Simulating the Evolution of Ant Behaviour in Evaluating Nest Sites

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Abstract. When an ant colony needs to find a new nest, scouts are sent out to evaluate the suitability of potential sites, particularly their size. It has been suggested that ant scouts of *Leptothorax albipennis* use a simple heuristic known as Buffon's needle to evaluate nest size. They do this in two stages: first laying a pheromone trail in the nest site, then, after a return to the old nest, coming back and wandering within the site assessing frequency of intersection with the pheromone trail ("two-pass" strategy). If a colony is forced to relocate from its current nest due to destruction of that nest, the time required to find a suitable new nest may be crucial. This paper details preliminary results from a computer simulation model of evaluation of nest size. The model aims to study why a "two-pass" strategy is used by ants when a "one-pass" strategy, in which the ant simultaneously lays pheromone and assesses the frequency at which it encounters its own trail, may be more time efficient. Analysis of the results indicates no clear advantage for the "two-pass" strategy, given the assumptions of the model. Possible implications of this result are discussed.

1. Introduction

Computer simulation modelling of social insects such as ants, termites and certain species of bees and wasps is an area of recent research, with models of task allocation [2], foraging in ants [3] and nest-assembly in wasps [7], among others. In this paper we consider size assessment of potential nest sites by ant scouts. Assessing the size of a potential nest site is a hard problem for a scout ant, and yet the decision of an individual scout about whether a site is suitable to house the whole colony can have a large impact on the colony's survival. Size assessment is difficult because scouts cannot simply measure diameter, since nests are often irregularly shaped. In addition, they are usually dark, and the ants' vision does not permit them to correctly estimate area. The evaluation method used by ant scouts of *Leptothorax albipennis* is therefore an interesting area of study. After discounting heuristics such as perimeter length or mean free-path length, Buffon's needle has been proposed instead [4, 5]. Fundamentally, Buffon's needle works on the principle that an ant lays a pheromone trail of defined length while wandering throughout a potential nest site, then evaluates the approximate size of the nest site by wandering again within the site while assessing the frequency at which it crosses its previously laid trail. All evidence suggests that *Leptothorax* ants assess sites by working alone and that they do this by deploying individual specific trail pheromones [4].

The original *in-vivo* investigation of Buffon's needle in *L. albipennis* was extended to *in-silico* experimentation by Şahin and Franks [6]. Their model replicated nest-integrity and size-assessment behaviour, and discovered a fundamental trade-off between thigmotaxis (wall-following behaviour) and exploration of the central area of the nest site in effective assessment.

One question begs an answer: In the scouting behaviour displayed by *L. albipennis*, why is the nest evaluation process carried out in two stages, the first consisting of laying a pheromone trail in the nest site, the second in assessing frequency of intersection with that trail while wandering within the nest site? In principle it would seem more efficient to compress the two stages into one. Hence we are interested in whether the "two-pass" strategy employed by the real ants is algorithmically superior to a "one-pass" strategy in which the ant wanders within the nest site, simultaneously laying pheromone and assessing the frequency of intersection with its own trail. Is there is an algorithmic reason why a one-pass strategy is not suitable? For instance, does a one-pass strategy bias area estimation in a way which an ant cannot compensate for when classifying a nest's size? Such a bias might occur because the ant is laying pheromone and detecting it in adjacent locations, which will result in a different frequency of path crossings compared to the two unrelated random walks used with the two-pass strategy. Here we present a computer simulation model that seeks to answer this question. In order to simplify the design and analysis of that model, we do not consider perimeter evaluation behaviour as was done by Şahin and Franks [6], but focus solely on size assessment behaviour. The independent implementation of two simulation models of the same behaviour is a prime candidate for validation of the models through model docking [1]. We hope to do this in the future.

2. Methods

The computer simulation model[1] was implemented using the Swarm[2] simulation toolkit and models the process of nest site evaluation by an individual scout ant using either the one-pass or two-pass strategy. The potential nest site has a simple representation as a hollow square with one entrance in the middle of the southern wall. The ant is defined by the characteristics shown below in table 1, which are explained in the following text. The ranges of these characteristics indicate the limits within which they are permitted to vary by the evolutionary component of the model, described in section 2.2, for which all initial values are selected randomly.

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[1] ftp://ftp.swarm.org/pub/swarm/apps/java/contrib/Buffon-1.0-2.2.tar.gz

[2] http://www.swarm.org

Table 1. Ant characteristics

Characteristic	Range
scouting strategy	one-pass or two-pass
scouting time	1-1000 time units
arousal decay rate	1-10 units per time step
classification divisor	1-3000

2.1 Model of Ant Behaviour

Note that the model only simulates the size-assessing behaviour of the ant, and not the boundary-checking behaviour. The simulation of scouting behaviour proceeds as follows:

1. Place ant at entrance to nest, facing nest centre, and initialise arousal level to 0.
2. Change ant's current direction with probability:
   a. 20% turn left 45 degrees
   b. 60% maintain current direction
   c. 20% turn right 45 degrees
3. If obstacle in path along new heading repeat 2 unless all three possible headings tried in which case rotate ant 45 degrees left or right with equal probability and repeat 2.
4. Deposit pheromone at current location as dictated by strategy.
5. Move to new location indicated by current direction.
6. If pheromone detected at new location increment arousal level by 10 units. Decrement arousal level by arousal decay rate (arousal level minimum = 0).
7. Repeat from 2.

The above process repeats for the number of time steps indicated in the ant's characteristics. If the ant is using a one-pass strategy then the ant deposits pheromone continuously. If the ant is using a two-pass strategy then the ant spends the first half of its scouting time depositing pheromone and the second half not depositing pheromone but simply assessing the frequency at which it encounters its previously laid pheromone trail (the ant is reset to the entrance of the nest at the beginning of the assessment phase, just as in the case of a real ant).

The assessment behaviour of the ant just described above is based on the concept of an arousal level. This is effectively a measure of the frequency of intersections with the pheromone trail over some recent time window defined by the arousal decay rate. Note that we are not proposing here that this is how ants actually measure intersection frequency with pheromone trails, but rather we are showing how a simple and cognitively plausible mechanism is sufficient to give rise to the desired result. The arousal level scheme certainly seems cognitively simpler than the counting scheme used by Şahin and Franks [6].

The movement behaviour of the ant given above is a constrained random walk, and was designed to correspond roughly with observed movement behaviours in real ant scouts. A visualisation of the ant's simulated behaviour is shown below in figure 1, and a visualisation of actual ant behaviour is given for comparison in figure 2 below. In figure 1 dark grey represents the walls of the nest site, and light grey represents the scout ant's pheromone trail. The entrance to the simulated nests shown in figures 1 and 2 is in the middle of the right-hand wall in both cases.

At the conclusion of the scouting process the ant's assessment of nest size *e* is given by

$$e = (c-1) - \min\left(\operatorname{int}\left(\frac{r}{d}\right), c-1\right), \qquad (1)$$

where *c* is the number of size categories (e.g. three categories: 0 = small, 1 = medium and 2 = large), *r* is the ant's arousal level at the end of the scouting process, and *d* is the ant's classification divisor (see table 1). This equation simply converts the ant's arousal level at the end of the scouting time, which is a measure of how often the ant encountered its own trail while scouting, into a normalised assessment of nest size.

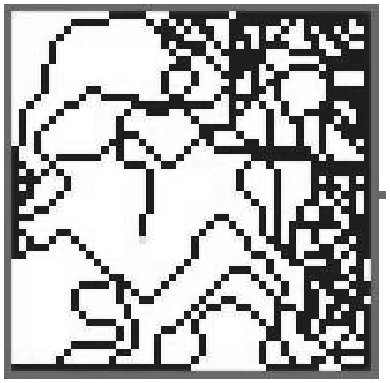

Fig. 1. Simulated ant movement in a potential nest site

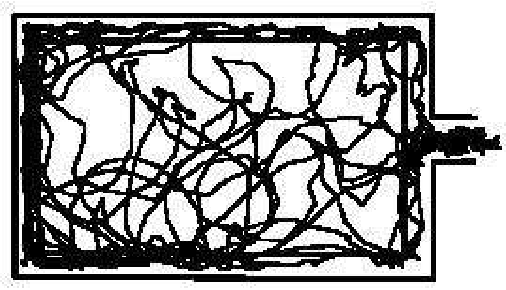

Fig. 2. Actual recorded ant movement in a potential nest site. From Mallon & Franks [4]

2.2 Model of Evolution of Ant Behaviour

A population of ants is evolved according to their average performance in assessing the sizes of potential nest sites as follows:

1. For all ants calculate average fitness based on assessment performance with three different sizes of nest (10 x 10, 30 x 30 and 50 x 50) where fitness *f* is given by

$$f = -q\left|e - s\right| - ta \ , \tag{2}$$

   where $-q$ ($q = 1000$) is the selection pressure on assessment quality, a ($a = 1$) is the selection pressure on assessment speed, e is the ant's estimate of nest size from equation (1), s is the actual nest size, and t is the total time the ant spends scouting.
2. Rank population according to average fitness and cull bottom 33% of population to be replaced by offspring of top 66% of population as follows:
   a. In ranked list of population mate pairs of ants with adjacent average fitness ranks to produce one offspring ant per pair, thus conserving the population size.
   b. For each mating produce offspring genotype using parameterised uniform crossover (crossover rate = 10%) and mutation operators (mutation rate = 1%, maximum value change from mutation = 10% of value range, mutations use a uniform distribution and are limited by the range of the value undergoing mutation).

The evolutionary algorithm described above is not intended realistically to simulate evolution in real ant populations, but rather to provide a simple way to apply evolutionary pressure to the behaviour under consideration.

At this point it is worth summarising the assumptions made in building our model of ant nest assessment behaviour. Table 2 below lists these assumptions.

Table 2. Model assumptions

Model Component	Assumption
ant movement	constrained random walk (see sec. 2.1)
nest shape	uniform (square)
path crossing calculation	arousal level with decay rate (see sec. 2.1)
selection pressure	relative importance of speed and accuracy is as defined in *q* and *a* in sec. 2.2

3. Results

Two different simulations were carried out: one in which all ants used the one-pass strategy, and one in which all ants used the two-pass strategy. Each simulation collected results from 40 experiments with each experiment run on a population of 21 ants over 60 generations. For each experiment, average scouting time (averaged over the fittest 66% of each generation) and number of generations required for the population to become 100% effective at assessing nest size were recorded.

The following hypotheses were tested: (1) that there is a difference in the number of generations required to establish robust nest assessing behaviour by the one-pass and two-pass strategies, and (2) that there is a difference in the time efficiency of the one-pass and two-pass strategies. Only those data where the population evolved to 100% assessment accuracy were included in the statistical analysis. In both cases the results of the analysis were non-significant, therefore the null hypotheses, that there are no differences between the one and two-pass strategies, cannot be rejected (U = 177.5 and U = 136 respectively, N_A = 20, N_B = 20; Mann-Whitney U test, Fig. 3). Furthermore for two simulations of 200 experiments each the one-pass strategy evolved to 100% accuracy in 45 cases, whereas the two-pass strategy evolved to 100% accuracy in 41 cases. Therefore the null hypothesis that there is no difference in the frequency with which one-pass and two-pass populations evolve to 100% assessment accuracy also cannot be rejected ($\chi^2 = 0.133$, $df = 1$).

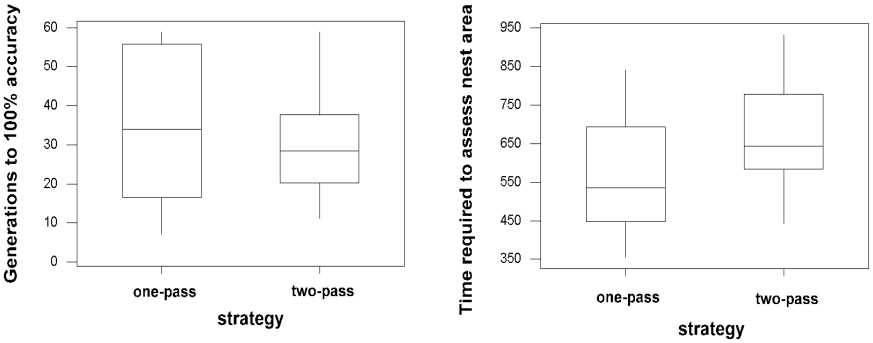

Fig. 3. Results from the simulations: neither in the number of generations to 100% accuracy (left) nor in the time then needed to perform the nest assessment (right) are the one-pass and two-pass strategies significantly different (boxes show quartiles, whiskers show range and the horizontal lines within boxes show medians; n = 20 for both strategies).

4. Discussion

Our simulation results showed no difference in effectiveness between the one-pass and two-pass strategies. That is, the evolutionary time required to establish robust nest assessing behaviour is not significantly different for the two strategies, nor is the frequency with which robust assessment behaviour is evolved using the two strategies. Furthermore, the evolved behaviours do not differ significantly in the time required to make an assessment. However, this can be qualified by two observations. Firstly as the two-pass strategy only lays pheromone for half of the scouting time, the two-pass strategy only uses half the pheromone of the one-pass strategy. So, if pheromone production is energetically costly, the two-pass strategy may be superior in energetic efficiency. On the other hand, the two-pass strategy actually takes more time outside the potential nest site than does the one-pass strategy, as the ants employing it return to their old nest between the two visits to the potential nest site. If the ant returns to the old nest site between visits, it will cover twice as much distance between nest and potential site using the two-pass strategy compared to the one-pass strategy, which costs both time and energy. These two observations each strengthen the case for a different strategy; the first indicates that the two-pass strategy may be better than the model suggests, while the second indicates that the one-pass strategy may be better than the model suggests. The fact that our model cannot distinguish the superiority of either strategy suggests that selection may not have influenced whether *L. albipennis* evolved one or two-pass strategies, and the fact that they use a two-pass strategy may be the result of a random course of evolution in that respect. Alternatively the use of a two-pass strategy by the real ants could suggest evolutionary constraint, or physical constraint based on the potential difficulty of simultaneously laying and detecting pheromone.

The main result of this paper is that the proposed one-pass strategy is able to assess nest area as quickly and as accurately as the two-pass strategy exhibited by the real ants, given the basic model presented here. That is, we have found no algorithmic reason why a one-pass strategy should not be used. To investigate the matter further, we intend to evaluate possible differences between the performance of the two strategies in more detail. In particular, the current model only utilises nest sites of differing size but uniform shape. Mallon & Franks [4] used several different shapes of nest site, including sites with a partial partition inside. We plan to use our model to assess the impact of different nest shapes on the two scouting strategies. Given more diverse nest site structures, is there any difference between the speed and effectiveness of the one-pass and two-pass strategies? Furthermore, it is possible that the arousal level profile generated by different nest shapes is a function of the movement behaviour used, therefore we plan to make this behaviour evolvable as well. Alternatively, the relative fitness of the one-pass and two-pass strategies could be evaluated if selection pressure is varied to favour speed over accuracy or vice-versa. It is also important to investigate in detail the specific effects of the assumptions used in the model. We are currently investigating the model in this manner and intend to present further results shortly.

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