

Synergy in Ant Foraging Strategies: Memory and Communication Alone and In Combination

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ABSTRACT

Collective foraging is a canonical problem in the study of social insect behavior, as well as in engineered systems inspired by this behavior. The use of pheromone trails is a well-studied mechanism by which ants coordinate their foraging. Another important mechanism for information use is the memory of individual ants, which allows an ant to return to a site it has previously visited. We hypothesized that there is synergy in the use of social and private information: ants with poor private information can follow pheromone trails; while ants with better private information can ignore trails and instead rely on memory. We developed an agent-based model of foraging by harvester ants, and optimized the model to maximize foraging rate using genetic algorithms. We found that ants' individual memory provided greater benefit in terms of increased foraging rate than pheromone trails in a variety of food distributions. However when the two strategies are used together, they out-perform either strategy alone. We compare the behavior of these models to observations of harvester ants in the field. We discuss why individual memory is more beneficial in this system than pheromone trails. We suggest that individual memory may be an important addition to ant colony optimization and swarm robotics systems, and that genetic algorithms may be useful in finding an adaptive balance with recruitment.

Categories and Subject Descriptors

I.2.8 [Artificial Intelligence]: Problem Solving, Control Methods, and Search; I.2.11 [Artificial Intelligence]: Distributed Artificial Intelligence – *multiagent systems*.

General Terms

Algorithms, Experimentation.

Keywords

Keywords are your own designated keywords.

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1. INTRODUCTION

Collective behavior among social insects is a subject that has caught the attention of computer scientists and engineers as a model for distributed problem-solving. For example, algorithms for ant colony optimization (ACO: [1]) and swarm robotics [2], [3], have been inspired by ants' use of pheromones to coordinate collective search. A great deal of attention has been paid to the mechanisms by which social insects share information, and how this shared information leads a colony to reach collective decisions, or to allocate its effort adaptively to different tasks or to different food sources. Less attention has been paid to the role of private information in individual insects' memory, but this is a subject that is attracting more attention recently (e.g [4], [5]).

Many species of ants and other social foragers make use of both private and social information in their foraging. Private information is information acquired through individual interaction with the environment, while social information is acquired through interaction with other individuals [6], for example via the use of pheromone trails in ants [7], [8]. Private and social information can conflict, however, as a worker with private information about one location and social information about another cannot simultaneously travel to both [5], [10]. If workers are to make optimal use of private and social information, they must adaptively resolve this conflict.

In this paper, we present an agent-based model (ABM) of ant colony foraging, based on published descriptions and our own observations of the foraging behavior of harvester ants, and which incorporates both shared and private information use. We use genetic algorithms (GAs) to explore this complex, nonlinear system, and to estimate the potential benefits of each of these sources of information in foraging on different distributions of food, as well as to find an optimal balance that allows colonies to take best advantage of both types of information. We make an empirical comparison of the foraging behavior of our optimized models to that of harvester ants, in order to make an inference about information use among ants in the field. We argue that the addition of individual memory to recruitment in engineered systems such as ACO and swarm robotics [11] may provide important benefits; and that GAs can be used to find the optimal tradeoff between the two, and thus maximize the benefits of each, for particular applications.

2. BACKGROUND

Pheromone recruitment is a well-studied mechanism by which ants and other social insects share information about the location and coordinate acquisition of food and other resources such as potential nest sites [12–15]. Successful foragers lay pheromone trails from foraging sites back to their nest. Foragers departing the nest can follow these trails to sites where food has previously been found and where, in environments where food is distributed patchily, there may be more food and search times may be lower than in other locations. Recruited foragers who also find food at these sites reinforce the trails, ultimately allowing the colony to allocate its foragers' effort to the best foraging sites on the territory.

However, pheromone recruitment can be detrimental if it causes recruitment of workers to low quality sites where workers waste time searching for scarce foods. This may happen because there was no more food to be found at the site when the first successful forager laid a pheromone trail, or because any additional food has already been collected by other recruited foragers (“overshoot” [16]). While there are mechanisms that reduce the problem of overshoot (for example a minimum volume of nectar in the crop is required to stimulate trail-laying among *Lasius niger* [17]; and *Pogonomyrmex* workers may sample the availability of nearby food before recruiting [18–20]) these mechanisms do not entirely eliminate the problem.

Another foraging strategy that is less prone to overshoot is site fidelity [18], [21–24]. Individual foragers retain private information about a location where they found food previously. If more food was available at the site, it can return there without reliance on pheromone trails or other social information signals, and with reduced risk that other foragers will have depleted the area before it completes its trip to the nest and back again.

Site fidelity and recruitment may complement one another. Honeybee foragers make use of both information shared via the waggle dance [9], and also private information about sites they have visited before; but it appears that honeybees very often ignore waggle dances they observe in favor of sites of which they have personal knowledge [25]. Similarly, *Lasius niger* foragers rely heavily on private information in their choices at trail junctions, even when the weight of pheromone trails contradicts their choice [5]. In these systems it appears that shared information about foraging sites is primarily for naïve foragers with no knowledge about foraging sites; after a forager obtains some personal information by visiting a site, private information is heavily favored. In this way ants and bees can maximize the benefits and minimize the costs of using both private and social information together [4], [25].

In the present study, we are interested in examining the benefits – in terms of increased food collection rate relative to uninformed, random search – of pheromone recruitment and site fidelity alone and in combination. We hypothesize that pheromone recruitment will increase foraging rate more than site fidelity in environments where food is distributed most patchily, i.e. where all food is found in dense piles, and where we hypothesize the benefit of rapid recruitment of ants to foraging sites will outweigh the cost of overshoot. We hypothesize that site fidelity will be of more benefit in environments where food is distributed patchily, but is found in less dense piles, as site fidelity allows ants to use personal information to exploit patchiness in the environment with reduced chance of over-recruitment to small piles of food.

Finally, we hypothesize that a strategy that balances use of both recruitment and site fidelity can increase food collection rate over either strategy alone.

We built an ABM of ant foraging, based on the foraging behavior and ecology of harvester ants as described in the literature, and based on our own observations. ABMs are particularly useful for modeling systems with spatial or temporal heterogeneity [26], [27], and systems in which complex behavior emerges as the result of interactions among individual agents with relatively simple behaviors, such as in ant colonies [15], [28], [29]. We designed our model to test the benefits of recruitment and site fidelity in different foraging environments. The particular behaviors expressed by these models and their efficacy at collecting food can vary with different parameter values [29] (described below, and see Table 1); and the optimal values for these parameters likely vary with model conditions (e.g. different food distributions, available foraging strategies). In order to observe each model making good use of the behaviors available to it, we selected parameters using GAs ([30], [31]; see also [3], [32], [33]) to maximize food collection rate.

We use GAs to optimize the behavior of our models to forage in three different food environments, using site fidelity alone, recruitment alone, neither strategy, or both together. We then observe the models foraging in the environments for which they were optimized, to evaluate overall foraging rate and search times. Finally we compare the behavior of our models to observations of harvester ant colonies in the field.

3. METHODS

Our model is based on that described in [19], [20], based on descriptions and observation of the foraging behavior of harvester ants of the genus *Pogonomyrmex*. Some parameters in the model are subject to selection, and produce important differences in foraging success depending on conditions, such as distribution of food (i.e. random vs. piled foods). Within each colony, every ant shares the same set of floating point parameters that determines their behavior. We describe the behavior of the GA-Integrated Ant (GIAnt) model and relevant parameters. We will then describe selection of parameter values using a GA.

3.1 Agent-Based Ant Foraging Model

Ants forage on a grid of 4000 X 4000 cells, with 25,600 pieces of food (seeds) placed on the grid in a random process in various distributions (described below). At model initialization, 100 ants begin at a nest located at the center of the grid. Pseudocode for the simulation is shown below. All ants carry out these instructions in parallel for 10,000 time steps.

3.1.1 ABM Pseudocode

3.1.2 Random Travel From Nest

Ants travel in a random from direction from the nest, in order to distribute themselves around the territory before beginning to search. They do this on their first trip from the nest, and may do this on subsequent departures from the nest if they have not chosen to follow trails or to return to a known site.

3.1.3 Uninformed Search

Ants that have traveled at random from the nest search for food by moving in a correlated random walk. At each time step their new direction of travel is selected from a normal distribution with a

Table 1: ABM Pseudocode

```

Initialize ants at nest, food on grid;
Do Random Travel From Nest;
Do Uninformed Search;
while t < 10,000 do
    if food is found then
        Pick up food;
        Sense count c of other food in neighborhood around current location  $l_f$ ;
        if rand(0,1) <  $\lambda_r + C / \mu_r$  then //Begin Recruiting
            Increment stop pheromone at  $l_f$ ;
            Begin incrementing recruitment pheromone at each location on return to nest;
        end
        while not at nest, Move at full speed in direction of nest; //Return To Nest
        Drop off food;
        if recruitment pheromone is present in neighborhood of nest and rand(0,1) <  $\lambda_t - C / \mu_t$  then
            // Follow Pheromone Trails

            while pheromone present out-bound and (stop pheromone is absent or rand(0,1) >  $\frac{\sum \Pi_{out-bound}}{\sum \Pi_{adjacent}}$  )
                Move to out-bound cells with probability proportional to pheromone weight
            end
            Do Informed Search;
        else if rand(0,1) <  $\lambda_s + C / \mu_s$  then //Return To Site
            while not at  $l_f$ 
                Move at full speed in direction of  $l_f$ ;
            end
            Do Informed Search;
        else
            Do Random Travel From Nest
            Do Uninformed Search;
        end
    end
    for all x, y, set  $\Pi_{x,y,t} = \Pi_{x,y,t-1} * (1 - \eta)$ ; //Evaporate Pheromones
    if  $\Pi_{x,y,t} < 0.001$ 
        set  $\Pi_{x,y,t} = 0$ ; //Pheromone is below ants' detection threshold
    end
end

Random Travel From Nest;
    Select random direction  $\theta$ 
    while rand(0,1) <  $\alpha$  do
        Random Travel From Nest
        Travel in direction  $\theta$  at full speed;
    end
end

Uninformed Search
    while food is not found, Select direction  $\theta_t$  from normal distribution  $N(\theta_{t-1}, \omega)$ , Move at  $\frac{1}{4}$  speed.
end

Informed Search
     $t_s = 0$ ;
    while food is not found
        Select direction  $\theta_t$  from normal distribution  $N(\theta_{t-1}, \omega + \gamma / t_s^{\delta})$ , Move at  $\frac{1}{4}$  speed;
         $t_s = t_s + 1$ ;
    end
end
end

```

constant standard deviation determined by a single parameter, ω , which gives a constant degree of turning that, after optimization, is adaptive for searching random areas on the grid. Searching ants move at $\frac{1}{4}$ the speed of ants traveling from the nest to foraging sites or returning to the nest with food [24].

3.1.4 Informed Search

Ants that have traveled to a location via pheromone trails or site fidelity, and are therefore searching an area where food may be more likely to be found than at a random location on the grid, search via a correlated random walk, by selecting from a normal distribution with a standard deviation that is a function of the time since beginning to search, t_s . This allows an increased degree of turning and more localized search early on in an ant's search in an area where food is likely to be found, but as t_s increases allows the degree of turning to decrease and approach ω if no food has been found. The ant then tends to move off to search for food in a new area.

3.1.5 Begin Recruiting

Ants detect and move to seeds within 1 grid cell ($\frac{1}{2}$ cm for *Pogonomyrmex* in the field [24]). When an ant arrives in a cell containing a seed, it takes a count C of the other available seeds in the Moore neighborhood of the location. Ants in the field may sample the availability of other food in the local area by handling other foods before returning to the nest [18], or perhaps by a scent of food in the vicinity. If the model has pheromone recruitment enabled, the ant decides to lay a recruitment trail probabilistically based on this count. We model two types of pheromone. Trail-laying ants deposit a 'stop' pheromone on the cell where they have picked up food, which marks the end of the trail to other ants that may follow the trail to the site. Then, as they return to the nest they deposit trail pheromone, incrementing the weight of pheromone on each cell across which they move.

3.1.6 Return to Nest

After picking up food, ants return to the nest by traveling at full speed in the direction of the nest.

3.1.7 Follow Pheromone Trails

After returning to the nest, ants decide to follow pheromone trails, if they are present, based on the count C of seeds at the last location where food was found. If so, ants move at full speed to cells out-bound from the nest, with probability linearly proportional to the weight of pheromone on those cells [34]. Ants stop following pheromone trails and begin searching when out-bound cells contain no pheromone; or they stop following trails probabilistically when they encounter cells with stop pheromone (cells where food has been found previously).

3.1.8 Return to Site

If the model has site fidelity enabled, and the ant has not decided to follow pheromone trails, the ant decides to return to the last location based on the count C of seeds at that location. It travels at full speed in the direction of that grid cell.

3.1.9 Evaporate Pheromones

At each time step, pheromones evaporate from the grid at an exponential decay rate. When the weight of trail or spot pheromone on a cell falls below a threshold of 0.001, it is considered to be below the ants' ability to detect it, and the weight of pheromone on that cell is set to zero.

3.2 Optimization by Genetic Algorithm

GAs are an optimization scheme inspired by natural selection. They operate on a population of potential solutions to a problem, in this case a population of parameter sets that control the behavior of our ant colony models. GAs discover solutions by iteratively evaluating each parameter set in the population against a fitness function, and then selecting successful parameter sets to populate the next generation. This process is repeated until the population converges on a solution to the problem. Here, we use the GA to select parameter sets for three different food distributions (piled, power-law distributed, and random; described below) and four foraging strategies (site fidelity alone, recruitment alone, both strategies together, or neither). By optimizing our model for each combination of food distribution and foraging strategy, we are able to observe how much each foraging strategy can improve foraging success above that obtained by foraging without information (i.e. neither site fidelity nor recruitment) in each type of food distribution.

Each colony is represented by 100 workers and a parameter set. We initialize a population of 200 parameter sets by randomly assigning values to each parameter. We evaluate each colony by running the model with each set of parameters, and assign a "fitness" value to each colony equal to the number of seeds it collects. Because the models are stochastic, and the number of seeds collected is subject to chance in the placement of food and the behavior of the ants, we repeat these evaluations in each generation. For each generation, we generate eight standard grids each with a randomly generated food layout. We evaluate each colony on each of the eight grids for 10,000 time steps each. Each colony's fitness is the sum of seeds it collects on all eight grids.

Following evaluation, we select successful colonies using tournament selection [35] and recombine their parameters to form the next generation. We compare the fitness of two colonies selected at random from the population, and select the one with greater fitness as the first parent. We then select another two colonies at random from the remaining 199, and keep the one with greater fitness as the second parent. Parental genomes are recombined with a crossover rate of 10% at each parameter. We then mutate the offspring's parameter values with probability 0.05, by selecting from a normal distribution with mean equal to the current parameter value and standard deviation equal to the current value * 0.05. We then return both parental colonies to the pool of potential parents, and repeat this 200 times to generate a new generation of colonies.

We repeat the above for 100 generations. Over time, the GA converges on good solutions to the foraging task given the distribution of food and the foraging strategies available in the model. In this way, we obtained models optimized for combinations of foraging strategy (with recruitment alone enabled, site fidelity alone, neither strategy enabled, and both strategies together) and food distribution (random, power-law distributed, and piled).

In all food distributions, the total number of seeds on the grid is 25,600, but seed placement differs (Figure 1). In the random distribution, all seeds are placed at random on the grid independently of one another, in a homogeneous spatial Poisson process; in the piled distribution all the available food is found in 25 large, dense, randomly placed piles of 1024, each with a radius of $\text{ceil}(\sqrt{1024/\pi}) = 19$ cells; while in the power-law distributed environment, 1/5 of the food is distributed at

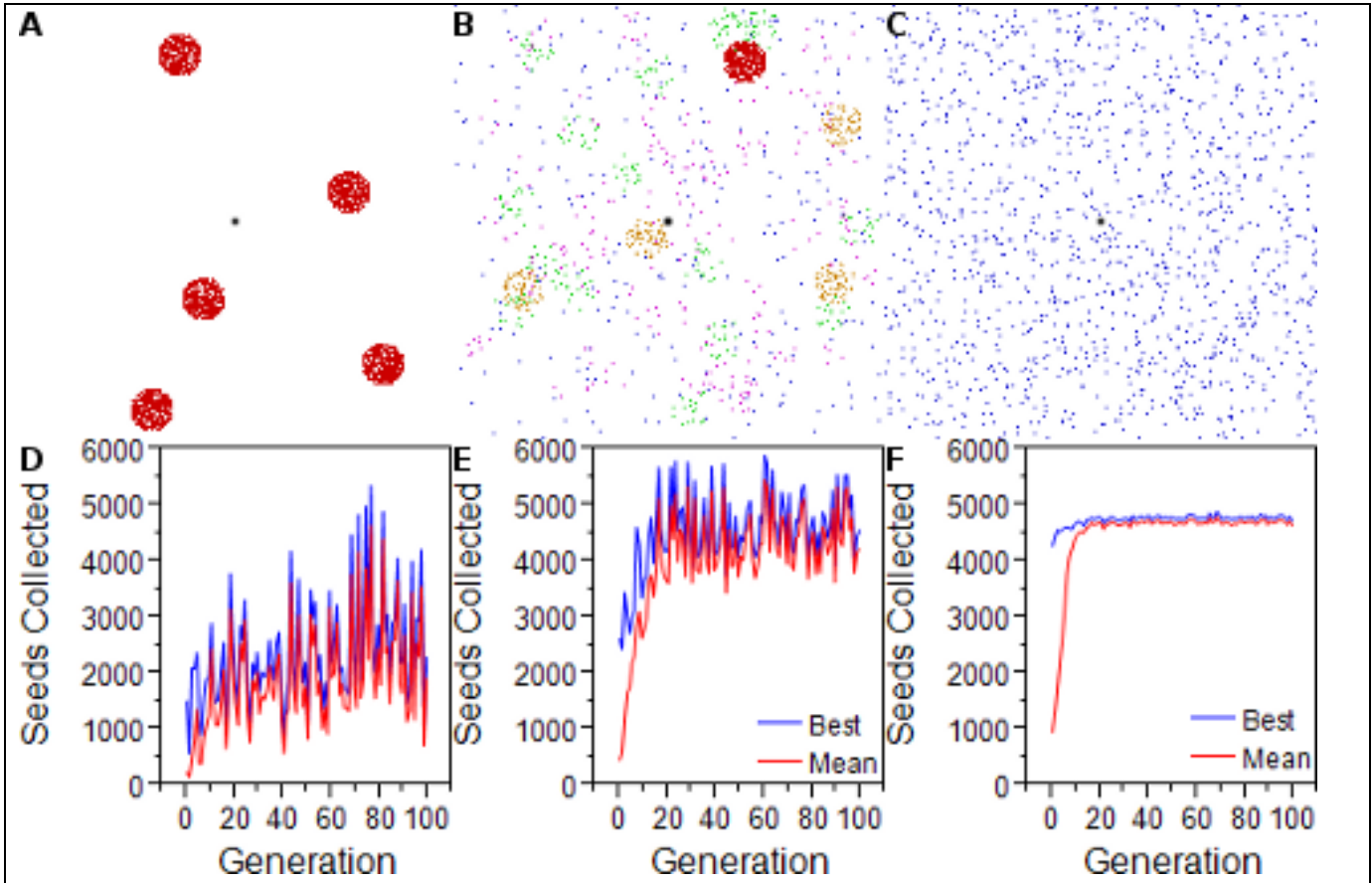


Fig. 1. Food distributions on which models were optimized and tested. A through C: Each grid contains the same number of seeds, but seeds are distributed **A**) in a piled distribution in which all available seeds are found in dense piles; **B**) in a power law distribution with a single dense pile (red), four piles of $\frac{1}{4}$ the density (orange), 16 piles of $\frac{1}{16}$ the density (green), 64 piles of $\frac{1}{64}$ the density (purple), and a random scattering of seeds (blue); **C**) or randomly scattered. Central black circle indicates the location of the nest. Note that for illustrative purposes, pile sizes and total number and density of seeds have been altered from that described in the text. **D** through **F**: Seeds collected in each of 100 generations during a GA run selecting parameters for the: **D**) piled food environment; **E**) power law food environment; and **F**) the random food environment. Variation in seeds collected from one generation to the next is greater for the piled and power law food environments than the random environment. Optimization occurs more quickly for the random food environment due to a less challenging search task.

random, $\frac{1}{5}$ is distributed in randomly placed piles of 16 seeds each, $\frac{1}{5}$ is distributed in randomly placed piles of 64, $\frac{1}{5}$ is distributed in piles of 256, and $\frac{1}{5}$ is distributed in piles of 1024 (all piles have radius of 19 cells so that they vary in density rather than area). All food is placed such that there is at most one food at each cell on the grid.

Food distributions and representative fitness curves are shown in Figure 1.

3.3 Observation of Optimized Colonies

3.3.1 Foraging Success

Following optimization, we observed GIANT models foraging on each of the three food distributions using parameters determined by the GA to maximize seed collection rates for those distributions. We recorded number of seeds collected in 10,000 time steps. In order to investigate the cause of differences in

foraging success, we also recorded time spent searching during each model run.

We also observed GIANT colonies foraging on distributions other than the one for which they had been optimized, in order to illustrate that the parameter sets and behaviors discovered by our GA produce important differences in the optimal behavioral response to different food environments. In addition, we test the hypothesis that the suite of behaviors that are optimal given a power law distributed food environment are an effective mixed strategy for unknown food distributions, because this environment selects for both the ability to find randomly distributed foods and also the ability to exploit piles of food when they are discovered. We focus this analysis on models using both recruitment and site fidelity together, because of previous research indicating that *Pogonomyrmex* in the field are capable of both behaviors [21], [36], [37].

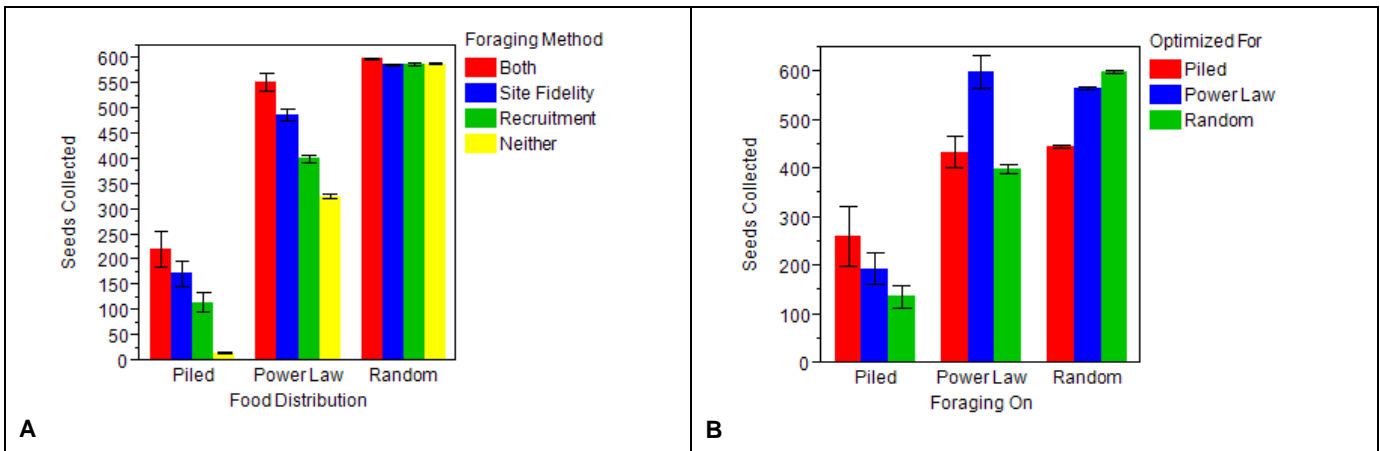


Fig. 2. Foraging success **A:** Seeds collected by models optimized for piled, power law, and random food distributions, using both site fidelity and recruitment together, site fidelity alone, recruitment alone, or neither. **B:** Seeds collected by models optimized to use both site fidelity and recruitment together, on one of three food distributions, and foraging on all three food distributions. Models perform best on the food distribution for which they were optimized. Models optimized for power law distributed food have best performance over all food distributions.

We report the results of our analyses of the effects of seed distribution, foraging method, and the distribution X method interaction, using full factorial general linear model (GLM) except where otherwise noted.

3.3.2 Comparison to Field Data

In order to compare the behavior of our optimized models to that of harvester ants in the field, we simulated bait experiments that we and colleagues carried out in a related field study [19], [38]. In that study, we baited colonies of *P. desertorum* (among two other species), a species whose colonies have on the order of 100 workers [39], with dyed seeds arrayed around the nest in four different distributions. In each observation, we baited a focal colony with a large single pile of 32 seeds; 32 seeds divided into four piles of eight; seeds divided into 16 piles of two; and 32 seeds scattered randomly. We placed seed baits within a minimum and maximum radius of 1 and 3 m respectively. Each pile of seeds was placed in a 10X10 cm area. We then observed the colony as it foraged for one hour, or until the colony ceased activity for the day, and recorded the time of retrieval of seeds from each of the four baits to the nest.

We simulated foraging observations using models parameterized by our GA. Because the seeds that make up the bulk of the diet of *Pogonomyrmex* in the field is spatially variable [40], [41] we simulated foraging by colonies that were optimized for power law distributed foods. Because the ant colonies we observed in the field also foraged on naturally occurring seeds while collecting our bait seeds, we initialized our simulated foraging observations with the same power law distribution of foods for which these parameter sets were selected, along with foods simulating the experimental baits we used in the field (described above, and see [19], [38]).

Following the procedure we used with our field data [19], [38], we produced cumulative intake curves from these observations, and calculated mean rates of seed collection from each seed distribution, by dividing the number of seeds collected by the time from the first to the last seed collected from each bait. We normalized the rates of collection from piled distributions by producing a ratio of the rate of collection from each piled distribution to the rate of collection from the random

distribution in each observation. Thus each ratio indicates how rapidly seeds were collected from each piled distribution relative to the rate of collection of randomly scattered seeds. This allowed us to produce a measure of the effect of heterogeneity on seed collection rate that is comparable to observations of ants in the field. For ant colonies in the field, the number of active foragers may vary from colony to colony or from day to day, producing variation in the rates of collection of all foods, and this normalization helps control for this variation as well. We analyzed these ratios using repeated measures ANOVA, a method that takes into account the non-independence between the rate of collection of food from each distribution (within a single observation, an ant retrieving a seed from one distribution is not at the same time available to collect seeds from other distributions). Repeated measures ANOVA accounts for this non-independence, and gives greater statistical power with data involving multiple measures within each observation.

4. RESULTS

4.1 Foraging Success

Across all foraging methods, we found that our models perform best, in terms of number of seeds collected, in the random food environment, followed by the power-law distributed environment, followed by the piled environment (Least Squares Mean seeds collected: 591.7, 442.8, and 132.3, respectively). The counter-intuitive result that randomly distributed seeds are collected faster arises because individual seeds scattered at random are found much more quickly than sparse piles of seeds, and this outweighs benefit of exploiting large piles after they are discovered, at least during the 10,000 time steps we observed.

We found that our models perform best across all food distributions when both recruitment and site fidelity are enabled, followed by site fidelity alone, followed by recruitment alone, followed lastly by models with neither method enabled (LS Mean seeds collected: 458.3, 417.2, 369.3, and 310.9, respectively; Figure 2a). In pairwise comparisons we found that site fidelity performs significantly better than recruitment alone in the power law, piled, and even the random food environments

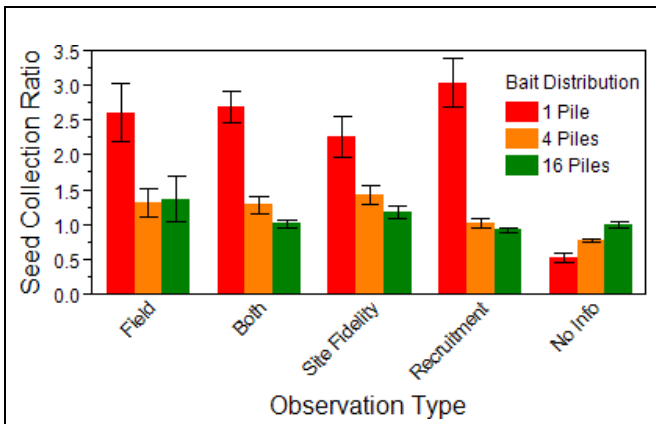


Fig. 3. Comparison of models to *Pogonomyrmex* foraging in the field. Seed collection ratios are the rate of collection of piles of seeds normalized by the rate of collection of randomly distributed seeds within each observation. A value of one indicates that seeds from a piled bait were collected at the same rate as randomly scattered seeds, while a value of two indicates piled seeds were collected twice as fast. Observations of *Pogonomyrmex* colonies in the field foraging on seed baits are compared to the foraging model using both recruitment and site fidelity together, each strategy on its own, or neither strategy.

(t-tests: all $p < 0.01$; $n = 160$ each); and that models using both foraging methods significantly out-perform either foraging method alone in all food environments (t-tests: all $p < 0.01$; $n = 480$ each). The improved performance of models with site fidelity in random food environments is due to the fact that site fidelity enables ants to retrieve seeds that are placed next to each other by chance.

4.2 Foraging Success on Other Distributions

We found that for each food distribution, the colony optimized for that food distribution had the greatest foraging success (Figure 2b). We test the hypothesis that the power-law optimized colony is the best strategy when the food distribution is not known a priori, by comparing the mean number of seeds collected across all three food distributions. The power law optimized colony collected the most seeds across all distributions (foraging on power law distributed food, piled food, and random), 474.2 seeds, as compared to 389.8 by the pile optimized colony and 397.8 by the random optimized colony. Thus the strategy for foraging on power-law distributed foods represents a good mixed strategy capable of foraging reasonably well on a variety of food distributions.

4.3 Comparison to Field Data

Pairwise comparison of each of our model strategies to field data reveal significant differences between field data and the no-information model in which ants use neither recruitment or site fidelity. A significant effect of data source (i.e. field data vs. model data: Repeated-measures ANOVA: $n = 29$ [9 field and 80 model]; $p < 0.001$) indicates that the no-information model collected piled seeds in general more slowly relative to random, compared to ants in the field. A significant interaction of data source and bait distribution ($p < 0.001$) indicates that the rates of collection of piled foods relative to piles of different densities differ from field observations as well. These can be seen in Figure 3, where the model colony using neither foraging strategy has lower foraging ratios overall than ants in the field, and also

the relative ratios for different bait distributions are opposite that seen in the other observations: increasingly densely piled baits are collected more slowly by this model, whereas ants in the field collected the most densely piled baits most rapidly.

We observed no other significant effects in pairwise comparisons of the other models to the field data (all main and interaction effects $p > 0.10$), because of the high variance in our field data. However we do see a significant interaction of bait distribution and model type when comparing models with site fidelity alone enabled vs. recruitment alone enabled ($p = 0.018$) which indicates that the site fidelity models are able to collect less densely piled baits more rapidly, while recruitment models are able to collect the densest piles more rapidly.

5. DISCUSSION

We found that site fidelity and recruitment together out-perform either strategy alone in all three food distributions, and that site fidelity alone out-performs recruitment alone in the power law and piled food distributions. Variation in search time per foraging trip explains much of the difference in foraging success using different foraging strategies. We found that site fidelity and recruitment together complement each other in a way that allows increased foraging rate over either strategy alone.

Other researchers have examined the value of private vs. social information based on imposed differences on the quality of that information (e.g. error in the communication of spatial information by the waggle dance in honeybees [42]). In this model, shared and private information are equally accurate; both recruitment trails and site fidelity guide ants to a precise location on the grid. Here, the difference in quality of shared vs. private information is not imposed as an assumption of the model, but is instead entirely a product of the collection and depletion of seeds in a pile by the ants as they forage. The greater benefit of site fidelity in our models is caused by the greater susceptibility of recruitment to the problem of overshoot.

We found that site fidelity out-performs pheromone recruitment in both the power law and piled distributions, and trends toward better performance in the random environment. The prevalence of pheromone recruitment across ant taxa suggests that there must be some foraging ecologies for which pheromone recruitment is more effective than site fidelity. The food distributions we experimented with here are based on the foraging ecology of seed-harvester ants. Seed-harvester ants' primary food is scattered across the landscape, but with significant spatial variation and in skewed distributions consistent with a power law distribution [40], with a few large piles of seeds, such as those dropped at the base of seeding plants, many small piles of seeds, and many randomly distributed seeds scattered by wind and other random processes. We imagine that for other types of food sources, e.g. animal carcasses, social insect colonies, or nectar sources, recruitment alone may be a more effective foraging strategy than site fidelity alone, as these may present foods where at a single point there may be enough food for multiple forager trips, reducing the problem of overshoot relative to the amount of food available. Additionally, recruitment may be more advantageous for ephemeral foods that will disappear or be taken by competitors before one or a few ants are able to collect it all.

We found that optimized models using neither recruitment nor site fidelity provide a poor fit to field observations of *Pogonomyrmex* foraging on seed baits. These models are able

to make no use of information about the location of food, and therefore search essentially at random – although aspects of their search behavior have been adjusted by the GA for particular types of food distributions, they cannot use information about where food has been found previously. As a result, they collect random foods fastest, and increasingly densely piled foods more slowly, as larger, denser piles of food are increasingly difficult to find by random search. This is opposite what we observed in ants in the field as well as in other models where ants are able to make use of this information, either by recruitment, or site fidelity, or both together. We found that our models of information use by ant colonies are statistically indistinguishable from the foraging behavior of ant colonies in the field. This is particularly interesting because we did not use GAs to fit our model behavior to field data, but rather we used GAs to maximize food collection rate given the constraints of the model. Presumably ants in the field have been selected to maximize food collection rate as well, among other goals and constraints.

6. CONCLUSIONS

We conclude that site fidelity as a foraging strategy has the potential to be more effective, at least in some environments more effective, than pheromone recruitment. In addition, we have quantified the extent to which site fidelity and recruitment may act synergistically to improve the success of colonies using both strategies over either strategy alone when foraging for seeds. Pheromone recruitment has benefits in sharing information about the location of food sources, and allowing rapid recruitment of ants to a site, as well as colony convergence on the most productive foraging sites; while site fidelity suffers less from the problem of overshoot and allows foragers to more reliably find seeds in a known patch. Once an adaptive balance is struck between reliance on these two sources of information, ants using these two foraging tactics in combination enjoy the benefits of both while reducing the associated costs. This synergy between private and social information may be an important feature of collective foraging in ants and social insects in general.

Finally, our approach to combining social and private information may be useful in the fields of ACO [1] and swarm robotics. Here, we used GAs to optimize models using different information use tactics for various food distributions, in order to observe the maximum benefit a colony might extract from various sources of information. GAs can also be used to optimize engineered systems. We believe the addition of site fidelity to recruitment may help reduce the problem of premature convergence in some ACO applications, by allowing individual agents to sample the solution space while minimizing the overhead of communication between agents. GAs have also been used to optimize swarm robots [3], [11], [43]. The combination of recruitment and site fidelity may be a valuable and important way to improve the performance of swarms in collective foraging tasks, using GAs to find an optimal balance between the two tactics for information use, potentially including communication overhead among the constraints to optimize.

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