

Decentralized communication, trail connectivity and emergent benefits of ant pheromone trail networks

Duncan E. Jackson · Mesude Bicak · Mike Holcombe

Received: 8 July 2009 / Accepted: 2 February 2010 / Published online: 14 March 2010
© Springer-Verlag 2010

Abstract Communication improves decision-making for group-living animals, especially during foraging, facilitating exploitation of resources. Here we model the trail-based foraging strategy of Pharaoh's ants to understand the limits and constraints of a specific group foraging strategy. To minimise assumptions we used model parameters acquired through behavioural study. Pharaoh's ants (*Monomorium pharaonis*) exploit the geometry of trail networks bifurcations to make U-turns, if they are walking the wrong way. However, 7% of foragers perform apparently incorrect U-turns. These seemingly maladaptive U-turns are performed by a consistent minority of specialist U-turners that make frequent U-turns on trails and lay trail pheromones much more frequently compared to the rest of the colony. Our study shows a key role for U-turning ants in maintaining the connectivity of pheromone trails. We produced an agent-based model of a heterogeneous ant community where 7% of agents were specialised frequent U-turners whilst the remaining 93% rarely U-turned. Simulations showed that heterogeneous colonies enjoyed significantly greater success at foraging for distant food resources compared to behaviourally homogeneous colonies. The presence of a cohort of specialised trail-layers maintains a well-connected network of trails which ensures that food discoveries are rapidly linked back to the nest.

This decentralised information transfer might ensure that foragers can respond to dynamic changes in food distribution, thereby allowing more individuals in a group to benefit by successfully locating food finds.

Keywords Agent-based modelling · Decentralized communication · Pharaoh's ants · u-turn · Self-organization

1 Introduction

Animals must make decisions throughout their lives, particularly about where to live or find food, and making informed choices means making the best use of available information [23]. A great advantage of living in a group or aggregation is that information can be shared, and group level behaviours can emerge that benefit group members [22]. Information transfer within groups is believed to play an important role in the evolution of sociality. Individuals in groups can simply exploit information generated by the activities of other group members, via eavesdropping [6]. However, more sophisticated information can also be transmitted directly or indirectly through multiple channels [6,5]. Valuable information is best transferred in an encoded form or by discrete means. For many social species, particularly social insects, this is often achieved by chemical communication using pheromones [33]. A common form of chemical communication used by many animals is substrate-marking with pheromones. In fact, the most complex form of chemical communication is found in the pheromone trails used by ants, termites and caterpillars [33]. Chemical trails allow personal information to be publicly communicated in the field, away from an information centre [31], and this optimises foraging in a dynamic environment [18]. Trail-following ants are some of the most abundant animals on earth [17].

D. E. Jackson (✉) · M. Bicak · M. Holcombe
Department of Computer Science,
University of Sheffield,
Sheffield S1 4DP, UK
e-mail: duncan@dcs.sheffield.ac.uk

M. Bicak
e-mail: m.bicak@dcs.sheffield.ac.uk

M. Holcombe
e-mail: m.holcombe@dcs.sheffield.ac.uk

The mechanism of pheromone trails is acknowledged as a paradigmatic self-organised process [4]. The process is governed by feedback where positive feedback, in the form of a pheromone trail, is provided by a fed ant returning to the nest. Other ants can follow this trail to food and subsequently provide further positive feedback by reinforcing the trail. If the food source is exhausted then they provide negative feedback by refraining from reinforcing with trail pheromone. The trail decays without reinforcement, and ants abandon the food source. However, the mechanism employed by most ants using trails is clearly much more complicated than this. This is because the most abundant ant species employ pheromone trails to organise their foraging activities when exploring, as well as exploiting, their environment [17]. Pheromone trails provide a reliable means of orientation in the environment and a means of communicating food presence. According to the definition of Meuth et al. [25] pheromone trail can be described as a ‘cultural artefact’, or a meme, because it constitutes a “unit of information used in higher order learning”. The advent of ant algorithms means that the general perception of pheromone trails is a simple feedback process where centralised communication occurs in the nest [9]. The success of real and virtual ant colonies is generally attributed to the deployment of massive search resources in parallel, but decentralised communication is likely another major factor in this success.

Ants dominate many environments, and the main source of that dominance is their ability to out-compete their rivals for food. But how can trails be the best strategy? We might assume that an equally numerous competitor will enjoy greater foraging success by searching solitarily rather than being constrained in their search by trails. The explanation for the foraging success of ants is that trails facilitate rapid transfer of information enabling rapid recruitment to the best available food resources, whereas a competing group not using communication relies solely on independent discoveries. In many social species the nest site serves as the information centre where communication is focussed [31]. However, a strategy of recruitment from the nest incurs extra time costs in addition to the time spent searching [8], because an individual must return to the information centre (the nest) to communicate and recruit. This strategy also limits the number of individuals engaged in food search as many wait for recruitment. Allocating a small proportion of foragers to searching might cede an advantage to a competing group where all individuals search.

Clearly the process is not as simple as we assume. For flying social insects costs incurred by recruitment travel are lower because of fast travel times but for ants large distances mean long travelling times, thus making decentralised communication away from the nest advantageous. In fact, this is what we find in colonies of trail-using ants. Exploratory pheromone trail marking of new territory is a more common

event than usually envisaged, because trails are often interrupted or disturbed by normal environmental events, especially rainfall [24]. Trails leading to persistent food sources must be maintained and fresh trails laid when new food finds are sought. Many ant species, most spectacularly army ants, form dense networks of trails during exploration, which link food discoveries allowing foragers to rapidly exploit them without an information centre [18]. Ants searching outside the nest can passively interact with a trail leading to food, meaning that decentralised communication facilitates rapid response to food finds.

Ant trails often form complex branching networks [1] and disorientated ants can make adaptive U-turns for correcting their course using visual cues [2], or trail geometry information [19]. However, the role of seemingly maladaptive U-turns on trails has only recently been investigated. In Pharaoh’s ants [19] 7% of individual foragers make U-turns that take them in the wrong direction i.e. away from the nest when fed or towards the nest when unfed. These spontaneous U-turns occur at any point on a trail and are not localised at trail branch points (bifurcations). Furthermore [15] a minority of ants consistently make frequent U-turns and lay pheromone trail at high frequency. In contrast, ants not making U-turns are highly unlikely to lay trail. These data show that U-turning ants specialise in maintaining the trail network and update its informational content. Here we present agent-based simulations which investigate the benefits derived from a cohort of trail maintenance specialists; the frequent U-turners.

The success of social foraging is hard to quantify without a suitable yardstick. It is impossible to find natural competitors that share the same colony size, search pattern and nutritional requirements as a model species of ant. However, by producing a model encapsulating all the key parameters employed in a study species’ search strategy we can readily compare strategies. Models must use a set of behavioural rules that are sufficient to generate patterns observed in real animals. Agent-based modelling has the advantage that spatial and temporal aspects of a model system can be investigated simultaneously [12]. For a dynamic process, such as pheromone trails, the accurate modelling of agents searching a space will be crucial in measuring foraging success over time. Small, seemingly trivial behaviours can be massively amplified leading to the emergence of unpredictable adaptive patterns [10]. This makes it preferable to model a real foraging process, based on actual behavioural parameters, rather than a generalisation that might overlook key behaviours. We model the pheromone trails of the Pharaoh’s ant and compare relative foraging success of populations containing individuals with homogeneous likelihoods of U-turning and populations containing specialist U-turning cohorts. We present our model using the X-machine formalism for computational agent specification [16].

2 Methodology and rationale

2.1 Purpose

Our model tests the hypothesis that populations of ants containing a cohort of U-turning specialists are more efficient at foraging than populations where all individuals U-turn with similar frequency. We further strive to deliver new insights into why this should be the case.

Several classes of models have already been produced to describe aspects of ant pheromone trail formation and traffic flow, particularly when selecting between food sources. Discrete models have proved very useful for studying emergent processes where space must be explicitly modelled. Cellular automata (CA) in particular have been successfully applied to the modelling of ant pheromone trails and yielded general theoretical insights into the spatio-temporal emergence of this process [10,29]. However, theoretical research has yet to evaluate the benefits of behavioural specialisation in group foraging strategies. The fact that many trail-using ants must construct trail networks for orientation might limit the breadth and depth of their search, relative to species that don't use trails. Our model attempts to understand how this problem is overcome in the case of Pharaoh's ants. It is likely that emergent population-level behaviours, especially decentralised communication, might facilitate greater search effectiveness than anticipated. In our model we ignore the role of recruitment from the nest, because it is poorly characterised for ant species. Because of this our model more closely replicates the common natural situation when ants encounter new territory and engage in a 'land rush', whereupon they rapidly explore the environment marking up a new trail network as they search for food [32].

2.2 Model parameters and scale

Pharaoh's ant is a 2 mm monomorphic pest ant forming colonies with less than 2,500 workers [26]. Colonies readily form trails to food and manipulation of colony size is simple, due to an absence of nest-mate recognition [17]. They have poor vision and rely on pheromone trails for orientation. They deposit trail pheromones constitutively when outside the nest [13] forming branching networks of pheromone trails even before food is discovered [19]. Pharaoh's exploit the geometry of trail bifurcations in trail networks to correct their orientation [19]. Our agent-based model comprises of three levels: individual; population; and environment.

2.2.1 Individual

Individuals are characterised by their identity number, nutritional status (internal food reserves), current heading, and environmental location. Each (ant) agent possesses no

internal memory to guide them between resource and nest-site locations. Memories of foraging routes are externalised as pheromone trails. The absence of stored memories of routes means that the memory each agent must possess is only a single 'memory' of their current internal food reserves. This is essentially an awareness of how hungry they are, and this parameter governs their motivation to leave the nest and forage or return to the nest when fed.

Individuals exit a nest site when their hunger drops below a threshold value and begin searching for food. They move non-randomly, according to a probabilistic turning matrix known as a 'turning kernel' [30], derived from behavioural observations, at a constant walking speed. Agents deposit pheromone in the environment as they walk and can sense the presence of pheromone in neighbouring cells if it exceeds a threshold value. If a pheromone trail is present they follow the trail, but if multiple cells with pheromones are detected their choice is biased first by pheromone concentration, then by a preference for walking ahead. Agents show high fidelity to trail following, but there is always a probability they will depart from the trail at each step. Agents also engage in U-turning, where they make a spontaneous 180° turn [15].

2.2.2 Population

Many simulations of social insect colonies lack authenticity because they fail to simulate colonies of natural sizes. The subsequent failure of simulated colonies to display the expected emergent properties found in the subject species is often attributed to the small colony size used in simulations. Pharaoh's ants have an advantage over many social insects in that the typical colony size is 500–2,500 workers [26]. For purposes of simulation we use colonies of 250 agents. Pharaoh's ant colonies are approximately equally divided into nest-workers and foragers [3]. Thus a colony with 250 foraging workers would contain 500 workers [26].

2.2.3 Environment

We simulate the environment as a 2-D square matrix of cells, where each cell has a side length of 2 mm (one ant body length). The dimension of matrix ranged from 125 to 750 cells thus simulating environments ranging from 25 to 150 cm (0.06–2.25m²), a realistic foraging space. A cell could contain ants, nest, food and pheromone, or be empty. All agents in a colony are initialised at the central place point of the environment. An inexhaustible, square patch of food with dimensions of 10×10 cells is placed in the top right-hand corner of the environment. As soon as an agent leaves the nest to begin foraging, the agent deposits 2 pheromone units in the cell it occupied. A cell's total pheromone content (p_i) decays exponentially such that at the end of each iteration the updated cell pheromone content (p_u) is $p_u = p_i - 0.0248p_i$ [20].

2.2.4 Temporal and spatial scale

A cell equates to a single ant body length and a single ‘step’ simulates a movement of 2 mm. Mean walking speed is 7.1 mm per second, thus one iteration simulates a time step of 0.28 s.

2.2.5 Parameterisation of U-turning frequency

In order to parameterise the overall U-turning frequency of the *M. pharaonis* colonies, a series of experiments were conducted. Complete descriptions of these studies can be found in references 15 and 19.

2.2.5.1 U-turning frequency on active trails

Frequency of U-turning behaviour on active trails was determined using three *M. pharaonis* colonies, each with approximately 1,200 workers and 10–50 queens [19, 15]. There was no significant difference in U-turning frequency (mean = 43.2%, range = 39.5–48%) among the three study colonies (Chi square = 1.98, $df = 2$, $N = 300$, $P = 0.372$), so data was pooled for all colonies to compare fed and unfed ants. 150 fed ants (50 from each colony) and 150 unfed ants (50 from each colony) performed at least one U-turn with similar probability; 45.1 and 38% respectively (Chi square = 1.73, $df = 1$, $N = 300$, $P = 0.188$). The overall U-turning frequency of 43% found on an active foraging trail was much higher than the 7% reported by Jackson et al [19] for individual ants on an empty trail. This high frequency is explained by the fact that if U-turning ants make many U-turns then they must also spend longer on the trail and are more likely to be observed. Indeed ants making U-turns were highly likely to make subsequent U-turns again within a short distance.

2.2.5.2 Fidelity to U-turning behaviour

Individual fidelity to U-turning behaviour was tested [15] so as to determine whether a specialist minority of ants were responsible for the high frequency of spontaneous U-turns. Individual fidelity to U-turning behaviour was tested using 20 fed and unfed ants from each of two colonies [15]. U-turning ants performed a mean of 4.1 U-turns in a single test (SD = 4.183, $N = 80$ ants), whereas non-turning ants made a mean of 0.14 U-turns per test (SD = 0.347, $N = 400$ [80 ants with 5 test each]). This difference was highly significant (Student’s t test: $t = 18.69$, $df = 478$, $P < 0.0001$) showing that Pharaoh’s ants demonstrate a remarkable fidelity to non-turning or U-turning behaviour. 77 of 80 ants (96%) identified as non-turners on their initial trial were also non-turners on their next trial. whilst 72 of 80 ants (90%) identified

as U-turners made subsequent U-turns. There were no significant differences between the frequency of U-turns made by fed and unfed non-turning ants from either colony (colony 1: $t = 0.8$, $df = 38$, $N = 40$, $P = 0.428$; colony 2: $t = 0.603$, $df = 38$, $P = 0.550$), or between colonies (fed and unfed non-turning ants pooled for each colony: $t = 1.44$, $df = 38$, $P = 0.150$).

2.2.5.3 Trail-laying and U-turning

Why is a strong behavioural fidelity to U-turning behaviour in Pharaoh’s ants so important? There is some evidence to suggest that behavioural specialisations might occur on pheromone trails [15]. For example, individual *Lasius niger* ants have been shown to differ in the frequency with which they perform trail laying behaviours. The hypothesis that U-turning was correlated with trail-laying behaviour in U-turning, but not non-turning individuals, was investigated by isolating 50 ants in both categories from each of three colonies (150 U-turning ants and 150 non-turning ants) and observing their trail laying behaviour. Trail-laying was defined as marking the soot layer with the stinger, which is an indication of trail pheromone deposition. Marks made by the stinger were visible between footprint markings as continuous lines, streaks, or spots. As a result, 263 of 300 (87.7%) U-turning ants made trail markings compared to only 67 of 300 (22.3%) non-turning ants. This difference is highly significant (Chi-square = 258.7, $df = 1$, $N = 600$, $P < 0.0001$) and is not significantly affected by colony, or nutritional status (log-linear likelihood analysis: by colony, $G^2=3.7$, $df = 4$, $N = 200$ ants \times 3 colonies, $P = 0.4481$; fed versus unfed, $G^2 = 2.08$, $df = 3$, $N_{fed} = 300$, $N_{unfed} = 300$, $P = 0.556$). Thus U-turning ants typically lay pheromone trail whilst non-turning ants rarely do so.

2.3 Process overview and scheduling

Agents are initialised in the nest with a nutritional status (food units) randomly selected from a normal distribution, and a proportion of this food is consumed at each iteration. As soon as an agent’s nutritional status drops below a hunger threshold, the hungry agent begins foraging and randomly enters one of the eight neighbouring cells, unless pheromone is detected in a neighbouring cell. If pheromone is detected in one or more cells, then the cell with the highest pheromone concentration is selected, but if an equal choice is available a preference is given to the cell directly ahead of the current cell (by a weighting). Agents also deposit pheromones in every cell they enter as they search. Agents search until they detect food, in which case their nutritional level is updated to a maximum food level, and the agent makes a 180° turn to return in the nest direction. We varied environmental dimensions, but the process always runs for 1,000 iterations.

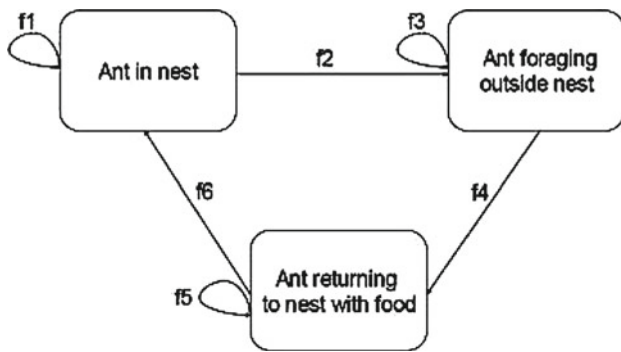


Fig. 1 Pharaoh's ant forager modelled as an agent specified using a simple, descriptive formalism. Ant agents were modelled with three readily observable behaviours (OB): ant in nest; foraging outside nest; returning to nest with food. Each of these OBs had a function or behaviour associated with it (f1, f3, f5) and transitions between OBs were labelled with event-driven functions (f2, f4, f6) described fully in the text

We specify agents as X-machines, a simple formalism used in computer science and well-suited to the robust, flexible description of processes where the components can have complex internal states [16]. As shown in Fig. 1, we model agents as having three readily observable behaviours (OB). These are: ant in nest; ant foraging outside nest; and returning to nest with food. Each OB has a function or behaviour associated with it (f1, f3, f5) and the transitions between the OBs are labelled with event-driven functions (f2, f4, f6). An agent tests simple conditions to determine its OB status and then steps through a further set of conditional tests in the appropriate function, which determines its next move (stay in nest, move cell, or feed). Each agent is tested in turn, and their position/memory is updated every iteration. The schedule for updating of global pheromone deposition and pheromone decay is of great importance. Pheromones decay at the start of each iteration before ants deposit more pheromone following their move (end of iteration). This ensures that pheromone does not decay until after the next time step and also prevents ants responding to pheromone until it has been deposited.

2.4 Design concepts

Emergence: Ant pheromone trails are truly self-organised, emergent phenomena. The system-level behaviour emerges from the individual behaviour of the interacting population components. A novel characteristic of our model is that a realistic test is given to our ant agents. The size of environment we use is always sufficiently large such that an individual agent must travel far from the nest to find food. A single agent cannot possibly return to the nest simply by following its own pheromone trail, because the trail connecting it to the nest will have decayed before it even reaches the food. Thus individual

agents are reliant on the trail-laying actions of other agents for orientation in the environment. Our model differs markedly from previous models in this respect, because in many models it is typical for trails to decay so slowly that the trail of a single agent will persist sufficiently long to guide it back from the food to the nest (for example: [27, 10]). Empirical study has shown that the trails laid by an individual ant only persists for approximately 8 s, which would limit the foraging range of an isolated individual to 56.8 mm (with a mean speed of 7.1 mm per second). This approximates to travelling 28 matrix cells, which means an ant cannot find the food alone and return using its own trail even in the smallest environment we tested (125 cells per side).

Stochasticity: Where behavioural parameters are poorly understood we have used probabilities. In our model U-turning and trail-leaving occur randomly with probabilities as determined in our empirical studies. Turning angle is determined by a probability matrix. There are also error rates (probabilities) associated with trail following (detection) and reorientation, both derived from empirical data. We do not imply that these behaviours are probabilistic, but acknowledge that at the current time we simply lack an understanding of the deterministic mechanisms underlying these choices.

Observation: During simulations the spatial distribution of agents, agent nutritional status and location of pheromone trails was constantly monitored, and where necessary visualised. For subsequent output analysis we measured the proportion of fed ants as a performance measure.

2.5 Initialisation

In our model agents were initialised with low food reserves from a normal distribution with a range of 0–10 food units. As stated previously, for an agent to begin foraging we assume that their internal food reserves must drop below a threshold value that triggers a behavioural transition. Food reserves decay linearly at a rate of 0.02 units per time step; therefore, all agents become active foragers when their food reserves equal to 1.0 food unit or less, and leave the nest within a narrow time window. Food reserves can drop to zero, but remain at zero until food is found, because we do actually model a social mechanism governing motivation to forage. The time period simulated begins in the morning, when the diurnal Pharaoh's ants begin foraging for resources between 8 and 9 a.m. after a night-time period of inactivity [28]. If the delay between individual foragers leaving the nest was large, then trails may not persist sufficiently long (8 s at a minimum) for ants to orientate themselves on their return. Resumption of foraging is undoubtedly a more complex process than modelled here, but irrespective of colony size, Pharaoh's ants commence foraging activity rapidly [28].

3 Experimental simulations

Agent communities were simulated using Matlab® on a PC with a Pentium IV 3.1 GHz processor and 512 MB RAM.

3.1 Homogeneous versus heterogeneous U-turning populations

We compared the foraging success of two types of agent communities. Firstly, colonies of behaviourally homogeneous agents, which all performed U-turns with a probability of 0.0005 at each iteration (an iteration was 2 mm and experimental trails were 300 mm in length). Secondly, we compared colonies of heterogeneous agents, which contained two cohorts of agents. Frequent U-turners comprised 7% of this population and performed U-turns with a probability of 0.018 at each iteration (an iteration was 2 mm and experimental trails were 450 mm in length). The remaining 93% performed U-turns with a probability of 0.00044 at each iteration, both employing the same foraging strategy but with a single behavioural difference. We used a simple indicator to compare performance by measuring the proportion of the agents that successfully located food in a fixed time period, i.e., the foraging success. We also tested control colonies that foraged individually without pheromones.

Environment size and foraging success: Colonies of fixed agent numbers (250 foragers) foraged for 1,000 iterations (approximately 4.8 min) in environments of variable size ($m \times m$), where $m = 125, 250, 375, 500, 625, 750$ cells or units (i.e. 25, 50, 75, 100, 125, 150 cm). Ten replicate trials for each environment size were performed using each strategy: heterogeneous U-turning; homogeneous U-turning; and control colonies that did not use pheromone trails. Reference to individual logs at each iteration, enabled us to investigate the behaviour of individuals over time.

4 Results

Simple emergence of branching pheromone trail networks through the activity of simulated ants has been previously investigated, and the form of the trail network has been shown to depend largely upon pheromone decay rate and individual fidelity to trail following [10, 11]. Modulation of these parameters determines degree of branching and the spatial limits of trail networks (breadth and depth of network). Similarly, using empirical parameters determined with Pharaoh's ants, we simulated communities of foraging agents, and predictably branching networks of trails emerged. However, our model is more refined than previous models because all parameters were obtained by empirical research at the individual level. A further major difference between our models and previous work is that the distance to food in our

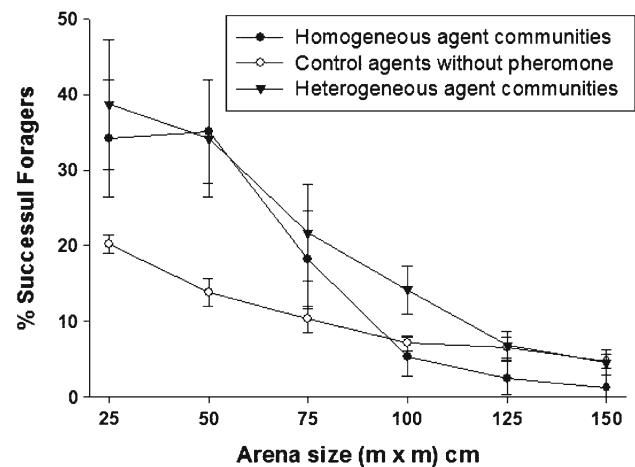


Fig. 2 Foraging success of heterogeneous U-turning (with specialists), homogeneous U-turning and control agent colonies in a foraging arena of variable size. Communities of 250 agents foraged for 1,000 iterations (approx. 4.7 min) in environments of 25–150 cm. We performed 10 replicates for each trial environment size

simulations exceeds the maximum distance an agent can travel and still return home simply by following its own decaying trail (for example: [27]). In this respect our models more faithfully represent ant trail use, where individuals must rely on cooperation with nest-mates to form trails.

Using our model we compared performance of the search strategy employed by Pharaoh's ants where agent communities contained individuals exhibiting heterogeneous U-turning behaviour with heterogeneous communities containing specialists. Results of the simulations (comparing colony foraging success) are shown in Fig. 2. Heterogeneous agent communities enjoyed greater foraging success than homogeneous agent communities in all trials except when the environment was small. We found no significant difference in foraging success between the two colony types when the environment dimension was small, 50 and 75 cm (Student's t test: 50 cm: $t = -0.28$, $N = 10$, $df = 18$, $P = 0.785$; 75 cm: $t = 1.214$, $N = 10$, $df = 18$, $P = 0.241$). However, heterogeneous colonies with U-turning specialists performed significantly better (heterogeneous mean = 8.5%, SD = 2.2%, compared to homogeneous mean = 3.0%, SD = 2.2%) when the environment dimension was 100 cm or greater (Student's t test: 100 cm: $t = 6.749$, $N = 10$, $df = 18$, $P < 0.001$; 125 cm: $t = 4.678$, $N = 10$, $df = 18$, $P < 0.001$; 150 cm: $t = 4.472$, $N = 10$, $df = 18$, $P < 0.001$).

In large environments (125 and 150 cm) the performance of heterogeneous agent communities was similar to that of control communities, which did not use pheromone trails. The exploratory success of behaviourally homogeneous colonies was poor in large environments, when compared to independent foragers (control colonies). The improved foraging success of heterogeneous colonies is attributable to

establishment and maintenance of multiple foraging trails, because of the activities of specialist U-turning agents. Homogeneous colonies were less likely to maintain multiple trails linking to the nest and instead were found to maintain only one or two main trails. Heterogeneous colonies benefited from maintaining numerous trails (typically 4–6) to the nest, because links to new food discoveries were more likely to be rapidly established and exploited by foragers in the local area. The successful establishment of pheromone trails to a food resource is a highly dynamic process and not all discoveries are guaranteed to be followed by trail establishment. Behavioural heterogeneity certainly increased the likelihood of trail establishment and this was reflected in the increased overall foraging success.

5 Discussion

It has been conclusively demonstrated that most U-turns are neither mistakes, nor corrections made by ants that were previously walking the wrong way. Here we have shown that U-turning coupled with increased trail-laying is an adaptive behaviour that is crucial for maintaining trail network connectivity, and facilitating responses to change. U-turning ants are well-informed to make decisions on trail persistence as they continually update their knowledge of food availability, by walking along trails repeatedly. This contrasts with ants not making U-turns, who make a single trip and could be misinformed if they fail to access a crowded resource, for example. In a competitive environment making quick decisions is vital and putting decision-making in the hands of a representative, well-informed minority of specialists probably speeds this process. U-turners could have greater control over the rapid abandonment of exhausted food sources, or switching to superior food sources.

Using a simple agent-based model we found that behaviourally heterogeneous populations of agents, where a small minority (7%) of agents made frequent U-turns, enjoyed greater colony foraging success than homogeneous colonies with a low level of U-turns. The reason for this greater foraging success was an improvement in trail network connectivity in colonies containing specialist high frequency U-turners. 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. Homogeneous colonies maintained less trails linking to the nest and, although individuals did discover the food source, were less likely to succeed in establishing new trails sufficiently quickly for other foragers to benefit.

Our model highlights some of the great benefits of agent-based modelling, in particular the fact that it “permits the user to trace back the system properties to the behaviour of individual animals” [21]. Kaiser was an early pioneer of

“individual-based modelling” in the 1970s who recognised that “we will never be able to understand a system’s properties unless we understand how they emerge”. Using individual-based modelling Kaiser [21] showed how the constant, low numbers of dragonflies observed patrolling shorelines of ponds could only be “attributed to certain behavioural properties of individual dragonfly males”. Using his model he “could correctly predict the outcomes of situations for which no data have been collected hitherto, or which do not occur at all in nature” [21]. This latter point is very important as many model analyses stop where the model has been corroborated to some degree, but Kaiser recognised that to achieve a better mechanistic understanding of the system dynamics it is vital to analyse these ‘unnatural’ situations. We have compared the performance of agent colonies behaving in an ‘unnatural’ manner with ‘natural’ heterogeneous colonies. This simple comparison provides a novel insight into the benefits of heterogeneous U-turning behaviour, demonstrating how a simple behavioural difference between individuals has major effects on the fundamental properties of a system.

The great benefit of agent-based modelling is that it treats individuals as unique and discrete entities with properties, other than age, that can change during their lives. Once the rules and characteristics of individuals have been identified and specified in an agent-based model “the population and community-level consequences ... emerge naturally” [7]. However, in a review Grimm [14] found that models are rarely fully explored to yield a deeper understanding of underlying mechanisms. Furthermore, 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 [14]. Our work here has demonstrated how a simple behavioural difference between individuals can have major effects on the fundamental properties of a system.

Our data, and agent-based model, suggest a key role for a cohort of specialist U-turning ants in establishing and maintaining pheromone trail connectivity. This finding contradicts the notion that all ants contribute equally to trail persistence, by laying trail on their return to the nest only if they find a rewarding resource. This ‘democratic’ system, termed the ‘electorate process’ by Wilson [32] (or collective decision-making [4]), would determine which trails persist because the ‘electorate’ decide whether trails are rewarding. Instead Pharaoh’s ants employ a more human, and entirely practical, implementation of democracy where a few representatives decide whether trails persist, while other colony members concentrate on foraging itself.

Our work highlights the importance of behavioural heterogeneity in determining system behaviour. This novel aspect of ant foraging behaviour might be emulated by colonies of virtual ants exploring search spaces, where the network topology is unspecified or needs to be discovered. We have also

shown that the presence of specialists might enable greater responsiveness to change in a dynamic environment because linkages are maintained allowing rapid mobilisation of other agents in the local to exploit the newly discovered solution. We also highlight a further key aspect of real ant foraging behaviour which might profitably be exploited in agent-based search, and that is the importance of decentralised communication via the environment. Future research will determine whether the allocation of 7% of the worker force to U-turning and trail maintenance behavior is an optimal commitment when faced with problems of balancing dynamic resource problems.

Traditional Ant Algorithms implement an information centre for communication which is more reminiscent of the centralised communication observed in honeybee (*Apis mellifera*) colonies [4] rather than ants. Current research into animal communication more fully recognises the use animals make of a wide variety of information sources, especially social information which can be passively acquired whilst foraging [6,5]. Opportunities to communicate at an information centre are far fewer than those available to acquire information by observing the behaviour of others or the consequences of their actions. A key goal of Nature-inspired Computing must be to recognise and emulate the wealth of information that can be exploited in search, with minimal memory use, so as to optimise decision-making.

Acknowledgements DJ was supported by the Novel Computation Initiative EPSRC grant ‘MASSING: Multi-Agent Search Strategies in Natural Groups’. MB was supported by BT Exact and EPSRC.

References

- Acosta FJ, Lopez F, Serrano JM (1993) Branching angles of ant trunk trails as an optimization cue. *J Theor Biol* 160:297–310
- Beckers R, Deneubourg JL, Goss S (1992) Trails and U-turns in the selection of a path by the ant *Lasius niger*. *J Theor Biol* 159:397–415
- Beekman M, Sumpter DJT, Ratnieks FLW (2001) Phase transition between disordered and ordered foraging in Pharaoh’s ants. *Proc Natl Acad Sci USA* 98:9703–9706
- Camazine S, Deneubourg J, Franks NR, Sneyd J, Theraulaz G, Bonabeau E (2001) Self-organization in biological systems. Princeton University Press, Princeton
- Dall SRX, Giraldeau L, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20:187–193
- Danchin E, Giraldeau L, Valone TJ, Wagner RH (2004) Public information: from nosy neighbours to cultural evolution. *Science* 304:487–491
- DeAngelis DL, Rose KA, Huston MA (1994) Individual-oriented approaches to modelling ecological populations and communities. In: Levin SA (ed) *Front Math Biol*. Springer, Berlin, pp 390–410
- Dechaume-Moncharmont F, Dornhaus A, Houston AI, McNamara JM, Collins EJ, Franks NR (2005) The hidden costs of information in collective foraging. *Proc Roy Soc B* 272:1689–1695
- Dorigo M, Di Caro G, Gambardella LM (1999) Ant algorithms for discrete optimisation. *Artif Life* 5:137–172
- Edelstein-Keshet L, Watmough J, Ermentrout GB (1995) Trail following in ants: individual properties determine population behaviour. *Behav Ecol Sociobiol* 36:119–133
- Ermentrout GB, Edelstein-Keshet L (1993) Cellular automata approaches to biological modelling. *J Theor Biol* 160:97–133
- Fahse L, Wissel C, Grimm V (1998) Reconciling classical and individual-based approaches in theoretical population ecology. *Am Nat* 152:838–852
- Fourcassié V, Deneubourg JL (1994) The dynamics of collective exploration and trail-formation in *Monomorium pharaonis*: experiments and model. *Physiol Entomol* 19:291–300
- Grimm V (1999) Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecol Model* 115:129–148
- Hart AG, Jackson DE (2006) U-turns on ant trails. *Curr Biol* 16:R42–43
- Holcombe M (1988) X-machines as a basis for dynamic system specification. *Software Eng J* 3:69–76
- Hölldobler B, Wilson EO (1990) *The Ants*. The Belknap Press of Harvard University, Cambridge
- Jackson DE, Ratnieks FLW (2006) Communication in ants. *Curr Biol* 16:570–574
- Jackson DE, Holcombe M, Ratnieks FLW (2004) Trail geometry gives polarity to ant foraging networks. *Nature* 432:907–909
- Jackson DE, Martin S, Holcombe M, Ratnieks FLW (2006) Longevity and detection of persistent foraging trails in Pharaoh’s ants, *Monomorium pharaonis*. *Anim Behav* 71:351–359
- Kaiser H (1979) The dynamics of populations as a result of the properties of individual animals. *Forts Zool* 25:109–136
- Krause J, Ruxton GD (2002) *Living in groups*. Oxford University Press, Oxford
- Krebs JR, Davies NB (1997) *Behavioural ecology*. 4th edn. Blackwell, Oxford
- Lugo AE, Farnworth EG, Pool D, Jerez P, Kaufman G (1973) The impact of the leaf cutter *Atta colombica* on the energy flow of a tropical wet forest. *Ecology* 54:1292–1301
- Meuth R, Lim MH, Ong YS, Wunsch DC (2009) A proposition on memes and meta-memes in computing for higher-order learning. *Memetic Comput J* 1:85–100
- Peacock AD, Sudd JH, Baxter AT (1955) Studies in Pharaoh’s ant, *Monomorium pharaonis* II. Dissemination. *Entomol Mag* 91:130–133
- Schweitzer F, Lao K, Family F (1997) Active Random walkers simulate trunk trail formation by ants. *Biosystems* 41:153–166
- Sudd JH (1960) The foraging method of Pharaoh’s ant, *Monomorium pharaonis*. *Anim Behav* 8:67–75
- Solé RV, Bonabeau E, Delgado J, Fernandez P, Marin J (2001) Pattern formation and optimization in army ant raids. *Artif Life* 6:219–226
- Vincent AD, Myerscough MR (2004) The effect of a non-uniform turning kernel on ant trail morphology. *J Math Biol* 49:391–432
- Ward P, Zahavi A (1973) The importance of certain assemblages of birds as “information centres” for food finding. *Ibis* 119:517–534
- Wilson EO (1962) Chemical communication among workers of the fire ant, *Solenopsis saevissima*. I. The organisation of mass foraging. *Anim Behav* 10:134–164
- Wilson EO (1971) *The insect societies*. Belknap Press of Harvard, Cambridge