

Modelling the Effects of Colony Age on the Foraging Behaviour of Harvester Ants

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Abstract. The colonies of certain species of ants, for example *Pogonomyrmex barbatus*, exhibit changes in behaviour as the colonies grow older, despite nearly all of the individual ants being replaced each year [1]. The behaviour of older colonies is more stable, and they are more likely to avoid intraspecific conflict [2]. Gordon hypothesised that the reason for this is that a 3-4 year old colony is in the steepest part of its growth curve, i.e. the 4000 workers of the 3 year-old colony are feeding 6000 larvae, and that the aggression of individual ants is based on colony level food requirements. This study aims to model this phenomenon using an individual-based simulation. The results from model are compared with field experiments taken over a period of years at the study site in New Mexico [3, 4]. The model provides support to the biological hypothesis by showing that both colony age and aggression of individual ants have significant effects on foraging ranges.

1 Introduction

Ant colonies are probably the most famous and most studied case of eusocial insects. There is extreme diversity to the extent that they occupy virtually every evolutionary niche available to them. Ant colonies have long been of interest to computer scientists due to their ability to solve complex tasks with relatively simple local rules. The modelling of ant colonies is also of interest to myrmecologists, who use the models in order to learn more about the biological systems they are studying. This report focuses on the development of a computational model of rival ant colonies in order to test one such biological hypothesis.

This study draws on data on a population of about 250 colonies of the red harvester ant, *P. barbatus*, studied in detail from 1985 to the present day. Colonies live for 15-20 years [1]. *P. barbatus* is a red seed-eating harvester ant that is common throughout the deserts of Arizona. Like many of the other *Pogonomyrmex* harvester ants, they have a powerful sting which is readily used. In the evening, a few *P. barbatus* workers will usually seal the nest entrance with gravel and twigs to keep intruders out of the nest. This often results in one or two of the workers ending up on the outside of the nest entrance after closing it.

Intraspecific competition is a term used by ecologists, which is defined as the struggle between members of a population for scarce resources. In this case different colonies of the same species of ant are fighting for limited food resources.

It differs from interspecific competition which is competition between members of different species for shared resources. The respective levels of intra- and interspecific competition have significant effects on the mortality and densities of the species in question [5]. In general, intraspecific competition is higher than interspecific competition for harvester ants, although there are instances of *P. barbatus* and *P. rugosus* sharing territory [6].

As colonies grow, the production of worker ants accelerates as the number of workers increases, until reaching equilibrium at their mature size. Over long timescales, the foraging range of *P. barbatus* is stable, but on the timescales of days and weeks, the trails are not stable. The short term behaviour depends partly on the behaviour of neighbouring colonies [1, 7, 8].

Of particular interest are the changes in behaviour exhibited by colonies as they grew older, despite (nearly) all the ants in the colony being replaced each year [1]. The behaviour of older colonies (i.e. over 5 years old) is more stable, and they are more likely to avoid intraspecific conflict [1, 2]. Gordon hypothesised that the reason for this may be due to the growth rate of the colony - that a 3-4 year old colony is in the steepest part of its growth curve, i.e. the 4000 workers of the 3 year old colony are feeding 6000 larvae. This hypothesis appears to be reasonable. The individual ants must therefore base their decisions on whether to engage in conflict over food requirements, leading to the global behaviour exhibited.

1.1 Hypotheses

Colony food requirements drive aggression. As a 3-4 year old colony is in the steepest part of its growth curve, the food requirement is high as a smaller population of workers requires energy to support a larger population of larvae. Therefore younger (i.e. developing) colonies should show more aggression. This aggression results in a propensity to engage in conflict with neighbouring colonies. However, the foraging ranges of 3-4 year old colonies are typically no different from those of 5 year and older colonies. Following on from this, the experimental hypotheses for the current study are as follows:

- H1.** *The foraging ranges of aggressive colonies are significantly larger than those of passive colonies.*
- H2.** *The foraging ranges of 5 year and older colonies are significantly larger than those of 3-4 year old colonies.*
- H3.** *The foraging ranges of aggressive 3-4 year old colonies are significantly different from those of passive 5 year and older colonies. (Null hypothesis)*

Thus the aggressiveness of the younger colonies should allow them to have foraging ranges typically found in older colonies despite their being smaller. This can be interpreted as the ‘plasticity’ of the developing system. This would give credence to the biological hypothesis that colony level food requirements drive the aggression of individual ants, leading to the changes in global behaviour observed in colonies of different ages.

2 The Model

An individual-based model was chosen as the most appropriate for the study of the effects of inter-colony interactions, based on the examination of previous studies (e.g. [9–11]) and the specific requirements of the problem. This method allows the addition of stochastic processes that are difficult to incorporate into mathematical models. All modelling was done using Matlab 7.04 (R14).

The temporal resolution for the model was chosen at 1 second per iteration. At this scale the ant behaviour must be fairly approximate as ants may change speed and direction during this period of time. To this end, the ants are modelled with random search behaviour and constant speed over this timescale. This provides the necessary level of abstraction for the global colony-level behaviours to emerge, and allows long simulation runs (5 hours ant time, which is roughly the amount of time ants spend foraging during a typical day).

In order to model at the right level of abstraction, certain modelling assumptions have been made. These are mainly in line with those used in previous models (e.g. [9, 10]), with some additional assumptions/simplifications. Some examples are given below, a full list of assumptions and justifications can be found in [12].

- Ants move at a constant speed [2], even if they are carrying food [13]
- The ants have a fixed mean departure rate from the nest, rather than being cued by the number of ants returning or any other factors [10]
- The foragers all follow fixed trail out of the nest for a period of time determined probabilistically and then start foraging. They later return to the trail at the point where they left it before returning to the nest [8]
- Ants search randomly until they are within 1mm of a food item, at which point they pick it up [14]
- The ants interact only with non-nestmates (quarrels or evasive behaviour); ants that meet from the same colony simply continue on. [6]
- Food items are homogeneous - i.e. the only food items are seeds and the seeds are all the same size. [10]

2.1 Simulation Environment

The simulation used a 50m x 50m toroidal world (as in [10]). This was divided into a 400x400 grid with each square representing 125mm x 125mm. These grid squares were then used for storing the locations of food and calculating local ant populations. At this size of the grid square, with the pickup range for food 1mm and the ant detection range 5mm, there is no particular distortion in using only the grid slot that the ant is currently in, as the probability of the ant being within 5mm of the edge of the grid slot is less than 1% and the probability of the ant being within 1mm of the edge of the grid slot less than 0.1%.

For each of the grid squares determined by the world grid there is a matrix of food locations with their coordinates. Each grid square can hold a maximum number of food items based on a maximum density of 1000 seeds/ m^2 . This is

based on an initial density of food items $625 \text{ seeds}/m^2$ and a renewal rate of $0.0017 \text{ seeds}/m^2/\text{sec}$, which equates to an average of $30.6 \text{ seeds}/m^2$ during a 5-hour simulation period. The food renewal is based on observations in the desert [10].

2.2 Ant Behaviours

The behaviours of individual ants are dependent on their state. The states are as follows: *1: In Nest; 2: On Outbound Trail; 3: On Inbound Trail; 4: Searching; 5: Returning to Trail; 6: Quarrelling; 7: Fighting; 8: Dead*. The simplification of reality that these states represent is justified by fact that the present study is concerned with interactions between ants during foraging excursions, and therefore is not concerned with activities of ants within the nest. Recruitment to food sources by scouts at the beginning of foraging activity is assumed to have already taken place, and as such is also not included as an element of the model (i.e. the trail directions are predetermined). These are in line with assumptions made in earlier studies [9, 10]. More details regarding ant states can be found in [12].

The ants leave the nest probabilistically according to a set departure rate and follow one of the foraging trails at a fixed speed until the trail departure trigger occurs, unless they encounter food or another ant during this time. Whether the ants have found food or are returning without food, they return to the trail at the point that they left it, then return to the nest along the trail. The ants search for food using a biased random walk, as in [10]. This is done by permuting the velocity vector between time steps by a normally distributed value with standard deviation of 0.6 radians and a bias of 0.01 radians away from the nest. These parameter values give results similar to observations that search is stochastic, but with a drift of about 0.25 cm/s away from the nest.

If an ant encounters an ant from another colony, they engage in a quarrel according to a colony level parameter for the ant that first made the detection. During a quarrel both ants are stationary. The result of a quarrel is either escalation to fighting, or a return to their previous states. Similarly, the end of a fight results in either death for one of the ants (according to the probability of kill), or a return to their previous states.

Food search was implemented by searching within a certain distance from the path of the ant within the last time step. This is superior to using a radius around the ant on each time step as it would be highly likely that the ant would ‘jump’ over food items. Observations of actual departure rates varied from ca. 0.1 to 0.5 ants per second [10]. After some experimentation, the higher of these figures was used in the present study. The number of seeds collected by ants in the model was around 3,000 to 4,000 per colony during a simulation run, considerably lower than predicted by [9] but in line with observations from the later [10] study.

Interaction between ants was handled by searching for intersections between the trajectories of an ant with its neighbours. Although this method is not perfect (see [12] for a full explanation), sophisticated modelling of this behaviour is unnecessary as the broad behaviour fits well with observations [2].

It was generally believed that harvester ants exhibited stable, non-overlapping territories [6, 15], as colonies were thought to use semi-permanent trails that never meet [16]. Gordon [2] demonstrated, however, that encounters are common among *P. barbatus*. During a 17 day period, 34 colonies engaged in a total of 1090 encounters with their neighbours, which equates to a rate of 1.9 encounters per colony per day. Since the main experiments in the simulation model involved three interacting colonies, the rate of encounters with neighbours was 2 per colony per day, which fits well with observations.

Foragers tend to travel away from the nest in straight lines and then fan out to search for food items [8]. The foraging ranges of *P. barbatus* vary between 1 and 20m [7]. The length of the trail with respect to the total foraging range varies considerably. It is not known how the ants decide to leave the trail. For that reason, various types of trail departure behaviour were tested. Exponential trail departure was chosen as it led to the most realistic foraging ranges (see [12]).

The distances between colonies were set to 10m during all experiments. This was derived from the distances between colonies in the crowded region studied in [2], as well as average nearest-neighbour distances ranging from 10.8m to 12.9m between the years of 1985 and 1988 [1]. For experiments with three colonies, the colonies were placed at the corners of an equilateral triangle, such that the distance from each colony to the other two was 10m. Trail angles were used that encouraged interactions. In general, trail angles at incident angles of 90 between neighbouring colonies were used (see Figure 1(b)).

3 Experiments

The parameter settings used in the experiments are shown in Table 1, along with the source of the given parameter values, if applicable. The simulation runs all lasted for 18,000 iterations, which represented 5 hours of ‘ant time’ - roughly the length of an average day’s foraging during peak season [10].

After a thorough exploration of the effects of various parameter settings on the foraging behaviour and inter-colony interaction of the simulated ants (see [12] for details of these), a series of experiments was designed to test the experimental hypotheses as stated in section 1.1: that the foraging ranges of aggressive colonies are significantly larger than those of passive colonies, those of 5 year and older colonies are significantly larger than those of 3-4 year old colonies, and those of aggressive 3-4 year old colonies are not significantly different from those of passive 5 year and older. Both the age of the colonies and the aggressiveness of the ants belonging to each colony were varied in such a way that the effects of each can be separated out. As such, the two main parameters of interest that were manipulated were:

Colony size. The age of the colony is determined by its size (number of active foragers, rather than spatial scale), as in all other behavioural aspects the colonies of different ages are identical. The number of foragers by age of colony is shown in Table 2 (values taken from [2]). The number of active

Table 1. Parameters used in all trials

Parameter	Value	Source
Number of colonies	1/2/3	N/A
Number of foragers	1890	Adler & Gordon 2003
World Size	50m x 50m	Schafer et al. 2006
Distance between colonies	5m - 10m	Gordon & Kulig 1996
Number of trails	2	Schafer et al. 2006
Trail length	4m	Gordon 1992
Ant speed	2.5m/min = 0.0417 m/s	Adler & Gordon 2003
Value of lost forager	50 seeds	Adler & Gordon 2003
Quarrel Range	5mm	N/A
Probability of quarrel	0-1	N/A
Probability of fight	0.07	Adler & Gordon 2003
Probability of kill	0.7	Adler & Gordon 2003
Quarrel Duration	40 sec (avg)	Gordon & Kulig 1996
Fight Duration	42 min (avg) = 2520 sec	Gordon & Kulig 1996
Initial food density	625 seeds/ m^2	Schafer et al. 2006
Food renewal rate	0.0017 seeds/ m^2	Schafer et al. 2006
Food pickup range	1mm	D.M. Gordon, personal comm.
Departure rate from nest	0.3 ants/sec	Schafer et al. 2006
Simulation time	5 hrs = 18,000 time steps	Schafer et al. 2006

foragers is estimated to be half the total number of foragers [9]; this is the number of foragers used in the model (there is no need to model inactive foragers).

Probability of quarrel (p. quarrel). The aggressiveness of the colony is manipulated here by a colony-wide parameter controlling the probability that an ant engages in a quarrel when two intraspecific ants meet. Experiments were conducted with various values for this parameter, ranging from 0 (complete passivity) to 1 (deterministic aggression). For the main experiments a value of 0.1 was used for passive colonies, and a value of 0.9 was used for aggressive colonies.

Table 2. Number of foragers by colony age

Colony Age	Total Foragers	Active Foragers
1	432	216
2	967	484
3-4	2604	1302
≥ 5	3780	1890

Table 3 shows the parameter values used in the experiments. The experiments were designed specifically to test the effect of varying the age between 3-4 years (the time at which the colony is in the steepest part of its growth curve) and

the probability of quarrel for the focal colony between 0.1 (passive) and 0.9 (aggressive). In addition to the *old-passive*, and *young-aggressive* conditions, the two reverse conditions of *old-aggressive* and *young-passive* were run as control conditions. The non-focal colonies in all seven experiments were old, passive colonies (5 years old, p. quarrel 0.1). The trail angles for the three colonies were [345,135], [15,225], [255,105], which meant that each of the trails intersected at right angles with the trail of one of the other colonies (see Figure 1(b)).

Table 3. Series of experiments to investigate effects of colony age and aggressiveness

Experiment	Colonies	Age (focal)	p.quarrel (focal)	Notes
1	3	3-4	0.1	Young, passive (control 1)
2	3	5	0.1	Old, passive
3	3	3-4	0.9	Young, aggressive
4	3	5	0.9	Old, aggressive (control 2)

4 Results

4.1 Non-overlapping foraging ranges

Figure 1 depicts the locations of food discovery from experiment 2, in which all three colonies were ‘old-passive’ (5 year old, p. quarrel = 0.1). It shows that despite trail angles that cause the foragers to come in contact on a regular basis, the foraging ranges of the colonies rarely overlap. In addition, there is a greater density of activity around the borders of the foraging ranges. This is in line with observed behaviour of *P. barbatus*, as well as of other harvester ant species [6, 9].

4.2 Combined effects of colony age and aggressiveness

This section presents the results of experiments 1-4, which were designed to show how the parameters alter the behaviour of the model in combination, and ultimately to test the experimental hypotheses. The mean distances from the nest of ants in the focal colony at the end of a the simulation run give a measure of the extent of the colony’s foraging range [12]. In Experiment 1 (*Young, Passive*) the mean distance was 3.48 metres, in Experiment 2 (*Old, Passive*) it was 3.57 metres, in Experiment 3 (*Young, Aggressive*) it was 3.59 metres, in Experiment 4 (*Old, Aggressive*) it was 3.71 metres. Increasing both aggressiveness (probability of quarrel) and colony age (number of foragers) increases the mean distances. Also note that the mean of the young-aggressive colony is similar to that of the old-passive colony.

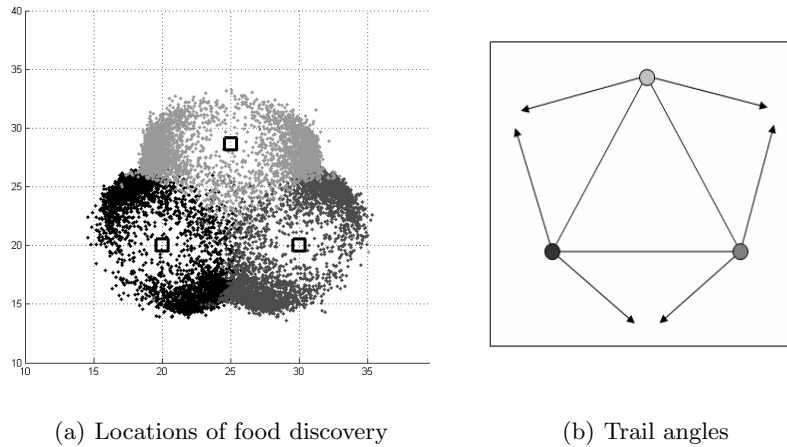


Fig. 1. (a) Locations of food discovery for the 3 colonies in experiment 2. Ants from the three colonies are represented by dots of differing shades of grey; colony locations are shown by black squares. Note that the foraging ranges of the three colonies rarely overlap. (b) Trail angles are shown as black arrows for each of the colonies

An analysis of variance (ANOVA) was run to see if the differences between the means were statistically significant. The results of this are shown in Table 4. The main effects of aggressiveness and colony age are both significant at the 0.01 level, whereas the interaction effect is not significant.

Table 4. Analysis of variance for distance from nest by age and aggressiveness

ANOVA - Constrained (Type II) sums of squares					
Source	Sum Sq.	d.f.	Mean Sq.	F	Prob.
Agression	21.4	1	21.37	10.65	0.0011
Age	14.6	1	14.55	7.25	0.0071
Agression * Age	0.2	1	0.24	0.12	0.7291
Error	11897	5927	2.01		
Total	11935.9	5930			

In the model, older colonies have larger foraging ranges than younger ones, and aggressive colonies have larger ranges than passive ones. This therefore supports hypotheses H1 and H2, as stated in section 1.1. In addition, young-aggressive and old-passive colonies tend to have foraging ranges of similar sizes. In order to verify whether these results hold statistically, post-hoc analysis was done using Tukey's least significant difference (L.S.D.) procedure. The results of this showed that the population marginal means of the young-aggressive and old-passive colonies are significantly different from the marginal mean of the

old-aggressive colony but not from the young-passive colony or each other. At the 95% confidence level, the null hypothesis that the young-aggressive colony and the old-passive colony have significantly different foraging ranges is rejected. This supports the experimental hypothesis H3, as stated in section 1.1.

Despite the increase in foraging range that the increase in aggression brings about, the benefits for the colony were not in evidence. In Experiment 1 (*Young, Passive*) 2843 food items were retrieved and 90 foragers lost; in Experiment 2 (*Old, Passive*) 3327 food items were retrieved and 102 foragers lost; in Experiment 3 (*Young, Aggressive*) 2787 food items were retrieved and 177 foragers lost; in Experiment 4 (*Old, Aggressive*) 3304 food items were retrieved and 208 foragers lost. The switch to aggressiveness caused a fall, albeit insignificant, in the amount of food items retrieved. An explanation for this is that time spent engaged in quarrels and fights leads to a reduction in the time available for foraging. In addition, time spent by foragers that are lost is also wasted. Naturally, the number of foragers lost by the focal colony increased in the shift from passive to aggressive. It seems that although aggression allows younger colonies to adopt foraging ranges that are roughly the same in extent as older colonies, the model is unable to explain the benefit of this in terms of short-term gains (food retrieved) or losses (foragers killed).

5 Conclusions

The model displayed the non-overlapping foraging ranges of *P. barbatus* described in [9], and showed sensitivity to both colony age and forager aggression. The main effects of age and of aggression on mean distance from the nest were both statistically significant. In addition, there was no significant difference between the foraging ranges of young, aggressive colonies and older, passive colonies. These results support the three experimental hypotheses from section 1.1. This is evidence that the model is behaving as expected, and that both colony age and the aggression of individual ants have significant effects on the foraging ranges of colonies. This could explain, in real ant behaviour, the aggressiveness of younger colonies, as it may allow them to have foraging ranges similar to those of older colonies. Passivity in older colonies leads to fewer lost foragers. This would suggest that aggression levels in *P. barbatus* are a trade-off between the foraging range and resources lost due to intraspecific interactions.

The number of food items retrieved did not increase when the aggression of the foragers was increased. This can be explained by the foraging time lost during quarrels or fights, as well as by foragers who are killed. It is likely that this also applies to real ants, so the benefits of having larger foraging ranges must be revealed over longer time spans. As the foraging ranges are fairly stable over time [8], the short-term losses in terms of lost time and resources must be outweighed by the longer-term benefits of a larger foraging range. This study would appear to agree with the biological hypothesis put forward by Gordon [2], although direct comparisons with real ants are made with caution.

It is hoped that this study might inspire further field studies into the behaviour of *P. barbatus* foragers from colonies of different ages (such as an attempt to measure the probability of quarrel directly).

Acknowledgements. Many thanks to Deborah Gordon for her advice, expertise, and her amazing dedication to the research of *Pogonomyrmex barbatus*.

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