An Agent-Based Model of ants' recruitment strategies compared to their colony size

Abstract

Ants can make use of different strategies for food foraging. In general, small colonies conduct individual foraging and as colonies grow in size, group recruitment and pheromone recruitment become increasingly stronger strategies. The changing habitat due to the increasing colony size can be an explaining factor for the change in behaviour, but recent research has shown that exclusively the increasing number of interactions that are caused by having a larger colony can explain this behaviour. By designing an Agent-Based Model (ABM) of foraging strategies in an ant colony, we tried to model these interactions with different colony sizes. We show that 1) bigger colonies rely more on pheromone recruitment, 2) a combination of different recruitment strategies at the same time is unstable, and 3) ABM's are a viable extension of differential equations when trying to model non-linear interactions.

Keywords— Agent-Based Modelling, ant foraging, recruitment strategies

"Everyone says, stay away from ants. They have no lessons for us; they are crazy little instruments, inhuman, incapable of controlling themselves, lacking manners, lacking souls. When they are massed together, all touching, exchanging bits of information held in their jaws like memoranda, they become a single animal. Look out for that. It is a debasement, a loss of individuality, a violation of human nature, an unnatural act."

-Thomas (1977)

Introduction

Ants are known for their ability to divide labour, e.g. in nest building, reproduction or foraging. They are considered efficient in the preservation of their species, which is evident in the fact that ants have colonised every continent on earth, except for Antarctica. With more than 12.000 different species known today, they account for 15-20% of earth's terrestrial animal biomass (Schultz, 2000) and their species is estimated to be 168 million years old (Moreau et al., 2006).

Different ant species adopt a mixture of foraging strategies. In the studies of Beckers et al. (1989), the authors studied the behaviour of over 98 ant species. They suggest a distinction between four different types of food recruitment strategies: group recruitment, tandem recruitment, pheromone recruitment and individual foraging.

Group recruitment happens when a group of foragers leave their nest to find food and when they do, they can guide other ants to their food source. This is a self-reinforced process because the follower ants can become leaders themselves for the next round of finding food. We can view tandem recruitment as a type of group recruitment were the group of following ants is one. With pheromone recruitment, ants create a pheromone trail from a food source to their nest. The ants release pheromones when they find food, creating a scented path for other ants leading to the food source. This too is a self-reinforced process, as the pheromone-following ants will too release pheromones on their way back to the nest when they found the food.

Recruitment strategies are influenced by habitat, species type and the size of the colony. Generally, ants rely more on pheromone recruitment as colonies grow in size (Hölldobler and Wilson, 1990; Beckers et al., 1989). Planqué (2010) confirmed this in their mathematical derivations of the stability of different recruitment strategies. In their research they propose five different equilibria, of which four are biologically possible. Furthermore, they pose four different predictions from their model:

1. The use of two or more strategies is never a stable situation. Only one of them is likely to be used consistently.
2. There is a certain minimal colony size required for all recruitment methods.
3. As colony size increases, ants should change from solitary foraging to pheromone recruitment, probably with tandem running and group recruitment as intermediate stages.
4. Very large colonies are always expected to use scent trails.

In this research, the relationship between colony size and recruitment strategies, as described by Beckers and Planqué, is further investigated. Planqué (2010) describes the system with differential equations, which has the obvious limitations: it assumes that the population is a homogeneous mixture and the terms are continuous. We overcome these limitations by reformulating the system into an ABM with space, which allows testing their predictions.

First, the relevant theory of Planqués paper is described in 'theoretical background', followed by the model description by ODD+D protocol. Finally, there will be the analysis of the results, discussion and future work.

Theoretical background

Beckers et al. distillate four different kinds of food foraging strategies in ants: tandem foraging, group foraging, individual foraging and chemical foraging. Foraging ants leave their nest and when they find food they can become become recruiters for group foraging, recruiting 'follower' ants of their colony and bringing them to the food source. A distinction between group and tandem recruitment can be made, depending on whether the leader ant recruits more than one other ant. The recruitment of pheromone trail ants depends on the level of pheromone the ant senses, with high levels of pheromones increasing the chance(Beckers et al., 1989). Pheromone recruitment has become well-known in the computer-sciences and has been the inspiration for the Ant Colony Optimization algorithm.

Beckers et al. distilled these different food recruitment methods to compare them against colony size to check their correlation. They found a correlation: the larger the colony size, the less the ants can rely on direct communication methods like group food recruitment and the more they are dependent on pheromone strategies.

Planqué (2010) investigates whether the viability of recruitment methods depend on the relationship between colony size and reliability of recruitment. In their paper, they demonstrate how one recruitment strategy compares to another when both are competing for recruits.

For these dynamics they require four ant roles; *unassigned, follower, leader* and *pheromone*. With the first role, an ant is uncommitted to any recruitment method, also called a solitary forager. Followers and leader take part in the same recruitment method: *group recruitment*. A *leader* recruits *uncommitted* ants, hence they become *followers*. When a group of a *leader* and its *followers* have success in finding food, the *followers* become *leaders* too and can recruit their own *followers* from the pool of *uncommitted* ants. Pheromone recruitment is based on scent. When an *uncommitted* ant picks up the scent of a *pheromone* ant, it has a chance to become a *pheromone* ant as well. Ants can take up another role based on the encounters they have with other ants (see fig. 3). The occurrences of recruitments methods can thus be described by ODEs, as shown below.

- $p(t)$ is the number of ants laying pheromone trails
- $f(t)$ is the number of ants in group recruitment as followers
- $l(t)$ is the number of ants in group recruitment as leaders
- $u(t)$ is the number of uncommitted workers
- c_1 is the per capita rate at which individual ants using pheromone trails recruit ants not currently engaged in any recruitment
- $\frac{c_2}{(c_3+1)}$ is the maximum per capita rate at which ants fail to keep following the trail (with $p = 1$ as the minimum)
- $l_{free} = l - \frac{f}{n}$

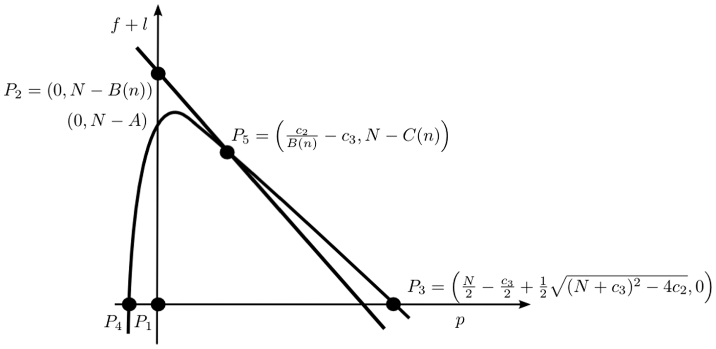


Figure 1: Equilibria found by Planqué et al.

- $c_4(n)$ is the change in numbers of follower ants
- c_5 is the sum of $successful$ and $unsuccessful$ group recruitment
- c_6 is the rate at which free leaders are assumed to stop recruiting for a food source

$$\frac{df}{dt} = c_4(n)ul_{free} - c_5 f \tag{1}$$

$$\frac{dl}{dt} = c_5\sigma(n)ul_{free} - c_6 l_{free} \tag{2}$$

$$\frac{dp}{dt} = c_1 pu - \frac{c_2 p}{c_3 + p} \tag{3}$$

$$\frac{du}{dt} = -c_1 up - c_1(n)ul_{free} - \frac{c_2 p}{c_3 + p} \tag{4}$$

Model Overview

Purpose

This paper is an extension of the work of Planqué (2010). As such, our purpose is twofold. Firstly, we investigate the same as Planqué, i.e. the effect of colony size on the balance between recruitment methods and the four discussion points that are raised in Planqué's paper. Secondly, we want to investigate whether ABM is a good method to extend differential equations, like the one on which we base our model. That is, to research how adding space and agents affects the dynamics of the model.

Entities, State Variables and Scales

Ants are the only agents in our model. Ants have a role, which represents their function in a recruitment scheme. Following Planqué (2010), ants can be a *follower*, *leader*, *pheromone*, or *uncommitted*. Apart from a particular role, ants are assigned a position and a list of *followers*. This list is empty when the ant's role is anything else than *leader*.

The behaviour of all agents is dependent on the probabilities of transitioning from one role in the recruitment strategy to another one.

We have added space to our model using a 2-dimensional torus, representing a piece of land on which ants are crawling around and looking for food. The grid points are spaces on which ants can walk. The distance between two neighbouring cells is arbitrary.

There are no environmental (external) forces in our model. Also, time and space scales are not relevant in our model. However, one could put the scales into perspective by noting that we are modelling a single colony, each agent is an ant and each step represents the movement of an ant to a surrounding position.

When group recruitment is used, follower ants are coupled to a leader. When they collectively do not find food, there is a chance that the collective falls apart and all the ants - including the leader - become unassigned. When the collective does find food, the collective has a chance that all follower ants become leaders.

Table 1: Parameter descriptions, symbols and their theoretical bounds

Parameter	Symbol	Bounds
Transition probability from *unassigned* **to** *follower*	p_{uf}	[0, 1]
Transition probability from *unassigned* **to** *pheromone*	p_{up}	[0, 1]
Transition probability from *pheromone* **to** *unassigned*	p_{pu}	[0, 1]
Transition probability from *follower* **to** *leader*	p_{fl}	[0, 1]
Transition probability from *leader* **to** *unassigned*	p_{lu}	[0, 1]
Maximum group size[a]	g	[0, 0.5]
Initial number of ants	N	[1, ∞)
Ratio between initial l and p[b]	ratio	[0, 1]
Grid size[c]	size	[1, ∞)
max number of iterations	max_iters	[1, ∞)

---

[a] The maximum number of *followers* per *leader*. This is a ratio of the total number of ants (N * ratio)
[b] Initial u is given by int(N/2), l by round(u * ratio) and p by $N - u - l$
[c] A value of n results in an $n \times n$ grid

Process Overview and Scheduling

Time is discrete in our model. Every time the model is advanced in time, each agent is called. Every agent does a random walk, i.e. it moves from its current position to a random adjacent position in its Moore neighbourhood. This can result in an ant staying at the same position as another ant. When this is the case, the ant has an encounter with only one of the other ants. It senses the role of the other ants and takes action according to its own role and the role of the ant is has an encounter with. Figure 2 is a flowchart of the agent's `step`. It is important to note that the model does thus not use a freeze-dried state. After a full iteration, the model can be displayed in the visualisation.

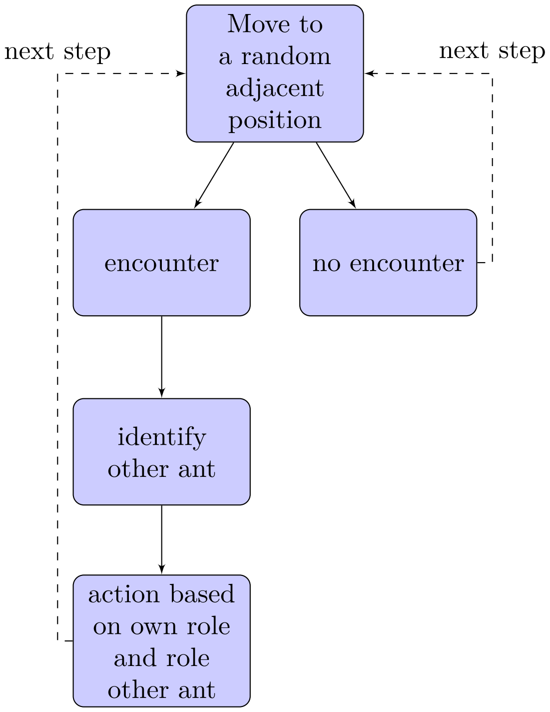


Figure 2: Flow chart of the model.

An important design choice for an ABM is the way the agents are scheduled. Executing agents in the same order each timestep can introduce experimental artefacts. To account for that we used a random activation scheduler. The pseudo-code of a timestep in the model can be seen below.

Algorithm 1 Role: Follower

```
Require: max_iterations, agents
  iterations = 0
  while iterations < max_iterations do
    shuffle agents
    for each agent in agents do
      step agent
    end for
    iterations += 1
  end while
```

Design concepts

Basic principles

The basic principle that connects this article to the work of Planqué (2010) on which we base our research is that of *recruitment methods*. The central thesis is that ants adhere to a particular method based on their encounters with other ants. Planqué (2010) used ODEs to describe the number of ants per role. This method was adapted to ABM and space was added, in turn making the transition from one method to another interaction-based.

The way ants move is crucial for the effects of these two additions. Our ants behave as random walkers, another basic principle of which the properties are well researched in the field of ABM. Whether an action will be taken (and which) depends on the interaction with other agents. This is further explained in the interaction section.

Emergence

The key outputs of the model are the continuous metrics pfl, pu, and flu, and the labelled equilibrium value. It is decided to design continuous output metrics, which is a requirement for most conventional high-dimensional model representation (HDMR) methods. To measure the effect on the dominance of recruitment methods, we use the number of ants in each of the nested groups. We can compare dominance of two methods using subtraction. Furthermore, normalisation allows us to compare the results of different colony sizes. As a result, the outcome variables are continuous on the domain $[-1, 1]$; plus one representing a total dominance of the first category in the subtract, minus one a dominance of the second and zero a point of balance. Continuous output is a prerequisite of all conventional sensitivity analysis methods.

The metrics are defined as such:

$$pfl = \frac{p - (f + l)}{total}$$

$$pu = \frac{p - u}{total}$$

$$flu = \frac{(f + l) - u}{total}$$

Where p is the number of ants using pheromones, l the number of leaders, f the number of followers, u the number of unassigned ants, and *total* the total number of ants. These metrics are bounded by the domain [-1, 1], where the size represents the dominance of one method versus the other and the sign which method dominates.

The different equilibria are defined (as defined in Planqué (2010)) as such:

- P_1 = only unassigned foragers
- P_2 = only group recruitment (+ unassigned) and no pheromone trail ants

- P_3 = only pheromone trail ants (+ unassigned) and no group recruitment
- P_5 = both group recruitment and pheromone trail ants (+ unassigned)

Equilibrium P_4 is deemed invalid since it has no biological meaning.

We assume an equilibrium to be stable when the model is in that state after 500 steps.

Adaptation

All changes in the agent rely on interactions with other agents. The environment itself has no influence on the behaviour or attributes of agents. There are no adaptive traits.

Objectives

Individuals exhibit no adapting (intelligent) behaviour[1], are purely reactive and therefore do not have objectives or intentions.

Sensing

An agent observes its interaction space and senses both the role of the ant it encounters (if any) and its own role.

Interaction

Interaction between agents only takes place if they are at the same position. Each ant that arrives on a new position has an encounter with a random other ant on this new position. Note that the choice of a particular ant does not affect the choice of the other ants. The active ant senses the role of the other ant. The action that follows depends on both the role of the active ant and the one with which it has an encounter. The roles and their actions are defined below:

- u**: Unassigned**. Has no current role. When meeting a leader, has a chance to become a follower of that leader. When meeting a pheromone ant, has a chance to become a pheromone ant.
- f**: Follower**. Has no special actions.
- l**: Leader**. Leads a group of followers. When finding one of its own followers, it will have a chance to change all followers into leaders. When finding anyone else, it has a chance to change all followers and itself into unassigned.
- p**: Pheromone**. Pheromone only has a chance to stop being a pheromone when meeting anyone but another pheromone.

Figure 3 shows the possible transitions given a certain role. For each of the six possibilities, there is a chance parameter. These chance parameters, combined with the grid size, the initial number of ants, and the group size, are the total set of parameters of our model.

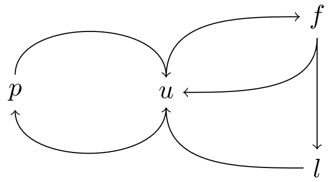


Figure 3: Possibilities in strategy change, with p=pheromone, u=unassigned, f=follower, l=leader

Stochasticity

Ants start their actions by randomly selecting a cell in its Moore neighbourhood, and moving there. When there is at least one other ant, it randomly selects one of those and interacts with it, with a certain chance defined in the parameters.

---

[1] Consequently, we have not created subsections on learning and prediction.

Collectives

Aggregates are defined as the complete collection of ants with the same role. When group recruitment is used, follower ants are coupled to a leader. When the leader is unsuccessful, there is a chance that the collective falls apart and all the ants - including the leader - become unassigned. When the leader is successful, the collective has a chance that all follower ants become leaders. These collectives are defined by us and non-emergent.

Observation

Every timestep the total number of ants per role is stored.

Details

For the complete codebase see: https://github.com/WouterVrielink/recruitment_strategies_ABM.

Initialization

The model is initialised as a two-dimensional square grid (*size* × *size*) in which N ants are placed at random locations. Half of the ants start unassigned, whereas the other half is either a follower/pheromone ant, depending on variable *ratio*.

Input data

The model does not require external inputs and does not mimic processes that change over time.

Submodels

Each agent's behaviour (`step()`) can be divided into two parts; `move()`, and `role_actions()`. The `move()` function selects a random location with uniform distribution in the agent's Moore neighbourhood. The `role_actions()` function depends on the present role of the agent.

Algorithm 2 Role: Unassigned

```
Require: Agent $X$, max_followers
  if $X$ has neighbours then
    Get random neighbour $Y$
    Get interaction probability $P$ with $Y$
    if random() $<$ $P$ then
      if $Y$.role is Leader and $Y$.followers $<$ max_followers then
        Add $X$ to $Y$.followers
        $X$.role = Follower
      else if $Y$.role is Pheromone then
        $X$.role = Pheromone
      end if
    end if
  end if
```

Algorithm 3 Role: Follower

```
Require: Agent $X$
  pass
```

Parameter Sweep

Before any analysis can be performed, reasonable parameter values have to be selected. Since no rational estimations can be made about transition probabilities, the starting ratio between l and

Algorithm 4 Role: Leader

```
Require: Agent $X$
  if $X$ has neighbours then
    Get random neighbour $Y$
    Get interaction probability $P$ with $Y$
    if random() $< P$ then
      $newRole$
      if $Y$ in $X$.followers then
        $newRole$ = Leader
      else
        $newRole$ = Unassigned
      end if
      for each $Z$ in $X$.followers do
        $Z$.role = $newRole$
      end for
      $X$.followers = []
      $X$.role = $newRole$
    end if
  end if
```

Algorithm 5 Role: Pheromone

```
Require: Agent $X$
  if $X$ has neighbours then
    Get random neighbour $Y$
    Get interaction probability $P$ with $Y$
    if random() $< P$ and $Y$.role is not Pheromone then
      $X$.role = Unassigned
    end if
  end if
```

p, and maximum group size g, we decided to take the whole range between 0-1. A large range of initial number of ants (10-500) and size of the system (3-20) was selected.

Consequently, these parameter ranges were Saltelli-sampled totalling 40.000 different parameter combinations. Each parameter combination was then run for with the total number of iterations (max_iters) fixed on 500 (Archer et al., 1997).

Results

Linear Discriminant Analysis

For analysis of labelled output with continuous inputs, one can use Linear Discriminant Analysis (LDA). LDA is a method that finds the linear combination of input parameters that maximises the separation of the labelled output.

Figure 4 shows this projection on a 2D plane for the parameter sweep. A surprisingly high ratio of the variance between the classes (0.998) can be explained by projecting the 9-dimensional data onto a 2D plane. Furthermore, since we have the projection matrix from 9D to 2D, we can predict the relative importance of variables from their values, see table 2.

Table 2: Projection matrix from the 8D space onto 2D space.

	p_{uf}	p_{pu}	p_{up}	p_{fl}	p_{lu}	g	ratio	N	size
x	0.10	4.25	-3.56	-0.03	-0.50	0.02	0.59	-0.00004	-0.005
y	-0.87	0.19	-0.34	-0.65	3.60	-0.35	-0.25	0.0005	-0.04

Even though not all parameter ranges are the same, which makes it impossible to directly compare values, one of the most striking properties of this matrix is that the number of ants and the size of the environment seem to have little to no effect in predicting the difference between the classes.

Although the projection seems to be successful, the distribution of the different classes is a bit off. The majority of the parameter combinations seems to result in a predictable final situation. A more interesting region is highlighted by a black square in figure 4. We can get a (lossy) estimation of the values in this square by multiplying its coordinates by the pseudo-inverse of the projection matrix, see table 2. This then gives us a prediction of the values within this space. Since these values should not be larger or smaller than the original bounds, we limit them to their original bounds. Furthermore, we have seen that N and `size` seem to have little effect on the final situation, so we fix them on 40 and 11 respectively, see table 3. A new parameter sweep was performed on these ranges which resulted in figure 5.

Table 3: Parameter bounds of the square in figure 4.

	p_{uf}	p_{pu}	p_{up}	p_{fl}	p_{lu}	g	ratio
min	0.55	0	0.41	0.54	0	0.27	0.45
max	0.68	0.62	0.97	0.64	0.31	0.32	0.57

Sobol Analysis

Figure 6 shows the first and total order explained variance for metric p_{fl}. We generally see a lower first order effect of the parameters for the subset generated from LDA than for the whole parameter range, but we see a higher total order effect for the same parameter subset. We see a clear effect of p_{lu}, p_{up}, and p_{pu} for both higher and lower order effects. Throughout all three metrics we see the same general pattern for N, size, ratio and g: they seem to have relatively little influence.

The second order interaction effects are insignificant for all combinations, except the interactions between p_{pu} and p_{lu}, and p_{up} and p_{pu}. For the complete parameter range and all three metrics the interaction between p_{pu} and p_{up} was significant, and for the bounded parameter range and all three metrics the second order interaction between p_{pu} and p_{lu} was significant.

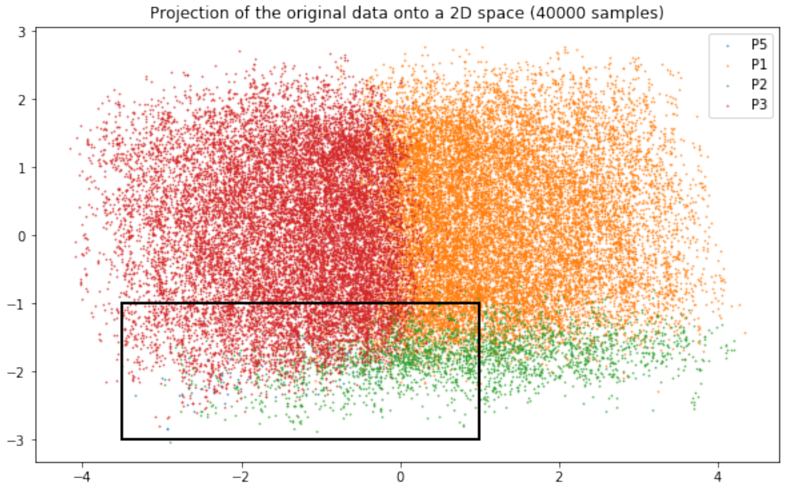


Figure 4: Projection of the original data onto a 2D space, with 40.000 samples P_1: 19531, P_3: 17725,P_2: 2664, P_5: 80

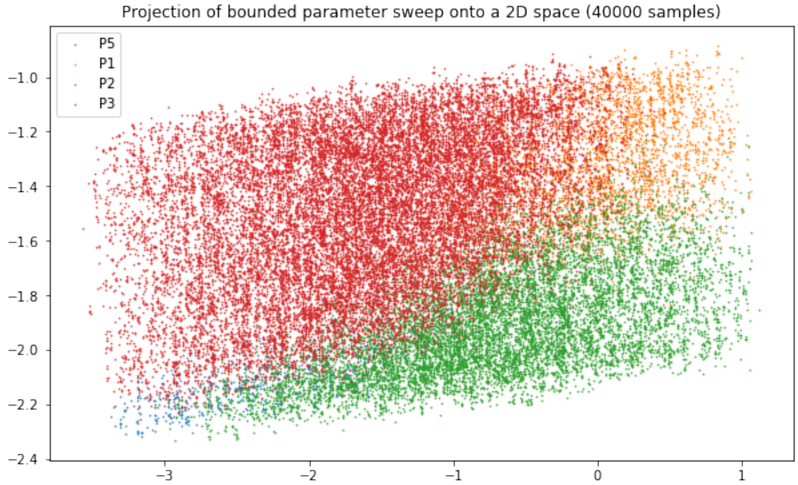


Figure 5: Projection of a bounded parameter sweep onto a 2D space with 40.000 samples. P_3: 23479, P_2: 11682, P_1: 3964, P_5: 875

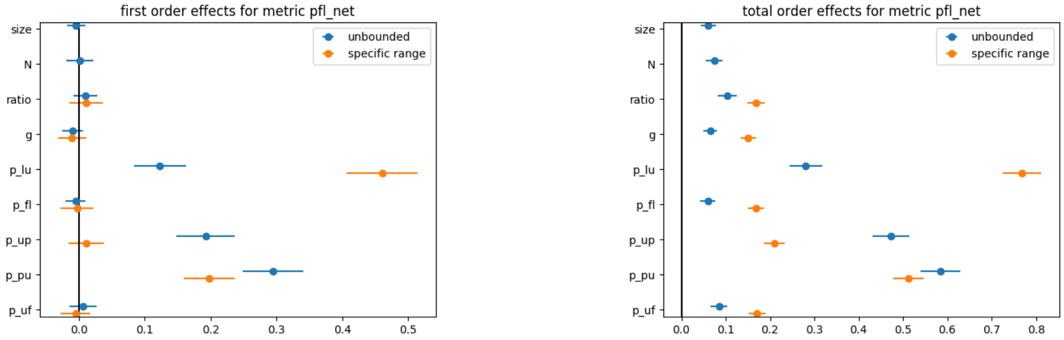


Figure 6: First and total order Sobol analysis for the complete parameter range, and the parameter subset.

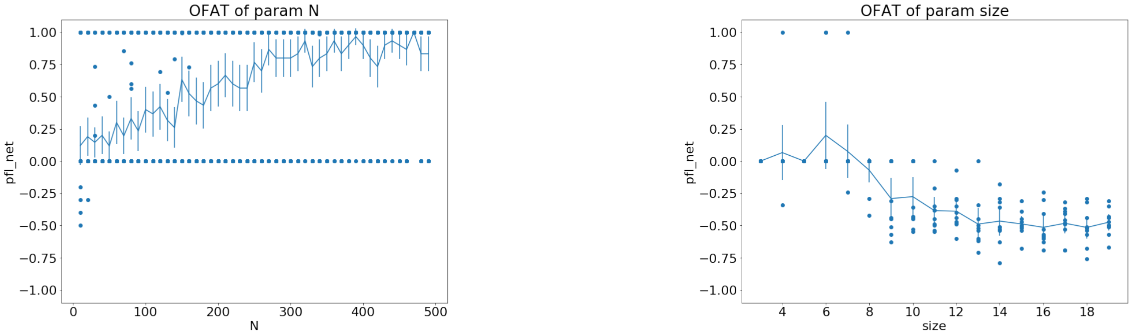


Figure 7: OFAT analysis that shows the effect of N and g on pfl

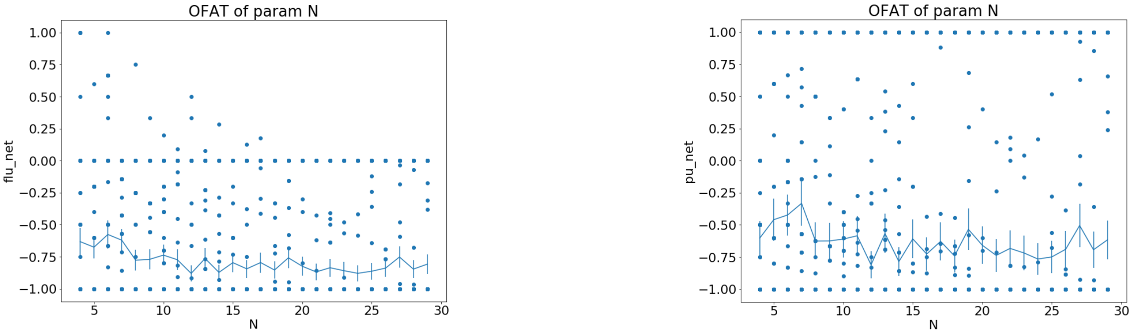


Figure 8: OFAT analysis showing the occurrences of each recruitment strategy for low values of N

One Factor at a Time

The one factor at a time (OFAT) analysis is an easy visual method to see the effects of a single parameter. Starting parameters (see table 4) were selected from the bottom-left corner of figure 5, which is dominated by P_5. This guarantees that P_5 is present in the new subset.

Table 4: Standard parameters of OFAT analysis.

p_{uf}	p_{pu}	p_{up}	p_{fl}	p_{lu}	g	ratio	N	size
0.56	0.49	0.52	0.54	0.25	0.27	0.52	100	12

We can see in figure 9 that a low lu value results in a high flu value. As p_{lu} increases, the number of unassigned ants increases and flu decreases. Once p_{lu} gets too high, group recruitment loses its competitiveness and pheromone recruitment becomes dominant.

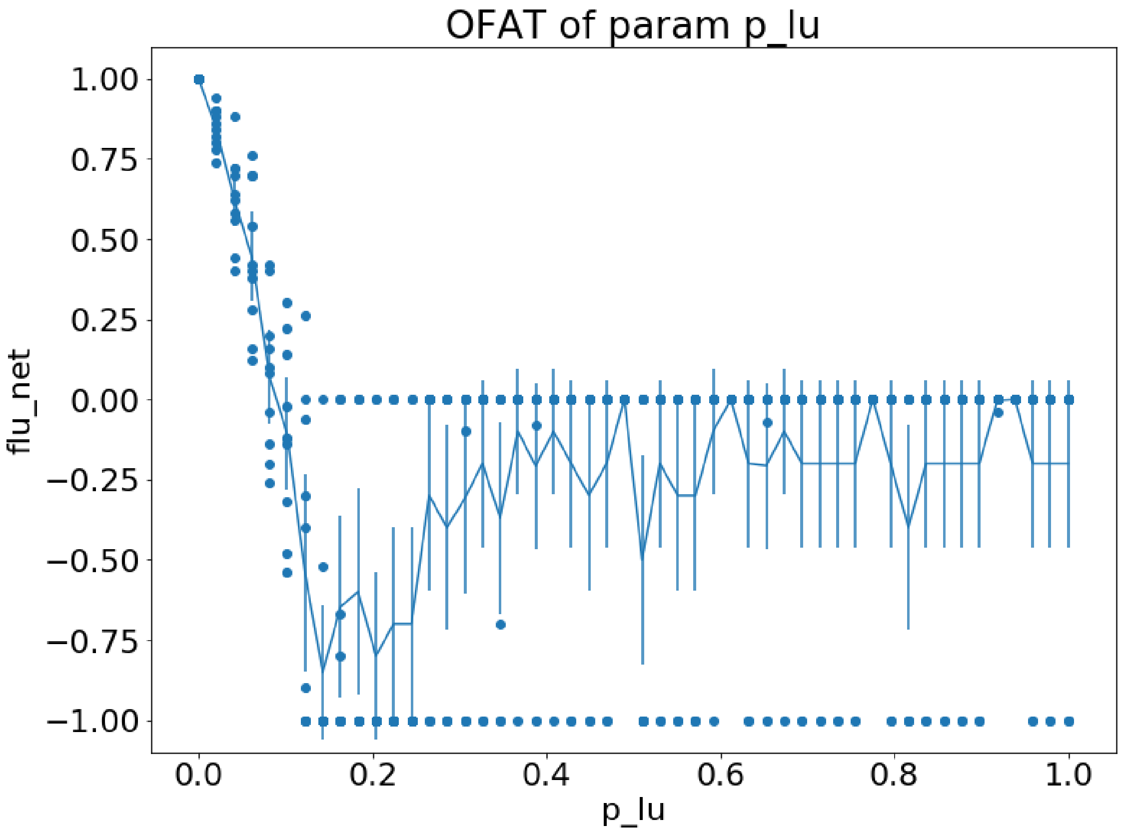
In figure 7 we see that as N increases, pheromone recruitment becomes dominant over group recruitment, as predicted by Planqué.

Increasing the size of the colony has a negative effect on metric pfl, as can be seen in figure 7. This is most likely caused by the effect that increasing the size, but keeping N static, results in a decrease in agent density, which makes pheromone recruitment less competitive.

Growing populations

Natural ant colonies are not static, and the number of ants is expected to grow over time in normal conditions. Furthermore, Planqué (2010) predicts that as colony size increases, ants should change from solitary foraging to pheromone recruitment. For these reasons we implemented a version in which every timestep one unassigned ant gets added to the system on a random location (figure 10).

The initial parameters chosen for the model resemble the OFAT parameters, but were slightly tuned such that in around half of the runs, the colony ends up with group recruitment and the other half with pheromone recruitment. A clear distinction between the two options is visible. Colonies that grow over time, tend to rely more on pheromone recruitment at the expense of group recruitment, but this does not seem to have a real effect on the relative use of unassigned (or solitary) ants, since the changes between the two groups are antagonistic.



.

Figure 9: OFAT analysis showing the occurrence of the group recruitment strategy for different values of lu

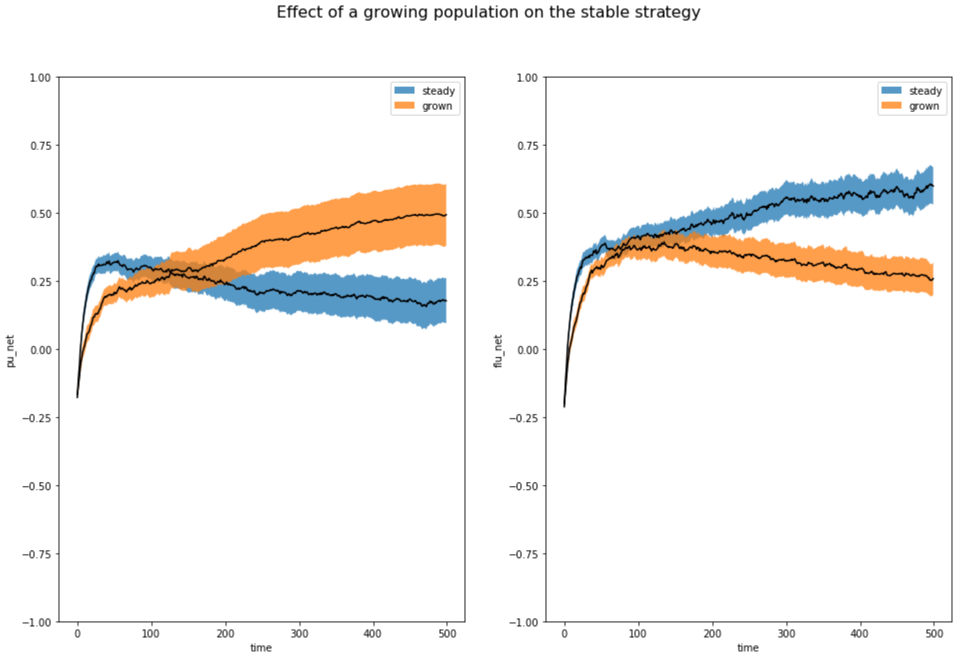


Figure 10: 100 replicates were used for both steady and grown. The confidence interval is 95%.

Discussion

The aim of this article was to investigate the four predictions raised by Planqué (2010), with an emphasis on the effect of colony size on the dominant recruitment strategy.

Their first prediction considers the co-existence of recruitment strategies and claims that two or more strategies can never lead to a stable situation. Stochastic/finite-size ABMs, like this one, generally have difficulty with reaching stable equilibria, with the positive-feedback of the strategies making it even less stable. One way to define stability in these models is the time it takes until it reaches its 'end-state'. Models that still remain in state P_5 after 500 iterations, can be considered stable, and increasing the total number of iterations can only make the possibility of ending up in P_5 lower.

The second prediction concerns the minimal colony size required for recruitment strategies. Our OFAT analysis could not confirm this, since running it with minimal ant numbers showed the use of all the three different strategies. The lowest initial N for which the outcome is not restricted is 4. Then we start with 2 *uncommitted*, 1 *leader* and 1 *pheromone* ant. Figure 8 shows that even for this number all recruitment methods occur. When we start with only one ant, there will be no change as all transmissions are interaction-based.

The third prediction is that as the colony size increases, the model tends to shift from a state dominated by solitary foraging - possibly with group recruitment as intermediate phase - to a pheromone dominated state. The effect of adding ants continuously to the system indeed generally results into a more pheromone dominated state. However, the cause of this effect is most likely due to the bigger population, as confirmed by the OFAT analysis, and not by the effect of growth.

The fourth prediction follows from the third: large colonies are expected to always use scent trails, which is confirmed by the OFAT analysis. Remember it becomes less probable for a leader to meet one of its own followers as the number of ants increases. This is not the case for pheromone ants, as they do not have groups, and can only become unassigned when meeting other –non-pheromone– ants. Consequently, the pheromone strategy scales better than the follower-leader strategy, as the number of ants increases.

The majority of data interpretation, and understanding, still relies heavily on visual cues. When sampling from a multivariate distribution, it can therefore be insightful to first reduce the dimensionality of the data to discover regions of interest. One important thing to notice is that as the number of parameters increases, the number of samples required grows exponentially. Interpreting the LDA, however, is tricky, and prone to misunderstanding. As LDA was used to find bounds over a wide range of parameters, the interpretation of these scales is only relevant over this wide range. Contrarily, the OFAT actually showed that the size and number of ants actually are relevant parameters in the region they were sampled, while LDA hinted that these parameters are relatively unimportant.

All in all, ABMs are an easy and intuitive way to model complex interactions between different agents. ABMs can be especially useful when mathematical analysis of the problem can not be done orisare particulary hard, as the case with some of the predictions of Planqué (2010). However, both the analysis as the interpretation of ABMs remains rather challenging. Ideally both ABMs and mathematical analysis are used for a complete understanding of a problem.

Future work

Future work could either extend the analysis performed on our model or extend the model itself. In the former category one could think of investigating a reverse of independent and dependent variables, i.e. will colony size change if a certain strategy dominates? Also, one could look at localities in the grid and if there will be segregation between regions, where certain recruitment method are dominant.

Alternatively, future research could extend the model itself. One could think of implementing scent trails, adding colony and food positions on the grid, change the movement behaviour of ants, and implementation of colony splitting. Below, a more detailed recommendation of pheromone scent implementation and empirical foundation can be found.

In our implementation of the pheromone recruitment method, ants did not interact with the pheromone trail, but only with the pheromone laying ant. This has allowed us to stay closer to Planqué's ODEs, but shows less resemblance to actual ant behaviour (Vander Meer and Alonso, 1998). Ants can follow pheromones when foraging, which in turn reinforces the pheromone path. If a pheromone path is not reinforced, the path will disappear with a certain decay rate. This leads to efficiently finding the shortest path to the food source, without ants having to directly communicate about a short path length. For this type of extensions, ABMs are especially suitable.

Earlier work

Earlier work involved the modelling of a biological interpretation of the Ant-Colony Optimization problem. See the GitHub link for the code and a nice video of how it works:
https://github.com/WouterVrielink/MC-ACO.

Notebooks

1. IPython notebook example on how to run
2. IPython notebook on LDA
3. IPython notebook on Sobol Analysis
4. IPython notebook on OFAT
5. IPyhton notebook on Growing population

MESA contributions

1. Issue #454: [Bug report] Setting iterations greater than 1 in Batchrunner has no effect.
2. Issue #455, pull request #456: [Feature Request]: Multiprocessing BatchRunner. (Pending)
3. Issue #458, pull request #459: [Bugfix] iter_neighborhood() now gives correct neighborhoods for both von Neumann and Moore. (**Accepted**)

References

Archer, G., Saltelli, A., and Sobol, I. (1997). Sensitivity measures, anova-like techniques and the use of bootstrap. *Journal of Statistical Computation and Simulation*, 58(2):99–120.

Beckers, R., Goss, S., Deneubourg, J.-L., and Pasteels, J.-M. (1989). Colony size, communication, and ant foraging strategy. *Psyche*, 96(3-4):239–256.

Hölldobler, B. and Wilson, E. O. (1990). *The ants.* Harvard University Press.

Moreau, C. S., Bell, C. D., Vila, R., Archibald, S. B., and Pierce, N. E. (2006). Phylogeny of the ants: diversification in the age of angiosperms. *Science*, 312(5770):101–104.

Planqué (2010). Recruitment strategies and colony size in ants. *PLoS One*, 5(8):e11664.

Schultz, T. R. (2000). In search of ant ancestors. *Proceedings of the National Academy of Sciences*, 97(26):14028–14029.

Thomas, L. (1977). The tucson zoo.

Vander Meer, R. K. and Alonso, L. E. (1998). Pheromone directed behavior in ants. *Pheromone communication in social insects, Westview Press, Oxford*, pages 3–33.