Coupled computational simulation and empirical research into the foraging system of Pharaoh's ant (*Monomorium pharaonis*)

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Abstract

The Pharaoh's ant (*Monomorium pharaonis*), a significant pest in many human environments, is phenomenally successful at locating and exploiting available food resources. Several pheromones are utilized in the self-organized foraging of this ant but most aspects of the overall system are poorly characterised. Agent-based modelling of ants as individual complex X-machines facilitates study of the mechanisms underlying the emergence of trails and aids understanding of the process. Conducting simultaneous modelling, and simulation, alongside empirical biological studies is shown to drive the research by formulating hypotheses that must be tested before the model can be verified and extended. Integration of newly characterised behavioural processes into the overall model will enable testing of general theories giving insight into division of labour within insect societies. This study aims to establish a new paradigm in computational modelling applicable to all types of multi-agent biological systems, from tissues to animal societies, as a powerful tool to accelerate basic research.
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1. Introduction

Modelling complex physical phenomena through computer simulation is an increasingly common approach to testing and improving our understanding of the natural world. Biological systems represent a great challenge for mathematical modellers because of their inherent complexity and the non-linear relationships amongst their individual components. Two main approaches have been successfully applied to modelling biological systems. The "top-down" state variable approach, based on ordinary or partial differential equations, approximates the behavior of many individuals by a single variable but in doing

so violates the basic biological principle that every individual is unique in behavior and physiology. In contrast the "bottom-up" approach models each individual, facilitating the study of the mechanisms underlying behavior and the consequences of interactions between individuals or with the environment. The "bottom-up" approach has many advantages principally in allowing the investigator to address general problems associated with the theoretical study of behavior and evolution. In the past a common objection to the production of detailed agent-based models of complex biological systems was the requirement for the quantification of many parameters and the fact that the simulation of the model made huge memory demands on even the fastest computers (Ermentrout and Edelstein-Keshet, 1993). Hence a common technique employed in simplifying individual-based modelling

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of biological systems are cellular automata (CA), which emulate real physical laws using a small set of simple rules and reduce the state space to only a few states (frequently no more than two). Cellular automata have effectively been used to explore many problems in biology but they generally treat biological communities as homogeneous without the flexibility, or variability, that is an essential characteristic of natural populations. The ready availability of powerful computers, and parallel computing, now makes the accurate modelling of communities of individuals a realistic endeavor (Nugala et al., 1998). This study shows how empirical research and modelling can be coupled to accelerate the rate of research into a social insect, the Pharaoh's ant (*Monomorium pharaonis*). We also apply a formal methodology to modelling the ant's behavior, X-machines, which we believe to be widely applicable to biological modelling and accessible to biologists.

1.1. X-machine modelling of behaviour

A great benefit of agent-based modelling is that it facilitates "individual-based modelling", which treats individuals as unique and discrete entities with properties, other than age, that can change during their lives. The belief is that once the rules and characteristics of individuals have been identified and specified in an agent-based model "*population and community-level consequences would emerge naturally*" (DeAngelis et al., 1994). The lack of an overall strategy for building and analysing individual-based models means that the original motivation for development of such models, the investigation of general theoretical issues, is largely being ignored Grimm (1999). Grimm (1999) tried to suggest a general approach to individual-based modelling of communities and after critical assessment found that "pattern-oriented" modelling has many advantages as a starting point. The most successful models aimed to explain patterns that can be observed in nature, as they were always testable to some degree and always led to new general insights (Grimm et al., 1996). He suggested starting with a very coarse model that reproduces a pattern then refining the model step by step, checking and testing the model rigorously with each refinement. This approach helps to solve the major problem of how to find the appropriate level of resolution when modelling a community, particularly now massive computational power is easily accessible. Grimm (1999) concludes that the potential of individual-based modelling will not be fulfilled until the actual process of modelling becomes as important as the individuals modelled. All too often many details are included in a model because they make the model seem more "realistic", when the aim should be to make a model as simple as practically possible as an aid to understanding.

The development of agent-based systems results in software with great inherent complexity, the "correctness" of which cannot be assured if the agent system's requirements have not been checked with some formal methodology. The agent system development process crucially requires attention to all the stages of "correct" system development: modelling, verification and testing.

X-machines are a formal method of modelling, which are particularly suited to the specification of dynamic agents that demand memory, as well as being reactive (Kefalas et al., 2003). A special case of X-machine, the communicating stream X-machine, has been shown to be suited to the specification of systems of co-operating agents, with preliminary models being produced for foraging honeybees and ants (Gheorghe et al., 2001; Kefalas et al., 2003). Instead of modelling individual agents as highly complex X-machines, Kefalas et al. (2003) advocate modelling complex agents as a set of simpler X-machines. These agent components can then model different behaviours of the agent, which are integrated into a situated agent with robust performance. Agent modelling could thus be separated into the specification of the X-machine components and the description of communication between these components. This modular approach has many advantages, particularly the possibility of reusing modules and the separation of modelling and communication as activities. Such an approach may be suited to modelling social insect behaviour but the preliminary work was at a trivial level and did not consider the complex chemical communication mechanisms regulating insect societies. Of particular importance is the fact that all ants are "totipotent", being capable of performing all tasks required of the colony (with the single exception of reproduction), such that all roles, and tasks within roles, are states accessible to every worker ant. This great flexibility requires that we model each individual as a complex

X-machine whose memory and environmental inputs determine its state, but it must be stressed that individual states are modulated by the environment, chemical communications and internal physiological variation (due, for example, to age or hunger). Roles are assumed when key parameters in the overall state of an individual satisfy criteria for performing a task (if the task is available), which is specified by a separate X-machine for the particular behaviour associated with that task (essentially a set of mechanistic rules). So individuals are modelled as complex X-machines with access to a repertoire of behaviours, which are modelled as simple X-machine modules.

1.2. Social insect communities

Social insect communities are groups of individuals (ants, bees, wasps, aphids and termites) that live together and reproduce as a single unit. The development of the colony phenotype is often regarded as being analogous to development in a multi-cellular community, often being referred to as a "super-organism". A colony represents a level of organisation above the individual with its own characteristic morphology, behaviour, organisation and life history. Individual workers in a colony may be compared to cells, although workers may differ genetically and have more independence and flexibility (Frank, 1999). The major challenge for social insect research is the integration of individual behaviours, thereby understanding the emergent colony-level behaviour.

Traditional approaches to the study of colony organisation have focussed on the adaptive value of social behaviour (Wilson, 1985) but there has been a recent shift towards understanding the mechanistic processes, or rules, that underlie colony behaviour. Self-organisational models have been increasingly used to describe how these colony processes emerge from the autonomous actions of individual workers (Camazine et al., 2001).

Many of the characteristic collective activities observed in social insect communities result in the formation of patterns, with apparent order and structure, that have in the past been interpreted as evidence of hierarchical control over a colony of complex individuals. However, recent research into a diverse range of physical and biological processes has illuminated the mechanisms by which such systems can acquire order and structure without any intervention by external direction. This principle of self-organisation has been defined as "*a process in which pattern at the global level of the system emerges slowly from numerous interactions among the lower-level components of the system. Moreover, the rules specifying interactions among the system's components are executed using only local information, without reference to the global pattern*" (Camazine et al., 2001).

In biological systems such patterns may be organised arrangements of living units in space and time that emerge from responses to local information, or structures arising from their collective actions. Self-organising systems must possess "emergent" properties, where a collection of interacting subunits exhibits qualitatively new properties that cannot be understood as the simple addition of the individual contributions. The term "complex system" is often used to refer to a system of interacting units, which display global properties that are not present at the lower level. It must be stressed that complexity in a system does not require complex components since non-linear interactions involving amplification and co-operativity can lead to the emergence of complex behaviour from similar components following simple rules. In biological systems these very simple rules of interaction have been shaped by selection and the products of group activity can be adaptive (Kauffman, 1993).

Because of their inherent complexity (at many levels) modelling of insect societies must start with simple assumptions, followed by rigorous testing of every feature before refining a model further. Frequently models are produced that exhibit key properties of a system, particularly when they simulate the emergence of some characteristic pattern, but rigorous testing of such models is rare.

Our study couples the process of agent-based modelling with empirical research into ant behaviour, new insights from each activity feeding back to accelerate the rate of elucidation of the overall process. We study one of the most striking examples of communication found in social insects; the formation of discrete ant trails between the nest and a food source. These pheromone trails are the visible evidence of highly sophisticated mass chemical communication processes, which show considerable variation between ant species. It is evident that very large societies, of small ants with poor vision, rely almost exclusively

on chemical based foraging strategies effectively dispensing with orientation using visual cues. Previous models of ant foraging have been simplistic, most frequently modelling ants where a trail is laid only on the return from food because visual navigation guides the return journey (reviewed in Camazine et al., 2001). Those models addressing foraging where orientation is solely by pheromone following have only succeeded in overcoming the many logistical problems by making biologically unrealistic assumptions (for example Schweitzer et al., 1997).

Here research we have conducted into the foraging system of *M. pharaonis* is presented, beginning with accurate analysis of the movement rules employed by the ant before advancing through the behaviours elicited by the numerous pheromones utilised in communication. The overall behaviour of ant foraging is separated into discrete behaviours with associated states, which can be studied, modelled and checked by simulation.

The process evolves by refinement of an initially very coarse model, establishing parameters with empirical biological research, until each component of the system has been satisfactorily understood. This approach aims to eliminate crucial assumptions that underlie the process by studying the system from the bottom-up, specifying fundamental rules of behaviour.

2. Biological research into foraging trails of *Monomoriumpharaonis*

The Pharaoh's ant is a familiar example of the "tramp ants", dispersed across the world via international trade (Holldobler and Wilson, 1990). It has been phenomenally successful in adapting from its native habitat to the artificial environments available in the world's cities. In heated buildings *M. pharaonis* is considered a pest and a significant vector of pathogenic bacteria, causing a significant problem in hospitals (Edwards and Baker, 1981). As a consequence of this pest role considerable effort has been directed to studying this ant with a view to developing effective methods for its control. This work has shed much light on many aspects of the behaviour of *M. pharaonis*, particularly its foraging method utilising trail pheromones, although the complexity of this

system has never been fully elucidated (Holldobler and Wilson, 1990; Ritter et al., 1977a).

Monomorium pharaonis is a small (2 mm long) mass-recruiting ant that forms pheromone trails to food, or water sources. The characteristics of organised trails produced by *M. pharaonis* are a consequence of key parameter values previously identified as crucial in determining trail dynamics, i.e. degree of random motion; fidelity to trails; pheromone deposition rate; attraction to trails; recruitment response; trail pheromone volatility; population size (Edelstein-Keshet et al., 1995). Clearly it is technically difficult to quantify some of these parameters without elucidating fundamental facts about the chemicals mediating the process.

2.1. Exploration

When exploring previously unmarked areas *M. pharaonis* engages in a "land rush", comprehensively described by Wilson (1962) of *Solenopsis saevissima*, where foragers explore a new area in large numbers laying pheromone trails constitutively. Such behaviour has been recorded in many other species of ants, e.g. *Oecophylla longinoda* (Holldobler and Wilson, 1977), *Myrmica rubra* (Cammaerts et al., 1977), *Leptothorax unifasciatus* (Aron et al., 1986) and *Solenopsis invicta* (Gordon, 1988). This is a remarkable phenomenon as workers are recruited to explore without the stimulus of a reward in the usual sense. It is imperative that workers mark virgin territory with pheromones, immediately it is encountered so as to advertise to competitors that the area is the exclusive foraging territory of *M. pharaonis*, and thereby monopolise any available resources. Several of the chemical components of the trail substance deposited by *M. pharaonis* also have a repellent effect on other insect competitors, whilst actually being insecticidal to some (Jones and Blum, 1982). The large number of individuals recruited to explore virgin territory ensures thorough exploration and territory marking of an area within a short period of time, dependent on the number of ants available to be mobilised in a colony as well as the size of the new area. A small colony of approximately 2000 ants rapidly establishes a divergent network of trails, covering 1 m^2 within 40 min. The characteristic shape of the trails in this bifurcating network is of irregular sinu-

soidal waves, which persist and do not straighten with the passage of time. The overall "hunger" of a colony is also considered to affect the efficiency (or speed) with which novel areas are explored (Wilson, 1962). This hypothesis was tested in *M. pharaonis* and the number of ants recruited to a new area was indeed found to be a function of the length of the preceding period of starvation, when corrections for colony size are made (Fourcassié and Deneubourg, 1994). Food deprivation is assumed to lower the threshold for foraging activity in workers, resulting in a switch to this role by many workers previously engaged elsewhere (Cassill and Tschinkel, 1999). Individual nutritional status affects role disposition in *M. pharaonis*, and consequently overall colony behaviour. It has been widely reported that *M. pharaonis* workers lay trail constitutively whilst foraging and exploring (for example Holldobler and Wilson, 1990), but an investigation of their trail-marking behaviour suggests that they lay trail frequently only when exploring new territory, particularly as compared to when operating on an established trail (Fourcassié and Deneubourg, 1994).

In an effort to understand how the characteristic wavy trail shape emerges from the behaviour of individual ants, video footage of ants exploring virgin territory was analysed.

The behaviour of individual ants ($n = 50$) and groups of 8–10 ants ($n = 80$) entering a large arena was observed and the following parameters recorded:

- direction taken (on an eight-point compass);
- distance travelled before turning;
- angle of turn;
- distance travelled before each turn or intersection with a previous ant path;
- direction taken and, if previously laid path followed, the distance path followed before losing it again;
- concentration (number of potential reinforcements) of trail followed was also recorded.

The rationale for this approach was that the same rules being employed by individuals in isolation and the first 8–10 exploring ants, in an environment initially devoid of information, should be employed by all subsequent ants, negating the need to track many interacting ants. Once many ants mark virgin territory it becomes very difficult to identify, or separate, the possible signals an individual ant might be responding to

in the environment. By minimising the available cues in the environment (initially to zero, on the substrate) it is possible to identify individual search patterns and responses to areas where known amounts of trail (as individual ant passages) may have been deposited. The results of this ongoing research, which forms the foundations of the simulation work, are presented as the preliminary movement rules for simulation in the next section. One of the most interesting characteristics of the non-random movement found in these ants is the high probability (0.39) of turning through 90° after advancing a short distance. When exploring virgin territory there is caution exercised when departing from the trail and exploration only occurs in increments of 1.9 ± 0.87 cm followed by a turn. Frequent turns through 90° lead to regular encounters with previously laid trails and maintain the link to the nest. The number of reinforcements the trail has previously received determines trail followed. Further factors affecting trail following, and departure, include the possibility of encountering a further intersection (select the trail with the highest concentration) and the high probability of losing a weak trail on a turn exceeding 45°. Further statistical analysis of this growing body of data will yield more accurate rules and possibly identify discrete, or continuous, differences in the way individuals explore.

The exploration of virgin territory as described briefly by Wilson (1962) is characterised by small "looping extensions" of the trail from an existing trail. The term "looping extensions" describes the process of departing from the trail, advancing a short distance then executing a protracted u-turn (two consecutive turns of 90° or greater) until a trail is encountered. This process describes an arc on the substrate, the shape of which is replicated by an intersecting ant following the path a previous ant has walked. This observation shows that exploring ants are laying trails constitutively but the trail of a single *M. pharaonis* worker ant cannot be followed when encountered over 25–30 s after deposition, suggesting a threshold of detection of 0.5 ant units and a half-life of 30 s. The amount of reinforcement a path section receives, by repeated trail deposition along its length, increases the distance an intersecting ant will follow it without departure. The antennal scanning range of the ants is the current heading $\pm 45°$ with right-angled turns rarely being followed successfully. Since this

means there is a high probability of losing the path on corners, these points of departure serve to link arcs together. It is hypothesised that this process results in the emergence of the sinuous trail network characteristic of *M. pharaonis*.

Movement of *M. pharaonis* during exploration was according to a search strategy, which is approximated by the rules in Box 1. It was not possible to analyse the fractal dimension as a measure of the randomness of movement paths of individual ants, because gross overestimates of fractal dimension occur when turn angles of $90°$ or greater occur with high frequency (Nams, 1996). An alternative method, applied by Nugala et al. (1998), was to fit the directional choice to a wrapped Cauchy distribution, but we preferred to use the actual probabilities generated by analysis of the large data set (>2000 turns measured) on directional choice. Animal movement is often simulated with active random walkers (for example Schweitzer et al., 1997), where the random walk tends to explore space thoroughly often returning to the same point many times, not filling space uniformly (Berg, 1983). Unlike *M. pharaonis* random walkers have no tendency to move towards regions of space that have not been occupied before because they have no memory of past movements. Constitutive chemical marking places such a memory of past movements in the environment thereby directing the future paths of *M. pharaonis* workers in a non-random manner.

2.2. Chemical trails

Studies have determined that seven chemical components of the trail substance deposited by *M. pharaonis* elicit trail-following behaviour of variable activity (Ritter et al., 1977a,b; Jones and Blum, 1982; Attygalle and Morgan, 1984). The most active of these compounds in a choice test is faranal, the only one of the trail compounds believed to be produced in the Dufour's gland. Workers, queens and males were shown to be attracted to faranal down to concentrations of $<1 \, \mathrm{pg \, cm^{-1}}$, four orders of magnitude less than the lower limit for the two most active alkaloid trail pheromones, monomorine I and III. This discovery resulted in faranal being referred to as the "true" trail pheromone of *M. pharaonis* (Ritter et al., 1977b). However, faranal is only produced in trace amounts whilst the alkaloid components are abundant,

so the difference in activity becomes difficult to separate when detecting substances differing in abundance by several orders of magnitude. One key attribute of faranal is that it is reputedly highly volatile and thus easier to detect with antennae, relative to the definitely low volatility alkaloids, which may require contact. A comprehensive elucidation of the roles of the alkaloid trail pheromones, produced by the poison glands, was never achieved, although studies demonstrated there was a synergistic effect when two were present.

One aspect of the contribution of different trail components to trail dynamics, which must be considered, is the relative volatility, and thus contribution to longevity, of the individual chemicals being deposited on a trail. It is highly likely that trail longevity is wholly appropriate to the foraging requirements of an ant species and demonstrably varies from minutes in *Aphaenogaster albisetosus* (Holldobler et al., 1995) to several days in some New World army ants (Torgerson and Akre, 1970). Differing volatility of chemical components enables ants to patrol and exploit areas of varying size but still permits the shift to richer feeding sites when old ones become depleted.

Investigations of the foraging methods employed by *M. pharaonis* suggest that they must utilise long-lasting pheromones as they can establish long trunk trails of up to 10 m from a nest containing only 1500 individuals (Sudd, 1960). In addition it has been observed that most *M. pharaonis* colonies become generally inactive at night, then resume foraging between 7 and 9 a.m., but are found to utilise the identical trunk trails followed the previous day (Sudd, 1957; Fourcassié and Deneubourg, 1994). Several trunk trails (1–4) radiate from a single nest and scouts are observed to explore the trunk trails to determine whether food is still available at their terminus, if unsuccessful scouts then leave the trunk trail they are following and try to locate alternative food sources or return to the nest.

Monomorium pharaonis forms tortuous trails with a wavy form such that it is difficult to envisage how such a trunk trail could be exactly replicated, in the same place, 1 or more days later by any other mechanism than long lasting marking of the substrate. This part of the investigation confirmed that long-term trail marking occurs in *M. pharaonis* and determined how long such trails last as a function of the number of ants laying the trail (Jackson et al., in preparation). The

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Box 1. Parameters and functions implemented in ant movement simulation

Environment data structure (memory) and specifications

xy, a	Ant coordinates
xy, f	Food coordinates and units
xy, n	Nest coordinates
xy, sp	Short-lived pheromone coordinates and units
xy, lp	Long-lived pheromone coordinates and units

One step = one ant length (2 mm)
One iteration = 0.33 s (mean
   ant speed = $6 \, \text{mm s}^{-1}$)

Ant data structure (memory) and specifications

xy	Coordinates	
d	Distance travelled since last turn	0–10 steps
h	Measure of hunger	0–1
v	Current direction	Compass 0–7

Functions

At each iteration	$\text{sp} = \text{sp} - (\text{sp} \times 0.01)$
	$\text{lp} = \text{lp} - (\text{lp} \times 5 \times 10^{-6})$

Exploration — new direction choice probabilities (when 10 steps completed)

Current heading		
	$+0°$ (compass 0) = 0.292	$-180°$ (compass 4) = 0.015
	$+45°$ (compass 1) = 0.170	$-45°$ (compass 5) = 0.177
	$+90°$ (compass 2) = 0.180	$-90°$ (compass 6) = 0.208
	$+135°$ (compass 3) = 0.080	$-135°$ (compass 7) = 0.054

At each step lay trail − 1 unit
   lp + 1 unit sp
Trail following
Scan compass positions 0, 1, 5
   for pheromone — select
   highest concentration
When trail is followed reset *d* to 0
Threshold for detection of
   short-lived pheromone (sp) =
   0.5 units
Threshold for detection of
   long-lived pheromone (lp) =
   134 units
At each step — if lp or sp <
   2000 units, lay 1 unit sp + 1
   unit lp

half-life of the longest-lived fraction of the trails was estimated at 6 h, with a minimum detection threshold of 134 ant units. An upper threshold for trail reinforcement was also determined, of approximately 4000 ant passages, the adaptive value of which is to prevent exhausted trails being searched repeatedly.

The ability to detect this long-lived fraction of the trail was investigated in order to identify possible differences in behaviour between those ants detecting and exploring the old trail and those failing. The rationale for this investigation was that some ants were observed to find the trail and re-establish it, in the experiments on trail longevity, whilst others failed. It was shown that to locate a long-lived, low volatility trail pheromone it is necessary to almost contact the trail on a surface with the antennae. This area of the study determined that ants constitutively dragging their antennae were those most likely to find trails, representing approximately 20% of all active foraging ants. A discrete subset of the colony were thus always capable of detecting long-lived trails but hunger was also found to shift other foraging workers into this state, thereby increasing the amount of ants searching these persistent trails. Individual states determine the ability to detect long-lived trails effecting a division of labour in the long-term use of foraging trails.

The preliminary investigations presented here form the foundations of a model of trail forming behaviour that already asks many questions, particularly about the contribution of individuals to trail formation. This area is currently under investigation using novel techniques for determining the chemical constitution of the trail as it is deposited.

3. Simulation of movement and trail formation in *M. pharaonis*

An X-machine is a general computational machine introduced by Eilenberg (1974) and extended by Holcombe (1988) that resembles a finite state machine (FSM) except for two significant differences:

- Data is held in a memory attached to the machine.
- Transitions are not labelled with simple inputs but with functions that operate on inputs and memory values.

X-machines are more expressive and flexible than FSM or other machine models like pushdown automata or Turing machines, which are too low level and hence of little use for specification of real systems. X-machines are capable of modelling both the data and the control of a system.

The machine, dependent upon the current state of control and the current values of the memory, processes an input symbol from the input stream to determine the next state, the new memory state and the output symbol, which will be part of the output stream (Kefalas et al., 2003).

The formal definition of a deterministic stream X-machine (Ipate and Holcombe, 1998) is an eight-tuple $M = (\Sigma, \Gamma, Q, M, \Phi, F, q_0, m_0)$, where Σ, Γ are the input and output finite alphabets, respectively, Q the finite set of states, M the (possibly) infinite set called memory, Φ a finite set of partial functions φ that map an input and a memory state to an output and a new memory state, $\varphi: \Sigma \times M \to \Gamma \times M$, F 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, $F: Q \times \Phi \to Q$, q_0 the initial state and m_0 is the initial memory.

X-machines can be used as a core method for an integrated formal methodology of developing correct systems. They are intuitive and at the same time facilitate formal description of data types and functions in any known mathematical notation. Adding new features to the original model can also readily extend X-machines.

3.1. Application to Pharaoh's ants — modelling individual ants as X-machines

The current parameters included in the X-machine model of *M. pharaonis*, and an outline of future parameters to be included as research progresses, are outlined below:

- $\Sigma = \{$chemical signals (particularly: pheromones from workers, eggs, queens and larvae; activators; inhibitors); other environmental stimuli (temperature, humidity, location, time of day, etc.); social inputs (proximity/contact with other ants, physical recruitment, recruitment displays, food exchange, antennation); physical attack/danger$\}$;

- $\Gamma = \{$chemical signals; recruitment (physical displays, physical contacts); food exchange; trail following; exploring; feeding; moving/carrying prey/brood items; alarm response; attack$\}$;
- Q is the finite set of states — we designate discrete states or roles (nurse, forager and scout) based on tasks performed and location, but roles are highly flexible in adult workers. In many studies large numbers of roles are identified by repetition of specific tasks (task fixation) but note that all workers are totipotent and will flexibly switch state (role/task) as conditions change to satisfy requirements. Nominal states may be identified by stereotypical responses as a consequence of many individuals sharing response thresholds in the same range. The number of states (as the individual's repertoire of response thresholds and memory symbols) is finite, but very high, because individual variation is high;
- $M = \{$hunger; experience at tasks; "excitement" by a food source; distance travelled since turning during exploring; physiological changes with age; activator/inhibitor levels; variable response thresholds$\}$;
- Φ By memory state we refer to the whole memory status because an input will be tested by a function against many separate memory parameters to determine the output (behavioural response) and equally many memory items will be modified in the process. Each iteration we test every agent's hunger and location (inputs are associated with the environmental locus) then, to determine state other requisite memory items are tested thus determining the response;
- F is the next state, or behavioural response (transition), after the relevant functions have been applied.

q_0 is the initial state — for modelling purposes a population of inactive ants in the nest and m_0 is the initial memory — initial memory values are set to zero but for preliminary simulation purposes hunger levels may be allotted from a normal distribution.

3.2. Rules and parameters used for computer simulation

Initial simulations using MATLAB^{TM} have focussed on producing a community of agents that move realistically whilst establishing a trail from a nest site. The functions and data structures employed are summarised in Box 1 and are derived from empirical investigation of ants in the laboratory.

The approach taken has been to implement rules incrementally and to test the effect of their addition using a community of agents. Agent-based simulation is computationally intensive and community sizes explored to date have not exceeded 250, although with the latest implementation a simulation of 2500 iterations (equating to a maximum distance explored of 2.5 m) will not exceed 45 min in duration. Natural *M. pharaonis* communities can function with worker populations as low as 100 individuals, although typical colony size is 1000–3000. Small population size will only restrict foraging range, although it has been suggested that a critical population size must be exceeded before "organised" chemically based foraging over a long-range can be achieved (Beekman et al., 2001). This hypothesis will be testable when further parameters have been determined. As further functions are included greater computational power will be applied to the simulation, in particular parallel computing.

Simulations are conducted on a square matrix generally of dimension 500–2000, with a centrally positioned nest, where agents behave according to the rules described. Agents originate from a single nest entrance and currently deposit one pheromone unit, of each type at every discrete step. Each agent has memory of the distance it has travelled since its last turn, or contact
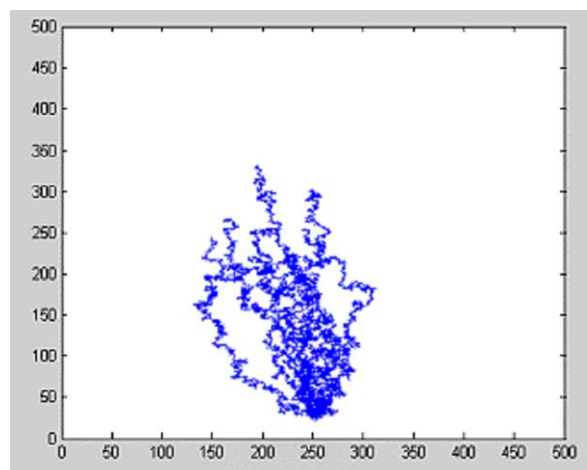

Fig. 1. Simulation using movement rules with 20 ants, 500 iterations. No pheromone is laid and the figure plots the tracks of individual ants.
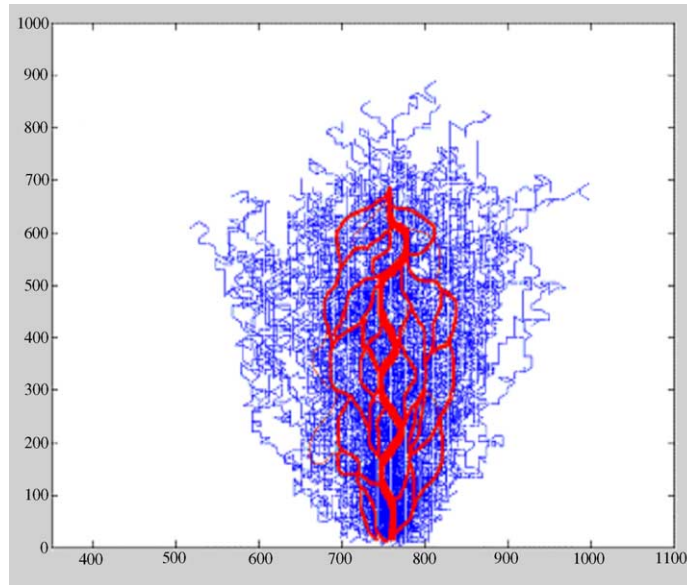
Fig. 2. Simulation using refined movement rules with 200 ants, 1000 iterations (with pheromone).

with a trail, and its hunger level or "motivation" to forage. The current implementation assumes all agents are maximally motivated to forage ensuring all agents leave the nest to explore the environment.

Agents can follow any pheromone detected in cells located within 45° either side of the direction of movement, with the probability of following dependent upon trail strength exceeding a threshold (see Box 1). When following a trail the strength of the pheromone on the trail determines trail fidelity.

Some stages in the implementation are briefly presented in Figs. 1–2. Fig. 1 shows the earliest stage where changes in direction are allowed at each discrete step (equals 2 mm or one ant body-length) and no pheromone is deposited.

A further stage in the implementation of the rules is shown in Fig. 2. The key addition at this stage is the process of advancing 10 steps (approximating to 1.9 cm) before turning, unless a pheromone trail is crossed. This step greatly increases the breadth of search achieved, matching the parameters of that found in the real ants. The proximity to other agents, or their trails, is much less than that seen previously but it is still close enough to maintain contact, thereby preventing agents becoming lost. The emergence of an irregularly shaped network of trails, and a main trunk

trail, is also apparent and the location of the strongest routes in this network has been superimposed upon Fig. 2. Rigorous testing of the importance of the departure distance before turning and the angle of turn will show the significance of these parameters to the *M. pharaonis* search strategy.

4. Conclusions and future work

The preliminary model of the movement rules accurately simulates the emergence of the characteristic trail shape manifested by *M. pharaonis*. Accurate quantification of the characteristics of the natural trail network will enable exhaustive comparison of trail network emergence in the natural and simulated environment. The foraging rules employed by *M. pharaonis* appear to be very simple but the discrete roles of the individual pheromones have yet to be elucidated. Current work will shortly reveal the exact roles of these pheromones, along with their accurate physical parameters including exact decay rates. Predictions of their roles currently require many assumptions, the biological plausibility of which is probably better tested before refining the model. This incremental approach to model development in tandem with empirical research

ensures the validity of the overall model by demanding rigorous testing of all parameters before progressing. Such parameters may be overlooked as irrelevant by a biologist or readily assumed by a computer science but a more correct approach is to couple the two modes of research. The model under development is then assuredly correct and it is valid to incorporate further aspects of foraging behaviour into the model and observe the emergent behaviour of the whole system. Modelling ants as individual X-machines, and ultimately a set of separate X-machines for specific behaviours, is proving to be a valuable aid to biological research into social insect communities.

From this initial study many avenues of research are now beginning to bear fruit and several novel methods of study have been developed to answer crucial questions. Aspects soon to be added to the model include:

- The accurate quantification of the decay rate of the major trail constituents employed during exploration, which will affect the longevity and size of the trail network.
- The affect of hunger on motivation to forage, particularly in the re-establishment of the trail network.
- The influence of hunger, age and brood (eggs, larvae and pupae) size on the role (state) of individual foragers.
- The mechanism of recruitment to a food source.
- Interaction effects between ants when following trails.
- Orientation using the trail network without recourse to visual cues.

It will be useful to express this individual-based model in a formal framework so that a mathematical link can be established between individual and population-level behaviour, facilitated by using the X-machine formalism. This link will facilitate the establishment of causal explanations for population-level patterns or events, by bridging the gap between complicated individual-based models and simplified top-down models. Formal specification of a model also facilitates model checking, the formal verification that the given properties of a system or agent are satisfied by the model. Model checking guarantees completeness of a model with respect to requirements, whilst simulation may only reveal inconsistencies or misconceptions in the model. Formal specification also stands independent of implementation, enabling other modellers to reproduce a simulation or explore other properties of a model.

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