Based Modelling of Decentralized Ant Behaviour using High Performance Computing

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Abstract

Ant colonies are complex biological systems that respond to changing conditions in nature by solving dynamic problems. Their ability of decentralized decision-making and their self-organized trail systems have inspired computer scientists since 1990s, and consequently initiated a class of heuristic search algorithms, known as ant colony optimization (ACO) algorithms. These have proven to be very effective in solving combinatorial optimisation problems, especially in the field of telecommunication.

The major challenge in social insect research is understanding how colony-level behaviour emerges from individual interactions. Models to date focus on simple pheromone usage with mathematically devised behaviour, which deviates largely from the real ant behaviour. Furthermore, simulating large-scale behaviour at the individual level is a difficult computational challenge; hence models fail to simulate realistic colony sizes and dimensions for foraging environments.

In this thesis, FLAME, an agent-based modelling (ABM) framework capable of producing parallelisable models, was used as the modelling platform and simulations were performed on a High Performance Computing (HPC) grid. This enabled large-scale simulations of complex models to be run in parallel on a grid, without compromising on the time taken to attain results. Furthermore, the advanced features of the framework, such as dynamic creation of agents during a simulation, provided realistic grounds for modelling pheromones and the environment. ABM approach through FLAME was utilized to improve existing models of the Pharaoh's ants (*Monomorium pharaonis*) focusing on their foraging strategies. Based on related biological research, a number of hypotheses were further tested, which were: (i) the ability of the specialist 'U-turner' ants in trail maintenance, (ii) the trail choices performed at bifurcations, and (iii) the ability of ants to deposit increased concentrations of pheromones based on food quality. Heterogeneous colonies with 7% U-turner ant agents were further shown to perform significantly better in foraging compared to homogeneous colonies. Furthermore, laying pheromones with a higher intensity based on food quality was shown to be beneficial for the Pharaoh's ant colonies in switching to more rewarding trails. The movement of the Pharaoh's ants in unexplored areas (without pheromones) was also investigated by conducting biological experiments. Video tracking was used to extract movement vectors from the recordings of experiments and the data obtained was subject to statistical analysis in order to devise parameters for ant movement in the models developed.

Overall, this research makes contributions to biology and computer science research by: (i) utilizing ABM and HPC via FLAME to reduce technological challenges, (ii) further validating existing hypotheses through realistic models, (iii) developing a video tracking system to acquire experimental data, and (iv) discussing potential applications to emergent telecommunication and networking problems.

Dedication

To my father, Professor Hasan Ali Bicak,

For his endless support and motivation, and for being the best father a daughter could ever have.

Babam Sağolsun!

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Declaration

I declare that this report was composed by myself, that the work contained herein is my own except where explicitly stated otherwise in the text. This work has not been submitted for any other degree or professional qualification except as specified.

(*Mesude Bicak*)

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Chapter 1

Introduction

Introduced by Darwin in 1850s, *natural selection* is referred to as 'one of the cornerstones of modern biology'. Coupled with *evolution*, biological systems in nature have been solving complex dynamic problems by adopting improved solutions over millions of years. Insect societies are perfect examples of such systems, who have been discovered to evolve elegant solutions, such as the mounds of termites, waggle dances of bees and the pheromone trails of ants. What was even more interesting for researchers to find out was that such elegant solutions were achieved through simple rules, where there was not much need for the individuals to possess 'intelligence'. Consequently, 'collective intelligence' achieved by *self-organized* behaviour in many *complex adaptive systems* of nature became a source of inspiration for human life, i.e. building designs inspired by termite mounds, job-scheduling routines in industries inspired by waggle dances of bees and Internet packet routing algorithms inspired by ant pheromone trails, to name a few.

This chapter introduces ant colonies as *self-organized complex adaptive systems*, followed by the research motivation, objectives and the approach applied.

1.1 Ant Colonies as Complex Adaptive Systems

Coined at the Santa Fe Institute by Gell-Mann (1995), complex adaptive systems are "macroscopic collections of simple (and typically nonlinear) interacting units that are endowed with the ability to evolve and adapt to a changing environment" (Complexity in a Changing Science, European Commission), where the order is *emergent* as opposed to pre-determined, with an unpredictable future. They are dynamic networks of many agents (which may represent cells, species, individuals, firms, nations) acting and reacting to each other in an unplanned manner, resulting in emerging regularities and patterns. For instance, in an ecosystem if a predator starts to deplete one species of prey, this results in a greater or lesser food supply for others in the system which in return affects their overall behaviour and population (Fryer, 20.11.2010).

Ant colonies have been shown to possess properties that characterize complex adaptive systems. Adapted from Bonabeau (1998) such properties are as follows:

- *Decentralized communication*: The absence of a global controller, thereby activities taking place via interactions between individuals and their environment.
- *Self-organization*: The existence of an emergent hierarchical organization which determines the partitioning of reproduction, resources, and tasks.
- *Adaptation to change*: Their ability to adapt to changing environmental conditions with robustness and resilience, i.e. food, competitors, predators.
- *Novel emergent behaviour*: As a result of adaptivity, arising novel emergent behaviour, such as division of labor.

Many group-living organisms exhibit complex and coordinated patterns, from the motion of fish and birds, to patterns of traffic flow in human crowds (Couzin and Krause, 2003). This is explained by self-organization; defined as the process, where global level patterns of a system emerge from local interactions among its individuals (Camazine et al., 2001). Individual organisms may use relatively simple behavioral rules to generate structures and patterns at the collective level that are relatively more complex than the components and processes from which they emerge. The mechanism of self-organization takes place through two different modes of interactions; negative and positive feedback. With positive feedback the system responds in the same direction of change; such as ants forming a pheromone trail to a food source by depositing pheromones. In negative feedback, the system responds in such a way as to reverse the direction of change; such as the evaporation of a pheromone trail when ants refrain from reinforcing the trail due to the depletion of the related food source.

1.2 Motivation

The discipline of Biomimicry, the remarkable foraging systems of the Pharaoh's ants and the Flexible Large-scale Agent-based Modelling Environment (FLAME) have been the motivation for this research as outlined below.

1.2.1 Biomimicry

Benyus (1997) defines Biomimicry as "innovation inspired by nature" which aims to; (i) study models in nature, (ii) take inspirations, and (iii) imitate processes to solve human problems. It stems from the idea that nature has already solved many of the problems through natural selection and evolution, where the animals, plants, and microbes are the engineers. Therefore, rather than re-inventing the wheel, Biomimicry suggests imitating the best adapted organisms in our habitat. There are many examples of biomimicry in our lives, such as aircraft wing designs based on inspirations from bird flights, bionic cars from the shape of boxfish, wind turbine designs from whale power and many more.

Another example of Biomimicry, Ant Colony Optimization (ACO) algorithms inspired by ant behaviour used in telecommunication are discussed in Chapter 7.

1.2.2 Pharaoh's Ants

Monomorium pharaonis species, more commonly known as the Pharaoh's ants, were chosen as the model species for this research, as they have the ability to solve dynamic problems as a routine in nature. They are small species, approximately 2 mm in length, which utilise multiple chemical pheromones for communication (and memory) over divergent time scales (Jackson et al., 2008). Having poor vision, they are wholly reliant on pheromones for orientation (Fourcassié et al., 1994) and unlike other ant species, they are known to readily form trail networks even before discovering food. The remarkable sophistication of the self-organised foraging system of the Pharaoh's ant exhibits many desirable properties, which led to their extensive investigation in the literature.

Pharaoh's ants and their unique properties are detailed in Chapter 2.

1.2.3 FLAME: The Agent-Based Modelling Framework

Agent-based modelling (ABM) is a popular bottom-up approach, where a system is modelled as a collection of autonomous decision-making entities called agents (Bonabeau, 2002). Each agent is able to make decisions on the basis of a set of rules. The most common use of ABM involves mimicking complex systems, such as ant and bee colonies, in which conclusions about the system behaviour are drawn according to the results of the simulations.

A successful general framework for agent-based modelling is the Flexible Large-scale Agent-based Modelling Environment (FLAME), which is being developed at the University of Sheffield, in collaboration with Science and Technology Facilities Council (STFC) (Coakley et al., 2006). FLAME, a flexible agent-based framework based on the theory of X-machines, was used as the modelling platform for this research. The biggest advantage of this framework was its support for High Performance Computing (HPC), which allowed complex models to be automatically parallelised on HPC grids, enabling large number of agents to be simulated over short periods of time.

1.3 Research Objectives and Approach

Following from the above motivation, the main objectives of this research are:

- To develop realistic agent-based models in order to contribute to the detailed understanding of the underlying mechanisms in foraging systems of Pharaoh's ants
- To identify potential applications for biomimicry solutions in telecommunications and networking.

These objectives are approached by:

- Utilising ABM through the FLAME framework to benefit from the cutting-edge technological advantages, such as HPC.
- Conducting biological experiments with Pharaoh's to obtain experimental data
- Developing a video tracking system to extract the experimental data obtained

1.4 Structure of the Thesis

This thesis is structured as follows:

Chapter 2. Communication in Ants: introduces the key concepts in ant communication and the unique behaviour observed in Pharaoh's ants.

Chapter 3. Methodology: provides a discussion on the common approaches to modelling and introduces the methodology used for this research.

Chapter 4. Ant Models to Date: provides an overview of the existing ant models in the literature.

Chapter 5. Biological Experiment: explains the biological experiments conducted in order to investigate the movement patterns of Pharaoh's ants.

Chapter 6. Investigating Foraging Strategies: explains the agent-based models based on the movement patterns and foraging strategies of Pharaoh's ants with a detailed approach to modelling pheromones.

Chapter 7. Investigating Specialist U-turners: explains the agent-based models based on the specialist U-turner Pharaoh's ants.

Chapter 8. Investigating 'Excited' Behaviour: explains the agent-based models based on the 'excited' behaviour (food quality assessment) of the Pharaoh's ants.

Chapter 9. Ants and MANETs: introduced the ACO algorithms and identifies potential applications for the investigated behaviour of Pharaoh's ants.

Chapter 10. Conclusions and Future Work: provides a summary of the findings and achievements of this research and discusses future work.

Chapter 2

Communication in Ants

Animals must make informed decisions throughout their lives by making the best use of available information, particularly about where to find food (Krebs and Davies, 1997). Living in a group can be advantageous for individuals in terms of information sharing as an emergent group level behaviour (Krause and Ruxton, 2002). For many social species, particularly social insects, this is often achieved by chemical communication using pheromones (Wilson, 1971). Pheromone trails optimise food finding (foraging) in dynamic environment as they enable information to be publicly communicated within the environment, away from an information centre (the nest). The intensive study of communication among ants over more than 50 years has yielded a wealth of results that has furthered our understanding of social organization. The demonstrated modes of communication are extremely diverse; tappings, stridulations, stroking, grasping, nudging, antennations, tastings /puffings and streaking of chemicals that evoke various responses from simple recognition to recruitment and alarm (Hölldobler and Wilson, 1990).

Ants dominate many environments, which is explained by their ability to out-compete their rivals for food. They achieve this by forming pheromone trails throughout the environment, which facilitates rapid transfer of information and enables rapid recruitment to food resources, whereas a competing group not using communication would rely solely on independent discoveries (Jackson et al., 2009). In many social species the nest site serves as the information centre (Wilson, 1962). This would introduce extra time costs in addition to the time spent searching (Dechaume-Moncharmont, 2005) as the individual would have to return to the nest to communicate and recruit, which in return would also limit the number of individuals engaged in food search. Sudd (1957) observed that the trails of Pharaoh's ants extend over 60 metres. Therefore, such decentralised communication of ant agents away from the nest is extremely advantageous, avoiding the need to travel large distances over long travelling times.

While the majority of the ant species (i.e. *Lasius niger* deposit pheromones only after finding a food source, Pharaoh's ants form trails even before a food source is found. Due to their poor vision, they are almost entirely reliant on these trails for orientation, which suggests that they have to utilise local information in a sophisticated manner.

The above suggests that ants, Pharaoh's ants in particular, inherently possess many characteristics desirable for complex computing systems, such as resilience, adaptation and self-organization. Therefore, this thesis studies the foraging strategies of the Pharaoh's ant (*Monomorium pharaonis*) aiming to identify potential mechanisms that could be applied to popular telecommunication and networking problems.

2.1 Introducing the Concepts

2.1.1 Pheromones

A 'semiochemical' is any substance used in communication, whether between species or between members of the same species (Law and Regnier, 1971). A pheromone is a type of semiochemical, usually a glandular secretion, used within a species; one individual releases the material as a signal and the other responds after tasting or smelling it (Karlson and Luscher, 1959). Carthy (1951) was one of the pioneers who conducted an experimental study of trail laying in ants. His technique of using artificial trails made from different glandular extracts, and analyzing the trail following response of ants to these trails, enabled him to identify the Dufour's gland as the source of pheromones in Fire ants (*Solenopsis invicta*). This technique is very popular as it has led to the discovery of trail pheromone glands in different taxonomic groups (Hölldobler and Wilson, 1990).

Pheromones are the key elements in the organization of ant societies. Hölldobler and Wilson (1990) states that a typical ant colony operates with 10 to 20 types of signals, most of them being chemical in nature. These chemicals are generated in the six key exocrine glands that occur widely through the ants; Dufour's gland, the poison gland, the pygidial gland, the sterna glands, the mandibular glands, and the metapleural glands (Hölldobler and Wilson, 1990).

In Pharaoh's ants, it has been found out that at least seven chemicals are utilized in their foraging activities (Ritter et al., 1977a; Jones and Blum, 1982; Hölldobler and Wilson, 1990). Faranal, the most active pheromone, was identified in Dufour's gland (Hölldobler, 1973; Ritter et al., 1977b), and six alkaloid monomorines have been identified in their poison glands, both of which were shown also to exhibit trail following activity (Ritter et al., 1977a).

The pheromone trails of ants have been extensively studied and modelled as single pheromone systems (Pasteels et al., 1986; Nicolis and Deneubourg, 1999). However, over the years it has been shown that multiple pheromones could be secreted from diverse glandular sources (Hölldobler and Wilson, 1990; Wyatt, 2003). Furthermore, it was found that multiple pheromones may exhibit different behavioural responses that are dependent upon concentration, context and their proportions (Hölldobler and Wilson, 1990). Due their significant importance in ant communication, it is essential for the modellers to have a good awareness of the pheromone deposition and detection mechanisms by ants in order to achieve realistic models, without losing the resulting interesting phenomena.

2.1.2 Trail detection and following in ants

Pheromones secreted by ants act within a short range and reach the receiver by diffusion, where the receiver ant can only respond after entering the 'active space'. Bossert and Wilson (1963) define the 'active space' as the zone where the pheromone concentration is at or above the detection threshold for the ants. From an instantaneous release of pheromones near the ground, the active space expands as a hemispherical cloud, where its radius rises to a maximum and then starts to contract and fade away to below the detection threshold as their diffusion continues (Wyatt, 2003). When a pheromone trail is formed, the 'active space' turns into a 'vapour tunnel'. As ants travel through this 'vapour tunnel' they sweep their antennae from side to side (Hölldobler and Wilson 1990).

Hangartner (1967) demonstrated the sinusoidal walk of ants along a trail and suggested that ants perform two types of chemical sensing: (i) Osmotropotaxis (bi-sensor simultaneous mechanism) and (ii) Klinotaxis (uni-sensor successive mechanism). It is believed that these mechanisms are the basis for chemo-orientation in ants (Leuthold, 1975). Osmotropotaxis suggests that the pheromone concentration is detected by the ants with both antennae, where a concentration difference is computed and the direction is changed towards the higher concentration accordingly. Whereas in Klinotaxis, information as to whether a direction change is necessary is provided. However, it is argued that for a bi-sensor process, tiny left to right movements would suffice to follow a trail, rather than the observed broad sweeping movements of the antennae (Jackson, 2005). Furthermore, Sharpe and Webb (1998) point out that the receptor cells on the antennae are very sensitive to odour concentration leading to non-linear response. This is further challenged by air turbulence, making it difficult for the ants to detect spatial and temporal differences in odour molecule concentrations (Osorio et al., 1994), thereby supporting the application of uni-sensor mechanism.

2.1.3 Recruitment

Recruitment in ants has been observed at three different levels: (i) individual, (ii) group and (iii) mass recruitment, which are described briefly as below.

- *Individual recruitment:*
  This is simply achieved by the chemical scents of pheromones laid by individual ants. Whenever an ant leaves the nest to forage, it is in search to locate a pheromone trail deposited by a fellow nestmate, leading to a food source. If a trail already exists, the ant will immediately join and follow, until a food source or a dead-end is reached. In the case of no trails being located, the ants are shown to wander around randomly (discussed in Chapter 5). In Pharaoh's ants, it has been also shown that they start depositing trails as soon as they leave the nest, even before finding food (Jackson and Cháline, 2007). This makes them highly valuable for modellers, as they are able to form robust networks of trails as soon as they leave the nest.

- *Group recruitment:*
  In this case, chemical trails are laid by foragers, where they are also obliged to lead discrete groups of five to thirty recruited ants from the nest to the food source along a pheromone trail. In order to achieve this, the ants have been observed to carry out the 'oscillatory recruitment dance' (Szlep and Jacobi, 1967), where the dancer vibrates its head and thorax to grab the attention as rapidly as possible and enable the fellow ant to follow it along the trail to a food source.

- *Mass recruitment:*
  Term coined by Wilson (1962), it is the transmission of information from one group of individuals to another group of individuals, via trails of many ants. This form of communication appears to be the most complex recruitment method of ants. The number of ants following a trail from the nest to food is controlled by the concentration pheromones secreted by workers already on the trail (Jackson, 2005); the better the food source, the greater the amount of workers laying a trail towards the nest. Consequently, as the food is being depleted, ants slowly reduce the activity of reinforcement, declining the trail strength due to evaporation.

The most common form of recruitment in ants is achieved via chemical trail communication, which are the most evident recruitment mechanisms observed in Pharaoh's ants. Therefore, the individual and mass recruitment mechanisms of Pharaoh's ants were the primary focus in this research. The movement, pheromone deposition and detection, such recruitment mechanisms of Pharaoh's ants were tested and successfully demonstrated with agent-based models. The Movement and Foraging Models, along with their details and results are explained in Chapter 6.

2.1.4 Tandem running

The expression “tandem running” was introduced by Wilson (1962), to describe a mechanism through which an ant communicates with its nestmates after a successful journey back to the colony. The “tandem-runner” was observed to take a special position called the “calling posture”, pointing its gaster upwards and deposit a pheromone which attracts and ‘calls’ the nestmates. When the first ant arrives, the tandem running commences after the touching the tandem-runner and the recruiting ant leads the nestmate to the discovered food source. During tandem running the follower was observed to keep close antennal contact with the leader, repeatedly touching its legs and gaster. Whenever this contact is interrupted, the leader was observed to stop and resume the calling posture, remaining for several minutes if necessary, continuously discharging the calling pheromone (Hölldobler and Wilson (1990).

2.1.5 Alarm communication

Worker ants are said to be in a state of alarm when they move away from a potentially dangerous stimulus, either calmly or in panic, or charge towards it aggressively (Hölldobler and Wilson, 1990). Furthermore, when an ant is seriously disturbed, it was observed to release pheromone along with alarm substance from her head, which both alarms nearby workers and attracts them to the threatened nestmate (Hölldobler and Wilson, 1990). In order to enhance attraction, ants are capable of making chirping sounds, in addition to pheromones, referred to as ‘stridulation’. Such behaviour can be classified into two broad categories: (i) aggressive alarm; where ants are drawn towards the threat trying to attack it, and (ii) panic alarm; where ants tend to run away from the threat. If the alarm is very strong, individuals are even observed to evacuate the nest (Hölldobler and Wilson, 1990).

To the best of my knowledge, tandem running has not been observed and alarm communication is yet to be investigated in Pharaoh’s ants, hence they are not taken into consideration in this research.

2.2 *Monomorium pharaonis*

The Pharaoh’s ant, *Monomorium pharaonis* (*Formicidae, Myrmicinae*), is a widely studied model system for investigating pheromone trails (Fourcassié and Deneubourg, 1994; Jackson et al., 2006; Jeanson et al., 2004). Forming colonies with less than 2500 workers (Peacock et al., 1955), they do not have nestmate recognition, which makes the manipulation of the colony size simple (Hölldobler and Wilson, 1990). Their poor vision and reliance on pheromone trails for orientation is advantageous as the visual cues do not need to be eliminated when conducting studies. This is identified as a major problem in *Lasius niger* colonies as they are known to possess excellent visual orientation skills. Furthermore, *L. niger* were observed to form short-lived trails, while *M. pharaonis* were found to form complex persistent trails.

Pharaoh's ants have been observed to possess further unique behaviour, making them more interesting for researchers. Such behaviour include: (i) the use of multiple pheromones, (ii) division of labour via multiple pheromones, (iii) division of labour by specialist U-turner ants, (iv) utilizing trail polarization and (iv) ability to distinguish between multiple food sources of different qualities, which are explained in the next sections.

Figure 2.1: *Monomorium pharaonis*, the Pharaoh's Ant..

2.2.1 Multiple pheromones

It has been suggested that Pharaoh's ants utilised three different types of pheromones for communication, which are (i) short-term attractive, (ii) long-term attractive and (iii) short-term repellent pheromones.

It was mentioned by Blum (1966) and Ritter et al. (1973) that the trails secreted by the Pharaoh's ants may persist for longer than one day, while Jeanson et al. (2003) found that they last for eight minutes on paper substrate. In his PhD research, Jackson (2005) observed that the trails produced by colonies of natural size can persist for more than 2 days, and demonstrated the co-existence of different types of pheromones allowing species to flexibly forage on persistent, as well as ephemeral food sources. It was suggested that the pheromones contained a chemical component (anticipated to consist of monomorines) with long-term persistence, serving a different role to the short-lived pheromone component (anticipated to be Faranal). Consequently, it was concluded that the Pharaoh's ants have a two-level memory as a result of utilizing multiple pheromones with different values of attractivity and volatility.

Recently, Robinson et al. (2008) hypothesised the use of short-term repellent pheromones by Pharaoh's ants. The results from biological experiments and agent-based models demonstrated successful results, proposing decay rates for such pheromones (Robinson et al., 2008).

2.2.2 Division of labour

The use of multiple pheromones provides Pharaoh's ants with memory over different time scales. Consequently, a division of labour between 'pathfinders' and 'foragers' was observed by Jackson et al. (2008). Only 17% of foragers always succeeded in detecting long-term attractive trails, no matter what the conditions of the ants were (deprived of food, isolated, etc.), whilst the remainder completely failed to detect them. However, other workers were capable of making a flexible transition to trail finding when deprived of food, although they always performed poorly in finding trails. It was observed that the workers, which could always locate and follow the long-lived trails (17% of foragers), 'pathfinders', left the nest early in the morning touching their antenna on the substrate following long-lived trails, aiming to investigate if a previously rewarding food source was still rewarding. On the other hand, the rest of the ants, 'foragers', were observed to leave the nest only whenever they were hungry following short-term attractive pheromones to locate food sources of immediate value. Such observed behaviour resulted in the pathfinder ants persistently searching for the optimal solution, where generalised foragers exploited the current best solution. It was concluded that this finding demonstrated the existence of behavioural castes within the same colony of Pharaoh's ants, which increased the foraging effectiveness by having individuals perform different tasks simultaneously.

As the differences in the concentrations of the multiple pheromones deposited by Pharaoh's ants are yet to be investigated and quantified, they were not taken into consideration in this research.

2.2.3 Trail geometry

The majority of the ant species can reorient on trails by using external cues, including landmarks and the position of the Sun (Hölldobler and Wilson, 1990), i.e. *Lasius niger*. Leafcutter ants were concluded to be using the Earth's magnetic field (Riveros and Srygley, 2008).

In 2004, it was also demonstrated that the Pharaoh's ant has a sense of geometry (Jackson et al., 2004). The structure of the pheromone trails formed by the Pharaoh's ants were investigated in depth, which were found to form Y-shaped branches with an internal angle of approximately 60 degrees as they led away from the entrance. It was observed that the ants walking the wrong way along a trail were unable to reorient at a trail bifurcation, if the angle was 120 degrees, whereas they successfully could if the angle was less. As a result, it was concluded that angles less than 120 degrees provided bifurcations with a 'nest-environment polarity', whereas at angles as large as 120 degrees only provided symmetrical information that was not of use. Consequently, it was demonstrated that the Pharaoh's ants use characteristic branching geometry of trail bifurcations to determine their heading, where their ability to reorient is maximized at the natural bifurcation angle of 60 degrees.

2.2.4 U-turning Behaviour

U-turning behaviour was first observed in *Lasius niger* ants by Beckers et al. (1992), who carried out a series of laboratory experiments to show how *L. niger* colonies systematically selected the shorter of two paths of varying length and formed trails between the nest and the foraging area. *L. niger* ants were observed to perform more U-turns on the longer branch compared to the shorter branch, where such behaviour was concluded to be a result of two potential reasons: (i) the unattractiveness of the longer branch after a relatively long journey, where the U-turns performed in this case were referred to as 'intrinsic U-turns', and (ii) the discovery of a branch with less traffic and less pheromone concentration, where in this case the U-turns were referred to as 'trail-based U-turns'. As a result, it was concluded that in both cases the U-turns were the result of 'mistakes' being made, as the ants were also observed to stop depositing pheromones on their way back.

In 2004, U-turns was also observed in Pharaoh's ants by Hart and Jackson (2004). However, the U-turns performed by Pharaoh's ants were concluded to have a completely different aim. 7% of the foragers were observed to perform 'apparently incorrect' U-turns throughout the trail network. These specialist U-turners made frequent U-turns on trails and deposited pheromones much more frequently compared to the ants not performing U-turns. As a result, U-turner Pharaoh's ants were concluded to be maintaining the trail network and updating its informational content.

Such behaviour of Pharaoh's ants was tested with an agent-based model using the FLAME framework, where the results further demonstrated the success of such a democratic system for increasing the foraging efficiency of Pharaoh's ants. The U-turn Model along with its details and results are explained in Chapter 7.

2.2.5 Food Quality Assessment

Choice of a path based on the quality of food source is a widely applied experiment among researchers, where ant colonies are provided with food sources of different qualities (Beckers et al., 1990, 1992b, 1993; Pasteels et al., 1987; Crawford and Rissing, 1983; Nicolis and Deneubourg, 1999; Sumpter and Beekman, 2003). Detailed experimental studies reported unexpected behaviour when two food sources were simultaneously made available to ant colonies. This was explained as a competition between two chemical trails leading to sources, giving rise to a bifurcation phenomenon, in which one of the trails attracted most of the population and pre-dominated over the other (Pasteels et al. 1987, Beckers et al. 1992b, Robson and Traniello, 1995, Detrain and Deneubourg, 1997).

Hangartner (1970) observed that *Acanthomyops interjectus* foragers increase trail laying activity when recruiting to richer sugar solutions, however the differences were not significant. Beckers et al. (1990) conducted experiments with *Lasius niger* and *Tetramorium caespitum*, and provided both colonies with: (i) two identical food sources simultaneously and (ii) two food sources of different qualities sequentially (after approx. 1 hour). *L. niger* foragers were observed to concentrate only on one of the sources in both cases (i) and (ii), irrespective of whether or not was there a difference between the qualities of the food sources provided. Even if the rich source was provided after the poor source, *L. niger* foragers continued exploiting the poor source until it totally diminished. This was explained as “cooperative transmission” as the stronger trail always had a higher preference over the others and a new trail to a good quality food source would not be able to compete with it. In contrast, *T. caespitum* foragers were observed to switch to a richer source, which was explained as “direct transmission”, enabling a recruiter from a newly discovered source to lead recruits to it, in spite of a well established recruitment to a previous source. In 1993, Beckers et al. used a Y-shaped experimental setup to observe the foragers of *Lasius niger* species, and found out that they deposited %45 more pheromones while exploiting 1 Molar sugar source, compared to when exploiting 0.05 Molar and 0.1 Molar food sources. Therefore, the overall finding was that mass-recruiting ants modulated their trail laying behaviour as a function of the sugar concentration.

Recently, Jackson and Chaline (2007) showed that Pharaoh’s ant foragers deposited pheromones during both outwards and the return leg of their foraging trips. Moreover, it was observed that the fed ants did not deposit significantly more frequently than unfed ants, but they deposited trails with significantly greater intensity when the quality of the food source was higher (1 Molar), whereas when the food source quality was low (0.1 Molar), no significant difference was found.

Such behaviour of Pharaoh’s ants will be referred to as the ‘excited’ behaviour and was tested with an agent-based model, where the results further demonstrated the success of such an efficient system in enabling the colony with the ability to distinguish between food qualities of different sizes and perform switches to the more rewarding trail branches accordingly. The Excitement Model along with its details and results are explained in Chapter 8.

Chapter 3

Methodology

3.1 Modelling

The aim of modelling is to create a realistic abstraction of the system. Due to inherent complexity of systems, it is not possible for a model to capture every detail. Therefore, models have to be fine-tuned and designed based on a specific hypothesis to be tested for the corresponding system. This further suggests that there could be many different ways to structure a model.

Modelling has proved to be very useful in understanding and predicting various properties of complex biological systems. Starfield et al. (1990) refers to models as “purposeful representations” and “tools for problem solving” as they help to capture the essence of a problem. They facilitate understanding and predicting properties of the system being studied. It involves a thorough analysis on the key parameters affecting the behaviour of the main components of a system and the interactions in between. This in return provides the modeller with valuable insights on the overall patterns of organization.

The product of a model is much more than a set of results which match experimental data (Robinson, 2006). The modelling approach allows us to test the role of mechanisms which may be almost impossible to manipulate in nature, for example the effect of pheromone diffusion on the way ants follow trails, or the effect of increased pheromone deposition by a fed ant on the overall foraging efficiency. Using models, it is possible to simulate and test various mechanisms and scenarios over and over again, simply by tuning parameters, which would be very difficult and time-consuming to achieve by conducting biological experiments.

Without computational simulations, traditional modelling approaches usually involve manually analysing biological data and deriving differential equations that approximate an “average” behaviour of a system. Such approaches tend to fail in capturing a large number of the interactions between components which could well be the factors leading to population-level behaviour. Consequently, recent research is increasingly favouring individual-based modelling, aiming to build more realistic models that capture interactions at the individual level to provide deeper insights into the reasons behind population level behaviour.

One of the key issues a modeller should be cautious about, is the number of iterations required for the model to be simulated. It is essential to have sufficient number of runs for the system to evolve from smaller parts, otherwise the community-level behaviour may not be observed efficiently.

There are two main approaches to modelling biological systems. These are top-down and bottom-up modelling, which are explained in the next sections. It should be noted that a combination of the two approaches, referred to as "integrated" or "middle-out" modelling, is also being widely applied by researchers, especially in the area of modelling the behaviour of bacteria, i.e. *E. coli*, where not so much is known about the characteristics of individual cells (Maleki-Dizaji et al., 2009).

3.1.1 Top-down modelling

Based on mainly ordinary or partial differential equations, systems are analyzed in a top-down manner in terms of a population of identical individuals, ignoring the differences in the population. The underlying behavioural rules are usually treated as a "black box", or approximated at the best case. Also referred to as state-variable models, these methods are essential and have proved useful in formulation of general theories. A popular example is the Lotka-Volterra model of the predator-prey interactions. However, biological systems tend to represent a great challenge for mathematical modellers, due to their inherent complexity and non-linear relationships among individual components.

In the study of the social insects, successful applications can be found in the works of (Beckers et al., 1992b; Beckers et al., 1993; Pasteels et al., 1987; Bonabeau et al., 1998; Nicolis and Deneubourg, 1999; Sumpter and Beekman, 2003). These models do often successfully describe ant behaviour, but they also limit the understanding of how patterns are formed. Such models may apparently work well, but in order to understand the flexibility and diversity of colony activity, it is also essential to investigate the agents at the individual level. Rather than carrying out a full investigation on the underlying mechanisms of the system, top-down models average individual behaviour over the whole population.

3.1.2 Bottom-up modelling

In bottom-up modelling, the system is modelled at the individual level, aiming to study the mechanisms for underlying behaviour as well as local interactions between the individuals. Bottom-up models emerge from low-level components of the system, in order to understand how the overall pattern of the system emerges. This method emulates the behaviour of the system under study in the most realistic way. Recently bottom-up approaches have started to attract more interest in modelling complex biological systems. This is due to researchers realizing the potential advantages of bottom-up approaches over top-down. For example, in a top-down model, it is not possible for a "user to trace back the system properties to the behaviour of individual animals" (Kaiser, 1979), which is essential when modelling complex biological systems. In contrast, this is easily achieved in bottom-up models.

Cellular Automata (CA) is a popular method in this regard, which emulates real physical laws using a small set of simple rules by limiting everything to a few states, frequently no more than two (Wolfram, 2002). Developed by Ulam and von Neumann, CA was founded upon the notion of one robot building another robot, aiming to address the problem of self-replicating systems. One such popular example is the 'Game of Life' by John Conway with four simple rules of generations, where CA models allow individual cells to react and change their states based on their interactions with the surrounding neighbouring cells. CA has been effectively used to explore many problems in biology but it treats biological communities as homogeneous, without any flexibility or variability, which are the two key characteristics of biological systems.

In bottom-up models, the individual components of a system are of prime importance. Consequently, another set of models conforming to this approach are referred to as individual-based modelling. A common way to achieve this is by treating these individuals as agents employing behavioural rules (agent-based modelling), where over time interactions between these agents will give rise to characteristic patterns at the population level. In modelling social insects, successful implementations of such models could be found in the works of (Deneubourg et al., 1989; Théraulaz et al., 1999; Jackson et al., 2004). Agent-based modelling is discussed in detail in the next section.

3.1.2.1 Agent-based modelling

Introduced by Reynolds with his Boids model in 1985 (Reynolds, 16.11.2009), agent-based models allow simulations of large number of agents and encourage bottom-up approaches allowing the modeller to focus on the individual elements interacting with each other, rather than looking at the population-level. The characteristic behaviours of the individuals are assigned to agents as simple rules, where each agent is able to make decisions based on these rules. As a result of various interactions between the agents through the environment they possess, certain population-level behaviour emerge. The most common use of agent-based models involves mimicking complex systems, i.e. foraging systems of social insects, in which theoretical lessons could be learned according to the results of the simulations.

An agent is a computer system that is situated in some environment and that is capable of autonomous action in this environment in order to meet its design goals (Wooldridge and Jennings, 1995). Once the lowest-level components of a system are identified as agents, simple rules governing their real behaviour are applied, which facilitates interactions between the agents and leads to emergent behaviour over time.

Obvious advantages of ABM over traditional modelling approaches, including CA are:

- *Asynchrony*: Agents do not need to simultaneously perform actions at constant time-steps, rather they can follow discrete event queues or a sequential schedule of interactions.
- *Spatial*: The environment does not necessarily need to be grid-based, nor the agents need to tile the environment, which allows cohabitation of agents with different environmental experiences.

Ant colonies are known for their decentralized communication system, as they do not have a leader influencing the colony members. Rather, their colony level behaviour emerges from the interactions between the individual ants, which is mainly via pheromones deposited in the environment. It is therefore more appropriate to apply bottom-up agent-based modelling to ant behaviour. This way, interesting features emerge over time, which are not pre-determined in the design at all. (Deneubourg et al. 1990).

3.1.3 Validating models

Grimm (1999), reviewed 50 individual-based animal population models, providing a detailed comparison between the two modelling approaches. According to Grimm the expectations from individual-based models were not fulfilled. This is because it was expected that once the rules and characteristics of individuals have been assigned to agents, the population and community-level consequences would emerge naturally (DeAngelis et al., 1994). However, out of the 50 individual-based animal population models reviewed, only 36% of them were found satisfactory as they were found to be generally inadequate. Grimm (1999) explains the reason behind this as the absence of a a general strategy for building and analyzing individual-based models. His suggestion upon this was to start with a very coarse model that reproduces a pattern, followed by refining the model step by step, and finally checking and testing the model rigorously with each refinement. It was concluded that bottom-up approaches alone will not lead to theories at the system level, due to the need for top-down approaches to provide an appropriate integrated view. However, it was also underlined that it will never be possible to fully understand a system's properties unless how they emerge is well understood.

On this issue, expressing individual-based models in a formal framework has been identified as a solution (Kefalas et al., 2003). Formal specification of a model facilitates model checking, which guarantees completeness of a model with respect to requirements, whilst simulations may only reveal inconsistencies or misconceptions in the model. This is where the FLAME framework comes into use, which is based on the X-machine theory, demanding formal specification of communicating agents, explained in the next chapter.

On the practical side, validation of models also have to be performed to assure quality. The validation levels are grouped into five categories by Carley (1996) as below:

- *Theoretical validity*: Adequacy of the underlying theoretical model in characterizing the real world
- *Internal validity*: Whether the underlying program is free of coding errors
- *Operational validity*: The adequacy and accuracy of the model results when compared with experimental data
- *Cross-model validation*: Comparison of two models against each other.
- *Data validity*: Accuracy of the data (real and computer generated) and the data's adequacy for addressing the issue of concern

In this research, attempts were made to fulfill each category by taking the following factors into consideration:

- *Face validity*: The model results or simulations 'appear' to fit with reality
- *Parameter validity*: The parameters of the model match the experimental data
- *Process validity*: The process described by the model corresponds to mechanisms of the biological system
- *Pattern validity*: The pattern of results generated by the model matches the patterns of biological results
- *Point validity*: The behavior of the model on each dependent variable has the same meaning as the experimental data
- *Distributional validity*: The distribution of the results generated by the model has the same characteristics as the real data

Furthermore, a number of validation techniques were used. Adapted from Carley (1996) these could be summarized as follows:

- *Grounding*: The simplifications made in the model design should not affect providing important insights. Parameters and states should be set in accordance to real rules, and wherever possible it should be demonstrated that the model results and behaviour are consistent with the real behaviour.
- *Calibrating*: Models should be extensively tuned to fit the mechanisms of the system under study by; parameter estimation, altering algorithms and rules within the model. If required experts should be consulted or experimental data should be obtained.
- *Verification*: The model results are compared graphically or statistically with experimental data and previous related findings.

3.2 FLAME

FLAME allows modellers from all disciplines to develop complex agent-based models. It is based on the X-machine theory, which is an extension of Finite State Machines (FSM). Introduced by Eilenberg (1974) and extended by Holcombe (1988), an X-machine is a general computational machine, which provides agents with a memory in addition to states and transition functions. As opposed to FSMs, the transitions are not labeled with simple inputs but with functions that operate on inputs and memory values. The X-machine, depending on the current state of control and the current values of the memory, consumes an input symbol from the input stream and determines the next state, the new memory state and the output symbol, which will be part of the output stream (Eleftherakis et al., 2005). The formal definition of an X-machine is an 8-tuple $M = (\Sigma, \Gamma, Q, M, \Phi, F, q_0, m_0)$, where:

- Σ, Γ is the input and output finite alphabet respectively,
- Q is the finite set of states,
- M is the memory,
- Φ is a finite set of partial functions φ that map an input and a memory state to an output and a new memory state, $\varphi:\Sigma \times M \rightarrow \Gamma \times M$,
- F is the next state partial function that given a state and a function from the type Φ, denotes the next state. F is often described as a transition state diagram, $F:Q \times \Phi \rightarrow Q$,
- q_0 and m_0 are the initial state and memory respectively.

Agent attributes, such as x, y coordinates, are stored in the memory, and are updated throughout the simulation. Communication between the agents is achieved through messages based on the interaction rules specified by the modeller. These rules involve posting and reading messages from message boards. In such a scenario, the possibility of deadlocks arising would be highly likely. FLAME handles deadlocks by using a distributed memory model, Single Program Multiple Data (SPMD), which inserts synchronisation points into the model, ensuring that all the data is coordinated among agents throughout the simulation.

FLAME requires the modellers to prepare three files (highlighted in figure 3.1), which should contain the following:

- *model.xml*: The model structure, such as agent descriptions, memory variables, functions, messages. It is possible to have multiple *model.xml* files.
- *functions.c*: The implementations of the agent functions specified in the *model.xml* files. It is possible to have multiple *functions.c* files.
- *0.xml*: The initial states or values of the memory variables of the agents specified in the *model.xml* files, i.e. the initial coordinates of the agents.

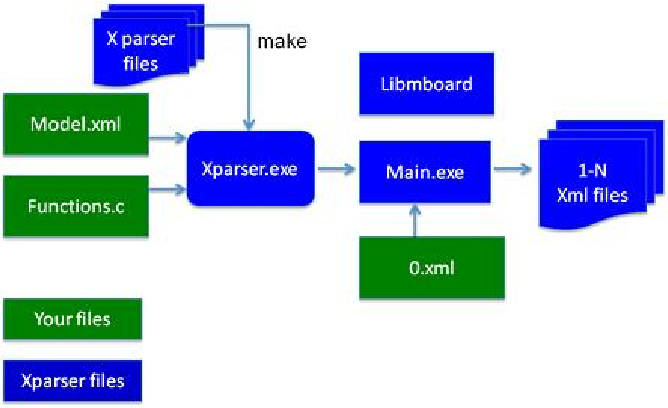


Figure 3.1: Block diagram of the FLAME framework.

The *Xparser.exe*, the simulation program generator of FLAME, is compiled with the modellers' files to produce a simulation package (*Main.exe*), which in return is used to run the simulation for a specified number of iterations. The outputs are generated as *XML* files, with identical structures to the *0.xml* file. The number of the resulting *XML* files depends on the number of iterations specified to run the model.

3.2.1 Communicating X-machine Agents

Modelled as communicating X-machines, agents exchange messages based on the rules specified in the *model.xml* file. Within the formal specification of X-machine theory, each agent should possess the following characteristics:

- A finite set of internal states of the agent,
- Set of transition functions that operate between the states,
- An internal memory set of the agent,
- A specification for sending and receiving messages among agents.

Figure 3.2 shows the structure of how two X-machines communicate. Communication between agents is handled by an intelligent message board library, called the *Libmboard*. It allows filtering of messages, reducing the work for the agents, hence improving simulation performances. This is simply achieved by specifying ‘conditions’ within the *model.xml* file and asking the *Libmboard* to filter out the messages that do not satisfy the specified conditions. As a result, the agents are prevented from iterating over unnecessary messages in the message board.

In order to describe a system in FLAME the following stages should be carried out:

- Identify the agents and their functions,
- Identify the memory variables for the agents,
- Identify the states to specify an order of function execution within the agent,
- Identify the input and output messages for each function.

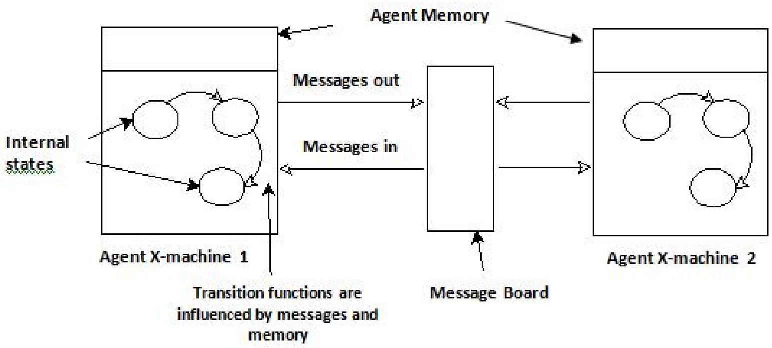


Figure 3.2: Communication between two X-machines in FLAME framework.

3.2.2 Advanced features

FLAME stands out from the other agent-based modelling frameworks as it supports high performance computing. Using FLAME, models can be automatically parallelised over parallel computers. Message Passing Interface (MPI) is used to send messages between agents which are located on different processors. Due to the flexible nature of FLAME, this is successfully achieved on various platforms. A number of HPC grids, such as SCARF, HAPU and Iceberg have been used to test and evaluate the efficiency of the FLAME framework in high performance computing.

Another advanced feature of the FLAME framework is the dynamical creation of agents throughout a simulation, which is an extremely useful feature for modellers. For instance, without such a feature, the pheromone agents would have to tile the environment, and become activated whenever an ant agent would come across them. This would limit both the movement of ant agents, as well as make an expensive approach in terms of memory and performance. The Pharaoh's ants under study were mentioned to deposit pheromones continuously, which is modelled by enabling ant agents to deposit pheromones agents at every iteration. If realistic colony sizes are simulated, long simulation periods would lead to large number of pheromone agents being created and would still eventually cause a big bottleneck in terms of performance. However, with the use of parallel runs, this is overcome by FLAME, which is explained in the next section.

Other advanced features of the framework include the ability to specify nested conditions for functions, thereby enabling the modeller to have increased control on the flow of the model. This facilitates faster compilation and increased performance, as well as more efficient design of the code, minimizing the amount of potential logical errors.

For every model developed, FLAME automatically generates a stategraph, which is a directed graph whose nodes correspond to internal states of an agent and edges correspond to transitions among these states. Different states are indicated by numbers in circles, whereas functions are represented by rectangular boxes. Furthermore, messages exchanged between functions as well as conditions defined are also noted. Stategraphs provide an overview of a model at an abstract level and are very helpful for modellers both for understanding and communicating their underlying codes.

The framework has been used in various disciplines, i.e. biology and economics, producing successful results. One such project is EURACE, where the European economy was modelled using many millions of agents. More recently FLAME has been ported to NVIDIA Graphics Processing Units (GPUs) allowing incredibly fast parallel performance with the ability to perform real time visualisation (Richmond et al., 2010).

3.2.3 Other Popular ABM Frameworks

Over the years various ABM platforms have been developed and released for public use. Each are based on specific characteristics, utilizing different technologies and programming languages. Such platforms have been recently reviewed and compared in detail by (Railsback et al., 2008; Berryman, 2008; Allan, 2010). Adapted from these reviews, below is a list of the most popular ABM frameworks along with their key features:

- SWARM:
  SWARM is a popular toolkit among researchers as it is fairly easy to build agents.

  Objective C++ is the primary language to develop agents, where the agents are represented as objects with functions and variables. It allows inheritance which makes it easy for the agents to have access to the environment (SWARM, 15.1.2009). It also supports Java, which facilitates parallelism via threads. Another advantage of SWARM is its user-friendly graphical user interface.

- MASON:
  MASON is a multi-agent simulation toolkit, written in Java, which allows discrete events to be simulated. It also includes 2D and 3D libraries for visualisation (MASON, 28.1.2009). It has been used to develop the Evolutionary Computation Journal (ECJ), a Java-based Evolutionary Computation Research System, which is claimed to be highly flexible with classes dynamically compiled at runtime by a user-provided parameter file (ECJ, 27.1.2009).

- Repast:
  Recursive Porus Agent Simulation Toolkit developed at the University of Chicago, supports a number of programming languages (Java, C#, Managed C++, Visual Basic.Net and Python) (North et al. 2006). Its features include logging simulation results and graphing tools, which make it attractive for users. It also allows users to dynamically access and modify agents and model at run time, and includes libraries for popular algorithms, i.e. genetic algorithms and neural networks.

- JADE:
  JADE is an agent development framework based in Java. It uses the Java Remote Object (RMI) registry to provide concurrent connection between machines (JADE, 16.1.2008). A super agent is defined within a class, where all other agents could inherit common attributes from this class. It is based on FIPA (Foundation for Intelligent Physical Agents) protocols.

- NetLogo:
  Authored by Uri Wilensky in 1999, NetLogo is a multi-agent simulation toolkit used to model natural and social phenomena (NetLogo, 28.1.2009). It is written in Java and it is in continuous development at the Centre for Connected Learning and Computer-Based Modelling. It is run as a stand-alone application, where the models can be run as Java applets inside a web browser, with the ability to view the models in 2D and 3D. For running simulations, an interface builder is available with buttons, sliders, switches, choosers, monitors, text boxes, notes and output area. It also has additional tools (command center, behaviour space, etc.) which make the process of modelling easy for a modeller.

FLAME is the modelling framework of choice for this project for many advantages it provides over the listed related frameworks. Adapted from (Allen, 2010) these could be summarised as follows:

- Based on a formal method X-Machines; specification and validation are inherently provided
- Stategraph outputs showing states and transitions in each agent cycle are generated automatically
- Parallelisation methods using MPI and testing techniques allow the development of large multiprocessor simulations
- Dynamic birth and death allocation ensure maximum simulation performance
- The syntax is mainly based on XML, therefore it is easily extendable

3.3 High Performance Computing

High performance computing (HPC) is the term given to the use of multiple computers or processors to solve various computational problems simultaneously, achieving results in significantly shorter periods of time, compared to when solving the problem individually. It involves running various calculations on different processors, dividing the load from one processor to another. This allows results, which sometimes takes days to solve, to be attained in hours or even minutes.

HPC has been used to speed up simulations. Researchers in this field focus on increasing the efficiency of communication among computers, as well as preventing extra computational overhead. However, this usually costs in terms of processing time or the time taken to develop elegant algorithms that would run in parallel. ABMs involve a number of individual programs (agents) constantly communicating with each other. This is a scenario of distributed computing where each program has its own private memory, communicating with each other through messages. Therefore, HPC will have to handle the distributed memory space for the individual programs, as well as the communication overhead among the programs. This is different from traditional parallel computing where all programs have access to a shared memory from which they read and write data.

Distributed HPC has been used in various applications like network routing problems, distributed databases and even file sharing applications. FLAME uses a similar approach to agent-based modelling, using a distributed structure for task parallelism among the agents.

3.3.1 FLAME in Parallel

High performance computing is essential for simulating complex problems using agent-based modelling. Researchers are hindered by complexities of porting models on parallel platforms and time taken to run large simulations on a single machine. FLAME is the only known supercomputing ABM framework which automatically produces parallelisable code. The framework handles the parallelisation of model code in a flexible fashion, allowing modellers to run simulations on a number of supported architectures.

FLAME utilises partitioned agent populations and distributed messages boards, which are linked through MPI communication. To help parallelisation, FLAME's message board, the *Libmboard* manages the data being requested between agents. As mentioned earlier, this is achieved by using message filters which limits the amount of data being requested. These boards are synchronised once all agents have finished 'writing' to them, which ensures that the agents who have completed 'reading' have obtained all message information needed for simulation. The agents are linked to the message boards and use them to transfer information among different nodes.

The most significant operation in the parallel implementation is providing the message information required by agents on one node of the processor array but stored on a remote node of the processor. *Libmboard* manages these data requests by using a set of predefined message filters to limit the message movement. This process could be considered as the 'synchronisation' of the local message boards within an iteration of the simulation. This synchronisation essentially ensures that the local agents have the message information they need as the simulation progresses.

Another advantage of implementing parallelism in FLAME through the *Libmboard* is that the development of the FLAME framework and the message board algorithms can continue independently to a great extent, as the Message Board API defines the interface between the two elements of the code. This should enable the message board routines to be developed and optimised without major re-engineering of the framework.

The two main areas of algorithmic and technical development needed to achieve an effective parallel implementation are load balancing and communications strategies. To address these, two basic methods of static partitioning have been developed in FLAME, which are: (i) round-robin and (ii) geometric partitioning.

- *Round-Robin Partitioning*:
  This is the simplest form of partitioning in which agents are distributed one at a time to each partition. This type of partitioning is applied in FLAME by default.

- *Geometric Partitioning*:
  Geometric partitioning, also known as separator partitioning, distributes the agents

> among the partitions based on one or more memory variables of the agent. Every agent must have these variables for this to work, where the variables can be either discrete or continuous numerical values, i.e. distributing agents using their position (x, y, z coordinates). This would provide a good initial distribution in scenarios where the communication is between the agents positioned close to each other. Therefore, the overall aim is to put such agents that would generate a lot of communication together onto the same partition.

For running ant models in parallel, the round-robin partitioning method was preferred as the geometric partitioning would not be advantageous. Ant agents create pheromone agents dynamically at every time step, at a coordinate nearby. Therefore if partitioned with geometric partitioning, ant and pheromone agents would be distributed among the same processors, and this would lead to an unbalanced distribution, thereby reducing the performance.

3.3.2 Iceberg

For high performance computing, Iceberg (Iceberg, 1.12.2010), the Sheffield Node of the White Rose Grid Computing Cluster, was used. Running 64-bit Scientific Linux (a Redhat varient of Linux), Iceberg comprises a head node connected to a farm of execution nodes, accessible to networked computers at Sheffield, where the jobs are managed using the scheduler Sun Grid Engine. For shared memory programming OpenMP; and for implementation of the MPI parallel programming standards OpenMPI and MPICH-GM are used, which facilitated the successful compilation and run of FLAME.

Current specifications of Iceberg are:

- Total number of processor cores: 568
- Scratch space on each node: 400 GB
- Performance : 435 GFLOPs
- Total Main Memory: 2.296 TB
- Filestore: 8 TB

3.3.3 Results from Models

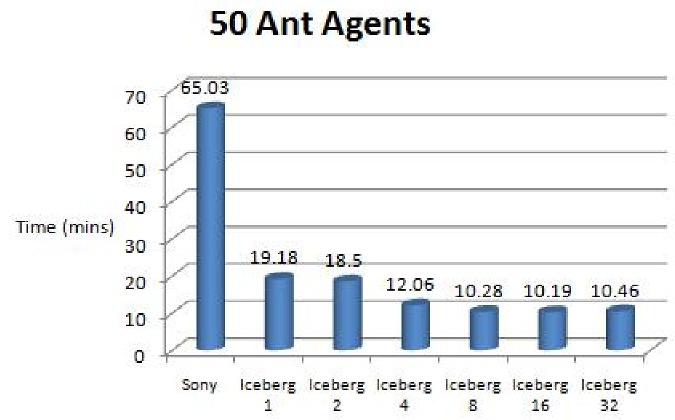
Previous models focus on simple pheromone usage with mathematically devised behaviour, which deviates largely from the real ant behaviour. Furthermore, simulating large-scale behaviour at the individual level is a difficult computational challenge; hence models in the literature fail to simulate realistic colony sizes and dimensions for foraging environments. To address these problems, HPC through FLAME was utilised on Iceberg, the HPC grid.

To demonstrate the dramatic effect of HPC; the Foraging Model in Chapter 6 was run with (n=50, 250, 500) ant agents for 5000 iterations on two different platforms using Round-Robin partitioning. The platforms were: Sony laptop (2.4 GHz processor, 4GB RAM) and Iceberg (568 processor cores (1, 2, 4, 8, 16 and 32 cores were used), 435GFLOPs). Figures in 3.3 demonstrate the performance results.

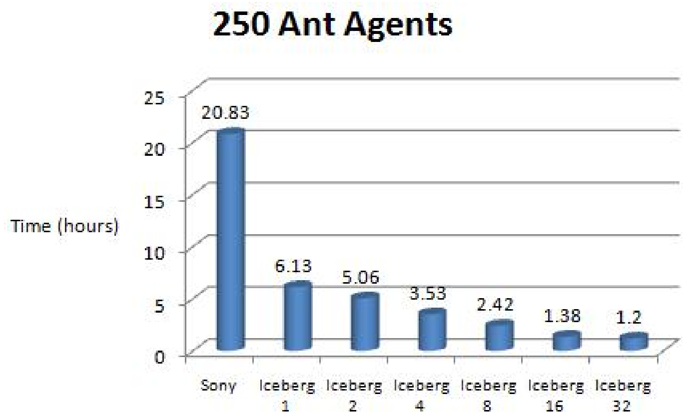
Results demonstrate that processing times were reduced by six times when the model was run in parallel compared to serial on the grid, and twenty times when ran in parallel on the grid compared to serial on the laptop, which is extremely desirable for processing complex biological models.

FLAME coupled with HPC enabled large-scale simulations of complex models to be run in parallel on a grid without compromising on the time taken to attain results. In ABM, models can scale up exponentially depending on the number of agents and the complexity of the functions to be performed, therefore this is a significant contribution. Furthermore, the advanced features of the framework, such as dynamic creation of agents during a simulation, provided realistic grounds for modelling the agents, especially pheromones, which sets this basic foraging model apart from the related models in literature. Further details are provided in Chapter 6.

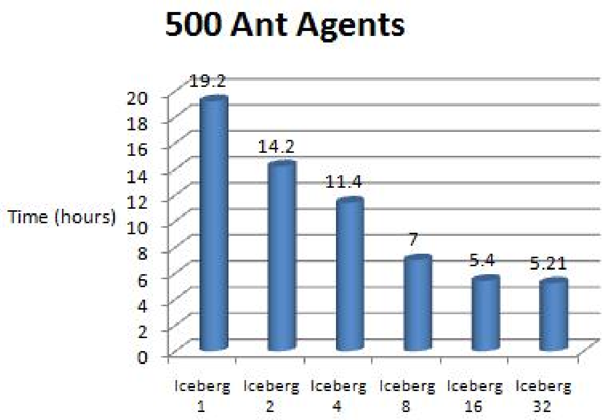
Unfortunately, the amount of time saved using Iceberg was negated by the length of time waited for the scheduler (large queues of jobs to be run). Therefore, the majority of the simulations were run on another platform with the following specifications: Intel Core 2 Quad CPU (2.66 GHz), 4GB RAM, with Windows 7x64 Operating System.



(a)



(b)



(c)

Figure 3.3: Performance results from running the Foraging Model in serial on a Sony laptop and in parallel on a grid.

Chapter 4

Ant Models to Date

Many different models have been employed by researchers to contribute to the understanding of the self-organised behaviour of ants. Modelling of insect societies is currently dominated by top-down approaches, which deal with a population of identical individuals using differential equations. Differential equations have been shown to provide a promising tool for analysing the mechanisms underlying colony-level patterns and they have frequently been applied to model the foraging behaviour of insects (Beckers et al., 1990, 1993; Deneubourg et al., 1990; Goss et al., 1989; Nicolis and Deneubourg, 1999). Sumpter and Pratt (2003) explain that the power of such models lies in their simple mathematical formalism for describing how populations change through time. For instance, during foraging, based on the number of ants being recruited to a food source, or abandoning a particular food source, recruitment and abandonment rates are written as functions of the number of insects foraging at a source, waiting at the nest or scouting for new sources. Through this approach, different recruitment mechanisms are represented by rate functions to model the foraging system of a particular species.

However, mathematical models lack flexibility. In order to overcome the rigidity of such top-down models, Monte Carlo models are employed by many researchers to facilitate the simulation of individuals in a population. In a Monte Carlo model, exogenous sensitive variables are allowed to change simultaneously within the boundaries of probability distributions. After carrying out sufficient runs (iterations), a cumulative probability distribution of the target variable (endogenous) is formed (Monte Carlo, 29.1.2009). Therefore, with the help of Monte Carlo models researchers are able to incorporate some randomness to their mathematical models, attempting to simulate the observed behaviour in biological systems.

This chapter provides a review of the existing models in the literature and where possible, technical issues emerging from these models are discussed. The models are categorized as: (i) initial formation of trails, (ii) the use of pheromones, and (iii) the choice of a path based on the quality of a food source.

4.1 Initial formation of trails

Formation of trails by ants have been extensively carried out on the army ant colonies, as they are among the largest and most cohesive societies (Deneubourg et al., 1989). Their foraging systems were observed to coordinate millions of individuals to cover around 1000 m^2 in a day (Rettenmeyer, 1963). The mathematical model by Denebourg et al. (1989) is one of the pioneering models in this field, aiming to show how the characteristic patterns could be generated from the interactions between many identical foragers via simple trail laying and following behaviour. This highly-cited model provided researchers with invaluable insights into the mechanisms of self-organization in ants. Other top-down models based on the initial formation of trails include the works of Edelstein-Keshet et al. (1995) a CA model, Watmough and Edelstein-Keshet (1995) a partial differential equation model, and Beekman et al. (2001) a differential equation based model.

These models were based on discrete environments, providing limited movement for ants, which in some cases were further constrained by limiting the direction of movement for the ants (i.e. ahead left or ahead right). Some models also introduced limits on points in the environment occupying only a pre-defined maximum number of ants, where the aim was to prevent all colony members from following the same trail. If there was not enough room at a point in the environment, the ants would have to move towards the opposite direction, which would initiate a branching trail. However, when both directions were fully occupied, the ants stayed where they were, which led to stagnations in the motion of the colony.

Simplified approaches to pheromone detection by ants were employed, such as; whenever an ant made a decision and took a step, this was modelled to have a direct effect on the following ant's probability of choosing the left or the right direction. Deneubourg et al. (1989) explained this as the key step in trail formation, and referred to as "an autocatalytic system". Rather than pheromones influencing the movement of the ants, portions of the trails were favoured by the occupance of colony members, by simply making one of the two points ahead (left or right direction) more or less preferred than the other. When there were no pheromones to follow, the ants was allowed to simply walk ahead. Considering that these models were all based on environments without any existing pheromones, it would be very likely for the ants with such rules to form straight trails. However, with the aid of Monte Carlo simulations, the results demonstrated the emergence of branched trails.

Refinements were attempted to improve the models by incorporating varying speeds of movement for the ants based on pheromone concentration detected. These enabled the foragers following a trail to move rapidly and directly, while the ones without having any pheromones to follow moved slower, more hesitant and random. This was simulated by making the probability of each ant's moving at each step increase 'sigmoidally' with the pheromone quantity ahead of it. Furthermore, pheromone evaporation was introduced, where a fixed fraction of the pheromone at each point evaporated at every iteration. However, generally such evaporation rates were not based on the actual evaporation rates of pheromones in nature.

4.2 Choice of a path based on the quality of a food source

As explained in Chapter 2, a number of ant species were observed to deposit pheromones more frequently after discovering a food source with a better quality, where this sometimes led to a switch of the colony to exploit the rich food source. Beckers et al., (1990), (Beckers et al., 1993), Nicolis and Deneubourg (1999) are some of the researchers who built top-down mathematical models to investigate such behaviour via different types of recruitment mechanisms.

These models generally operated on one key parameter, called the 'recruitment accuracy', which was defined as the proportion of successful ants that reached a food source. Depending on the type of recruitment (i.e. cooperative or direct transmission (Beckers et al. (1992)), different functions were utilised to define this parameter. For instance, cooperative transmission implied that the recruitment accuracy was to be represented by a 'monotonic increasing function', enabling the accuracy to increase with the number of recruiters as the trails were reinforced; whereas in direct transmission, this parameter was represented by a linear combination of the accuracy with which it was transmitted.

In such models, even though trail recruitment was considered to be the fundamental, the concentrations of pheromones were modelled as rate constants, where their deposition were calculated as a function of the food source quality. However the evaporation of pheromones and their detection by the ants were not considered in detail.

Attemps were made aiming to test how far the trail laying and following behaviour of individuals could generate the overall choice of food source by a colony using Y-shaped trail setups. 'Choice functions' were utilised to determine the choice of a path based on the pheromone quality of the branches. However, the control parameters were chosen with such care that, even a small difference between the numbers of ants choosing either branch was sufficient to induce a large majority of foragers to choose the stronger branch.

Models also incorporated environments with arbitrary number of sources, where the choices of ants were defined as functions of the rate of deposition on the trail, the number of sources and the colony size. Consequently, results demonstrated different behaviour of the colonies based on the number of available sources and colony size. The simulated behaviour was explained as the colony's ability to focus its activity preferentially on one particular source rather than on another, with an ability to switch to a better source when provided. However, it was admitted that the variability of the system should be facilitated better, i.e. based on behavioural rules rather than random, as in mathematical models, the common way to achieve this numerically is through Monte Carlo type of simulations, which was explained by the authors as "viewing the process as a probabilistic game and assigning transition probabilities associated with the choice of each trail" (Nicolis and Deneubourg, 1999).

4.3 Use of pheromones

Key to collective foraging is the sharing of information, so that the nest-mates can be recruited by successful foragers to profitable food sources. The best known example of sharing of information is mass recruitment via pheromone trails. Almost all of the models described in the previous sections demonstrated the huge benefit of the pheromone trails in ants' lives (for orientation, recruitment, etc). Models to date are based on the use of a single pheromone. However, as stated in Chapter 2, recently the use of multiple pheromones were hypothesised, where the existence of short-term repellent pheromones was tested with an agent-based model (Robinson et al., 2008).

This model was based on the foraging system of Pharaoh's ants, which utilised a positive pheromone along with a negative repellent pheromone, with an aim to demonstrate that using a repellent pheromone could make foraging more successful; unsuccessful foragers would deposit unrewarding areas with repellent pheromones and prevent the nest-mates from wasting their time re-exploring them. The model was based on a simple environmental setup, consisting of four cells, which were: (i) the nest, (ii) the stem, representing a bifurcation point, (iii) right branch, and (iv) left branch, where one of the branches contained a food agent. Based on an already established network, the initial formation of trails was not considered and the ants to leave the nest were decided according to the order of their IDs, as well as a traffic flow rate, allowing two ants per iteration.

A time-step was defined as the time taken to traverse one cell, i.e. it would take two time-steps for an ant leaving the nest to reach the food source and another two time-steps back to the nest, given that they make the right choice at the bifurcation. The decisions of the ants at the stem (bifurcation point) was modelled based on observations from biological experiments with Y-shaped environment setup, which introduced error rates

(5% when walking outwards and 1% when returning towards nest). The concentration of the pheromones deposited were also based on findings from biological experiments with Pharaoh's ants, which resulted in the parameters of 2 units for the positive pheromone and -26 units for the negative pheromone.

The results successfully demonstrated the positive contribution of the repellent pheromones; with only repellent pheromones in the foraging system, the switch occurred more slowly than only with the positive pheromones, whereas without the repellent pheromones, the switch to the new branch never happened, as the ants were locked in the positive feedback loop attracting them to the previously attractive branch; only a few ants, which were assumed as to have made mistakes, were observed to find the food. Therefore, the existence of repellent pheromones were successfully shown to increase the Pharaoh's ants' foraging system more efficient in terms of the number of ants returning to the nest fed.

This model is a working example of a bottom-up agent-based model, where variability in the system was successfully demonstrated, which had not been possible in previously mentioned mathematical models without the use of Monte Carlo simulations. The model has an emergent result, which is the highly variable attractiveness of the branch without the food source. Communication via multiple pheromones among the ant agents were successfully demonstrated, resulting in the colony performing switches.

This agent-based model was extended with a continuous environment and a detailed approach to modelling pheromone deposition and detection by ant agents, where an alternative approach to utilising negative pheromones was demonstrated, explained in Chapter 8.

4.4 Discussion

The models constructed have been useful for improving our understanding of social complexity. However, the major challenge in social insect research is understanding how colony-level behaviour emerges from individual interactions. Models to date focus on simple pheromone usage with mathematically devised behaviour, which deviates largely from the real ant behaviour.

Both top-down and bottom-up modelling approaches have successful examples in the literature. Top-down models provide theory and pose general questions, whereas in bottom-up models, such theories are tested in terms of a population of individuals. However, only the bottom up approach attempts to understand the causality of the phenomenon under investigation. Considering the contributions of both approaches to the understanding of complex biological systems, models should become a requisite in this field as they allow us to relate causes and patterns from the individual to colony level that cannot be generated by intuitive approaches alone (Beshers and Fewell, 2001).

Another challenge modellers face and lack is simulating realistic colony sizes and dimensions for foraging environments, where both have big influences on ant behaviour, as observed in nature and biological experiments performed. However large-scale behaviour at the individual level is a difficult computational challenge, due to large number of agents producing large number of data, thereby introducing memory and performance problems.

In this research, such problems were addressed by using the agent-based modelling approach, a bottom-up modelling approach, which enabled the system under study to be investigated in detail, where behaviour and heterogeneity of interacting components were not reduced to a simplified mechanism. Realistic colony sizes and foraging areas were simulated, where the challenges with modelling, performance and memory were addressed by using the supercomputing agent-based modelling platform, the FLAME framework.

Chapter 5

The Movement Patterns of Pharaoh's Ants

In computational biology, in order to achieve realistic models it is of utmost importance to ensure that the rules and parameters used in the model are based on biological facts (experimental findings). For this purpose, a thorough literature review was carried out and recordings of Pharaoh's ants were obtained from Dr. Duncan Jackson. Required parameters were extracted from the literature, and the recordings were analysed digitally using video tracking. However the movement of ants in virgin territory were not clearly distinguishable in these videos, as they contained a colony of around 1500 ants foraging together. The possibility of ants forming pheromone trails, hence influencing each other's movement, made it necessary to carry out biological experiments with the aim of obtaining experimental data on the movement patterns of Pharaoh's ants. The coordinates of the ants were extracted from the recordings of experiments. The extracted coordinates were statistically analysed and a probability distribution of the turning angles were derived for the Pharaoh's ants, which formed the basis for the models developed, as explained in the next chapter.

5.1 Related Work

Establishing the rules underlying the movement of animals has been the fundamental interest for many biologists and researchers of related disciplines. Their research is mostly based on the concept of 'correlated random walk' where the direction of a single step of the walk is statistically related to the direction of previous steps (Codling et al., 2008). Random walk of animals are considered to take place in discrete steps, occurring at discrete times. Furthermore, the mean distance moved in a single step is estimated, as well as the mean cosine of turning angles between consequent steps.

Well-known related work includes Kareiva and Shigesada (1983), McCulloch and Cain (1989), and Nouvellet et al. (2009), who have discussed the theory of correlated random walk models and developed different mathematical formula to investigate movement patterns of insects. Their findings suggest that the mean squared displacement and angular distribution are the two key concepts for analysing movement patterns of animals. Mean squared displacement, is the average squared distance between two consecutive steps of movement; whereas angular distribution, is the set of directional changes throughout the path of the animal. They also note that when determining the two concepts, the distribution of times between the discrete steps plays a key role.

In order to analyse movement patterns, recordings of experiments are used, where animal positions are noted at a set of equally spaced times. The positions are then plotted via a piecewise linear approximation and the corresponding path of animals is constructed by joining the consecutive positions with straight lines. This is followed by the calculation of mean squared displacement and the turning angles for the animals' movement at different time intervals, by re-sampling the data. Finally, the findings are compared against each other for different time intervals.

Another area of interest in random walk research is the turning kernel. This is a probability distribution of the turning angles of an animal moving in an environment, derived as a result of a correlated random walk. It has been widely applied to cell movement models (Dolak and Schmeiser, 2005; Xue and Othmer, 2009). Turning kernel was also used to form the basis of foraging models, where ants walk non-randomly, without being under the influence of any other environmental factors, i.e. virgin territory without any existing pheromones to follow. Related work includes Jackson (2005), who studied individual movements of 50 Pharaoh's ants from recordings of six colonies. Each step of the ant was encoded as a sequence of directional changes using an eight point compass and turning data was analysed for each individual ant. As a result, a turning kernel was derived.

The majority of the foraging models in the literature utilize simple environmental setups. Examples include cells, to limit the movement of ants, or existing pheromone trails to lead the ants. These help to avoid potential complex problems that could arise, and focus on the specific mechanism under study according to the hypothesis tested. However, in order to have a good understanding of foraging strategies and trail reinforcement, it is of prime importance to understand the initial formation of trails by the first ants leaving the nest. Therefore, with the aim of targeting realistic foraging models, it was decided to investigate the movement patterns of Pharaoh's ants, when they had no pheromones to follow.

Biological experiments similar to that of (Jackson, 2005) were conducted with Pharaoh's ants, which were recorded and digitally analysed to derive a turning kernel, as explained in the next sections.

5.2 Experimental Setup

Movement patterns of *M. pharaonis* colonies were studied at the Ant Lab at the University of York, U.K., under the supervision of Dr. Elva Robinson. Due to frequent splitting within the colony, three colonies of Pharaoh's ants were studied over a period of three months. The colonies contained 1500 – 2500 workers, as well as brood of all stages and queens (3 to 8 in one colony), and were housed in wooden nest boxes that were held within large plastic foraging boxes. The walls of the foraging boxes were coated with Fluon in order to prevent the ants from climbing up and escaping. While the room was maintained at 24 degrees Celsius, colonies were given fresh water ad libitum in glass tubes sealed with cotton wool and were fed with mealworm larvae, as well as sugar syrup in Eppendorf tubes.

The pictures in figures 5.1 and 5.2 show the setup used for this experiment. Individual ants were allowed to walk into the foraging arena via a metal bridge. The dimensions of the foraging arena used was 65x45 cm. A big arena was chosen to minimize limitation on the movement of the ants. As soon as an ant stepped into the arena, the bridge was removed. The movement of each ant was recorded for a duration of 10 minutes, and the recorded ant was then removed and placed in another temporary box. The inner surface of the foraging arena, as well as the sides and the back of the bridge were covered with white paper, as; (i) paper is a commonly used substrate for foraging experiments (the decay rate of the pheromones deposited by Pharaoh's ants has been determined on paper (Jackson, 2005)), and (ii) light-brown coloured Pharaoh's walking on white paper was a good contrast for recording purposes. Prior to recording a new ant, the papers were replaced with fresh ones, to ensure that the next ant would not be influenced by any potential pheromone markings laid by the previous ant. A total of 45 ants from three colonies were recorded.

5.3 Video Tracking

Recordings of the experiments were digitally analysed using video tracking, in order to derive a 'probabilistic turning kernel' for the Pharaoh's ants. This was done by using RoboRealm (RoboRealm, 15.10.2009), a robot vision-detection framework, which has the ability to link image processing with motion. This framework was configured to track ants throughout the videos. The ants in the recording were defined as blobs with the dimensions of a Pharaoh's ant. Once a blob is detected, RoboRealm assigns this a

Figure 5.1: Experimental setup for recording Pharaoh's ants individually: ants were allowed to walk into the foraging arena through a bridge.

Figure 5.2: Experimental setup for recording individual Pharaoh's ants individually: blocks of LED bulbs were attached onto metal bars and placed above the foraging arena to provide effective, harmless lighting.

unique ID and tracks its coordinates throughout the video (the modules used and their brief details are included in the Appendix). This is a great advantage as the majority of related work involves playing videos in slow motion and manually tracking the corresponding coordinates. An alternative but rather expensive approach is to attach RFID tags on ants, which has been used to track *T. albipennis* ants to investigate their nest selection behaviour (Robinson et al., 2009). This method produced successful results for investigating nest selection behaviour, as the aim was to detect the coordinates of ants only when they were outside the nest entrance. However, given the size of the RFID tag, the RFID reader has to be a maximum of a few millimeters apart from the tag in order to receive signal efficiently. Therefore, this would not be a feasible solution on its own for tracking movement patterns of ants, as it would facilitate limited monitoring of movement.

From three ant colonies, a total of 45 ants, each for about 10 minutes, were recorded as they moved freely in the arena. Out of 45 ant videos, 15 of them were sampled and analysed, where an average of 80 second sequences were extracted. A discrete step of an ant governed by the related pair of coordinates is referred to as an 'observation'. During the tracking process, the tracking speed was reduced to its minimum (1/4 of the original speed), which led to an average of 18 observations per second, while Nouvellet et al. (2009) recorded a maximum of 8 observations per second. This meant smaller time intervals, thereby increased accuracy in detecting the path that the ant followed. Overall, a total of 21,443 turns were noted, which corresponds to an average of 1,430 observations per ant and 18 (21,443 / (80*15)) observations per second. Thus the time interval (t) between the two observations were approximately 0.056 seconds.

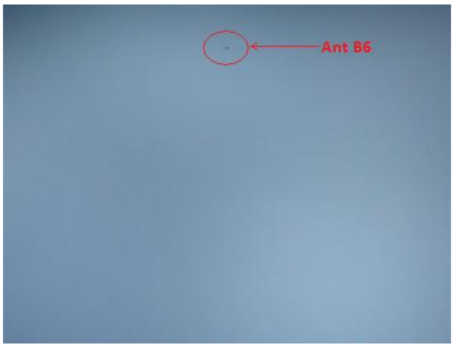


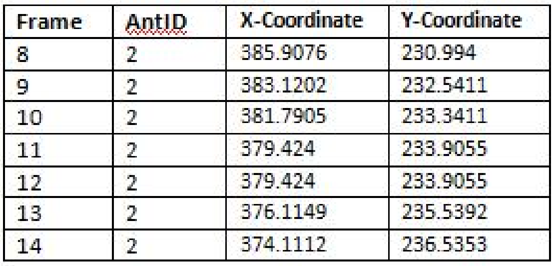
Figure 5.3: Snapshot taken from the recording of Ant #6 from Colony B.

Figure 5.4: Snapshot taken during tracking of the recording in figure 5.3 using RoboRealm (Ant #6 is being tracked with ID=2).

The analysis of the movement patterns of Pharaoh's ants were solely based on the recordings of the individual Pharaoh's ants, as shown in figures 5.3 (original recording) and 5.4 (tracked version).

5.4 Determination of the Turning Angles

As a result of the tracking process, the positions of individual ants are extracted at discrete times (*t*=0,1,2,...) from the recordings. Snapshot below in figure 5.5 is a sample output from RoboRealm, where the columns represent the frame number, ant ID, x and y coordinates, respectively.



Frame	AntID	X-Coordinate	Y-Coordinate
8	2	385.9076	230.994
9	2	383.1202	232.5411
10	2	381.7905	233.3411
11	2	379.424	233.9055
12	2	379.424	233.9055
13	2	376.1149	235.5392
14	2	374.1112	236.5353

Figure 5.5: Sample output of extracted coordinates from a video.

Extracted coordinates were used to construct a piecewise linear approximation of the ant's path, by joining the positions of the coordinates at discrete times (*t*=0,1,2,...) via straight lines. An example piecewise linear approximation is shown in figure 5.6. The angular changes throughout the adjacent straight lines will give the turning angles of the ant.

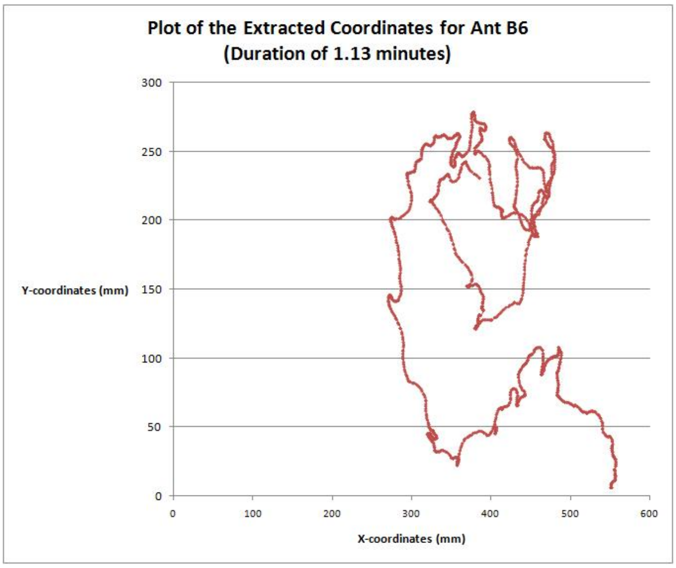


Figure 5.6: Plot of Ant #6 from Colony B.

The displacement of an ant at time t_i is its position at this time relative to its position at time t_{i-1}. As the ant is assumed to move in two dimensions, the mean displacement

(MD) and the mean squared displacement (MSD) are calculated using the equations given below;

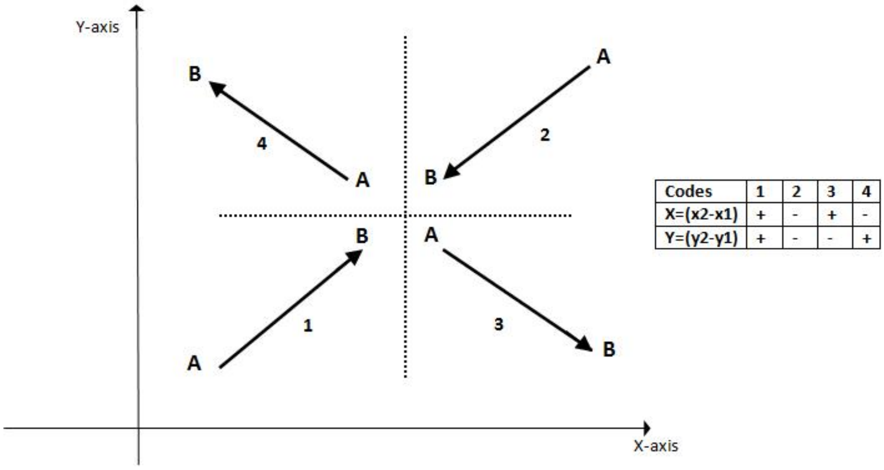
$$d_{(t)} = \sqrt{(x_{(t)} - x_{(t\text{-}1)})^2 + (y_{(t)} - y_{(t\text{-}1)})^2}$$

$$MD(t) = E[d(t)]$$

$$MSD(t) = E^2[d(t)]$$

In order to determine the direction of the movement of the ants, the extracted coordinates were further analysed through the following steps:

1. The path of an ant is formed by joining the two consecutive observations with straight lines.
2. The gradient of the line joining the two consecutive recordings of ant movement is given by Y/X, where $Y = y_2 - y_1$ and $X = x_2 - x_1$.
3. When both X and Y are positive i.e. a positive gradient, this indicates a direction of movement upwards to the right; while when both X and Y are negative, the direction of movement is downwards to the left. Similarly, when X is positive and Y is negative, the direction of movement is downwards to the right; and when the opposite takes place, the direction of movement is upwards to the left. To denote this, numbers 1, 2, 3 and 4 are used as codes, respectively, as indicated in figure 5.7 below.



Codes	1	2	3	4
X=(x2-x1)	+	-	+	-
Y=(y2-y1)	+	-	-	+

Figure 5.7: Codes for potential directions of the ant based on X and Y.

4. The movement is categorized in terms of 4 main directions as shown in figure 5.7, where the potential combinations of these directions (figure 5.8) would lead to 16 different cases. For example, a movement towards right upwards (both X and Y positive) would have four options in its consecutive movement direction: (i) right upwards (1 → 1), (ii) left upwards (1 → 4), (iii) right downwards (1 → 3) and (iv) backwards (1 → 2). It is important to note that in the case of 1 → 2, it makes a

difference if the ant turns back from right (1 → 2a) or from left (1 → 2b). This is explained in the following sections.

5. In order to determine the turning angles of an ant, the follow-up line of the previous step (B-D in figure 5.9) is compared against the new line (B-C) based on the new direction of the ant. Thus, the previous direction (angle) is important in determining the turning angle.

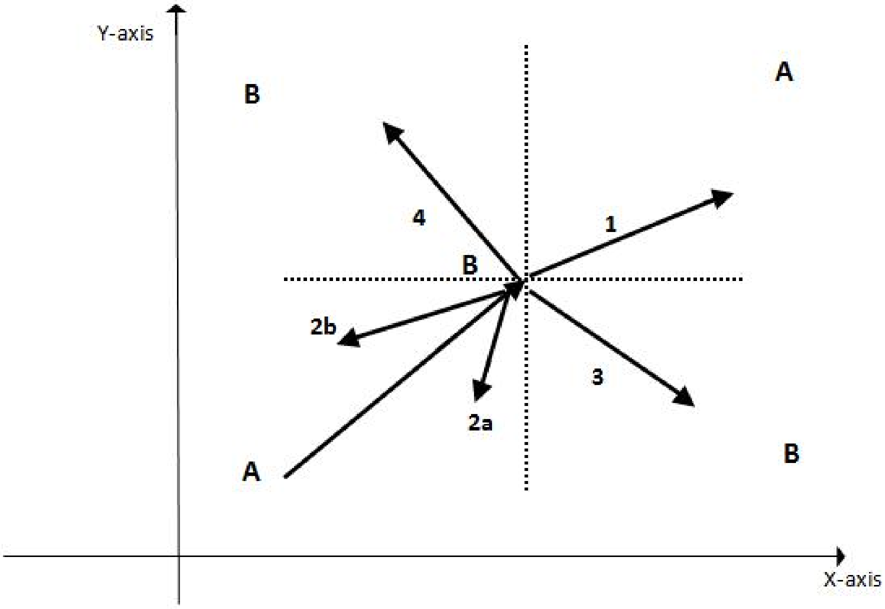


Figure 5.8: Options of directions.

The method used to determine turning angles is further clarified in the following two of the 16 cases, demonstrated in figures 5.8 and 5.9.

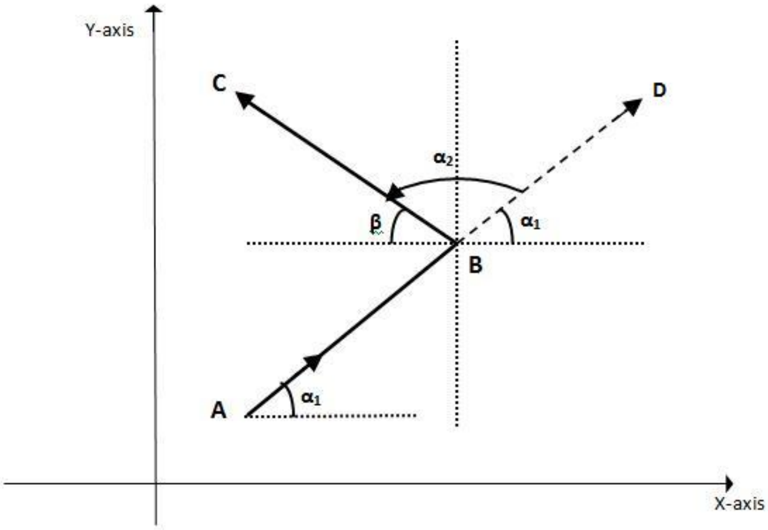


Figure 5.9: Determining Turning Angles: Case 1.

- Explanation of Case 1: (1 → 4)
  Ant walking with a positive gradient (upwards to the right), where α_1 is the

starting angle (previous angle), β is the angle obtained from the new line (B-C) and α_2 is the turning angle. The turning angle in this case is calculated by $180 - \alpha_1 - \beta$.

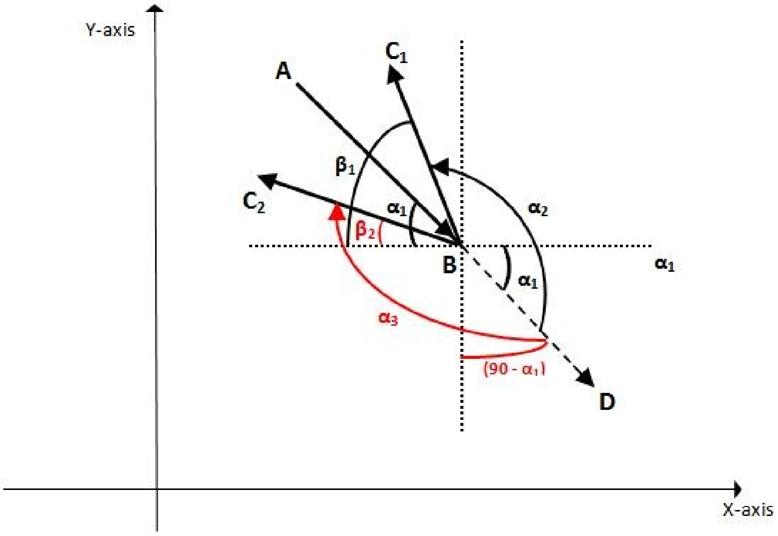


Figure 5.10: Determining Turning Angles: Case 2.

- Explanation of Case 2: (3 → 4)
  Ant walking downwards to the right (3) is turning back (4) from the left or from the right of its previous path. The turning angles in these cases are then calculated as following:

A → B → C1 (left):

$$\alpha_2 = \alpha_1 + 90 + (90 - \beta) \qquad (\text{when } \beta > \alpha)$$

$$= 180 + \alpha_1 - \beta$$

A → B → C2 (right):

$$\alpha_3 = (90 - \alpha_1) + 90 + \beta_2 \qquad (\text{when } \beta < \alpha)$$

$$= 180 + \beta_2 - \alpha_1$$

For determining the turning angles of the other 14 cases the same approach used for the two cases above (Case 1 and Case 2) is utilised and similar formula are developed. These formulations are applied to each and every recordings of ant movements (except X = 0, Y = 0) in order to determine their turning angles.

One other turning angle in ant movement in the recordings that needs careful attention is the first movement from the starting point. Out of 4 options with regard to the direction of ant facing, two options were noted in figure 5.11. Thus an ant coming straight down from above will have α_1 angle with X and Y coordinates, giving a turning angle as $\alpha_2 = 90 - \alpha$. In case the movement is to right $\alpha_1 = \alpha_2$.

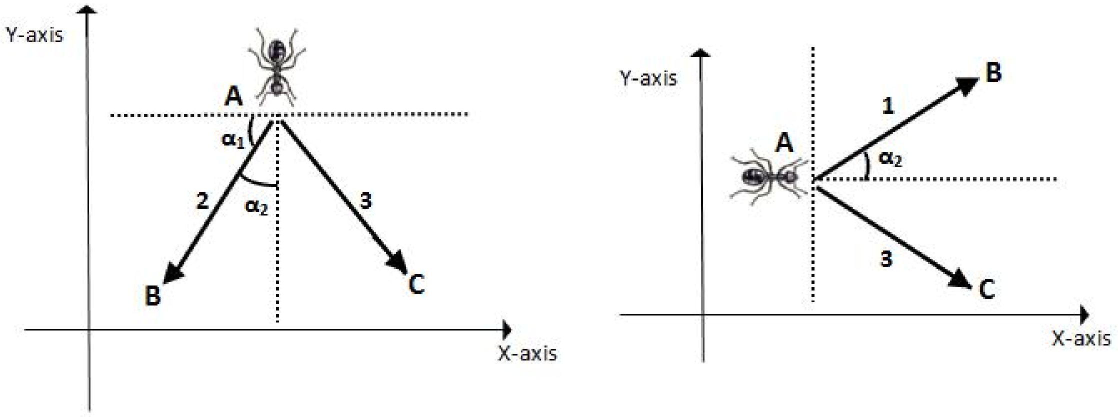
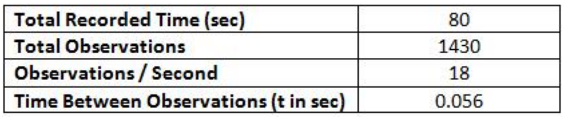


Figure 5.11: Starting angle.

5.5 Results and Discussion

As indicated in the previous section, the starting point for the biologists and researchers of related disciplines interested in animal movement is: the determination of the mean squared displacement, the mean displacement, the turning angles and their relations with the time (sampling).

Our research involving pooled data from 15 ants, each analysed for an average period of 80 seconds, producing a total of 21,443 observations. This corresponds to 18 observations per second, indicating a time period of 0.056 seconds between each observations. These are summarised in figure 5.12.



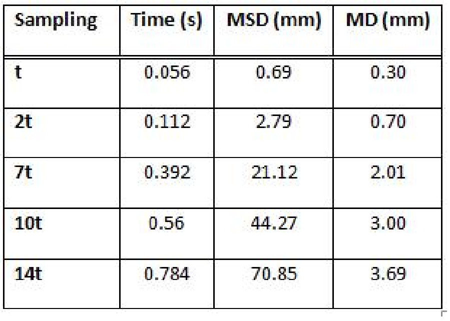
Total Recorded Time (sec)	80
Total Observations	1430
Observations / Second	18
Time Between Observations (t in sec)	0.056

Figure 5.12: Details of analysis.

The mean squared distance calculated from our observation is 0.69 mm and the mean distance covered by an ant on the average is found to be 0.303 mm between the two consecutive observations. As this distance is covered at 0.056 seconds, the ants' speed on the average is calculated as 5.4 mm per second. Considering the length of an ant to be 2 mm, the ants in the recordings have moved on the average almost three times of their lengths in a second. Jackson (2005) noted a speed of 7.1 mm per second for the ants he investigated, while Nouvellet et. al's findings of a movement of 200 body lengths of an ant in 30 seconds implies an average speed of 13.3 mm per second.

Considering the sensitivity of the mean squared displacement and the turning angles to time (sampling) at which the observations are recorded, the path the ants followed is re-sampled at t, $2t$, $7t$, $10t$, and $14t$. It is expected that as the time interval of observations increase, the mean squared distance and the mean distance covered would increase.

When sampling takes place in analysing the searching behaviours of animals, Bell (1991) notes that it is most appropriate to take body length of an animal in deciding the length between the two observations. This could be true if the time interval in sampling is so high to generate observation intervals more than two to three times the body length of the animal. In our case, sampling at t with 18 observations per second corresponds to 0.303 mm gap between two observations and this is only about 1/3 of the body length of the ant. It is believed that such an observation interval enables tracing the path followed by the ant more precisely. The body length of the ant, for the interval between the observations is best captured with sampling at time $7t$ giving an interval of 2.1 mm (1 ant step). The mean squared displacement and the mean displacement at various times resulting in different samples are shown in figure 5.13.



Sampling	Time (s)	MSD (mm)	MD (mm)
t	0.056	0.69	0.30
2t	0.112	2.79	0.70
7t	0.392	21.12	2.01
10t	0.56	44.27	3.00
14t	0.784	70.85	3.69

Figure 5.13: Average MSD and MD.

It is quite clear that both the mean square displacement and the mean displacement increase as the time increases. That is, there is a positive relationship between the time and the mean squared displacement and the mean displacement. Nouvellet et. al (2009) in their research concluded that the mean squared displacement of ants' paths deviates considerably from being directly proportional to time. However, in many related models of animal movement, mean squared displacement is taken to be proportional to time. On the other hand, angular distribution was found to vary according to the precise value adopted for the sampling time interval. The impact of the re-sampling on angular distribution could be seen in the studies of Codling and Hill (Codling and Hill 2005).

Similar to Jackson (2005), each observation was encoded as a sequence of directional changes, and fitted using an eight point compass (see figure 5.14). The turning kernel in an ants movement giving a probability distribution of the possible turning angles for an ant is obtained from the normal curve derived at time t, as the observations at time t is tracing the path more precisely than any other time interval between the observations. According to the findings, which are summarized in table 5.15, ants predominantly chose to continue on their current course (50.3%) and there was a high incidence of 45^o turns almost equally to the right (19.5%) and left (20.1%). Vincent and Myerscough (2004) explain turning kernel as a symmetric distribution, which decreases with the magnitude of the angle of the turn. They express this further by a statement from Pasteels et al.

(1986), which states that an ant is less likely to choose a path that involves a large turn as opposed to one that involves a small turn. The turning kernel derived from the recordings of the ants are in unison with these statements.

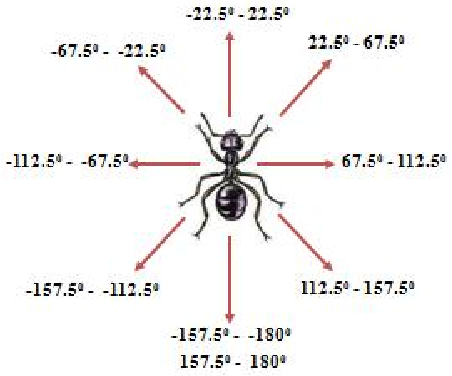
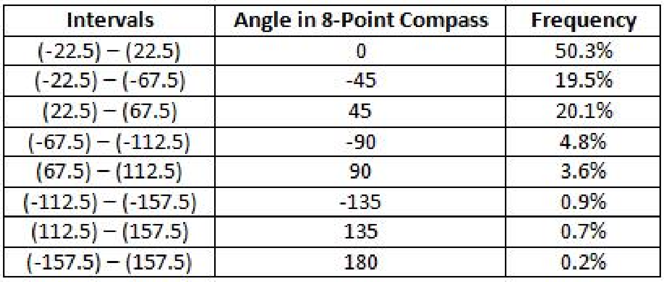


Figure 5.14: The turning kernel based on 8-point compass.



Intervals	Angle in 8-Point Compass	Frequency
(-22.5) – (22.5)	0	50.3%
(-22.5) – (-67.5)	-45	19.5%
(22.5) – (67.5)	45	20.1%
(-67.5) – (-112.5)	-90	4.8%
(67.5) – (112.5)	90	3.6%
(-112.5) – (-157.5)	-135	0.9%
(112.5) – (157.5)	135	0.7%
(-157.5) – (157.5)	180	0.2%

Figure 5.15: The derived turning kernel for Pharaoh's ants.

The set of all turning angles at each observation of the path of an insect's movement gives a distribution of angular changes. It is expected that as the time interval of observation increases the turning angles would be wider, corresponding to relatively less direct forward movement and more side ways movement. The sets of turning angles for different time intervals (t, $2t$, $7t$, $10t$ and $14t$) at each observation resulted a distribution of the turning angles corresponding to each time interval. Distributions of turning angles for time intervals t, $2t$ and $7t$ are given in figures 5.16 and 5.17. One observation common to all of the distributions of turning angles is that they all have a normal distribution. The distribution of the turning angles for t has the highest peak while the distribution of the turning angles for $14t$ is the flattest. This means that the probability of ants choosing a direction forward is higher in the distribution of turning angles for t compared with $14t$ while the probability of ants going sideways or turning backwards is higher in the distribution of turning angles for 14t compared to t.

During the recordings, the stationary period of ants were also calculated and found to be 38% of the total observations.

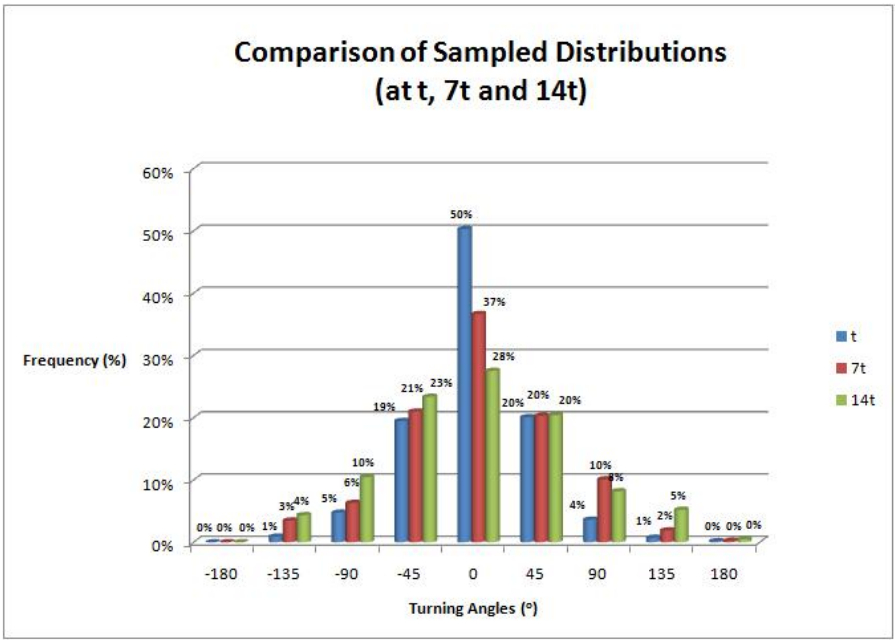


Figure 5.16: Comparison of sampled distributions of turning angles (3D bar chart).

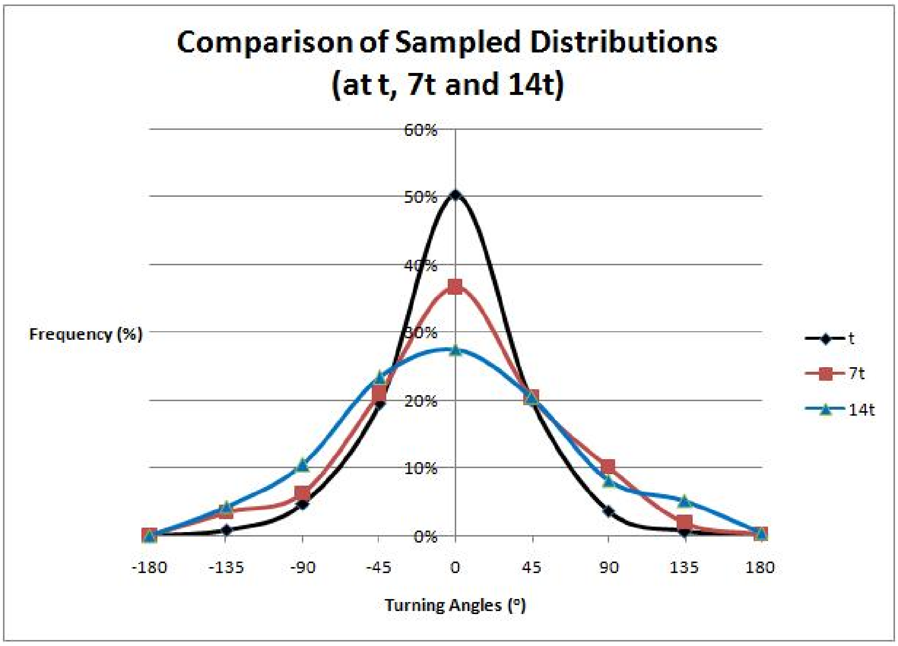


Figure 5.17: Comparison of sampled distributions of turning angles (Scatter graph).

5.6 Conclusion

The main objective of this chapter was to derive a turning kernel for the ants based on a well established experimental setting. A sufficient number of ants and their corresponding movements were analysed in an environment free of various distortions, i.e. previous pheromones laid by other colony members. While working for this objective, MSD, MD and their relations with the time interval between the observations on the path followed by the ants were also investigated.

While determining the MSD and MD at different time intervals of the observations, it was concluded that as the time increased, MSD and MD both increased, indicating a positive relationship in between. Another finding from the experimental work on the ants was that the distribution of the turning angles have normal distributions whose shape flattens as the time interval of the observations is increased. In tracking the movement of ants from recorded videos, relatively more frequent observations were noted (18 observations per second), which led to a more precise follow up of the path.

The turning kernel derived from the distribution of angular changes reflected a normal distribution, where the values extracted are used in the models, as explained in the next chapter.

Chapter 6

Investigating the Foraging Strategies of Pharaoh's Ants

It was discussed earlier in Chapter 3 that both top-down and bottom-up modelling approaches have successful examples in the literature, and ABM, a bottom-up approach, was identified as the best for modelling complex biological systems.

In this chapter, ABM was utilized to improve existing models of the Pharaoh's ants, focusing on their foraging strategies. Based on related biological research, a number of hypotheses were gathered to investigate the potential mechanisms employed by *M. pharaonis* colonies during foraging. Several models were developed to help demonstrate the effect of these hypothesis on overall foraging efficiency of *M. pharaonis* colonies. These were: (i) division of labour in Pharaoh's; trail maintenance by 'U-turner' ants, (ii) the effect of trail choices at a bifurcation, and (iii) the effect of laying pheromones with higher intensity for food assessment. Detailed description of the models developed, along with the interpretation of results are provided in the next sections. For every model, a list of the parameters is provided in the Appendix.

Throughout the modelling process, the FLAME framework was efficiently utilized and a number of technological challenges commonly faced by modellers were addressed, which were:

- Dynamic creation of pheromone agents, which saved memory and improved performance, as well as providing agents with flexible cohabitation within the environment
- Dynamic creation of food agents, which facilitated the demonstration of a dynamic environment
- Parallel runs coupled with high performance computing formed a ground to simulate realistic colony sizes, as well as foraging space, which is identifed as a severe

bottleneck for many related models in the literature

- Environment was simulated as continuous space, where the 'discreteness' of agents was reduced to a minimum
- The agent-based modelling approach facilitated the complex mechanisms under study to be simulated in a detailed and realistic manner.

Furthermore, a visualizer was developed to parse the outputs of the FLAME framework and visualize the behaviour of agents throughout the simulations. This facilitated in-depth understanding of the results, as well as provided good means for testing the algorithms governing the models. For further analysis of the results, workflows using Taverna (Missier et al., 2010) were developed, which facilitated efficient automated analysis of large sets of results. Appendix A contains the list of parameters, whereas Appendix B contains the stategraphs for the models developed.

6.1 The Movement Model: Initial Formation of Pheromone Trails

In the previous chapter, the average walking speed of the Pharaoh's ants, as well as a turning kernel estimating their movement patterns were derived. These are used to form the basis of all the models described in this chapter. The walking speed was found to be 5.4 mm/s (n=15). Therefore, it was assumed that the simulated ant agents moved at a mean speed of 5.4 mm/s, where a single iteration approximated to a time period of 0.37s. Given the body length of Pharaoh's ant as 2 mm, a single step of the Pharaoh's ants was assumed to correspond to 2 mm (Jackson, 2005).

The aim of the movement model is to demonstrate the movement patterns of Pharaoh's ants based on the turning kernel. The model details along with the results are explained in the next section.

6.1.1 Model details

The environment contained a nest agent with dimensions 20x20 mm, positioned at the centre of the environment. Ant agents were initially positioned with random coordinates within the nest. Food agents with random coordinates and sizes were also included, along with two 'environment' agents for technical purposes; for dynamic creation of pheromone and food agents (when depleted). It was mentioned earlier that the FLAME framework supports dynamic creation of agents during simulations, which highly improves the performance of the models, decreasing the run times; opposed to having static agents initialized in the environment waiting to be activated one at a time, which would consume plenty of memory space, as well as decreasing performance. The dimensions of the environment was 500x500 units, which corresponds to 500x500 mm, a realistic foraging space (Jackson, 2005). Initially there were no existing pheromone agents (or trails) within the environment, simulating a virgin territory.

Ant agents are characterised by their identity number, nutritional status, current heading and environmental location. In all the models, the nutrition levels of the ant agents are used as motivation to leave the nest, which were randomly generated, i.e. a (double) value between 1 to 10, ensuring a random distribution of ant agents leaving the nest, as observed in nature, rather than applying traffic control rates utilised in previous related models. As soon as the nutrition levels fall below a threshold, ant agents leave the nest and commence foraging. Once the ant agents leave the nest, they walk non-randomly based on the probabilistic turning kernel. Unlike the majority of the ant species (i.e. *Lasius niger*), Pharaoh's ants have been observed to lay pheromones continuously and as soon as they leave the nest. This is due to their poor vision, which leads to their complete reliance on the deposited pheromones for orientation. Therefore, ant agents deposit a pheromone agent at every time step.

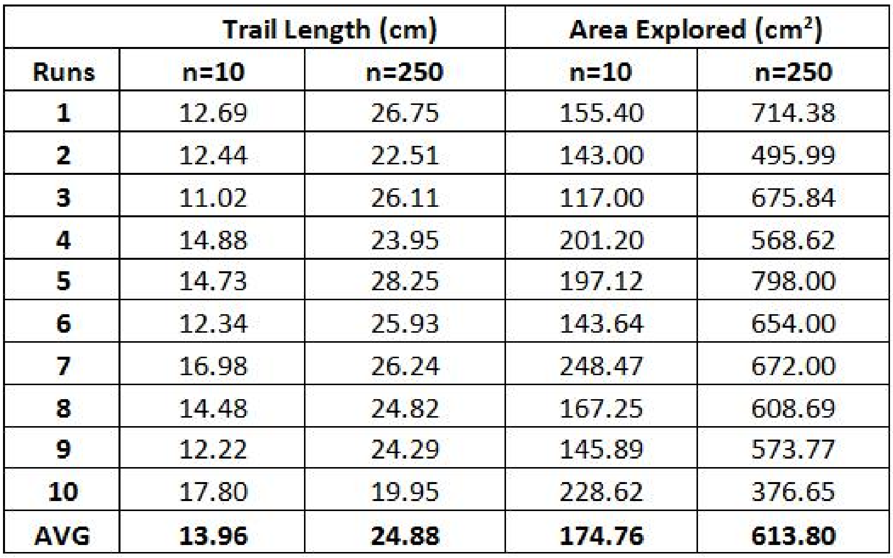
Pheromone agents are created dynamically through the Generator agent. Ant agents test the environment to 'detect' pheromones at every step, and a priority is given to following the detected pheromones. Pheromone deposition and detection by ant agents are described in detail in the next section. Studies have shown that pheromones are volatile chemicals and decay over time. Consequently, a decay rate was determined by Jackson (2005) for the pheromones secreted by Pharaoh's ants. This rate is used in all models, where the concentration of pheromone agents is decreased accordingly at every iteration.

It was observed in biological experiments that ants show high fidelity to trail following. However it was also observed that there is always a probability that the ants will depart from the trail. Furthermore, ant agents were observed to engage in U-turning, where they make a spontaneous 180 degree turn (Jackson et al., 2004). These observations were parameterised by Jackson et al. (2008) and are included as behavioural rules in all the models presented in this chapter.

6.1.2 Results

According to Sudd (1960), Pharaoh's ants can produce trails with lengths exceeding 10 metres. Similar to Jackson (2005), the lengths of the trails formed by the ant agents (n=10 and n=250) after 1000 iterations (corresponding to 6.2 minutes) were calculated for 10 runs. The results are summarized in table 6.1, which fit with the findings of

Jackson (2005), whose ant agents produced 20-50 cm long trails after a period of 4.8 minutes. Furthermore, the total area explored by the ant agents (relative to the position of the nest) was calculated for every run. The results summarized in figure 6.2 demonstrate that the simulated movement patterns serve as an efficient search strategy for Pharaoh' ants, enabling them with the ability to explore large foraging spaces.



	Trail Length (cm)		Area Explored (cm^2)	
Runs	**n=10**	**n=250**	**n=10**	**n=250**
1	12.69	26.75	155.40	714.38
2	12.44	22.51	143.00	495.99
3	11.02	26.11	117.00	675.84
4	14.88	23.95	201.20	568.62
5	14.73	28.25	197.12	798.00
6	12.34	25.93	143.64	654.00
7	16.98	26.24	248.47	672.00
8	14.48	24.82	167.25	608.69
9	12.22	24.29	145.89	573.77
10	17.80	19.95	228.62	376.65
AVG	**13.96**	**24.88**	**174.76**	**613.80**

Figure 6.1: The lengths of the pheromone trails produced and the total area covered by the ant agents (n=10,250) throughout 1000 iterations (6.2 minutes).

6.2 Modelling Pheromones

Communication in Pharaoh's ants is achieved solely through pheromones, therefore trail following behaviour is the key to understanding the underlying mechanisms of foraging. It is essential that any modelling approximation reflects the real mechanism as closely as possible, otherwise the interesting phenomena will be absent. Bearing this in mind, extra effort was spent to model pheromones in the most realistic manner.

An overview of the mechanisms underlying trail following in ants was provided in Chapter 2 and it was mentioned that as evaporation takes place, this leaves a semi-ellipsoidal area of gaseous pheromone around the trail, which is referred to as the 'vapour tunnel' (Bossert and Wilson, 1963). Sharpe and Webb (1998) further stated that the ants following the trail travel through the 'vapour tunnel' testing the air for the pheromone molecules, often moving their antenna about. Therefore, pheromone modelling was achieved under two categories: (i) pheromone deposition by the ants and (ii) pheromone detection by the ants.

6.2.1 Pheromone deposition

Each pheromone is deposited as a spot, which contains many molecules that evaporate over time. As a result of diffusion, the molecules move in space from their original point of direction, as well as decaying up to a point that they no longer elicit activity. It was mentioned earlier that pheromone can be in two different states; liquid (at the point of deposition) and gas (diffusion of molecules). To simulate this in a realistic manner, pheromone agents are deposited as spots, and represented with two radii; the operating width and the maximum functional width, each representing the dimensions for the two different states of the pheromone agent.

Pheromone trails appear to be very wide, especially after reinforcement. However according to smoked-glass experiments, they are in fact multiple trails braided together and very narrow. Assigning values to these parameters is challenging, due to our limited knowledge on the chemical properties of the pheromones. However, the decay rate for the pheromones secreted by Pharaoh's ants was previously determined by Jackson (2005). The operating width of the trail was also observed to be around 2 mm (Jackson (2005)), whereas the trail pheromone is predicted to be detectable from 20 mm or more from the centre of the trail (based on discussions with Dr. Jackson). However, it should be noted that there is no spatial limit to where the pheromones can evaporate. Therefore, the maximum radius should only be determined by how much the ant agents can detect. This is further explained in the next section.

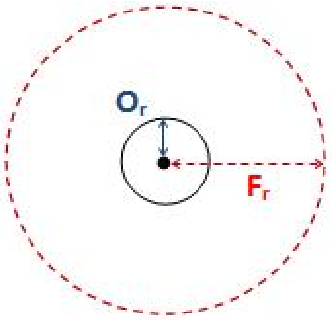


Figure 6.2: Pheromone Model (O_r is the operating radius, F_r is the maximum functional radius).

6.2.2 Pheromone detection

Ants have been observed to perform sinusoidal walk around the trails, hugging the centre of the trail. This is because the centre of the trail is where the concentration of the pheromone is the highest. Pheromone detection was discussed in Chapter 2, where it was mentioned that the areas away from the trail will have a lower detection threshold for ants. Therefore, the maximum radius of a pheromone would be determined by the lower detection threshold of the ants.

According to Calenbuhr and Deneubourg (1992) osmotropotaxis is the key mechanism employed by ants for detecting pheromones, which requires an ant to perceive local pheromone trail concentration with each antenna and compute the difference, then change direction towards the higher concentration. Jackson (2005) argues that this definition is rather problematic as, if the ants are computing a difference then, based on behavioural observations, this cannot be a simultaneous bi-sensor sampling mechanism and must instead be a successive uni-sensor mechanism. Osmotropotaxis also implies the use of memory by ants to perform calculations of difference in pheromone concentrations.

Models of pheromone detection in this thesis are based on klinotaxis, the uni-sensor mechanism, where the models successfully demonstrated the 'wiggly' movement of ants, along with successful detection of higher pheromone concentrations, without having to use a memory to calculate concentration differences. Furthermore, Pharaoh's ants were never observed to walk backwards (Sudd, 1960), therefore in related models ant agents are only allowed to follow the pheromones ahead.

6.2.3 Model details

Bossert and Wilson (1963) modelled the diffusion of pheromone molecules and showed that the active space is related first to the quantity of pheromone, second to the sensitivity (threshold) of the receiver, and third to the diffusion coefficient of the pheromone which is correlated with its molecular weight. In response to the selection pressures on the signalling system, over evolutionary time each of these values can be changed to give an active space which is larger or smaller, quicker or slower to expand to its maximum, faster or slower to fade. Sharpe and Webb (1998) also produced a mathematical model based on ostropotaxis, composed of the parameters; amount of pheromone deposited, diffusion coefficient of pheromone, antenna distance, length of time since trail deposited.

It was mentioned earlier that the pheromone agents decay over time, and a corresponding decay rate was determined by Jackson (2005). Based on this decay rate, the pheromone agents decay at every time step, where the formula could be expressed as follows:

$$\mathrm{p}_u = \mathrm{p}_i - (\mathrm{p}_i * 0.0248)$$

If the concentration falls below a certain threshold then they become extinct and the pheromone agent is killed. This simulates the evaporation and decay of molecules with an exponential decay from the origin of the pheromone agent, as well as contributing to the performance of the model, as the environment will be free of molecules at very low levels. Any pheromone molecule that has a concentration falling below the detection threshold of the ant, which is described as the 'sensitivity of the receiver' in related literature, will not be detected by the ant agents. This will correspond to the odours that have probably diffused farther than the maximum functional width of the pheromone, and will be considered as negligibly small to be sensed by an individual ant agent.

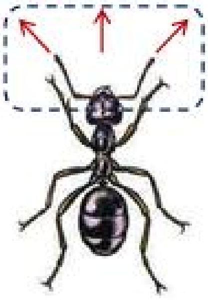


Figure 6.3: Antennal range for an ant agent based on body length (2 mm).

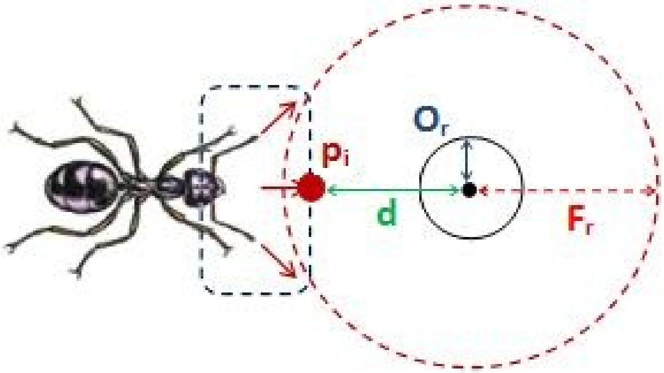


Figure 6.4: Pheromone detection by an ant agent.

Pheromone detection by ant agents could be explained step by step as follows:

1. Ant agents test to sense any pheromone agents nearby:
   Whether the antenna range of the ant agent intersects with the operating or maximum functional width of a pheromone agent.
2. Ant agents follow the pheromone agents ahead:
   To simulate the antennal range, the vicinity of an ant agent is defined within 45 degrees clockwise and anti-clockwise angles. Therefore, the ant agents will only follow the pheromone agents that are within the antennal range.
3. Diffusion of the pheromone molecules is expressed in a linear form:
   If there are multiple pheromone agents within the antennal range; for every pheromone that is within the antennal range, their relative concentration at the point of intersection with the antennal range (shown by the red dot in figure 6.4) could be detected, with the following formula:

$$p_i = p_c * (1 - d / F_r)$$

where;

p_i = Concentration of the pheromone at the point of intersection (red dot)

p_c = Concentration of the pheromone

d = Distance between point of intersection and pheromone

F_r = Maximum functional width over which pheromone molecules could diffuse

4. Ant agents decide which direction to walk towards: It was mentioned in the previous section that the ant movement is categorized into 8 directions (based on an 8-point compass). Therefore for every direction (0, 45 degrees clockwise and anti-clockwise), the total concentration for the diffused molecules falling within the antennal range is calculated. The direction with the highest concentration is chosen and the coordinates of the ant are updated accordingly.

Figure 6.5: Snapshot from U-turn model: Demonstration of pheromone agents with their operating radius (red circles) and maximum functional radius (blue circles).

Trail reinforcement is modelled by the ant agents depositing a brand new pheromone agent at every step. As mentioned earlier whenever a pheromone agent is deposited, it is created with an operating width as well as a functional width for the molecules to disperse. The added advantage of simulating the environment as continuous space provides ant agents with flexible cohabitation (coordinates with a precision of 'double') within the environment. Therefore, when the ant agents start following pheromone trails, they will be reinforcing the trail further with brand new pheromone agents deposited at close but different coordinates, adding to the total concentration of the diffused molecules. This simulates the observed 'multiple but narrow trails' from the smoked-glass experiments.

6.3 The Foraging Model

Sudd (1960) wrote a detailed paper on his observations of *M. pharaonis* colonies in western Nigeria while foraging in nature. Consequently, he classified the potential problems that could arise during foraging under three categories: (i) how foragers are able to find their way to and from the nest, (ii) how they recruit workers to foraging activities, and (iii) how they guide recruits to the food they discover. However, similar to previous related models (Jackson, 2005) the details of the recruitment process in the trail-building was ignored as it is poorly understood and yet to be quantified for the Pharaoh's ants. Therefore, in these models, ant agents were recruited to pheromone trails simply by detecting them.

The aim of this model was to produce a basic foraging model based on simple behavioural rules discussed in the previous section, to demonstrate the potential of agent-based modelling coupled with FLAME, as well as the outcomes of the approach to modelling pheromones. A basic hypothesis was also tested to be able to evaluate and provide a comparison of the model results. The hypothesis tested the effect of improved sensitivity of ant agents towards food sources within the environment on the overall foraging efficiency of the colony.

6.3.1 Model details

The environmental setup was identical to that of the movement model. Food agents are placed at random coordinates with random sizes, where the size is decreased by 0.02 units whenever an ant agent comes across. When the size of a food agent equals to 0.2 units, the food agent is killed, and a new food agent with random coordinates and size appears, simulating a dynamic foraging environment.

Ant agents search the environment until they detect a food agent, in which case their nutritional level is updated to a maximum food level, and the agent makes a 180 degree turn. Then the ant agent follows pheromone agent trails to return to the nest agent. Once an ant agent is back in the nest, it does not leave until her nutrition level falls below the threshold. Their nutrition levels are decreased by a small amount at every step.

Based on the findings on increased trail laying by fed ants, compared to unfed ants, fed ant agents were allowed to deposit higher concentration of pheromones (2 units), where unfed agents deposited a lower concentration (1 unit). During experimental trials, this was found to be very helpful, as this prevented other colony members from following the initial pheromones deposited by the first few ant agents (after leaving the nest). It also ensured that unrewarding pheromones decayed sooner, while the pheromones deposited by the fed ants persisted for longer, facilitating an efficient foraging strategy. Considering that Pharaoh's ant agents deposited pheromones at every step, this was a significant advantage.

Colonies of (n=50, 250, 500) ant agents were simulated for 1000 iterations (6.1 minutes). Jackson (2005) states that Pharaoh's ant colonies are approximately equally divided into nest-workers and foragers, therefore a realistic colony size was simulated in all models, which is rare to come across in related models in the literature.

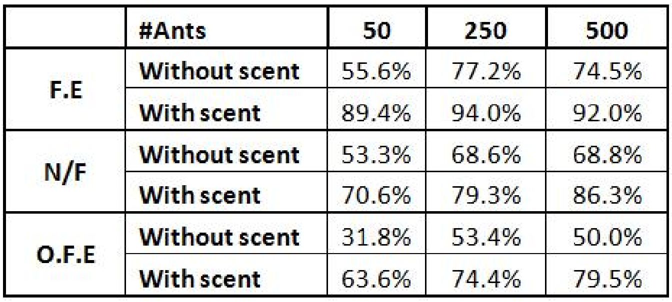
Based on the hypothesis to be tested, two versions of the model were produced, which were:
Version 1: Based on the simple behavioural rules explained above.
Version 2: In addition to the rules in version 1, the food agents were introduced with a radius of scent, representing diffusion of food scent.

6.3.2 Results

The results from the models were analysed under three categories:

- Foraging Efficiency (F.E): Proportion of fed ants
- Overall Foraging Efficiency (O.F.E): Proportion of fed ants that successfully returned to nest
- Nest to Fed Ratio (N/F): Ratio of O.F.E to F.E

In both versions of the model, when an ant agent came across a food agent, pheromone trails were successfully established between the food source and the nest, demonstrating the successful deposition and detection of pheromones by ant agents. As mentioned earlier in Chapter 2, due to the irregular shapes of trails and limited antennal range of the ants, it is very likely for the ants to accidentally walk off the trails. With the added effect of modelling the environment as as continuous space, the chances of the ant agents missing a food source nearby was very high. This is clearly evident in Version 1 (please see the videos of the simulations). However, in Version 2 introducing a food scent based on the food size provided a ground for faster discovery of the food agents, thereby facilitating the establishment of stronger trails between the food source and the nest. Furthermore, increased number of ant agents (n=50, 250, 500) resulted in an increase in the overall foraging efficiency (O.F.E) and nest-to-fed ratio (N/F) as this meant that at any time step, more ants were actively exploring the environment. A summary of the F.E, N/F and O.F.E results are provided in figure 6.6.



	#Ants	50	250	500
F.E	Without scent	55.6%	77.2%	74.5%
	With scent	89.4%	94.0%	92.0%
N/F	Without scent	53.3%	68.6%	68.8%
	With scent	70.6%	79.3%	86.3%
O.F.E	Without scent	31.8%	53.4%	50.0%
	With scent	63.6%	74.4%	79.5%

Figure 6.6: Summary of the F.E, N/F and O.F.E results from the models with colonies of (n=50,250,500) ant agents after 1000 iterations (average of 10 runs).

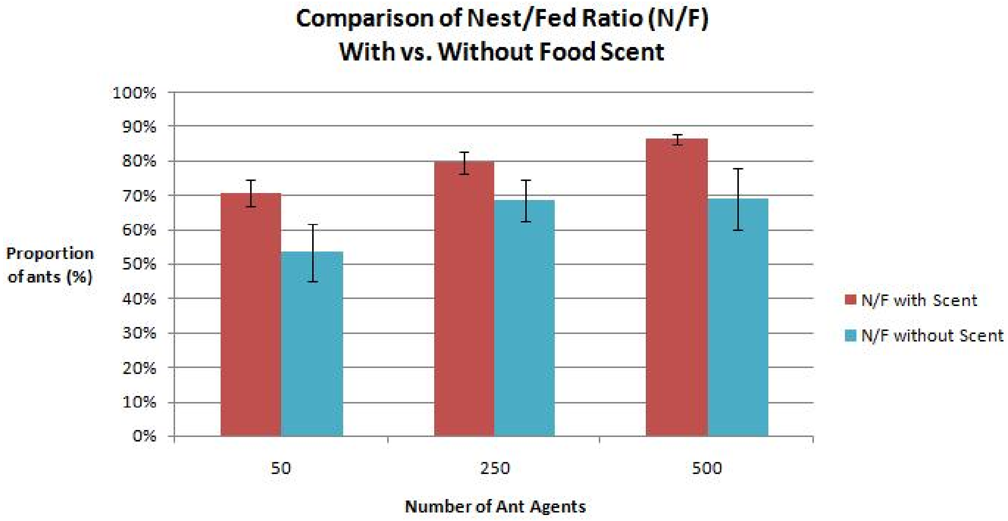


Figure 6.7: N/F Ratio results from two versions of the model with (n=50, 250, 500) ant agents. Each model was run for 10 times for a period of 1000 iterations.

Figure 6.7 shows the N/F ratio, while figure 6.8 shows the O.F.E results from the two versions of the model. For a better visual comparison, figure 6.9 shows the complete results (F.E, N/F, O.F.E) from both versions of the model. The results were further analysed by a Difference of Means test with t-distribution (Two-sample Assuming Equal Variances), which was applied to test the significance of means between the models with and without the food scent at a 0.05 (two tail p-value) significance level. If the t-statistical (calculated) value was greater than the t-critical (table) value, the null hypothesis of no difference was rejected and it was concluded that there was a significant difference between the two means. Standard Error (Standard Deviation / Sqrt(Total number of runs), where the total number of runs was 10) is also demonstrated by error bars on the bar charts.

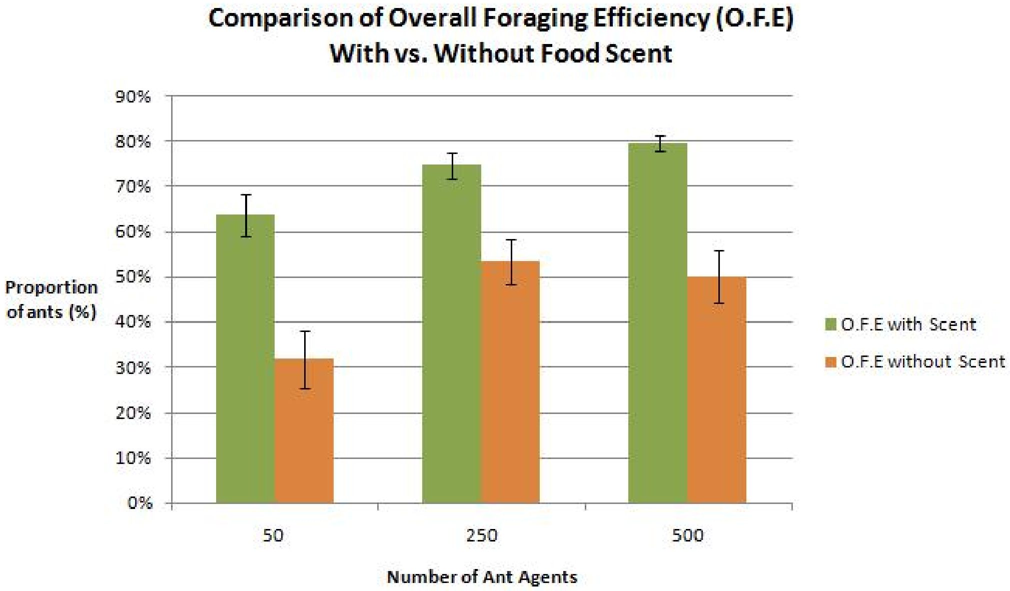


Figure 6.8: O.F.E results from two versions of the model with (n=50, 250, 500) ant agents. Each model was run for 10 times for a period of 1000 iterations.

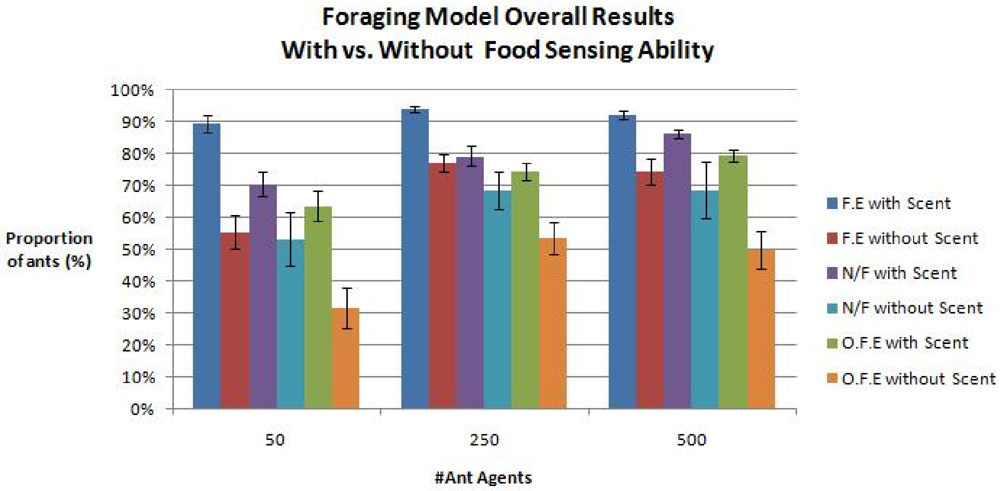
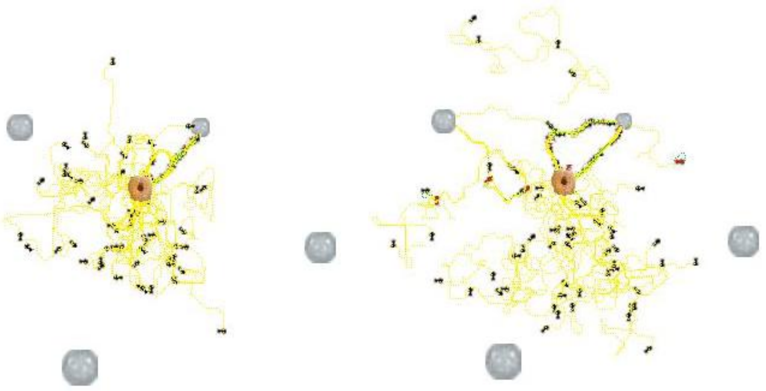


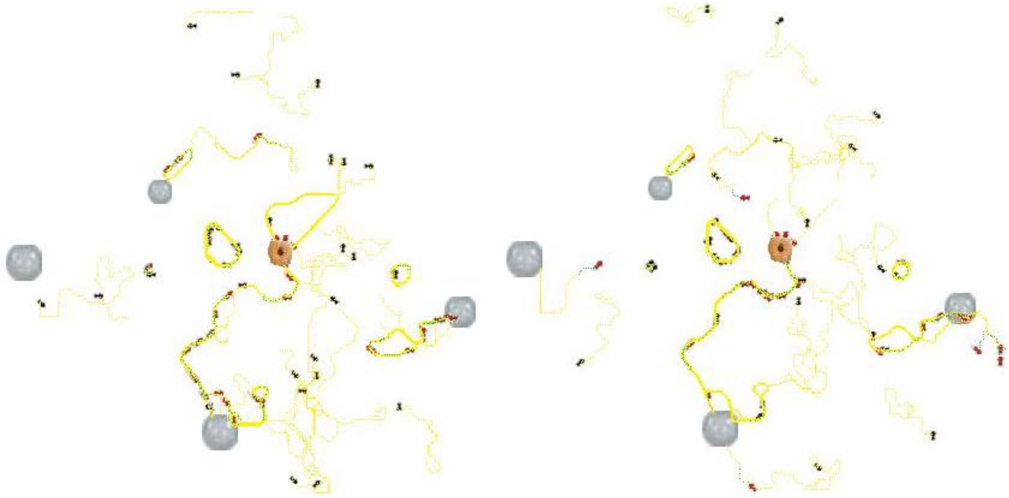
Figure 6.9: All results (F.E, N/F, O.F.E) from two versions of the model with (n=50, 250, 500) ant agents. Each model was run for 10 times for a period of 1000 iterations.

As shown in figures 6.6 to 6.9, the models incorporating a food scent resulted in improved results. For all colonies (n=50, 250, 500) introducing the food scent led to a significant increase in the overall foraging efficiency (O.F.E), as when n=50; (t-statistical: 4.048, t-critical: 2.101, p: 0.001), when n=250; (t-statistical: 3.644, t-critical: 2.101, p: 0.002), and when n=500; (t-statistical: 4.875, t-critical: 2.101, p: 0.0001).

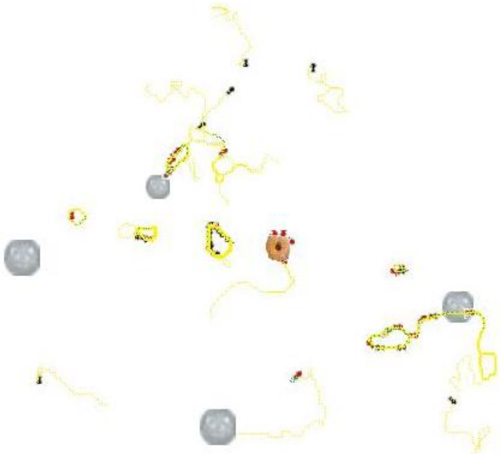
Figures in 6.10 shows the snapshots from the simulation captured at different time steps. As shown in figure 6.7a, ant agents successfully establish a strong trail to a nearby food source within 1.1 minutes, and in figure 6.10b another trail from the same food source to the nest is established successfully facilitating faster depletion of the food source. After 3.8 minutes, other members of the colony successfully establish a trail to distant food sources (figure 6.10c), where one of the trails is successfully further reinforced as



(a) 176^{th} iteration (1.1 mins). (b) 311^{th} iteration (1.9 mins).



(c) 612^{th} iteration (3.8 mins). (d) 693^{th} iteration (4.3 mins).



(e) 1000^{th} iteration (6.2 mins).

Figure 6.10: Snapshots from the model with (n=250) ant agents.

shown in figure 6.10d. It can also be observed that the initial trails leading to the nearby food source have now decayed due to the depletion of the food source and ant agents no more reinforcing those trails. However as time progresses and the ant agents attempt to establish trails between distant food sources and the nest, their success levels decrease as they are unable to maintain long trails between the nest and the distant food sources, leading to an increased number of lost ants, as shown in figure 6.10e.

A simple hypothesis was successfully tested through a basic foraging model, and realistic colony sizes were simulated in a realistic foraging space. Technological challenges addressed in related models in the literature were improved with a continuous environment, as well as dynamic creation of agents throughout the simulations. Turning kernel derived from video tracking coupled with a detailed approach to modelling pheromones facilitated simulations of the 'wiggly' walk of the Pharaoh's ant agents (please see the videos of the simulations), as well as the successful formation and detection of pheromone trails. However, the overall foraging efficiency (O.F.E), which is the proportion of the fed ants that were back in the nest at the end of the simulation, was quite low in both versions of the model. This is due to the ant agents not being able to find their way back to the nest by efficiently utilizing the deposited pheromone trails within the environment. This is a problem addressed by many researchers in related literature, which suggest that Pharaoh's ants in nature must be using more sophisticated mechanisms to maintain trails between the nest and the food sources. Consequently, the effect of the specialist U-turner Pharaoh's ants, as well as the ability of colony members in assessing food quality were investigated using agent-based models, as explained in the next chapters.

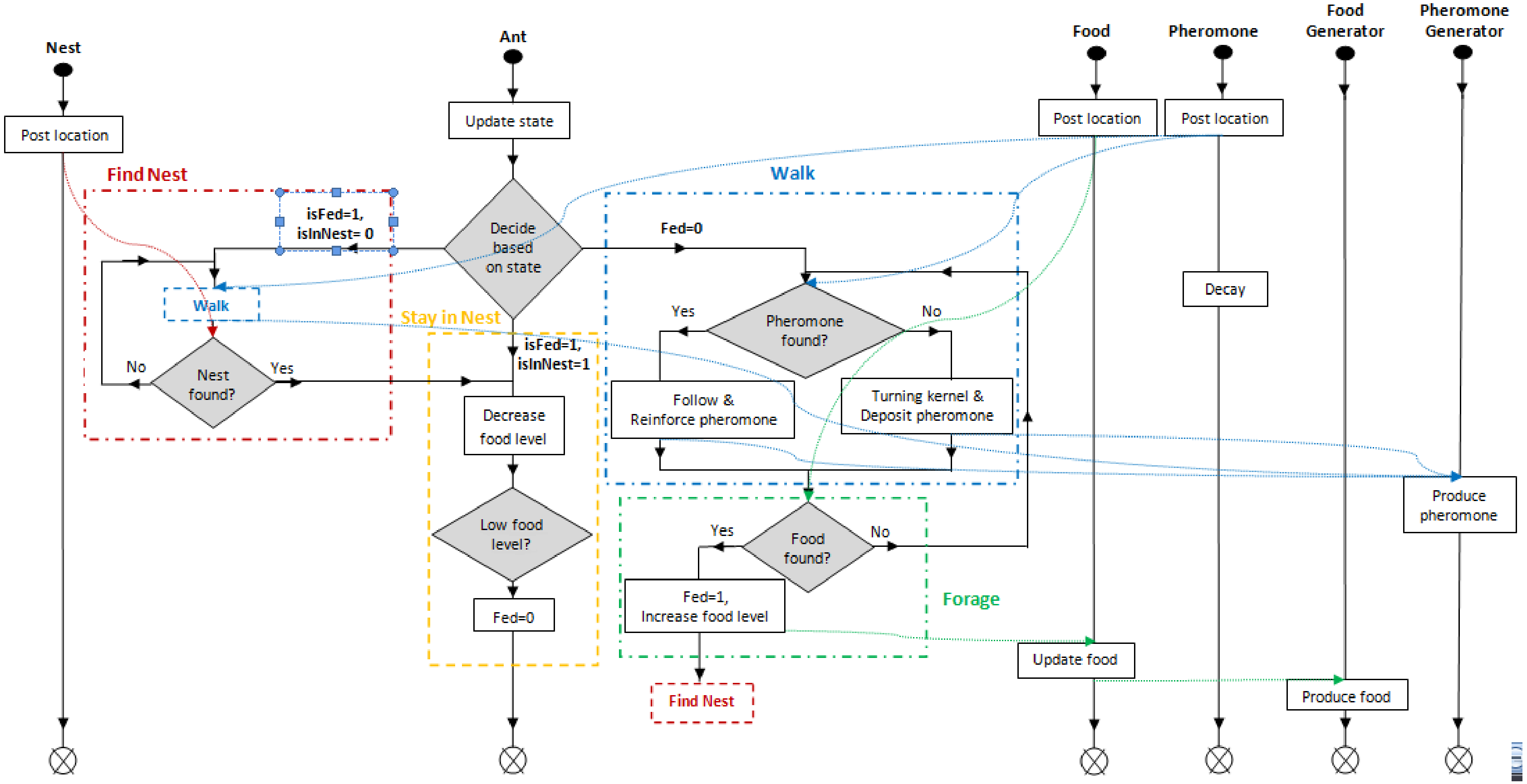


Figure 6.11: Overview and Time-line of Models Developed (Curved arrows are colour-coded to indicate the exchange of messages within related functions).

6.4 Discussion

Figure 6.11 provides an overview and shows the time-line for the models developed. Rectangular boxes contain functions, whereas the diagonal boxes contain conditions affecting the flow of functions. Curved arrows are colour-coded to indicate the exchange of messages within related functions of agents. All models developed in this thesis are based on this structure. Implementation details for every model could be viewed in depth via the stategraphs, which are provided in Appendix B for every model.

The turning kernel derived from biological experiments, coupled with a detailed approach to modelling pheromone agents produced successful simulations in the Foraging Model, hence they formed the basis for all the models in this research. Compared to the related models in the literature, this is a significant improvement, where the first set of successful results were demonstrated with the movement model. The 'wiggly' walk of the ant agents, as well as their efficient detection of pheromone detection were simulated. The results of the model were further analysed by carrying out calculations of the trail lengths produced by the Pharaoh's ant agents along with the total area covered.

The movement model was extended with a number of behavioural rules obtained from the related literature and formed the foraging model. Aiming to demonstrate the abilities of the modelling approach and the framework used, the model was used to test a basic hypothesis; whether introducing scent to food sources would increase the foraging efficiency of the colonies. As expected, the results showed positive response and more ant agents were fed at the end of the foraging trips. However, the results for overall foraging efficiency, which corresponds to the proportion of fed ant agents back in the nest, were low in numbers. This fell in line with the findings from related models in the literature, and further suggested that the Pharaoh's ant agents must be employing more sophisticated underlying mechanisms for efficient foraging strategies.

Chapter 7

Division of Labour by Specialist U-turner Pharaoh's Ants

As introduced in Chapter 2, the U-turning behaviour was first observed in *Lasius niger* ants by Beckers et al. (1992), who concluded that the U-turns performed by this ant species were the results of a 'mistake' being made, where the ants returning stopped marking (laying pheromones) on their way backwards.

In 2004, similar behaviour was also observed in Pharaoh's ants by Hart and Jackson, which were concluded to have a completely different aim; 7% of foragers performed 'apparently incorrect' U-turns at any point in a trail network, where these specialist U-turners made frequent U-turns on trails and laid trail pheromones much more frequently than ants not performing U-turns. Therefore, U-turner Pharaoh's ants were concluded to be determining the continuity of pheromone trails.

Agent based models based on U-turning behaviour of Pharaoh's ants were implemented to further demonstrate the ability of U-turner ants in maintaining pheromone trails, as well as the overall success of heterogeneous colonies over homogeneous colonies. Model details along with results and their interpretations are provided in the next sections.

7.1 Model details

As mentioned in the previous section, two versions of the model were produced:

- A model with a heterogeneous colony where 7% of the colony consisted of U-turner ants
- A model with a homogeneous colony without any U-turner ants.

Both versions of the model were based on similar environments, which contained two existing trails (see figure below). Both trails contained a food source each, positioned at the end of the trails. Models were run with (n=10, 50, 100, 250) ant agents for 2000 iterations (12.2 minutes), each for 10 runs. Furthermore, both versions were simulated with two different dimensions for environment:

- 500x500 mm environment which contained trails with 450 mm length
- 750x750 mm environment which contained trails with 700 mm length

Figure 7.1: U-turn model with 500x500 mm environment.

The general behavioural rules for the agents were almost identical with those employed in the Foraging Model. The differences introduced by the U-turning behaviour were as follows:

- Ant agents were provided with an additional memory variable called 'turn' to distinguish between the U-turner and regular ants throughout the simulation
- 7% of the population for every colony was calculated and U-turners were introduced to heterogeneous colonies accordingly (i.e. a heterogeneous colony with 250 ant agents contained 232 regular and 18 U-turner ants)
- Based on Hart and Jackson (2004), U-turner ants had a probability of 1.8% to perform 180 degree turns, whereas regular ants had a probability of 0.044%.

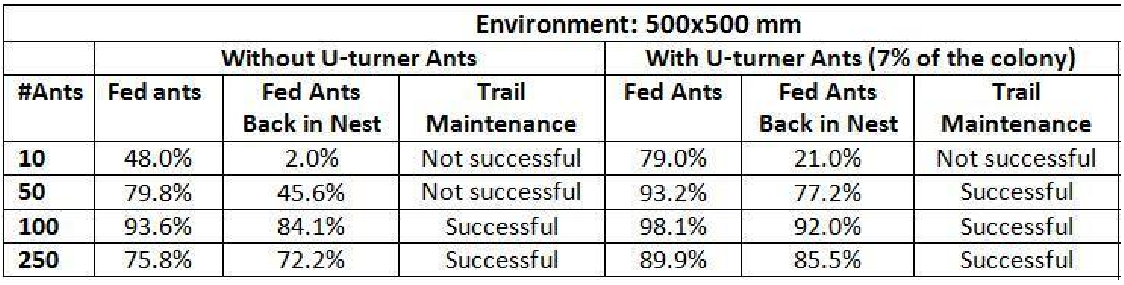
- U-turner ants were observed to perform frequent turns and lay pheromones mostly at active trails (Hart and Jackson, 2004). This was used as a motivation for U-turner ant agents to leave the nest. Unlike regular ant agents, which leave the nest when their nutrition levels fall below a threshold, U-turner ant agents only left the nest when the pheromone concentration outside the nest entrance was higher than a specified threshold. This ensured that U-turner agents would be reinforcing and maintaining rewarding trails

7.2 Results and Discussion

Similar to the Foraging Model, the results from the models were analysed under three categories:

- Foraging Efficiency (F.E): Proportion of the fed ants
- Overall Foraging Efficiency (O.F.E): Proportion of the fed ants that successfully returned to the nest
- Nest to Fed Ratio (N/F): Ratio of O.F.E to F.E

A colony was considered successful if the proportion of the fed ants back in the nest (O.F.E) was above 50% of the overall population. The results were further analysed by a Difference of Means test with t-distribution (Two-sample Assuming Equal Variances), which was applied to test the significance of means between the homogeneous and heterogeneous colonies at a 0.05 (two tail p-value) significance level. If the t-statistical (calculated) value was greater than the t-critical (table) value, the null hypothesis of no difference was rejected and it was concluded that there was a significant difference between the two means. Standard Error (calculated by; Standard deviation/Sqrt(Total number of runs), where the total number of runs was 10) is also demonstrated by error bars on the bar charts.



Environment: 500x500 mm						
	Without U-turner Ants			With U-turner Ants (7% of the colony)		
#Ants	**Fed ants**	**Fed Ants Back in Nest**	**Trail Maintenance**	**Fed Ants**	**Fed Ants Back in Nest**	**Trail Maintenance**
10	48.0%	2.0%	Not successful	79.0%	21.0%	Not successful
50	79.8%	45.6%	Not successful	93.2%	77.2%	Successful
100	93.6%	84.1%	Successful	98.1%	92.0%	Successful
250	75.8%	72.2%	Successful	89.9%	85.5%	Successful

Figure 7.2: Summary of results (homogeneous vs. heterogeneous, n=10,50,100,250) in 500x500 mm environment.

Results in 500x500 mm environment after 2000 iterations:

Figure 7.2 is a summary of the results for homogeneous and heterogeneous colonies in

500x500 mm environment, which demonstrate that colonies with (n=10) ant agents were unsuccessful in trial maintenance due to insufficient number ants. However, the positive effect of U-turners was still evident as 20% more ants were fed and back in the nest at the end of the simulation (t-statistical: 2.357, t-critical: 2.101, p: 0.03). Homogeneous colonies with (n=50, 100, 250) ant agents were all successful in maintaining trails, as the length of the trail (400 mm) was not a challenge for such populations. However, with the inclusion of 7% U-turners in heterogeneous colonies with (n=50) ant agents, the overall foraging efficiency of the colony was significantly higher as, 30.6% more ants were fed and back in the nest at the end of the simulation (t-statistical: 2.902, t-critical: 2.101, p: 0.01). In heterogeneous colonies with (n=100, 250) ant agents, the inclusion of 7% U-turners still led to an improvement in the results. When n=100; 8% more ants were fed and back in the nest at the end of the simulation, and when n=250; 13.3% more ants were fed and back in the nest at the end of the simulation. The increase in overall foraging efficiency for the heterogeneous colonies with (n=100) ant agents was not significantly higher, showing that the contribution of U-turners to a colony with (n=100) ant agents was not significant. (t-statistical: 1.575, t-critical: 2.101, p: 0.133). However, the increase with heterogeneous colonies with (n=250) ant agents was significantly higher compared to the homogenous colonies with (n=250) ant agents, as well as to the heterogeneous colonies with (n=100) ant agents (t-statistical: 2.996, t-critical: 2.101, p: 0.008). This was due to the food sources being depleted by the ant agents rapidly

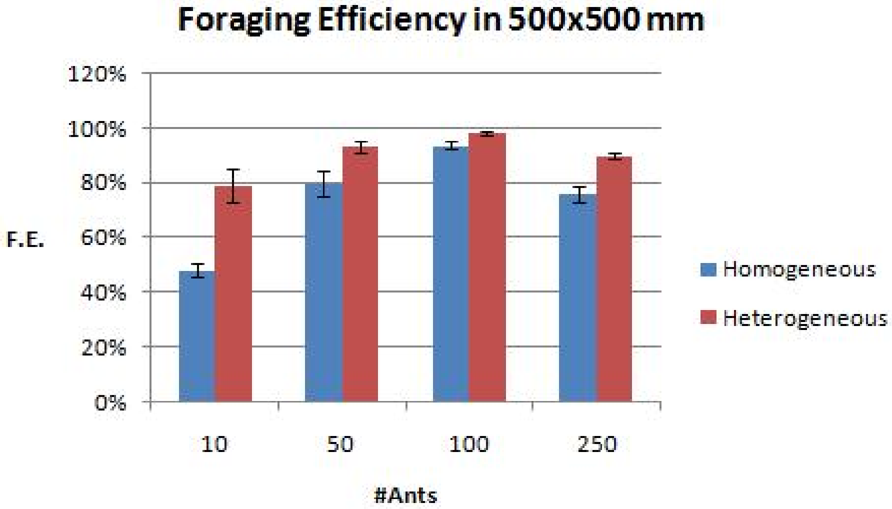


Figure 7.3: Foraging efficiency in 500x500 mm environment.

Figures 7.3, 7.4 and 7.5 demonstrate the differences between homogeneous and heterogeneous colonies in 500x500 mm environment, based on F.E, N/F and O.F.E respectively. In all categories, the efficiencies were higher in the heterogeneous models, where the increased number of ant agents were proportional to an increased efficiencies. However, this was not the case for the colonies with (n=250) ant agents. This was due to the food sources being depleted as a result of high population of foragers (see video). Consequently, after a short period of time there were no food available, which led to a higher proportion of unfed ant agents at the end of the simulation reducing the values for all categories, compared to the results with 50 and 100 ant agents.

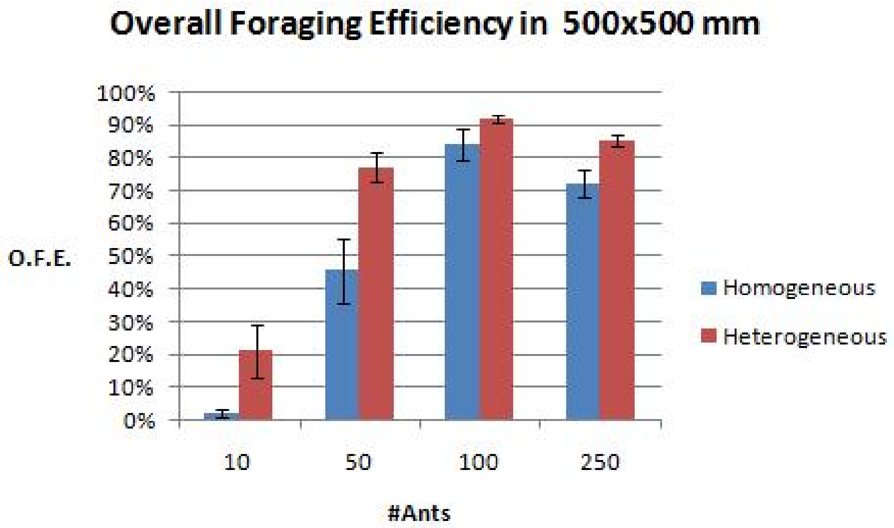


Figure 7.4: Overall foraging efficiency in 500x500 mm environment.

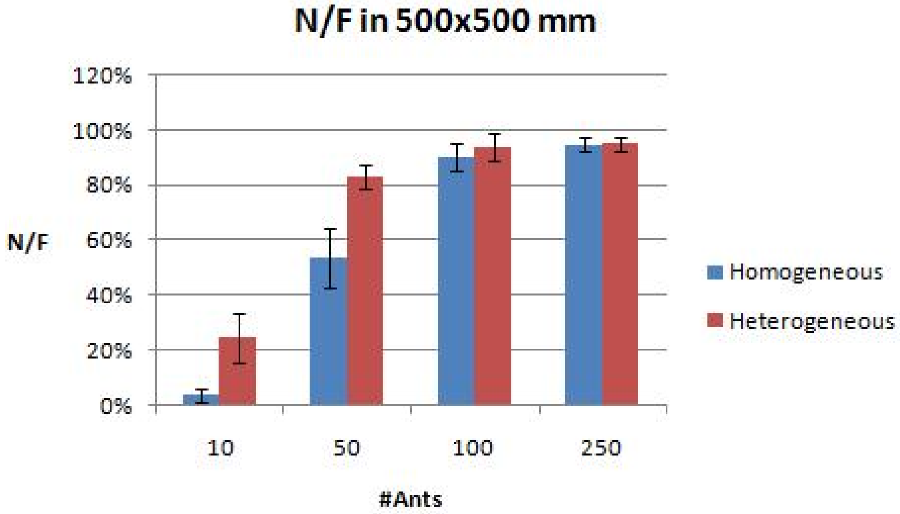
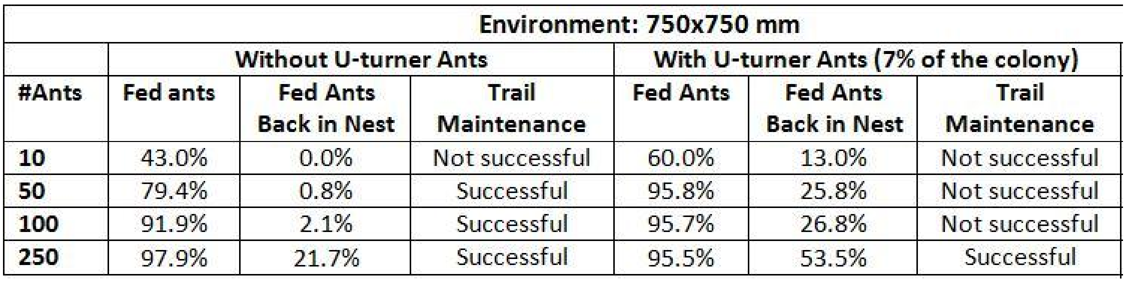


Figure 7.5: Nest to Fed Ratio in 500x500 mm environment.



Environment: 750x750 mm						
	Without U-turner Ants			With U-turner Ants (7% of the colony)		
#Ants	Fed ants	Fed Ants Back in Nest	Trail Maintenance	Fed Ants	Fed Ants Back in Nest	Trail Maintenance
10	43.0%	0.0%	Not successful	60.0%	13.0%	Not successful
50	79.4%	0.8%	Successful	95.8%	25.8%	Not successful
100	91.9%	2.1%	Successful	95.7%	26.8%	Not successful
250	97.9%	21.7%	Successful	95.5%	53.5%	Successful

Figure 7.6: Summary of results (homogeneous vs. heterogeneous, n=10,50,100,250) in 750x750 mm environment.

<u>Results in 750x750 mm environment after 2000 iterations:</u>

Figure 7.6 is a summary of the results for homogeneous and heterogeneous colonies in 750x750 mm environment, which demonstrate that both homogeneous and heterogeneous colonies with (n=10, 50, 100, 250) ant agents were unsuccessful in the maintenance of a 700 mm trail due to insufficient number ants. However, the positive effect of U-turners was evident in heterogeneous colonies with (n=10, 50, 100, 250) ant agents as when n=10; 13% more ants were fed and back in the nest at the end of the simulation (t-statistical: 6.091, t-critical: 2.101, p: 0.00000936), when n=50; 25% more ants were fed and back in the nest at the end of the simulation (t-statistical: 6.636, t-critical: 2.101, p: 0.00000314), and when n=100; 24.7% more ants were fed and back in the nest at the end of the simulation (t-statistical: 3.76, t-critical: 2.101, p: 0.001), when n=250; 31.8% more ants were fed and back in the nest at the end of the simulation (t-statistical: 7.919, t-critical: 2.101, p: 0.00000028).

Figures 7.7, 7.8 and 7.9 demonstrate the differences between homogeneous and heterogeneous colonies in 750x750 mm environment, based on F.E, N/F and O.F.E respectively. In all categories, the efficiencies were higher in the heterogeneous models, especially in figures 7.8 and 7.9 N/F ratios and O.F.E show a dramatic increase with the addition of 7% U-turners.

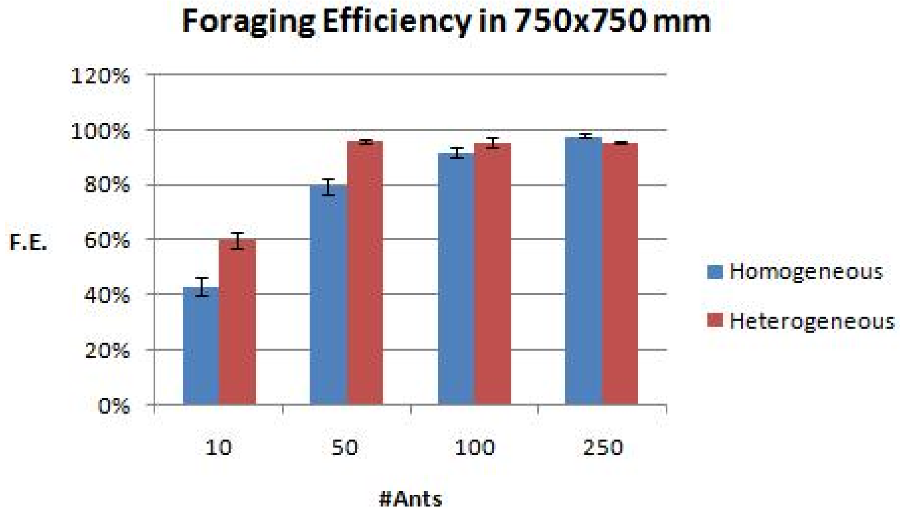


Figure 7.7: Foraging efficiency in 750x750 mm environment.

Overall, the positive influence of 7% population of U-turner ants on the foraging success of Pharaoh's ant colonies was successfully demonstrated, further validating the hypothesis of Hart and Jackson (2004) that U-turning behaviour could be a vital component of the pheromone-trail maintenance process, as making quick foraging decisions is vital to colony success, and leaving decision-making to a specialised, well-informed minority would certainly speed the process. As a result, U-turner ant agents in heterogeneous colonies successfully helped in maintaining rewarding trails, leading the rest of the colony members to the food sources and back to the nest efficiently.

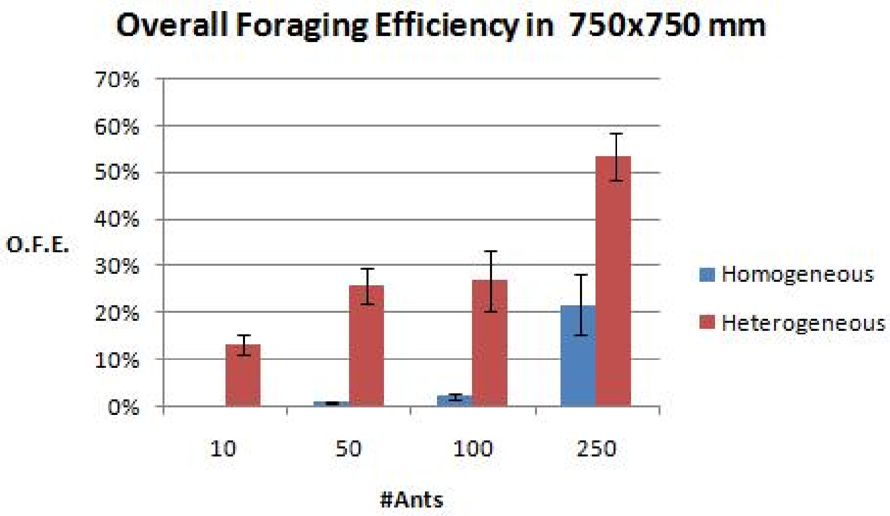


Figure 7.8: Overall foraging efficiency in 750x750 mm environment.

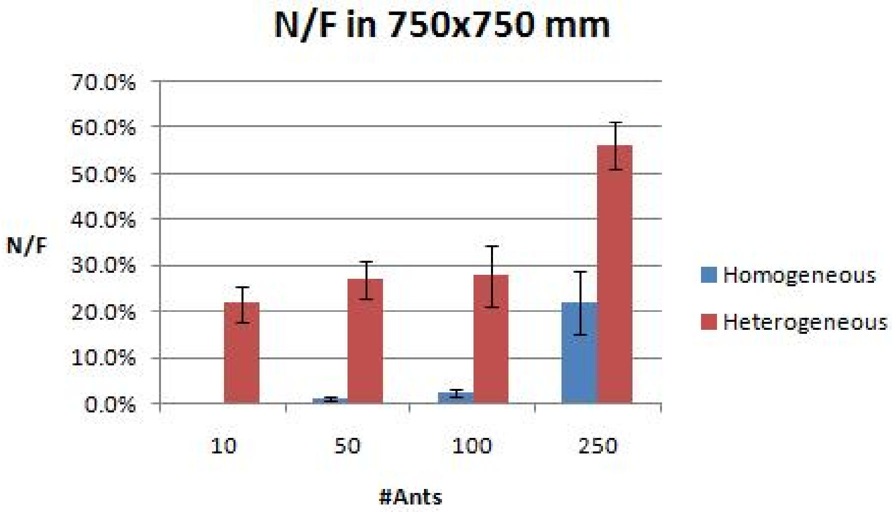


Figure 7.9: Nest to Fed Ratio in 750x750 mm environment.

Chapter 8

The 'Excited' Behaviour of Pharaoh's Ants Based on Food Quality Assessment

The ability of ants in assessing food quality was described in Chapter 2, where it was stated that Jackson & Chaline (2007) showed that in Pharaoh's ant colonies, fed ants deposited pheromones with significantly greater intensity when the food source quality was high (1 Molar), whereas there was no significant difference found when the food source quality was low (0.01 Molar). Such observed behaviour of Pharaoh's ants will be referred to as the 'excited' behaviour.

Models investigating the ability of food quality assessment by ants were discussed in Chapter 4. In this section, the 'excited' behaviour of Pharaoh's ants demonstrating their ability to assess food quality is investigated. The environment for this model is based on a Y-shaped experimental setup, hence an existing pheromone trail with two branches containing a food source each of different qualities; leading the ant agents to food sources was included. Using Y-shaped experimental setups for investigating various behaviour of ant species is a very common practise. Nicolis and Deneubourg (1999) explained the importance of this setup by stating that experiments need to be performed in deliberately idealized situations, in order to reduce the potential complications in the real world to a minimum. Due to the nature of such an environmental setup, the behaviour of Pharaoh's ants at a bifurcation point was also investigated.

Therefore, the model aims to address the following questions:

- How do individuals make decisions at a bifurcation point?
- If the branch with the poor food source is exploited first;
  Can the colony manage to switch to the branch with the good food source? If yes, how long does this take?

How does the 'excited' behaviour affect this in terms of switching time as well as overall foraging efficiency?

- If the branch with the good food source is exploited first;
  Can the colony discover and maintain a trail to the branch with the poor food source?

Robinson et al. (2008) previously investigated the repellent pheromones of Pharaoh's ants using an agent-based model, where their observations of Pharaoh's ants' choice of branches at bifurcation points were also parameterized. This observed behaviour and the corresponding parameters were included in the excitement model, which formed the ground to investigate the observed behaviour further. The two versions of the model along with the results and their interpretations are provided in the next sections.

8.1 Model details

Two versions of the model were developed based on the observed behaviour of Pharaoh's ants at bifurcation points by Robinson et al. (2008):
Version 1: Choice of ant agents at the bifurcation point when walking outwards
Robinson et al. (2008) observed that a certain minority of the ants always made an error and walked onto the weaker branch no matter how strong the other branch was. This was determined by 5%. Therefore, in this version, the ant agents had a probability of 5% (error rate) to choose the weaker branch when arrived at the bifurcation point.
Version 2: Choice of ant agents at the bifurcation point when walking towards the nest
In this version, in addition to the error rate specified in version 1, ant agents were also provided with a probability of 1% (error rate) when walking back to the nest. This was based on Robinson et al. (2008)'s observation of a certain minority of *fed* ants always choosing to walk onto the other branch, instead of walking back towards the nest.

Both versions of the model were based on the same environment, which contained an existing trail, based on a Y-shaped experimental setup. The right branch of the trail contained a food source with poor quality (size = 5 units representing a 0.01 Molar sucrose solution) and the left branch contained a food source with good quality (size = 100 units representing a 1 Molar sucrose solution). Both food sources were positioned at the end of the trails and both trails were of the same length (40 mm). The food source with poor quality was deliberately initialized with a very low size (5 units), to investigate the behaviour of ant agents and the system once the food source was completely depleted. Figure 8.1 is a snapshot of the environment for this model.

Similar to the previous models, ant agents leave the nest when their nutrition levels fall below a threshold and begin following the existing pheromone trail in the environment,

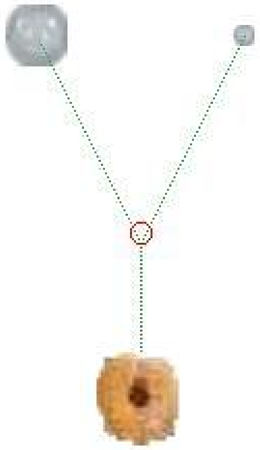


Figure 8.1: Initial environmental setup for the excitement model. The right branch contained the poor food source (size = 5 units) and the left branch contained the good food source (size = 100 units). The bifurcation point is circled.

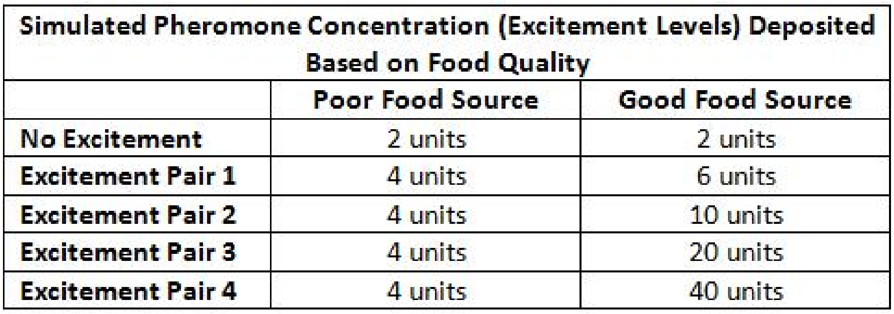
foraging for food sources. As stated earlier, ant agents walk towards the direction with higher pheromone concentration. Once an ant agent arrives at a food source, it consumes 0.02 units, and performs a 180 degree turn, following the pheromone trail back to the nest. If a fed ant agent reaches another food source, a 180 degree turn is performed, and the pheromone trail is followed back towards the nest; whereas if an unfed ant agent reaches the nest, again a 180 degree turn is performed, walking outwards following the pheromone trail, continuing the search for a food source. Once a fed ant agent successfully finds the nest, it stays in the nest until the nutrition levels again fall below the threshold.

Jackson and Chaline (2007) observed increased pheromone deposition after a food source was found, however due to the nature of volatile pheromones, it was not possible to quantify the concentrations of pheromones deposited. Therefore, five sub-versions of the model were developed, where the first sub-version simulated ant agents without the ability of food quality assessment (no excitement), and the other four sub-versions simulated ant agents with varying excitement levels. When ant agents did not possess 'excited' behaviour, they deposited constant amount of pheromones (2 units) throughout the simulation, whereas when they did, different excitement levels were simulated. The values used for the excitement levels are shown in Figure 8.2.

8.2 Results and Discussion

All versions (including the sub-versions) of the model were run with (n=50, 250) ant agents, for 2000 iterations (12.3 minutes) and each was repeated for 10 runs.

The results investigated the effect of 'excited' behaviour on:



Simulated Pheromone Concentration (Excitement Levels) Deposited Based on Food Quality		
	Poor Food Source	**Good Food Source**
No Excitement	2 units	2 units
Excitement Pair 1	4 units	6 units
Excitement Pair 2	4 units	10 units
Excitement Pair 3	4 units	20 units
Excitement Pair 4	4 units	40 units

Figure 8.2: Pheromone deposition (excitement levels) based on food quality.

- The overall foraging efficiency (O.F.E)
- The switching time when the colony successfully switched from the branch with the poor food source to the branch with the good food source
- The ability of the colony to maintain trails to both branches.

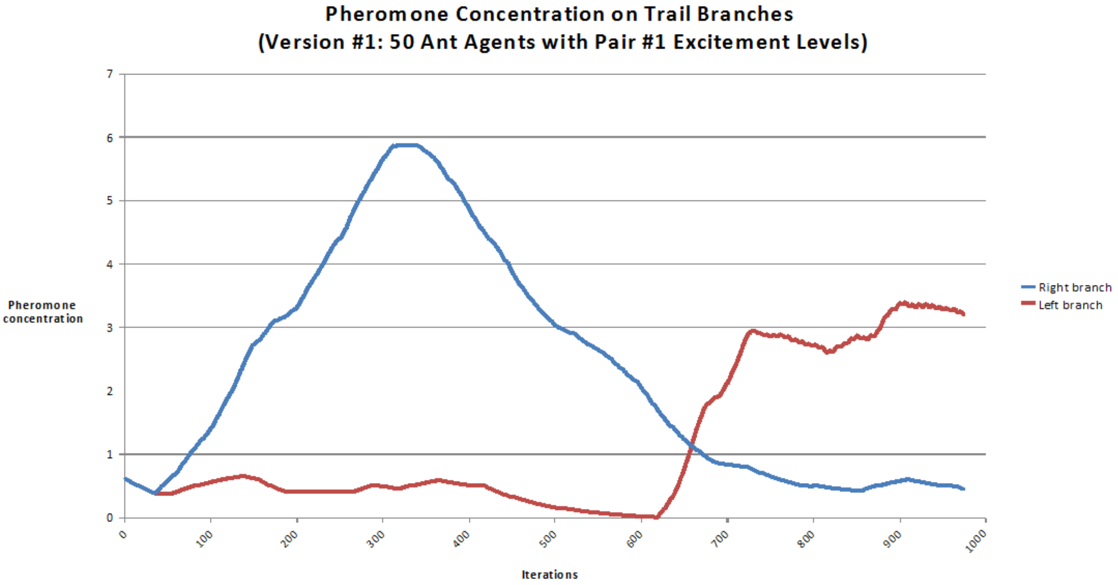


Figure 8.3: Pheromone concentration on branches: Version 1 (n=50) with excitement levels (pair 1).

Related research analysed model results based on the pheromone concentration on the branches. Figure 8.3 demonstrates the results (n=50 ant agents, version 1, depositing varying excitement levels (pair 1)) based on pheromone concentration and figure 8.4 demonstrated results for the same model based on the proportion of the ant agents on the trail branches. As could be seen from the figures, graphs based on the proportion of ants gave a more in-depth view of the process, hence the analysis of model results were based on the proportion of ant agents on branches.

Figures 8.5 and 8.6 provide a summary of the results for when the right branch was discovered initially, which are explained as below.

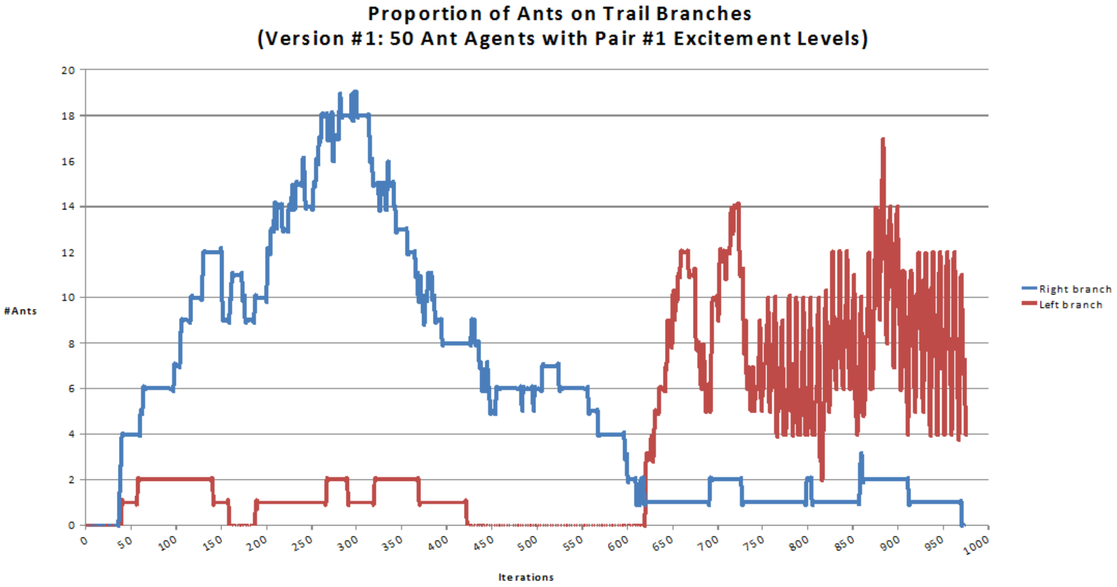
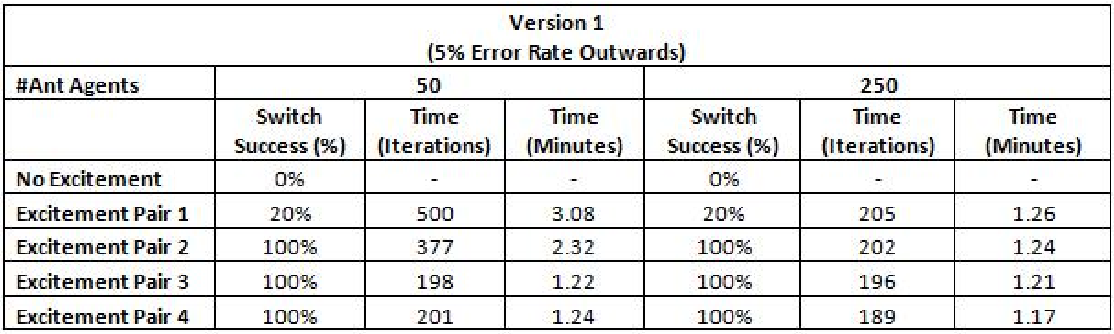


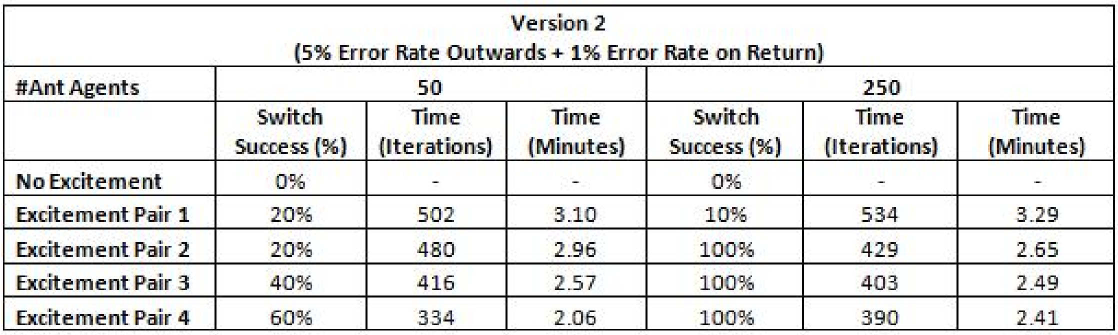
Figure 8.4: Proportion of ants on branches: Version 1 (n=50) with excitement levels (pair 1).



Version 1
(5% Error Rate Outwards)

#Ant Agents	50			250		
	Switch Success (%)	Time (Iterations)	Time (Minutes)	Switch Success (%)	Time (Iterations)	Time (Minutes)
No Excitement	0%	-	-	0%	-	-
Excitement Pair 1	20%	500	3.08	20%	205	1.26
Excitement Pair 2	100%	377	2.32	100%	202	1.24
Excitement Pair 3	100%	198	1.22	100%	196	1.21
Excitement Pair 4	100%	201	1.24	100%	189	1.17

Figure 8.5: When the right branch was explored initially: Summary of switching results from version 1 (n=50,250).



Version 2
(5% Error Rate Outwards + 1% Error Rate on Return)

#Ant Agents	50			250		
	Switch Success (%)	Time (Iterations)	Time (Minutes)	Switch Success (%)	Time (Iterations)	Time (Minutes)
No Excitement	0%	-	-	0%	-	-
Excitement Pair 1	20%	502	3.10	10%	534	3.29
Excitement Pair 2	20%	480	2.96	100%	429	2.65
Excitement Pair 3	40%	416	2.57	100%	403	2.49
Excitement Pair 4	60%	334	2.06	100%	390	2.41

Figure 8.6: When the right branch was explored initially: Summary of switching results from version 2 (n=50,250).

(i) When the right branch was explored initially:

Results from ant agents without the ability of food quality assessment (No Excitement):

For both high (n=250) and low (n=50) numbers of the ant agents, in both versions of the model, the colonies failed to switch to the left branch (with the good food) and the ant agents stayed on the branch that was initially discovered (the right branch), shown in figure 8.7. With (n=250) ant agents, even though the poor food source was depleted after a certain period of time, the ant agents remained stuck on the right branch, unable to switch to the left branch with the good food source.

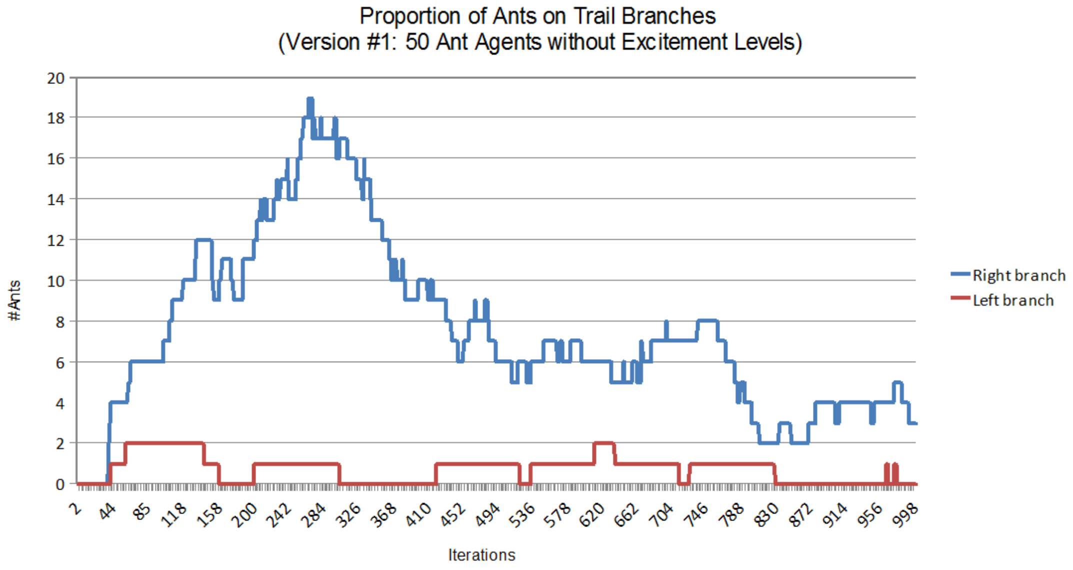


Figure 8.7: Proportion of the ants on branches: Version 1 (n=50) without excitement.

Results from ant agents with varying excitement levels (Pair 1):

For both high (n=250) and low (n=50) numbers of the ant agents, in both versions of the model, only 20% of the runs resulted in a successful switch to the branch with better food source. This demonstrates that the difference between the excitement levels after assessing the quality of food is meaningful and important for the ants to switch efficiently.

Results from ant agents with varying excitement levels (Pairs 2, 3 and 4):

When the model was ran with varying excitement levels of pairs 2, 3, and 4, the results demonstrate that the switching time decreased as the differences between the pheromone levels (based on the quality of the food source) was increased. Therefore, the ant agents were able to distinguish between the quality of the sources more efficiently and a faster decision of was made by the colony.

The error rate introduced in version 1 ensured that a trail to the branch with the poor food source was maintained, while the branch with the good food source was explored. With (n=250) ant agents, once the poor food source on the right branch was depleted, the colony successfully switched to the left branch with the good food source.

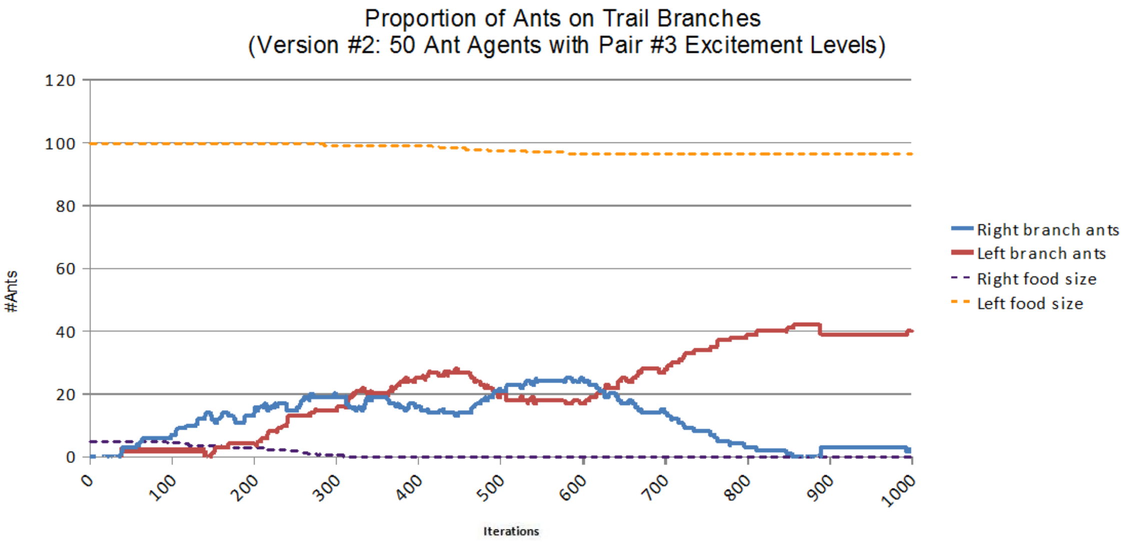


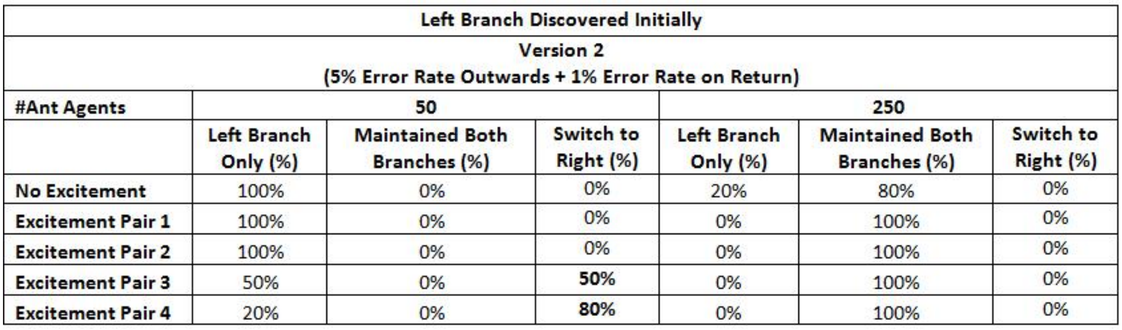
Figure 8.8: Proportion of the ants on branches: Version 2 (n=50) with excitement levels (pair 3).

On the other hand, the additional error rate introduced in version 2 resulted in failure and the majority of the ant agents failed to switch to the left branch with the good food source. This is because, fed ants returning from the good branch had the opportunity to walk on the branch with poor source due to the 1% error rate. Even though this facilitated a trail to the poor source to be maintained, it also led to circumstances where the right branch became stronger than left branch, thereby leading the colony to the branch with poor source rather than the branch with good source over time. With (n=50) ant agents, this led to a complete failure and the colonies were not able to switch at all, getting stuck on the right branch with the poor source; whereas with (n=250) ant agents, the colony was confused and switched between branches multiple times, shown in figure 8.8.

Figures 8.9 and 8.10 provide a summary of the results for when the right branch was discovered initially, which are explained as below.

Left Branch Discovered Initially						
Version 1 (5% Error Rate Outwards)						
#Ant Agents	50			250		
	Left Branch Only (%)	Maintained Both Branches (%)	Switch to Right (%)	Left Branch Only (%)	Maintained Both Branches (%)	Switch to Right (%)
No Excitement	100%	0%	0%	100%	0%	0%
Excitement Pair 1	100%	0%	0%	0%	100%	0%
Excitement Pair 2	100%	0%	0%	0%	100%	0%
Excitement Pair 3	100%	0%	0%	0%	100%	0%
Excitement Pair 4	100%	0%	0%	0%	100%	0%

Figure 8.9: When the left branch was explored initially: Summary of trail maintenance results from version 1 (n=50,250).



Left Branch Discovered Initially						
Version 2 (5% Error Rate Outwards + 1% Error Rate on Return)						
#Ant Agents	50			250		
	Left Branch Only (%)	Maintained Both Branches (%)	Switch to Right (%)	Left Branch Only (%)	Maintained Both Branches (%)	Switch to Right (%)
No Excitement	100%	0%	0%	20%	80%	0%
Excitement Pair 1	100%	0%	0%	0%	100%	0%
Excitement Pair 2	100%	0%	0%	0%	100%	0%
Excitement Pair 3	50%	0%	**50%**	0%	100%	0%
Excitement Pair 4	20%	0%	**80%**	0%	100%	0%

Figure 8.10: When the left branch was explored initially: Summary of trail maintenance results from version 2 (n=50,250).

(ii) When the left branch was explored initially:

In version 1, (n=50) ant agents always explored the left branch and colonies were unable to maintain a trail to the right branch. However in version 2 with (n=50) ant agents, as the gap between excitement levels increased, results demonstrated failure. Due to the 1% error rate, fed ants had the opportunity to walk onto the right branch, depositing high levels of pheromones. Over time, this led to a higher overall pheromone concentration on the right branch and resulted in the colony switching from the left branch with the good food source to the right branch with the poor food source. Even after the poor source was depleted on the right branch, the colony was unable to switch back to the left branch.

With (n=250) ant agents, version 2 did not have a negative influence on the switching behaviour, and in both versions (n=250) the ant agents successfully maintained both trails. Once the poor source was depleted on the right branch, colonies completely switched to the left branch with the good source. This is possibly due to the environmental trail setup being too small for (n=250) ant agents; individual ants were able to quickly deplete the poor food source on the right branch, without 1% error rate having effect on the switching behaviour of the colony. It is anticipated that if the same model is run with a longer trail in a larger environment, similar results with (n=50) ant agents will be obtained.

The overall switching times for both versions of the model with (n=50, 250) ant agents are shown in figures 8.11 and 8.12, which demonstrate that increased excitement levels led to decreased switching times and facilitated the colonies to perform switches to more rewarding branches faster. This was the outcome from the both versions of the models, however the figures help to conclude that the colonies based on Version 1 performed better with faster switches.

A summary of the overall foraging efficiency results are provided in figure 8.13. The

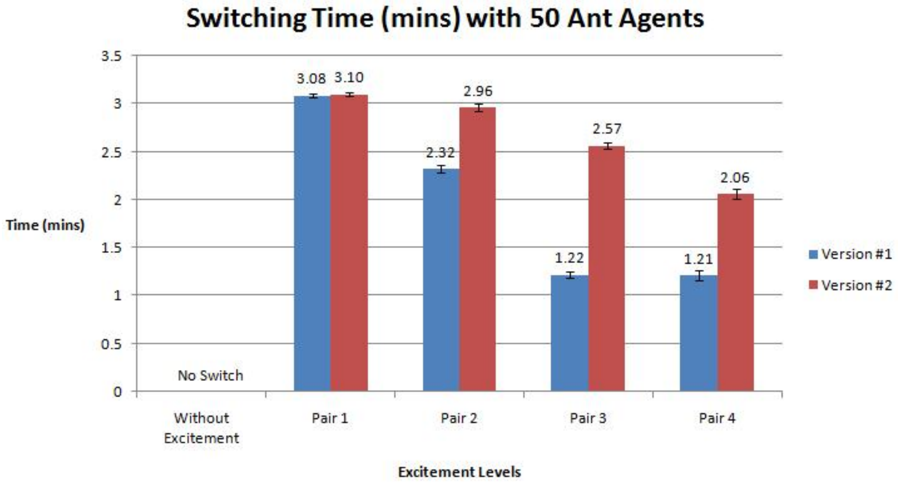


Figure 8.11: Switching time for (n=50) ant agents.

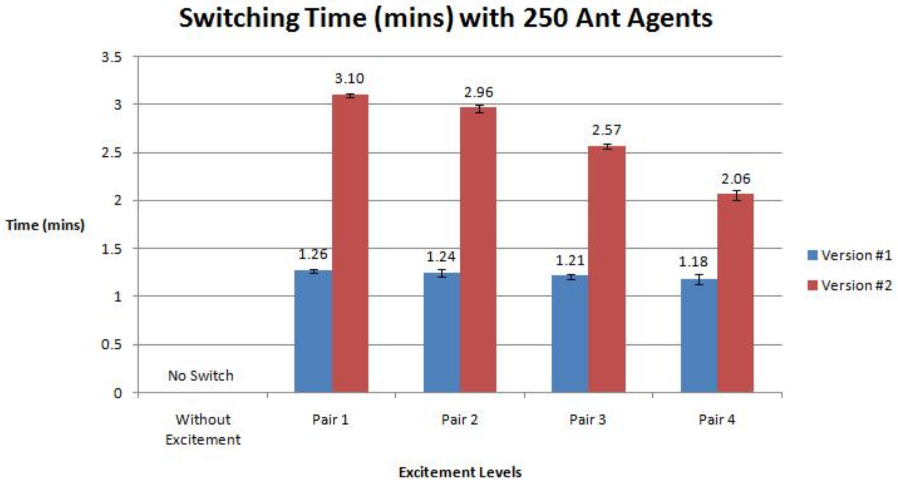
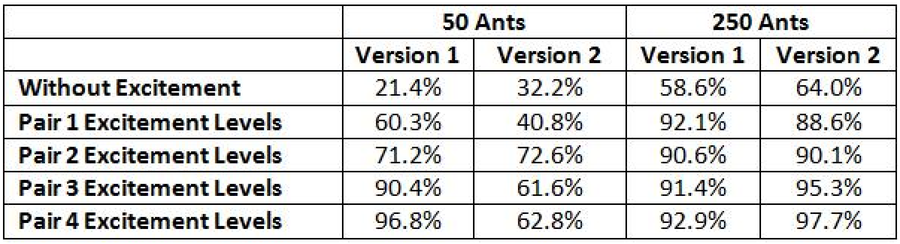


Figure 8.12: Switching time for (n=250) ant agents.

results demonstrate an increasing number of fed ant agents back in the nest at the end of the iteration when the excitement levels were present, suggesting that the trails were maintained more efficiently when the ant agents possessed the 'excited' behaviour. Furthermore, in version 1 the colonies with (n=50) ant agents compared to colonies with (n=250) ant agents achieved approximately equal percentage of success when the excitement levels were present. However, in version 2 the colonies with (n=50) ant agents were not as successful, suggesting that the error rate (backwards) introduced in version 2 were not advantageous for the ant agents. Figures 8.14 and 8.15 show bar charts for the overall foraging efficiency achieved in both versions of the model.

The O.F.E results were further analysed by a Difference of Means test with t-distribution (Two-sample Assuming Equal Variances), which was applied to test the significance of means between the colonies with and without the 'excited' behaviour at a 0.05 (two tail p-value) significance level. If the t-statistical (calculated) value was greater than the t-critical (table) value, the null hypothesis of no difference was rejected and it was concluded that there was a significant difference between the two means. Standard Error



	50 Ants		250 Ants	
	Version 1	Version 2	Version 1	Version 2
Without Excitement	21.4%	32.2%	58.6%	64.0%
Pair 1 Excitement Levels	60.3%	40.8%	92.1%	88.6%
Pair 2 Excitement Levels	71.2%	72.6%	90.6%	90.1%
Pair 3 Excitement Levels	90.4%	61.6%	91.4%	95.3%
Pair 4 Excitement Levels	96.8%	62.8%	92.9%	97.7%

Figure 8.13: O.F.E results from both versions of the models with (n=50, 250) ant agents.

(calculated by; Standard deviation/Sqrt(Total number of runs), where the total number of runs was 10) is also demonstrated by error bars on the bar charts.

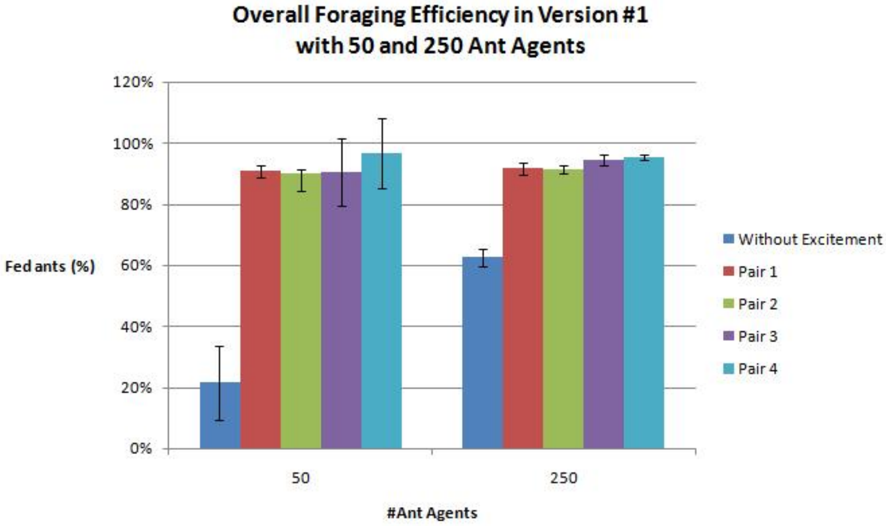


Figure 8.14: O.F.E results from the models with (n=50, 250) ant agents in version 1.

As shown in figures 8.14 and 8.15, the colonies with 'excited' behaviour resulted in improved results. The results from the models without excitement were statistically compared against the results from the models with varying excitement levels. In Version 1, in both colonies (n=50, 250), there was a significant increase, as when n=50; without excitement against pair 1 excitement levels resulted in (t-statistical: 30.129, t-critical: 2.101, p: 7.43x10^{-17}), against pair 2 excitement levels resulted in (t-statistical: 8.577, t-critical: 2.101, p: 8.96x10^{-8}), against pair 3 excitement levels resulted in (t-statistical: 16.753, t-critical: 2.101, p: 2.0x10^{-12}) and against pair 4 excitement levels resulted in (t-statistical: 46.768, t-critical: 2.101, p: 3.0x10^{-20}). When n=250; without excitement against pair 1 excitement levels resulted in (t-statistical: 30.129, t-critical: 2.101, p: 7.43x10^{-17}), against pair 2 excitement levels resulted in (t-statistical: 8.577, t-critical: 2.101, p: 8.96x10^{-8}), against pair 3 excitement levels resulted in (t-statistical: 16.753, t-critical: 2.101, p: 2.0x10^{-12}) and against pair 4 excitement levels resulted in (t-statistical: 46.768, t-critical: 2.101, p: 3.0x10^{-20}).

In Version 2, for colonies with (n=250) ant agents, though not as evident compared to Version 1, there still was a significant increase between the colonies without excitement and colonies with varying excitement levels. When colonies without excite-

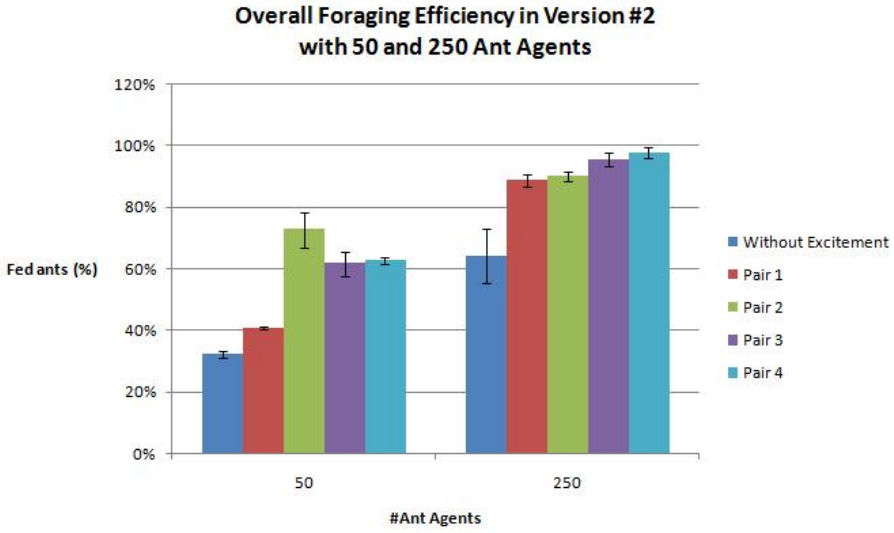


Figure 8.15: O.F.E results from the models with (n=50, 250) ant agents in version 2.

ment were compared against colonies with pair 1 excitement levels, this resulted in (t-statistical: 2.224, t-critical: 2.101, p: 0.584), against pair 2 excitement levels resulted in (t-statistical: 2.41, t-critical: 2.101, p: 0.002), against pair 3 excitement levels resulted in (t-statistical: 2.878, t-critical: 2.101, p: 0.06) and against pair 4 excitement levels resulted in (t-statistical: 3.123, t-critical: 2.101, p: 0.056). However this was not always the case for colonies with (n=50) ant agents, which further demonstrated the confusion introduced by the error rate introduced in Version 2. The comparison of colonies without excitement against colonies with pair 1 excitement levels resulted in (t-statistical: 0.557, t-critical: 2.101, p: 0.039), against pair 2 excitement levels resulted in (t-statistical: 3.627, t-critical: 2.101, p: 0.027), against pair 3 excitement levels resulted in (t-statistical: 2.004, t-critical: 2.101, p: 0.01) and against pair 4 excitement levels resulted in (t-statistical: 3.123, t-critical: 2.101, p: 0.006).

Overall, the results demonstrate that the increased trail laying upon assessing food quality helps ant agents in switching to better food sources and maintaining a more efficient foraging strategy. Increased excitement levels based on different food qualities decreases the switching time, therefore improving the performance of the colony. The results further demonstrated that the choices of ant agents at the bifurcation point (as observed by Robinson et al. (2008)) could influence the switching behaviour. The outwards error rate (5%) was found to be advantageous as it ensured that both branches were explored by ant agents, whereas an error rate on the return leg of the foraging trip (1%) could lead to confusion among the colony and failure to switch to a branch with the poor food source. Therefore, it could be concluded that an outwards error rate coupled with 'excited' behaviour (with increased gaps between excitement levels (concentration of pheromones deposited) upon assessing food quality, would be the optimum foraging strategy for Pharaoh's ants.

The 'excited' behaviour of Pharaoh's ants were investigated through detailed agent-based models, where the increased trail deposition based on food quality assessment was shown to increase the success of the colonies even further, enabling them to switch to branches of trails which would lead to more rewarding food sources. For this model, a Y-shaped bifurcation environment, a popular experimental setup amongst biologists, was utilized, which formed a strong ground to investigate the behaviour of ant agents at bifurcation points. The results suggested that no matter the how strong a trail branch is equipped with pheromones, the fact that a minority of the ants still preferred to explore trail branches with low pheromone concentrations is advantageous for the colony. It was shown that this facilitates the simultaneous exploitation of multiple food sources. Furthermore, when this behaviour was coupled with deposition of different concentrations of pheromones based on the food quality, multiple trails would be maintained efficiently.

Chapter 9

Ants and MANETs

The increased use of laptops with 802.11/Wi-Fi wireless networking have made mobile ad-hoc networks (MANETs) a popular research topic since 1990s. A MANET is a decentralized group of mobile nodes with an unstructured network topology, which exchange information by means of wireless transmission. Nodes move around freely and communicate with each other based on their transmission range, forming temporary communication links. In order to establish communication between nodes that are outside the range, a node uses its neighbour nodes as a 'bridge' to receive and forward messages (Wang et al., 2009). This flexibility, however, comes at a price, as communication is difficult to organize due to frequent changes in topology.

Nature-inspired algorithms, specifically Ant Colony Optimization (ACO) algorithms, have been extensively applied as routing algorithms to address the problems of routing in MANETs. This is because MANETs and ant colonies posses similar fundamental properties, which are (adapted from Chen and Heinzelman, 2005):

- *Dynamic nature*: Hosts change their positions randomly, leading to an unpredictable topology. This means an established route to a destination may not be available after a while; analogous to ephemeral (dynamic) food sources and their depletion by ant colonies.
- *No centralized control*: All nodes function independently without being controlled by a centralized node, thereby resources cannot be assigned in a predetermined manner; analogous to the decentralized fashion of ant colonies, functioning without a leader, relying on the local information pheromones deposited in the environment.
- *Limited detection*: Based on wireless channel, nodes have a limited radio range; analogous to ant colonies relying on pheromones, which decay and evaporate over time.

ACO is a population-based, general-purpose search technique for solving difficult combinatorial problems, inspired by the pheromone trail laying and following behaviour of ant colonies (Dorigo and Sttzle, 2006). Routing in ACO is achieved by transmitting ants rather than routing tables or flooding link-state packets (LSPs) across the network. Since the ants are represented by small agents, they can be piggy-backed in data packets, where frequent transmission of ants (updates of routing information) is possible.

This chapter provides an overview of existing routing protocols for MANETs in the literature, focusing on those based on ACO. Where possible, links between the findings from Pharaoh's ants and challenges in MANET routing algorithms are identified and potential improvements are proposed.

9.1 Background

In the absence of a fixed infrastructure, MANET nodes communicate directly with one another in a peer-to-peer fashion. The mobility of the nodes impose limitations on their power capacity and consequently, on their transmission range. While nodes move in an out of range with respect to other nodes, the instantaneous topology changes must be communicated to all other nodes. Furthermore, the limited bandwidth of wireless channels and their transmission characteristics impose additional constraints on how much and how often control information can be exchanged (Chakrabarti et al., 2001). Therefore, ensuring effective routing for ad-hoc networks is one of the great challenges that need to be addressed. A common solution is for each node to update its routing table frequently by flooding control packets throughout the network. However, in dynamic networks transmitting large routing tables or flooding packets at regular intervals may incur large routing overheads and result in slower responses to changes in network topology. A great amount of resources has been devoted to research in the MANET field in the past three decades (Garcia-Macias and Gomez, 2007), introducing various routing protocols with an aim to propose solutions for effective routing in MANETs. The evaluation of such protocols tend to be based on bounded space, with nodes sending data at a constant rate, and compared against each other based on a number of criteria, such as end-to-end delay, packet delivery ratio, and the routing overhead.

Much of this work is targeted at finding a feasible route from a source to a destination, without considering current network traffic or application requirements. However, the lack of fixed base stations in ad-hoc networks implies that there is no dedicated agency to manage the channel resources, suggesting that there must be mechanisms available to recover efficiently from the inevitable packet collisions (Chakrabarti et al., 2001). Otherwise, the network may become overloaded, where the application will have no way of improving its performance. This paved way to implementations of "Quality of

Service (QoS) aware routing protocols", where QoS refers to maintaining consistent performance on a network by managing a number of performance related metrics in a coordinated fashion, where bandwidth and latency are some of the key metrics. Therefore, QoS-aware protocols aim to utilize an approximate bandwidth estimation to adapt to network traffic. (Chen and Heinzelman, 2005). Routing protocols for MANETs and the QoS concept are discussed in the next sections.

9.2 Routing in MANETs

MANET routing protocols are classified into three categories: (i) proactive, (ii) reactive, and (iii) hybrid routing protocols. The diagram below summarizes the key differences in between the three categories along with examples of existing algorithms.

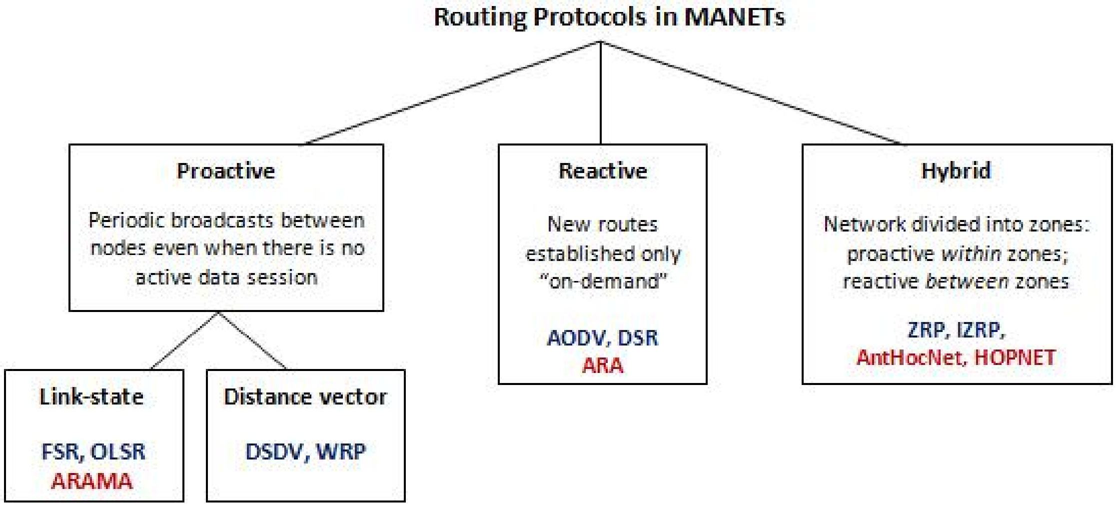


Figure 9.1: Routing protocols in MANET.

9.2.1 Routing protocols for MANETs

Proactive routing protocols:

In proactive routing protocols, each node attempts to maintain a consistent view of the network, which is done by periodically broadcasting its routing information to every other node within its neighbourhood. They are classified into two, which are (i) link-state routing and (ii) distance vector routing.

Most of today's wired network routing algorithms, as well as the Internet, use the link-state method (Clausen et al., 2003), where the outgoing link cost is sent to every node in the network in order to construct a routing tree. Nodes then refer to their routing trees to forward packets. Popular examples include Optimized Link State Routing (OLSR) and Fisheye State Routing (FSR), where FSR is regarded as the most efficient protocol among these (Wang et al. 2009). In FSR the LSPs are not broadcasted, but periodically exchanged with the local neighbor nodes, whilst in OLSR, each node periodically broadcasts a list of its 1-hop neighbours (adjacent nodes). However, both approaches were concluded to be insufficient for MANETs due to large overhead.

In distance vector routing, routing tables are forwarded which for each node contain the destination node, next hop and the hop count. The nodes compare the received entries against their own and modify their routing tables accordingly, which is followed by broadcasting the updated routing table. A sequence number is generated by the destination, which provides the packets with a unique ID. This was introduced to avoid potential routing loops which was a common problem in distance vector routing. Popular examples include the Wireless Routing (WRP) and Destination Sequenced Distance Vector (DSDV) protocols, where DSDV is well known as it is based on the popular distributed Bellman-Ford routing algorithm (Wang et al., 2009). DSDV utilizes two types of packets: (i) full dump and (ii) incremental. Full dump packets carry the available routing information, while the incremental packets carry only the information changed since the last full dump. The two types of packets aim to lower the overhead and shorten the update latency, however, overall the overhead of DSDV is still quite large due to the need for frequent updates, thereby large amount of information to be carried. In WRP, each node maintains four tables: (i) distance, (ii) routing, (iii) link-cost tables, and (iv) a message re-transmission list. These tables lead to high memory consumption at each node, and result in routing overhead.

The advantage of these protocols is the short response time in determining a good route from source to destination, as a result of frequent up to date information on the current network topology in each node. However the flooding of control packets consumes a large portion of the network bandwidth. Furthermore, most of the established routes are never used, which is a waste of network resources. Overall, although proactive routing protocols have a very low response time, considering the constant changes of network topology, proactive routing protocols alone do not provide a feasible solution.

Reactive routing protocols:
Also known as on-demand routing protocols, reactive routing protocols have been proposed with an aim to reduce the overhead caused by flooding of control packets. This is achieved by maintaining routing information only for the active routes, rather than maintaining all the routes periodically. Therefore, *route discovery* is initiated ‘on demand’ when required. This protocol consists of two phases: (i) route discovery and (ii) route maintenance.

In the route discovery process, a route request packet (RREQ) is usually flooded until it reaches the destination (or a node that contains the route to the destination). Then, a route reply packet (RREP) is generated and sent back to the source to inform the available route. This route is maintained as long as the connection is active and removed once it is no longer required.

If the link is broken due to node failure or a dynamic change, the *route maintenance* phase is initiated, where the node sends out an error packet to the source. Upon receiving the error packet, if the source still needs a route to the destination and cannot find an alternative route, the source re-initiates an RREQ to find a new route.

Popular examples include ad-hoc On-demand Distance Vector (AODV) and Dynamic Source Routing (DSR) protocols. DSR is a standard reactive algorithm without any additional properties, which means that if there are no topological changes in the network, no control packets will be sent across. In AODV, a list of unidirectional links tracked by the RREQ is kept, which are used to prevent RREP from visiting them. In the event of a route failure, an error packet is broadcasted until it reaches the source node. Once the source node receives it, RREQ and RREP packets are sent across in the same manner, however it is possible to reduce the delay by sending packets from the node that detected the error, rather than the source. DSR was found to perform better than AODV in terms of both delay and overhead in simple scenarios, i.e. a few source nodes and low mobility, whereas shorter delays but higher overhead were produced by AODV in complex scenarios.

Overall, reactive routing protocols seem to result in a reduced control overhead, along with increased packet delivery ratio and improved network efficiency. However, if the nodes move frequently, the network would again spend a lot of resources on maintaining its current routes, thus leading to an increase in overhead. Furthermore, the response time could be very long, leading to dropped data packets during the route discovery period. Despite all the disadvantages, related work in the literature has shown that in general, reactive routing protocols are more applicable for MANETs than proactive routing protocols (Wang et al. 2009).

Hybrid routing protocols:
Hybrid routing protocols were introduced with an aim to combine the advantages of proactive and reactive routing protocols. In hybrid protocols, the network is partitioned into zones. A proactive routing method is used within each zone while a reactive routing method is used for inter-zone communication. With this method, the overhead is reduced as the inefficiency of the proactive approach is limited only within the zone, while reactive routing enables efficient connectivity across zones. In such protocols, the zone radius plays a key role in the overall performance as it determines the size of the zones. For instance, if the zone radius is too large, then the hybrid protocol behaves like a proactive protocol, whereas if it is too small, then the protocol will behave like a reactive protocol. Popular examples include Zone Routing Protocol (ZRP) and Zone-based Hierarchical Link State (ZHLS) protocols.

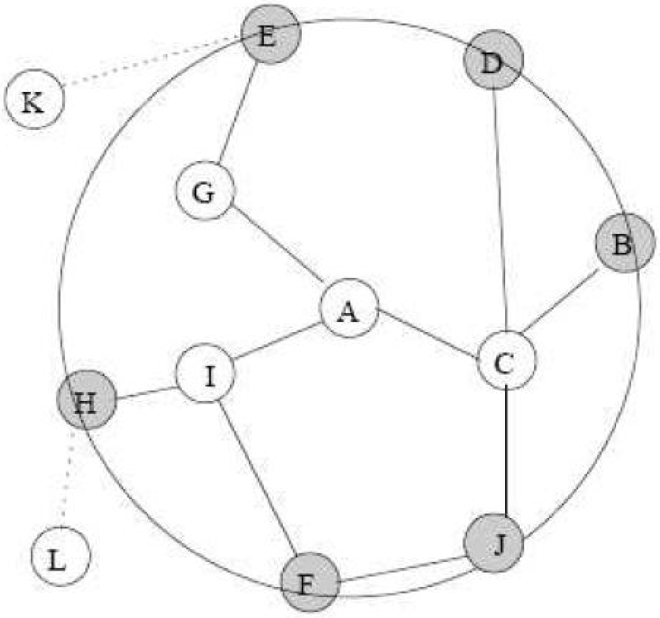


Figure 9.2: Hybrid routing protocol (Zone radius=2, A's zone=B, C, D, E, F, G, H, I, J, Interior nodes=C, G, I, Border nodes=B, D, E, F, H, J).

ZRP (Haas, 1997) applies 'bordercasting' for reactive routing, where the RREQ packet is forwarded only by the border node of the zone. When the RREQ packet is received by the receiver border node, it looks up the proactive routing table in its zone and sends back a RREP packet if it has the route to the destination, otherwise repeats bordercasting. In ZHLS, the global positioning system (GPS) is also utilized to obtain locational information on the zones, which is used to define overlapping zones and assign each node a 'node ID' and a corresponding 'zone ID'. This forms a hierarchical topology of two levels: (i) node and (ii) zone level, which handles link failures in an efficient manner. Once the source node becomes informed of the node ID and the zone ID for the destination node, even if the link breaks ZHLS can find another route to destination with less control packets sent across, thereby causing less overhead compared to reactive routing protocols. However, the need to use GPS to obtain information on locations is a significant disadvantage.

Overall, hybrid routing protocols use the integration between proactive and reactive protocols to increase the scalability. Even in large scale networks, they perform better compared to proactive and reactive protocols, achieving less delay and overhead. However, they are not fully adaptive, parameters like zone radius require to be finely adjusted and pre-programmed.

9.2.2 Ant-Based Routing Protocols

As stated above, the traditional routing protocols face many problems due to the dynamic behavior and resource constraints in MANETs. To overcome this limitation, a routing protocol is required to have a self-organizing or an autonomous feature. An approach to achieve such feature is to use a biologically-inspired mechanism. In nature, many biological systems possess the ability to maintain their stable condition themselves regardless of the external influences or dynamic conditions. Ant colonies are complex biological systems that respond to changing conditions in nature by solving dynamic problems. Their ability of decentralized decision-making and their self-organized trail systems, have inspired computer scientists since 1990s, and consequently initiated a class of heuristic search algorithms, known as ant colony optimization (ACO) algorithms. These have proven to be very effective in solving combinatorial optimisation problems, especially in the field of telecommunication.

ACO is based on the ant foraging behaviour, utilizing pheromone deposition as a means of evaluation for the travelled route. Rather than RREP and RREQ packets, 'forward' and 'backward ant' agents are sent across the routes, where the ant agents deposit pheromones at the nodes arrived. In the long term, this approach is used to determine the shortest path between the source and the destination. The first ACO system was introduced by Marco Dorigo in his Ph.D. thesis (1992), and was called the Ant System (AS) (Ant Colony Optimization, 06.03.2008). This is the first algorithm that was inspired by the trail-following behaviour of ants and was initially applied to a discrete optimization problem, the Travelling Salesman Problem (TSP). Although the results obtained were not state-of-the-art on the TSP, AS compared well with other general purpose metaheuristic methods, such as simulated annealing, evolutionary computation, and tabu search and consequently gave rise to a whole set of ant behaviour based algorithms. Popular ACO algorithms along with their brief details are as follows:

AntNet: (Di Caro et al., 1997)
Designed for a wired network, forward ants move based on a 'visited nodes list', pheromone information and the outcome of a heuristic function based on the length of the link to the next node. To avoid congestion, the forward ant is released based on a probability value which changes according to the current traffic load. The backward ant returns to the source node by following the same path as the forward ant. While returning, the pheromone information and other statistical information gathered by the forward ants are used to update the routing table of each intermediate node. AntNet has been extensively tested under different traffic patterns, proving to be highly adaptive and robust, outperforming its competitors.

ARA:
Based on AntNet, ARA was designed for MANETs. It is an ordinary reactive routing protocol consisting of three phases: (i) route discovery, (ii) route maintenance, and (ii) route failure handling. ARA sets up the path reactively using the forward ant and the backward ant in the route discovery process. It differs from AntNet, by not keeping

the visited nodes in memory. Instead, each intermediate node uses the source and the previous hop of the forward ant to create a route entry. Routing loops are avoided by using a sequence number generated by the destination node and route maintenance is performed via reinforcement by data packets. The failure handling phase re-initiates route discovery when there is no alternative link in the routing table.

AntHocNet: (Di Caro et al., 2004)
Possibly the most popular MANET algorithm due to its performance, AntHocNet is a hybrid routing algorithm which combines both reactive and proactive routing strategies. Similar to AntNet, it utilizes pheromone deposition and the ‘visited nodes list’. A route is set up reactively using reactive forward ants which gather a ‘path quality’ while travelling in the network. Upon arrival at the destination, backward ants return on the path taken by forward ants to the source node and update the routing tables of nodes as they go along. Unlike ARA, AntHocNet uses proactive forward ants to maintain the paths. Therefore, by being reactive, the algorithm does not try to maintain up-to-date routing information between all the nodes in the network, but instead concentrates its efforts on the pairs of nodes between which communication sessions are taking place, whereas by being proactive, for ongoing communication sessions it continuously tries to maintain and improve existing routing information. When compared to AODV, AntHocNet was found to be twice as efficient in terms of end-to-end packet delivery, while the packet delivery ratio remained the same.

HOPNET: (Wang et al., 2009)
The first routing protocol that combines the concept of ZRP and ACO, is an improved version of AntHocNet in terms of scalability. It utilizes five types of ants, which are: (i) internal forward ant, (ii) external forward ant, (iii) backward ant, (iv) notification ant and (v) error ant. The internal forward ant is responsible for maintaining the proactive routing table continuously within its zone. The external forward ant performs the reactive routing to nodes beyond its zone. When an external forward ant is received at the destination, it is converted to a backward ant and sent back along the discovered route. If a new route is reactively discovered, then a notification ant will be sent to the source node and to all nodes on the route to update their reactive routing table. The error ant is utilized to communicate any changes in the network topology and restart a new search by the destination if the source still needs a route. In route discovery, priority is given to unvisited nodes, rather than routes with pheromones. The forward ants explore all adjacent links, aiming to ensure that no link is missed. In addition to scaling much better than AntHocNet, HOPNET was also shown to have a higher overall packet delivery ratio, where the size of the network had very little impact on the overall performance of the algorithm.

9.2.3 Pharaoh's Ants and Routing in MANETs

Even though ACO is inspired by ant behaviour, it does not faithfully follow ant biology. This is because a computer algorithm does not need to be constrained in the same way as real ants. For example, in ACO, "pheromone" is normally applied after an agent has identified a 'food source', on its way back to the 'nest', whilst real ants deposit pheromones as they walk. Therefore, it should be noted that the inspiration taken from the behaviour of ant colonies are applied to routing algorithms through ACO at a high level.

However, they also have a large degree of commonality. For instance in the hybrid zone routing protocol, HOPNET, the network is divided into zones based on a zone radius, which is similar to the concept of 'vapour tunnel' in ant colonies, discussed earlier in Chapter 6. This is because pheromone molecules both decay and move over time and a combination of pheromones lead to a 'tunnel' of pheromone molecules. The ants which are within the tunnel follow the trail locally, whereas the ants that are outside the tunnel are not informed of the trail, walking non-randomly based on the turning kernel within the environment. Ants within the tunnel correspond to nodes within the zone, proactively maintaining routes; whereas ants outside the tunnel correspond to a node outside the zone, where a link needs to be established reactively.

In ACO there is always a possibility of stagnation. Once an optimal path is chosen by all ants, this recursively increases an ant's preference, which may lead to the congestion of this path or a dramatic reduction in the probability to select other paths. Furthermore, this could result in packets queueing at nodes increasing its probability of being dropped. These scenarios are undesirable for a dynamic network, and could potentially be improved by the observed behaviour of Pharaoh's ants at bifurcations; no matter how strong a trail is in terms of pheromone concentration, a certain minority of Pharaoh's ants 5% for outwards, 1% for back towards the nest) were observed to follow the trail with lower concentration. Overall, this ensured that multiple trails were maintained, which resulted in multiple food sources being exploited simultaneously. It was further demonstrated that if one of the food sources were depleted or removed, the colony would have an alternative rewarding route to exploit (explained in detail in Chapter 8). If such a technique is applied to routing protocols, it could potentially enable a more efficient search strategy for route discovery and facilitate route maintenance; multiple routes to destination could be established so that an alternative route would be readily available in the event of a link failure. Therefore nodes will be able to send packets through the alternative route avoiding queues, hence minimizing the amount of dropped packets and reducing the overhead. However, it is anticipated that maintaining such alternative routes require additional overhead, suggesting that there has to be a compromise between increase in overall efficiency and routing overhead.

Pharaoh's ants also have division of labor among the forager workers, some of whom specialise in laying and detecting pheromone trails, by performing U-turns and laying pheromones more frequently. The U-turner ants were found to play a key role in improving trail network connectivity (see Chapter 6), which led other colony members to food sources more effectively, thereby increasing the overall foraging efficiency. Maintaining a well-connected trail network ensured that trails leading to new food discoveries were rapidly linked to the nest and thus available for other foragers to follow (Jackson et al., 2010). Such behaviour clearly represents a potential for improving route maintenance if applied to routing algorithms. Once a route is established from source to destination, U-turner ants could be sent across the established route, facilitating continuous reinforcement of the exploited route. U-turner ants would especially be useful when the distance between the source and destination is large, i.e. when there is a greater probability of idle links. However, similar to the previous case, it should be noted that an increased routing overhead would again be anticipated due to more packets being sent across the network, suggesting a compromise between increased efficiency and routing overhead. The U-turn Model (in Chapter 7) demonstrated that as observed in nature, a population of only 7% of U-turners were sufficient to increase the success of the colonies with populations of (n=10, 50, 100, 250) ant agents. Even though a working model of a routing scenario is not developed, the small proportion of U-turners required indicates that the increase in overall efficiency could be much greater than the overhead introduced. To achieve the optimum performance, it should also be noted that the compromise between the introduced overhead and the overall efficiency targetted to achieve may need to be dynamic. For instance, if the discovered food source was close to depletion, a dynamic increase in exploration would be advantageous for the colony, where the U-turners would not be maintaining trails until a fresh trail to a new source is established. Therefore, balancing such a compromise would enable to track the problem effectively.

9.3 Quality of Service (QoS) in MANETs

Two key elements of network performance are bandwidth and latency. Although the theoretical peak bandwidth of a network connection is fixed according to the technology used, the actual bandwidth experienced varies over time and could be affected by latencies. Latency refers to any of several kinds of delays typically incurred in processing of network data, such as propagation delay, transmission delay and processing delays. Excessive latency creates bottlenecks that prevents data from filling the network pipe, thus decreasing effective bandwidth. The impact of latency on network bandwidth can be temporary or persistent depending on the source of the delays. QoS refers to measuring and maintaining consistent performance on a network by managing both bandwidth and latency, as well as a number of other performance metrics, such as dropped packets, errors, jitter and out-of-order delivery, in a coordinated fashion. In this context, the main focus of QoS is on bandwidth and latency.

QoS involves a variety of techniques and requirements to ensure that certain application-specific performance needs are met. In order to achieve this, the MANET must be aware of the applications' QoS requirements, which can be a challenging task as different services types, i.e. video streaming, voice, file transfer, have significantly different objectives for delay, bandwidth and packet loss (Chakrabarti et al., 2001). To address this, the first essential task is to find a route between the source and destination that will have the necessary resources available to meet the QoS constraints for the desired service. Therefore, the design of a routing protocol in an ad-hoc network has a significant impact on the achievable QoS. As a result, it is important to consider the impact of different application-specific QoS requirements on the routing process.

Crawley et al. (1998) states that QoS routing offers serious challenges even for today's Internet, which has only supported 'best effort' service; "it will do its best to transport the user packets to their intended destination, although without any guarantee". With the Internet as the basic model, the same has also been true for ad-hoc networks, especially given their peculiar challenges compared to traditional wireline or even conventional wireless networks (Chakrabarti et al. (2001)). In recent years however, QoS in ad-hoc networks as a research topic has started to receive attention from a growing number of researchers. Related work in this area include Chen and Heinzelman, (2005), Chen et al. (2004) and Chakrabarti et al. (2001).

9.3.1 Pharaoh's Ants and QoS

Considering the above, the 'excited' behaviour of Pharaoh's ants (explained in Chapter 8) could possibly be a source of inspiration to provide some awareness of QoS within a routing algorithm. It was observed in Pharaoh's ants that increased trail laying based on food quality assessment helped the ant colonies choose branches with good food sources, even if the branch with poor food source was exploited initially. Therefore, through the 'excited' behaviour, the colony was able to add an additional bias to those sources of food which had higher quality, possibly even if they were further away. This could be concluded as a balance between multiple requirements affecting the overall foraging efficiency, such as the distance to food source (the speed that food can be acquired) and the quality of the food source (for a large colony to depend on for a longer period of time). However, this balance varies based on the needs of the colony, which is analogous to application-specific QoS requirements. This scenario is similar to a network of heterogeneous nodes with network links offering varying latency and bandwidth, i.e.

network links with low latency but low bandwidth versus those with higher latency and higher bandwidth. Therefore, based on the requirements of the application (e.g. video conferencing or file transfer), modulating routing ‘excitement’ levels (i.e. amount of pheromones deposited by ant agents based on link quality) could contribute to maintaining a balance between demand and supply, thereby adapting routing accordingly and achieving a desirable QoS.

Hence it is clear that in order to achieve effective routing, it is essential to address QoS issues. It is a complex problem with many facets, where algorithms, policies and protocols for coordinated admission control, resource reservation and routing for QoS are only recently beginning to receive attention (Chakrabarty et al., 2001). It is all about a subtle balance and relevant adaptation in order to satisfy the changes in requirements.

9.4 Conclusion

In this chapter, a review of routing algorithms for MANETs was provided, focusing on ant behaviour inspired routing algorithms. Overall, the hybrid zone routing algorithm, HOPNET, based on the most ant inspired behaviour, was concluded to outperform the rest. Further improvements were suggested from the findings of Pharaoh’s ants, such as the application of the behaviour observed at bifurcation points and U-turning, for route discovery and maintenance. It is anticipated that the application of such behaviour could potentially increase the efficiency of current algorithms by improving the ability to discover and maintain alternative routes respectively.

A brief discussion on the concept of QoS and its application for MANETs was also provided. In the literature QoS provisioning has been identified as a serious issue for MANETs that needs to be addressed in order to achieve more effective routing. The ‘excited’ behaviour of Pharaoh’s ants observed was suggested as a potential solution to improve the overall QoS.

There are further mechanisms proposed in the literature that are hypothesised to improve the foraging strategies of Pharaoh’s ants, such as the use of multiple pheromones (short and long term attraction and short term repellent pheromones) for communication. Research on the organization of Pharaoh’s ant foraging systems has shown that ant foraging trail networks are much more complex than generally perceived, where this complexity was shown to be not accidental but exists to make the foraging system of a colony more effective at collecting food. Therefore, it could be concluded that by incorporating further inspirations from the unique mechanisms of ant colonies, ACO (and routing algorithms based on ACO) algorithms could be further optimised, but further work needs to be done to account for the challenges, such as the overhead introduced from the additional complexity of adding ant inspirations to routing algorithms.

Chapter 10

Conclusions and Future Work

The main objectives of this research was to develop realistic agent-based models in order to contribute to the detailed understanding of the underlying mechanisms in foraging systems of Pharaoh's ants, and to identify potential applications for biomimicry solutions in telecommunications and networking. To achieve these objectives, ABM was utilised through the FLAME framework to benefit from technological advantages such as HPC; Biological experiments with Pharaoh's ants were conducted to obtain experimental data in order to minimise assumptions and achieve realistic models; and, A video tracking system was developed to extract the experimental data obtained, which enabled parameter estimation for the models developed. As a result, the movement patterns of the Pharaoh's ants were estimated and expressed in terms of a probabilistic turning kernel. This enabled simulating the movement of Pharaoh's ants in territories without pheromones, facilitating a realistic search strategy and formation of pheromone trails to the discovered food sources. Furthermore, the observed behaviour of specialist ants performing U-turns and their frequent pheromone deposition was modelled and their successful contribution to the overall foraging efficiency of the colony was demonstrated. Increased pheromone deposition by the colony members based on food quality was also modelled, and its potential to be an underlying mechanism for the sophisticated foraging strategies of Pharaoh's ant colonies was confirmed. Based on such observed behaviour and the model results, potential links were identified with routing algorithms for MANETs, including QoS considerations.

The sophisticated foraging behaviour of the ant colonies has been extensively investigated. More than 50 years of research unearthed their remarkable trail systems achieved through robust, decentralized communication. Their collective intelligence has been shown to be one of the best examples of self-organization, which has inspired many researchers from various disciplines. Early research revealed their ability to detect shortest paths in static environments, whereas recent research discovered fundamental mechanisms in the foraging systems of Pharaoh's ants, such as the use of multiple pheromones

(Jackson and Cháline, 2007; Robinson et al., 2007), their ability to exploit trail network topology (Jackson et al., 2004) and division of labour through specialist U-turner ants (Hart and Jackson, 2004).

This chapter summarises the achievements of this research and outlines future work, concluding with an overview of potential applications via Biomimicry.

10.1 Experiments, Models and Achievements

Agent-based modelling, as opposed to other approaches (discussed in Chapter 3), enabled to focus on individuals rather than the population, facilitating a detailed understanding of the mechanisms under study at the individual level. The interactions between agents based on simple rules led to emergent behaviour, providing better insights into the foraging strategies of ant colonies.

The FLAME framework, which allows high performance agent-based modelling on parallel architectures, was used as the modelling platform. Various technological challenges in modelling were addressed, making the models more realistic and the results more credible. The addressed challenges included: (i) dynamic creation and death of agents during a simulation; simulating a dynamic environment, (ii) environment with continuous space; enabling precise and flexible movement of ant agents, and (iii) runs of simulations in parallel; facilitating realistic colony sizes with large number of agents.

Related models in the literature were extended with a detailed approach to modelling pheromone agents, which involved their deposition and detection by the ant agents. Where necessary, different environmental settings were developed to test the mechanism under study in a more efficient manner, i.e. large foraging space without any existing pheromones, existing Y-shaped trail introducing bifurcation. Model parameters were based on experimental data either from the literature or by conducting experiments of my own, and it was ensured that the relationship between the parameters were preserved, i.e. ant body length versus ant step size. It should be noted that assumptions were made for a number of unknowns, including the concentration of pheromone deposition, ant step size and ant antennal range. These assumptions were based on related literature and discussions with biologists.

Based on the above, four models were developed: (i) Movement Model, (ii) Foraging Model, (iii) U-turn Model and (iv) Excitement Model, whose aims, results and achievements are summarised as follows:

Movement Model (Chapter 6.1):

The initial aim was to investigate and identify whether the Pharaoh's ants had a pattern of movement in territories without any pheromones. The Movement and Foraging Models, unlike related models in the literature, were based on an environmental setting without any existing pheromones. Therefore, it was important to know how the first few Pharaoh's ants leaving the nest would walk within the environment. Considering that Pharaoh's ants deposit pheromones at each step, such movement patterns would characterise the initial pheromone trails to food sources.

Due to limited experimental data, biological experiments were conducted (Chapter 5), where the movement of individual Pharaoh's ants in a large foraging arena was recorded. The recordings were digitally analysed by video tracking to extract the coordinates of the Pharaoh's ants. The extracted coordinates were statistically analysed, which demonstrated the existence of a pattern; Pharaoh's ants were found to have a higher percentage for walking ahead, where the probability decreased as the angle of turn increased, suggesting that overall, Pharaoh's ants performed small turns. A probabilistic turning kernel (based on 8 directions) was derived to represent this pattern. The Movement Model (and all other models) were based on the derived turning kernel, where Pharaoh's ant agents were allowed to leave the nest agent when hungry and explore the environment looking for food agents.

A detailed approach was taken to model the pheromone agents (Chapter 6.2), enabling the ant agents to deposit and detect the pheromone agents in a 'realistic' manner. Based on the decay and the diffusion of pheromone molecules, the pheromone agents were deposited with an operating width (representing the liquid phase) and a maximum functional width (representing the gaseous phase) by the ant agents. For pheromone detection, the antennal range for Pharaoh's ants was taken into consideration, and the ant agents were allowed to 'sense' any pheromone agent molecules falling within this range.

The Movement Model was simulated with (n=10, 250) ant agents in an environment with dimensions (m=500x500 mm) for 1000 iterations (6.1 minutes). The results were analysed in terms of the lengths of the pheromone trails formed, as well as the total area explored by the ant agents, which fit well with the findings in the literature, demonstrating the simulated movement patterns as an efficient search strategy. Furthermore, despite not modelling the antennae of the ants explicitly, the antennal detection range and the diffusion of pheromone molecules for trail detection facilitated simulations of the 'wiggly' walk of the ant agents, as observed in nature.

Foraging Model (Chapter 6.3):

The aim of this model was to show that the simple rules employed by the related foraging models in the literature were not sufficient to explain the success of Pharaoh's ants foraging system. A basic agent-based model was developed based on the rules gathered from the literature, such as (i) ant agents leave the nest when hungry in search of food agents, (ii) ant agents deposit pheromone agents at every step, and (iii) once fed ant agents search the nest by following pheromone agents deposited in the environment. Furthermore, the food agents were introduced with a ‘scent’ to test whether this would facilitate more efficient locating of the food agents by the ant agents. The sole aim of this simple hypothesis was to demonstrate the functionality of the model and test the ant agents’ ability to respond to a basic parameter (food scent).

Two versions of the model including, (i) food agents without food scent and (ii) food agents with food scent, were developed and simulated with (n=50, 250, 500) ant agents for 1000 iterations (6.1 minutes) in an environment with dimensions (m=500x500 mm). As expected, the results showed an increasing Foraging Efficiency (F.E; proportion of fed ants), Overall Foraging Efficiency (O.F.E; proportion of fed ants back in the nest) and Nest to Fed Ratio (N/F; O.F.E/F.E) for the model with food scent, which were also proportional to an increased number of agents (n). However, the results showed that O.F.E was always the lowest compared to F.E and N/F, demonstrating that fed ants were not very successful at finding the nest agent by following pheromone trails.

Considering the success of the Pharaoh’s ants in nature, these results suggested that there has to be further underlying mechanisms contributing to the foraging strategies of the Pharaoh’s ants, and provided further motivation to develop subsequent models; the U-turn and the Excitement Models.

U-turn Model (Chapter 6.4:)

The aim of this model was to demonstrate the effect of division of labour in Pharaoh’s ant colonies by specialist ants, who were observed to perform frequent U-turns and deposit pheromones frequently. Model rules and parameters were based on the observed behaviour in the literature, such as (i) population of the U-turner ant agents were 7% of the colony, (ii) U-turner ant agents performed U-turns with a certain probability, (iii) U-turner ant agents deposited higher concentrations of pheromones, and (iv) U-turner ant agents left the nest when the pheromone concentration outside the nest entrance was higher than a threshold.

Two versions of the model, (i) homogeneous (without U-turner ant agents) and (ii) heterogeneous (with U-turner ant agents), were developed and simulated with (n=10, 50, 100, 250) ant agents for 2000 iterations (12.3 minutes) in two different environments with dimensions (m=500x500 mm, 750x750 mm).

The results showed that the heterogeneous colonies were always more successful than the homogeneous colonies in all three categories (F.E, O.F.E, F/N), demonstrating the positive contribution of U-turner ants. As concluded in the literature, their ability in maintaining and reinforcing rewarding trails, thereby increasing the chances for the other colony members to be informed of the rewarding trails was demonstrated.

Excitement Model (Chapter 6.5:)
The aim of this model was twofold: to demonstrate the effects of (i) increased pheromone deposition by Pharaoh's ants based on food quality assessment, and (ii) decisions made by the Pharaoh's ants at bifurcation points. Model rules, parameters and the environmental setting (an existing Y-shaped pheromone trail with each trail branch leading to a food source of good and poor quality) were based on the related observed behaviour in the literature, such as (i) when walking outwards, upon reaching the bifurcation point, a certain minority of Pharaoh's ants preferred to walk onto the weaker branch (referred to as 'outwards error rate'), (ii) after eating food when returning back, upon reaching the bifurcation point, a certain minority of the Pharaoh's ants preferred to walk onto the other branch rather than walking towards the nest (referred to as 'return error rate', and (iii) ant agents deposited a varying concentration of pheromones after discovering food agents.

Two versions of the model based on the observed behaviour of Pharaoh's ants at the bifurcation point: (i) outwards error rate and (ii) outwards and return error rate, with five subversions based on varying excitement levels (pheromone concentration deposited based on food quality): (i) no excitement (constant deposition), (ii) - (v) different pairs of pheromone concentration deposited, were developed and simulated with (n=50, 250) ant agents for 2000 iterations (12.3 minutes) in an environment with dimensions (m=500x500 mm).

The results showed that the decisions made by the ant agents at the bifurcation point had an important effect on the overall behaviour:

The outwards error rate and excitement levels:
The outwards error rate proved to be useful, as the ant agents had the chance to explore both trails. Regardless of whichever trail branch was explored first, the ant agents had the opportunity to explore both trails as a result of the outwards error rate. However, without the excitement levels, if the trail branch with the poor food source was explored initially, the ant agents were not able to switch to the branch with the good food agent, as they did not have a mechanism to tell the difference between the qualities. When excitement levels were applied (differing concentrations of pheromones deposited), the colonies of n=50 ant agents were able to switch to the branch with the good food source for the most of the time, whereas the colonies of n=250 ant agents were always successful at switching. As excitement levels increased (different pairs of deposited pheromones), a faster switch took place for both colonies. When the branch with the good food source was explored initially, this branch was explored by the majority of the ant agents, and no switching to the other branch occurred.

The return error rate and excitement levels:
The return error rate led to an interesting phenomenon. Without excitement levels, the ants were not able to show any switching behaviour. However when the excitement levels were introduced, a confusion was observed. This is because the return error rate enabled the returning ant agents to walk onto the other branch. If these were fed ant agents which discovered the good food source, they would be depositing high concentrations at every step, thereby reinforcing the branch with the poor food source. As a result, if this occurred too many times, the branch with the poor food source could become stronger than the branch with the good food source, leading to a wrong switch.

Overall, it was concluded that the outwards error rate coupled with excitement levels would be the best approach. Robinson et al. (2008)'s agent-based model was extended and an alternative mechanism demonstrating the ability of the Pharaoh's ants to perform switches between trail branches was introduced.

10.2 Future Work

As an extension to the models developed throughout this research, a model incorporating all of the mechanisms studied could be implemented. This could help to provide a better understanding of the foraging strategies employed by the Pharaoh's ants, where the results could be compared against the results obtained from the Foraging Model. It would be interesting to see the effect of the combined mechanisms on the Foraging Efficiency (F.E), Nest to Fed Ratio (N/F) and especially on the Overall Foraging Efficiency (O.F.E).

It would also be interesting to run the models in different environmental settings, such as the U-turn and Excitement Models in environments containing:

- An existing pheromone trail with a number of bifurcation points
- An existing pheromone trail with branches of different lengths

It is stated in the literature that the Pharaoh's ants employ three different pheromones for communication, which are short-term and long-term attractive pheromones and short-term repellent pheromones. As there are many unknowns with these chemicals, they were not incorporated in this research. Further to U-turner specialists, so-called pathfinder and forager ants of Pharaoh's ant colonies were observed to perform different tasks simultaneously (as explained in Chapter 2); after days of being deprived of food, pathfinder ants were observed to walk slowly touching their antenna on the substrate, following previously deposited long-term attractive pheromones, whereas foragers only followed short-term attractive pheromones. Quantitative studies are yet to be performed on this concept, currently making it challenging to be tested with agent-based models. However, further experimental work coupled with agent-based models could possibly lead to interesting discoveries; maybe the pathfinders are the wise U-turners of the Pharaoh's ant colonies?

10.3 Further Inspirations and Biomimicry

Biomimicry is based on the principle that nature has already found solutions to many of the problems we are trying to solve (Biomimicry, 6.11.2010). This resulted in successful applications of ideas from nature into various disciplines. Some examples are aircraft designs inspired by bird flights (Liu, 2006), climate control designs for buildings inspired by termite mounds (French et al., 2010) and wind turbine designs based on whale power (Howle, 2009).

The foraging system of ant colonies has also been a source of inspiration for various applications in different disciplines. A popular example is the ant-based routing algorithms, which mimic the behaviour of ants to find shortest paths between source and destination nodes, as discussed in Chapter 8. Other examples include job scheduling (Campos et al., 2001), vehicle routing (Fuellerer et al., 2009), data clustering (Tsai et al., 2004), and even crowd behaviour modelling (Nishinara et al., 2006). Decades of research has clearly shown that the trail systems of ant colonies are far more complex than generally perceived, and there is still plenty of room for further work. The key areas of social insect study were identified to span for at least the next ten years by Boomsma and Franks (2006), in order to further investigate: the robustness of insect sociality against environmental stochasticity; multiple forms of division of labour to enable long-term food storage, collective defence, policing and punishment of selfish individuals. This is based on the belief that only humans and social insects can build and manage large-scale societies according to complex economic decision rules.

Therefore, it can be concluded that further research involving experimental work coupled with agent-based modelling into insect behaviour, has great potential to reveal novel interesting phenomena. With the ever increasing applications of multi-disciplinary research, the future of further inspirations stemming towards Biomimicry for solving various complex problems is promising.

Appendix A: List of Parameters for the Models

1 Movement Model

List of parameters used for this model:

- antFoodLevel = rand(1..10)
  (Nutrition levels of the ant agents were initialised to a random (double) value between 1 and 10)
- antFoodLevelDecay = 0.2
  (Nutrition levels of the ant agents were decreased at every iteration)
- antStepSize = 2 mm
  (Distance walked by an ant agent per iteration)
- environmentSize = 500 mm
  (Dimensions for the environment: 500x500 mm)

2 Modelling Pheromones

In addition to the parameters used for the Movement Model, the following parameters were also used:

Ant agents:

- antAntennalRange = 2 mm
  (Antennal span of Pharaoh's ants)
- antMinPheromoneDetectionUnit = 0.2 units
  (Minimum concentration of pheromone that can be detected by an individual ant agent)

Pheromone agents:

- pheromoneMaxConcentration = 2 units
  (Maximum concentration of an individual pheromone agent)
- pheromoneMinConcentration = 0.1 units
  (Minimum concentration of an individual pheromone agent)
- pheromoneMinRadius = 2 mm
  (Operating width of the pheromone, denoted as O_r)
- pheromoneMaxRadius = 20 mm
  (Maximum functional width of the pheromone, denoted as F_r)

3 Foraging Model

In addition to the parameters used for the Movement Model and Pheromones, the following parameters were also used for this model:

Ant agents:

- antHungryPheromoneDepositionUnit = 1 units
  (Concentration of pheromone deposited by an individual hungry ant)
- antFedPheromoneDepositionUnit = 2 units
  (Concentration of pheromone deposited by an individual fed ant)
- antFoodConsumptionUnit = 0.02 units
  (Amount of food consumed by an individual ant agent)
- antFedFoodLevel = 100 units
  (Food levels of the fed ant agents were increased to allow their stay in the nest until they are hungry again)

Food agents:

- food1Size = 5 units
  (Size of the first food agent)
- food2Size = 100 units
  (Size of the second food agent)
- food3Size = 75 units
  (Size of the third food agent)

- food4Size = 25 units
  (Size of the fourth food agent)

4 U-turning Model

In addition to the parameters used for the Movement Model, Pheromones and the Foraging Model, the following parameters were also used for this model:

- antTurnProbability = 0.00044
  (Probability for 180 degree turn for normal ants (0.044%))
- uturnerTurnProbability = 0.018
  (Probability for 180 degree turn for U-turner ants (1.8%))

Pheromone agents:

- initialTrailStrength500 = 3 units per pheromone agent
  (Initial strength for the existing trail in 500x500 mm environment)
- initialTrailStrength750 = 30 units per pheromone agent
  (Initial strength for the existing trail in 750x750 mm environment)

5 Excitement Model

In addition to the parameters used for the Movement Model, Pheromones and the Foraging Model (ant agent), the following parameters were also used for this model:

Ant agents:

- antOutwardsErrorRate = 0.05
  (Error rate at the bifurcation point when ant agents are walking outwards: 5%)
- antBackwardsErrorRate = 0.01
  (Error rate at the bifurcation point when ant agents are walking back towards the nest: 1%)

Food agents:

- rightBranchFoodSize = 5 units
  (The poor food on the right branch representing 0.1 Molar sucrose solution)
- leftBranchFoodSize = 100 units
  (The good food on the left branch representing 1 Molar sucrose solution)

Appendix B: Stategraphs for the Models

1 Foraging Model

The stategraph for this model was as follows:

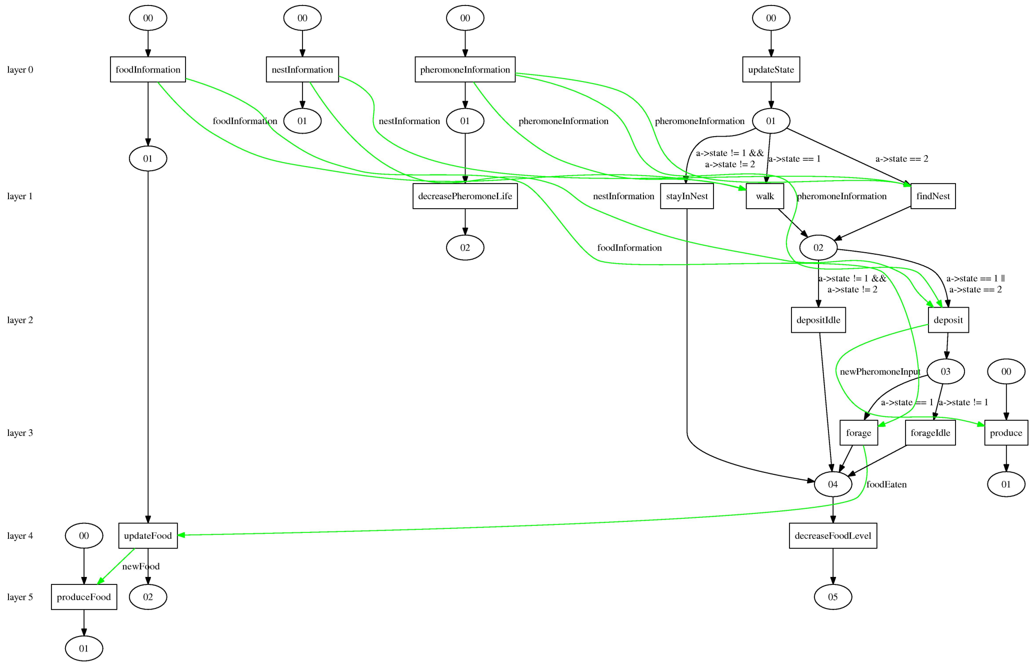


Figure 10.1: Stategraph of the Foraging Model generated by FLAME.

2 U-turn Model

The stategraph for this model was as follows:

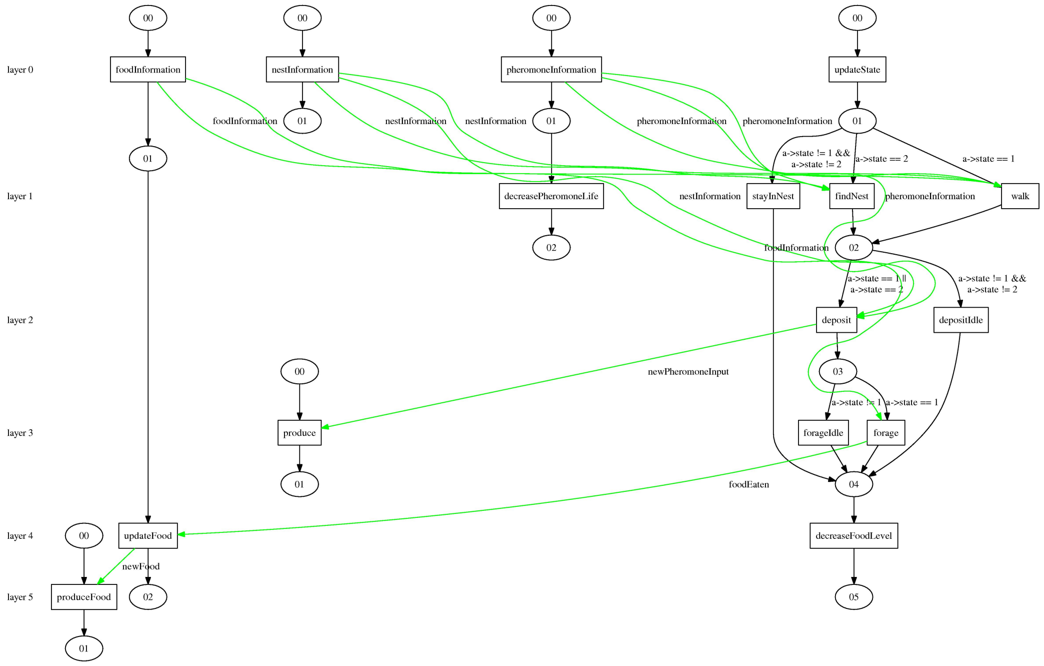


Figure 10.2: Stategraph of the U-turn Model generated by FLAME.

3 Excitement Model

The stategraph for this model was as follows:

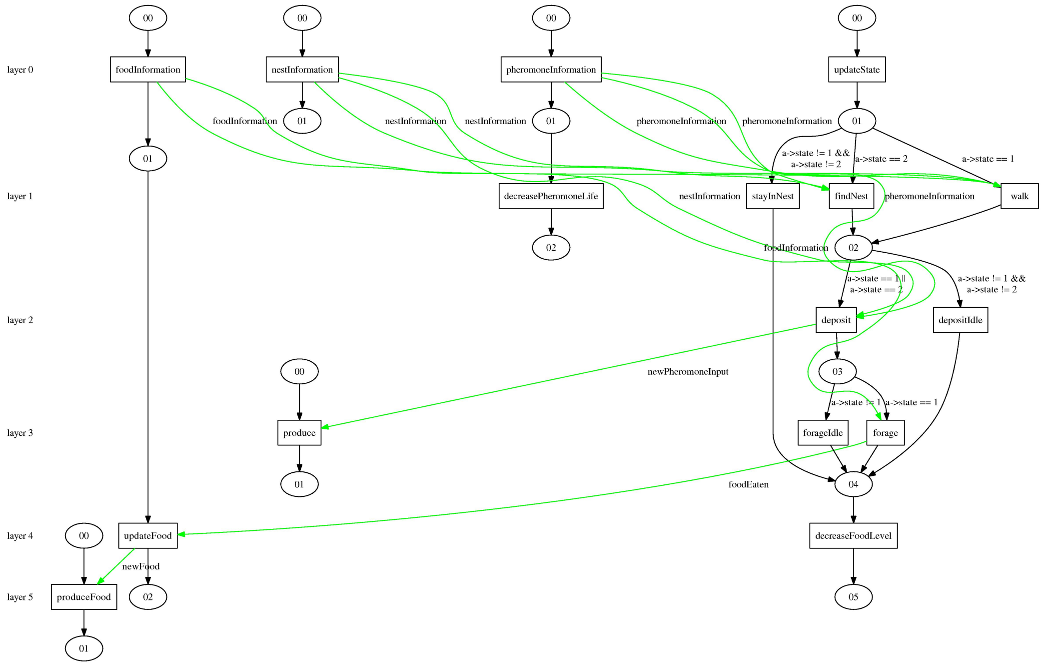


Figure 10.3: Stategraph of the Excitement Model generated by FLAME.

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