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Simulating the evolution of recruitment behavior in foraging Ants

Kenneth Letendre

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and form for publication:

Approved by the Thesis Committee:

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**SIMULATING THE EVOLUTION OF RECRUITMENT
BEHAVIOR IN FORAGING ANTS**

BY

KENNETH LETENDRE

B.S., BIOLOGY, TOWSON UNIVERSITY, 2003

THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Master of Science

Computer Science

The University of New Mexico
Albuquerque, New Mexico

December, 2010

DEDICATION

I dedicate this thesis to my mother, who taught me the curiosity about the world and the interest in science that have driven me constantly to do and learn new things. I dedicate this thesis to my father, whose passion for technology introduced me at a young age to piles of parts that could be assembled and made to compute.

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ABSTRACT

Spatial heterogeneity in the distribution of food is an important determinant of species' optimal foraging strategies, and of the dynamics of populations and communities. In order to explore the interaction of food heterogeneity and colony size in their effects on the behavior of foraging ant colonies, we built agent-based models of the foraging and recruitment behavior of harvester ants of the genus *Pogonomyrmex*. We optimized the behavior of these models using genetic algorithms over a variety of food distributions and colony sizes, and validated their behavior by comparison with data collected on harvester ants foraging for seeds in the field. We compared two models: one in which ants lay a pheromone trail each time they return to the nest with food; and another in which ants lay pheromone trails selectively, depending on the density of other food available in the area where food was found. We found that the

density-dependent trail-laying model fit the field data better. We found that in this density-dependent recruitment model, colonies of all sizes evolved intense recruitment behavior, even when optimized for environments in which the majority of foods are distributed homogeneously. We discuss the implications of these models to the understanding of optimal foraging strategy and community dynamics among ants, and potential for application to ACO and other distributed problem-solving systems.

TABLE OF CONTENTS

INTRODUCTION.....	1
METHODS.....	6
Density-Dependent Recruitment Model.....	10
Optimization By Genetic Algorithm.....	11
Comparison to Field Data.....	14
RESULTS.....	16
GA Results.....	16
Comparison to Field Data.....	19
DISCUSSION.....	22
REFERENCES.....	30

Introduction

Spatial heterogeneity in the distribution of food is an important ecological determinant of the optimal foraging strategy of a species (Charnov, 1976), and of the dynamics of populations and communities (Schoener, 1974; Wiens, 1976).

Heterogeneously distributed foods present foragers with an opportunity to take advantage of reduced search times within patches where food is more densely concentrated than in the environment as a whole. Foraging strategies that are best adapted to the scale and degree of heterogeneity in the environment are favored (Charnov, 1976). Heterogeneity influences the distribution of consumers (Wiens, 1976) and can provide a dimension along which food niches are partitioned, allowing the coexistence of species (Schoener, 1974).

Socially coordinated foraging behavior can be part of a species' strategy for exploiting heterogeneously distributed foods (Wiens, 1976). Social organisms in patchy environments can take advantage of others' knowledge of the location of food patches, either through active sharing of information or by observing others' foraging success (Ward and Zahavi, 1973). Information sharing may be particularly important for eusocial insects. Because of the high relatedness among nestmates (Trivers and Hare, 1967), and the fact that the reproductive success of an insect colony is mainly or entirely the result of the queen's reproductive output, workers are selected to maximize foraging success of the colony as a whole (Oster and Wilson, 1979). Therefore, cooperative foraging may be selected for among eusocial insects if it increases the foraging success of the colony, even if it comes with some cost to individual foragers.

Among many species of ants, information is communicated between foragers with the use of recruitment pheromones, which in some species are used to leave a trail along the ground as a forager makes a return trip to the nest with food (Wilson and Hölldobler 1990). When departing the nest, other foragers may follow these trails to sites where food has been found previously, and where, in environments where food is distributed heterogeneously, there may be more food available. In this way, foragers communicate information about the location of food sources, which allows reduced search times, and increased rate of food collection.

This recruitment behavior is of particular interest to computer scientists as a distributed problem-solving system. Observation of the collective action of foraging ants and the use of pheromones to coordinate collective activity inspired ant colony optimization (ACO) algorithms (Bonabeau et al., 2000). This optimization technique emulates the fairly simple, distributed interactions of individual ants to arrive at optimal colony-level solutions to complex problems. ACO's have been applied to approximations of NP-hard problems such as the traveling salesman problem (*ibid.*) and engineering applications such as the design of VLSI chips (Arora & Moses, 2009). However Timmis et al. (2006) point out that biologically inspired computation has not yet reached its full potential, as biocomputing techniques are based on the behavior of only a small sample of natural behaviors, the diversity of which is still largely unexplored.

Harvester ants of the genus *Pogonomyrmex* provide an excellent model system to study the influence of heterogeneity in the distribution of food on the evolution of foraging strategies and social behavior. They feed primarily on small seeds that foragers carry individually, yet their food sources exist in a mixture of homogeneous sources and

heterogeneous patches (Gordon 1993, Reichman 1984). Many seeds that harvester ants feed on are carried by the wind and are scattered at random; however depressions and other soil features may create pockets where seeds tend to fall out of the wind in greater concentrations, and some seeds may fall from plants in patches or be harvested directly from plants' stems by the ants. Mature colonies among species in this genus range in size over more than an order of magnitude, from hundreds of foragers to more than ten thousand (Johnson 2000). The general foraging strategy of *Pogonomyrmex* varies from one species to the next, from solitary foraging to social foraging with persistent trunk trails (Johnson 2000), with a general trend toward more intense social foraging with greater colony size (Beckers et al. 1989; Johnson 2000). Within a species, foragers may engage in solitary or social foraging depending on the density of available foods (Hölldobler 1976, Mull and MacMahon 1997).

In a study of the scaling of territory area with *Pogonomyrmex* forager number, Moses (2005) predicted a sub-linear scaling relationship between territory size and forager number, as a result of the ants' need to strike an optimal trade-off between the cost of increased search times on a small territory depleted of seeds, and the cost of increased travel times to and from the nest with increasing territory size. However, while Moses (2005) found a sub-linear scaling relationship between territory area and forager number, and an increasing density of foragers on the territory with increasing forager number, she did not find a predicted increase in search time with forager number. This led to the hypothesis that, given some heterogeneity in the distribution of food sources, larger colonies, by virtue of having larger territories, have access to more information

about this distribution, and can exploit this information to direct foraging effort to the densest, highest quality patches where foraging times are reduced.

In order to investigate the influence of forager number and heterogeneity in the distribution of food on foraging strategy, we developed agent-based models (ABMs) of foraging by harvester ant colonies, based on descriptions of their behavior in the biological literature and our own observations. We used these models to test the prediction that more intense recruitment behavior will be optimal for larger colonies and for colonies foraging in environments with more heterogeneity in the distribution of food. ABMs simulate systems by iteratively executing rules that govern the behavior and interactions of agents within the system. On each iteration, the state of the system is updated based on the actions or interactions of the agents over each discrete time step. ABMs are particularly useful for modeling systems with spatial or temporal heterogeneity (Berec 2002, Nonaka and Holme 2007) and systems in which complex behavior emerges as the result of interactions among individual agents with relatively simple behaviors (Grimm et al. 2005), just as the group behavior of an ant colony emerges as the result of actions and interactions among the individual ants.

ABM's allow us to investigate the effects of forager number and food heterogeneity on the evolution of recruitment behavior by allowing perfect control over these independent variables, while controlling for other factors that are difficult or impossible to control in the field. For example, one wants to compare species that share enough similarity in their foraging habits and environment, and that vary only in the traits of interest; but it may be that traits covary among related species in the field as a result of phylogenetic dependence (Freckleton et al. 2002). Heterogeneity in the distribution of

seeds in the field has been estimated by taking soil samples (e.g. Reichman 1984), however such estimates may not provide a relevant measure of the heterogeneity of foods for a given ant species, as ants do not collect all seeds indiscriminately. Even sympatric species may vary systematically in their preference for seeds of different sizes – and thus seeds that may be found in different spatial distributions – based on the size and morphology of the workers (Hölldobler 1976). ABM's allow us to control all confounding factors and experimental conditions, and thus provide a perfect experimental environment so that we can study only the behaviors of interest.

We are interested in the effects of forager number and food heterogeneity on the optimal foraging behavior of ant colonies, specifically colonies' use of pheromone recruitment to food sources. Therefore we optimized our ABMs using genetic algorithms (GAs), an optimization technique that simulates the process of evolution by natural selection (Forrest 1996, Mitchell 1998). GAs optimize functions or programs by repeatedly evaluating the success of a population of different possible parameter combinations, and recombining and mutating successful parameter sets to arrive at good solutions to the fitness problem over the course of generations. In the field, the behavior of *Pogonomyrmex* species is optimized by natural selection to maximize foraging success (among other goals and constraints) given each species' particular ecology. Therefore, GAs and other evolutionary algorithms are a particularly appealing method for selecting parameters for models of biological systems (e.g. Hamilton et al. 1990, Solé et al. 2000, Buchkremer and Reinhold 2008).

We used GAs to determine behaviors, encoded as parameters in our ABM, that maximized seed intake. The fitness function in our GA was seed intake rate. We

executed GAs over a range of forager numbers, and over a range of food distributions from fully homogeneous to fully heterogeneous, selecting for fastest rate of food collection under these varying conditions. We then used the resulting, optimized models to simulate experimental foraging observations, and compared the behavior of the resulting models to that of ants in the field.

METHODS

Simple Recruitment Model

We developed an ABM of recruitment by a colony of ants, and a GA to evolve parameters to maximize the rate of seed collection by the colony. Our model is similar in some respects to the search and recruitment behaviors in the models by Haefner and Crist (1994) and Crist and Haefner (1994); however we sought to simplify our model to reduce computational complexity and run-time, since optimizing our model for each combination of forager number and food heterogeneity requires running the model thousands of times.

Under this simple recruitment model, each time a searching ant picks up a piece of food, it lays a pheromone trail as it returns to the nest. Ants leaving the nest to begin another foraging trip follow pheromone trails to return to sites where food has previously been found. Ants that arrive in high-density food patches have lower search times on average than those in lower density patches, and reinforce the pheromone trails leading to these sites. Pheromones evaporate at an exponential decay rate, and over time the foragers are expected to converge on the highest quality patch based on its density and its distance from the nest, as more and more foragers are recruited to the highest quality sites (Beckers et al. 1990, Detrain & Deneubourg 2008).

At model initialization, all ants begin at the nest site located at the center of a grid of 4000 X 4000 cells. Each ant picks a direction at random and begins walking. At each time step, each ant stops walking with a constant probability determined by the parameter α , and begins to search. For high values of α , ants generally will walk short distances from the nest; whereas for low values, ants will generally walk long distances from the nest before beginning to search.

Like *Pogonomyrmex* in the field (Crist and MacMahon 1991), searching ants move in a correlated random walk. The degree of turning in searching ants' correlated random walk allows them to search more thoroughly in a local area if turning more, or to move in a straighter line and cover more distance if turning less. We found that there may be different optimum degrees of turning at different times in an ants' search. At the end of a pheromone trail where there may be more food to be found, ants may randomly select the wrong direction to begin moving and walk away from a pile of food; however if they are able to turn more and therefore do a more thorough, local search when they begin searching (a behavior suggested by our personal observations of *Pogonomyrmex* foraging on piles of bait seeds in the field), they are more likely to find more food in a patch. If searching ants decrease their turning behavior over time, this allows ants to move off and search more widely for new food sources if they fail to find food early on.

We determined searching ants' turning behavior as follows. At each time step t , each searching ant selects a direction Θ_t to move from a normal distribution with mean equal to Θ_{t-1} and a standard deviation (SD) determined by three parameters, which allow degree of turning to change with the number of time steps since the ant began searching, t_s :

$$SD = \omega + \gamma / t_s^\delta \quad (1)$$

The parameter ω determines ants degree of turning. For lower values of ω , the direction searching ants move at each time step t is more tightly correlated with the direction the ant moved at time step $t-1$, and ants tend to turn less. For higher values, searching ants' movements are less correlated from one time step to the next, ants turn more and cover less distance. The parameter γ allows ants an extra degree of turning with low values of t_s , and to return to the baseline degree of turning ω as t_s becomes large, and therefore γ / t_s^δ becomes small; the exponent parameter δ determines how quickly this term approaches zero as t_s increases. Searching ants move at $1/4$ the speed of walking ants or trail-following ants, a relative rate supported by observations of ants in the field (Crist and MacMahon 1991).

Upon finding food, ants pick up the food and begin to return to the nest. *Pogonomyrmex* in the field navigate by landmarks and the polarization of sunlight, and have a keen ability to navigate even if displaced significant distances (Hölldobler 1976). Therefore, in our model, ants returning to the nest move at each time step so that their distance from the nest is non-increasing. They select an adjacent, in-bound cell to move to with probability proportional to the amount that a move to that cell would decrease the ant's distance to the nest. While returning to the nest, ants lay pheromone trails by incrementing the weight of pheromone on each cell they move through by a constant amount. Returning ants move at $1/2$ the speed of walking or trail-following ants (Crist and MacMahon 1991).

After returning from the first foraging trip, ants leaving the nest again follow trails if any exist, or if not (if no pheromone trails have been laid yet – see section 3.2 below), they begin searching at the nest entrance. Trail-following ants move at each time step so that their distance from the nest is non-decreasing. They select an adjacent, out-bound cell with probability proportional to each cell's pheromone weight, as a fraction of the total pheromone weight on all such cells. This allows ants to bias their movement onto cells on which more pheromone has been laid, and gives ants a greater probability of arriving at sites from which more pheromone trails have recently been drawn. At each time step, trail-following ants abandon the pheromone trail and begin to search with probability determined by the parameter ε . When an ant arrives at a cell whose out-bound neighbors have no pheromone, it has reached the end of the trail, and it begins to search.

At each time step t , the weight of pheromone $\Pi_{x,y,t}$ on each cell x,y is evaporated at a rate determined by a colony-specific evaporation rate η :

$$\Pi_{x,y,t} = \Pi_{x,y,t-1} * (1 - \eta) \quad (2)$$

Over time this evaporation approximates an exponential decay rate. When the weight of pheromone on a cell falls below a threshold, it is considered to have fallen below an ants' ability to perceive it, and the pheromone on that cell is set to zero.

See Table 1 for a summary of parameters used in this model.

Density-Dependent Recruitment Model

During fieldwork, we observed that individual *Pogonomyrmex* foragers may sometimes travel back and forth to collect bait seeds without recruiting any other foragers to the effort (site fidelity, or patch fidelity; see Crist & MacMahon 1991, Buchkremer & Reinhold 2008, Beverly et al. 2009); and that this may go on indefinitely, or after some time a number of other foragers may quickly join the effort and a foraging trail develops. We therefore developed an alternate to the simple recruitment model above. This density-dependent recruitment model is identical to the simple recruitment model, except that instead of leaving a pheromone trail on the return trip to the nest each and every time an ant picks up food, ants make a decision to leave a pheromone trail or not. We introduced two new parameters to facilitate this.

The first parameter relevant to this decision is λ , which determines an ant's constant probability of leaving a pheromone trail each time it picks up a piece of food. Thus if λ is 1.0 or higher, the behavior of this model is identical to the simple recruitment model above; if λ is less than 0.0, the colony can abandon the use of pheromones entirely.

The second parameter μ determines ants' sensitivity to the presence of other food in neighboring cells in making the decision to lay a pheromone trail or not. Upon picking up a piece of food, an ant takes a count C of other seeds in the eight cells immediately adjacent to the cell where it found food, and decides to leave a pheromone trail on the return trip to the nest with probability p :

$$p = \lambda + C / \mu \quad (3)$$

(Note that if $p < 0$ then ants leave a trail with probability 0; if $p > 1$ then ants leave a trail with probability 1.)

The ability of ants in the field to detect other food in the neighborhood may be based on a scent of nearby seeds detectable by a foraging ant. Alternatively, Hölldobler (1976) noted that ants often handle a number of seeds before picking one up and returning to the nest; he speculated that ants may be sampling the availability of food in an area.

Optimization By Genetic Algorithms

As described above, the behavior of these models is subject to the selection of a variety of parameters. We are interested in differences in the behavior of ant colonies of different sizes after their behavior has been optimized by natural selection in environments with different degrees of heterogeneity in the distribution of food. Thus we are interested in the optimal behavior expressed by our models for simulated foraging environments.

An exhaustive exploration of the space of all combinations of parameters for the global optimum is not feasible. For the density-dependent recruitment model described above, we have eight floating-point parameters. If we assume a discretization of each parameter to two significant digits, and if all parameters were restricted to the interval $[0,1]$ (some are not so restricted), the search space of all possible parameters contains more than $(10^2)^8 = 10^{16}$ parameter combinations. Assuming the quarter-second run-times we experienced for our smallest and quickest simulations of ant colonies with ten foragers, an exhaustive exploration of the search space would take on the order of 10^6 years to complete. The search for optimal parameter sets for environments varying in

food heterogeneity is further complicated by the fact that the random placement of heterogeneous foods means that sometimes a colony might find a dense pile of food placed very near its nest, while at other times there may be no piles of food nearby. In order for a colony to behave optimally in such a stochastic environment, it must perform well overall given the possibility of all such eventualities, rather than being optimized to perform well in only one such configuration. Given the infeasibility of finding provable global optima for these models, we instead used genetic algorithms (GAs) to find parameters that approximate the optimal behavior possible for our models under each set of conditions.

Our GA works as follows. Each parameter is a floating point number.

Parameters for each colony in the initial generation of each GA run were randomly selected from a uniform distribution. Each colony's genome is made up of one number for each parameter. The behavior of workers in our models is determined by a single set of parameters for the colony as a whole. Individual variation in the behavior of workers may be an interesting area of study; but given the high degree of relatedness among the workers in an ant colony (Trivers and Hare 1967), we expect that stochasticity in the behavior of ants modeled here will produce functionally similar variation for the purposes of this study.

Each GA run used a population of 100 colonies, over 100 generations. We ran GAs over a range of forager numbers, from 10 to 1000 foragers, and over a range of food heterogeneity. Food heterogeneity was manipulated by placing food in piles of 256 seeds, and scattering the remaining seeds at random over the grid. The grid was always set up with the same number of total seeds, but the number of seed piles ranged from zero

(heterogeneity 0) to 100 (heterogeneity 1). We ran the GA multiple times for each combination of forager number and food heterogeneity.

All colonies were evaluated on eight food configurations per generation, with piles and seeds placed at random on the grid, but each with the particular degree of heterogeneity for that GA run. The eight food configurations were standard for each generation, such that each colony was evaluated on the eight configurations identical to those given to all other colonies in that generation.

Each colony was evaluated on each food configuration for 20,000 time steps per configuration. Because the energetic cost of foraging is a tiny fraction of the energetic value of a seed retrieved by *Pogonomyrmex* foragers (Fewell 1988, Weier and Feener, 1995), time costs dominate in selection on foraging efficiency; therefore the measure of fitness we used was the total number of seeds collected by each colony in the eight food configurations in each generation. An equal value was assigned to seeds collected from any of the distributions of food, whether piled or randomly scattered.

In each generation, tournament selection for the greatest number of seeds collected determined the parents for the next generation. Tournament selection is an efficient selection method whose selection pressure is robust to noisy fitness evaluation methods (Miller & Goldberg 1996), such as the sampling of colonies' performance on stochastically determined food distributions used here. Two colonies (parameter sets) were selected at random from the population, and their fitness (the number of seeds they had collected) were compared. The one with greater fitness was selected as a parent. Another two colonies from the remaining 99 were then selected at random, and the one with the greater fitness from this pair was selected as a second parent. These two parental

genomes were recombined with a crossover rate of 10%. Inherited parameters were mutated 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 parameter value * 0.05. Both parental parameter sets were then returned to the pool of potential parents, and this was repeated 100 times to produce the next generation of parameter sets.

Comparison to Field Data

We attempted to validate our models by comparison with observations of *Pogonomyrmex* foraging in the field. In a separate field study, we (Paz et al. in review) studied the foraging behavior of three *Pogonomyrmex* species that range over more than an order of magnitude in maximum colony size: *P. desertorum*, up to 500 workers; *P. maricopa*, up to 1000 workers; and *P. rugosus*, up to 10000 workers. We baited focal colonies with dyed seeds arrayed around the nest in four different distributions. We baited with a large single pile of seeds; an equal number of seeds divided into four piles at one-quarter the density; seeds divided into 16 piles at one-sixteenth the density; and seeds scattered randomly. Seed baits were placed within a minimum and maximum radius, forming a donut around the nest entrance. We then observed the focal colony as it foraged, and recorded the retrieval of seeds from each of the four baits to the nest.

We simulated foraging observations using models parameterized by our GAs. We initialized models with food distributions that mimic the experimental baits we used in the field (Paz et al. in review; see Fig. 1). Based on the assumption that *Pogonomyrmex* in the field have evolved to exploit a mixture of heterogeneous and homogeneous food sources, we selected parameter sets for our models that were optimized for 50% piled and 50% random food distributions (heterogeneity 0.5 in Figs. 3 and 4). We compared the

behavior of models of our largest colonies of 1,000 ants, with the behavior of *P. rugosus*, a species whose colonies can grow as large as 10,000 workers, but many or most of which have fewer workers, and only a fraction of which workers forage (as opposed to engaging in other tasks or remaining idle) at any time (Moses 2005).

Following the procedure we used with our field data (Paz et al. in review), we produced cumulative intake curves from these observations, and from these calculated mean rates of seed collection from each seed distribution. 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. 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. 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, and therefore the rate of collection of piled foods is not independent of the rate of collection of randomly scattered foods. 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. Repeated measures ANOVA accounts for this dependence, and gives greater statistical power with these kinds of data.

RESULTS

GA Results

We found that variation in foraging success (fitness for the purposes of our GA) from one generation to the next was greatest in the smallest colonies of ten ants, in environments where all available food is in piles. This results from a small territory size and the chance placement of piles of food relatively close to or far from the nest. The territories of larger colonies are more likely to encompass multiple piles, and therefore these colonies experience less variation in foraging success from one generation to the next. The foraging success of colonies foraging on distributions with greater proportions of randomly scattered foods is less subject to the chance placement of dense piles of food.

Nevertheless, because we evaluated each colony on eight food configurations in each generation, we achieved sufficient stability in fitness from one generation to the next to observe optimization on the foraging task over the course of the GA runs. Fig. 2a illustrates the mean and maximum fitness (total number of seeds collected over eight evaluations foraging for 20,000 time steps) in each generation over one GA run, with a ten-ant colony foraging on a fully heterogeneous food distribution. It was with this combination of small forager number and high degree of heterogeneity in the food distribution that we saw the greatest variation about the mean in number of seeds collected from one generation to the next. For contrast, Fig. 2b illustrates the mean and maximum fitness during one GA run for a 1000-ant colony foraging on a fully heterogeneous food distribution, where foraging success from one generation to the next is reduced. We tested this difference in variance for the ten- and 1000-ant GA runs illustrated in Fig. 2, selecting generations 50 and greater, after all or most optimization

was complete. After normalizing mean fitness for each colony to 1, we found that the variance in foraging success was significantly greater for the ten-ant colony (F-test for equality of two variances: ten-ant variance = 0.053, 1000-ant variance = 0.009; $F = 6.136$, $df = 49,49$, $p < 0.001$).

We are interested in the degree to which forager number and heterogeneity in the distribution of food select for the use of pheromone trails to direct the foraging activity of the colony. Two parameters are indicative of the intensity of recruitment behavior: with decreasing rate of pheromone evaporation η , pheromone trails are less ephemeral, and it is possible for ants to follow trails longer distances from the nest; and with decreasing probability that a trail-following ant will abandon a pheromone trail at each time step, ε , ants are more likely to follow pheromone trails to their end. To some extent, these parameters may be traded off against one another as GAs converge on an optimal degree of trail-following behavior. Below, we use as a measure of the intensity of recruitment a derived Recruitment Factor, which is the geometric mean of trail persistence ($1 - \eta$) and ants' trail fidelity ($1 - \varepsilon$):

$$\text{Recruitment Factor} = \sqrt{(1 - \eta)(1 - \varepsilon)} \quad (4)$$

Thus, ants of a colony with Recruitment Factor equal to 1 could theoretically follow pheromone trails an infinite distance, as trails would be permanent, and ants following trails would unfailingly follow them to their end. Ants of a colony with Recruitment Factor equal to 0 would be unable to follow pheromone trails any distance,

because either pheromone trails would evaporate instantly, or because ants would have no tendency to follow pheromone trails leading from the nest.

Simple Recruitment Model

In the simple recruitment model, we found significant, positive, main effects of both food heterogeneity and forager number on recruitment factor (GLM, standardized β coefficients throughout. Heterogeneity: $\beta = 0.624$, $p < 0.001$; Forager Number: $\beta = 0.373$, $p < 0.001$. $N = 133$ GA runs.) and a significant, negative interaction effect of forager number with food heterogeneity (GLM: $\beta = -.295$, $p < 0.001$). Recruitment behavior increased with forager number, and in environments with more heterogeneously distributed foods. The relationship of recruitment behavior with forager number and food heterogeneity is illustrated in Fig. 3a.

Density-Dependent Recruitment Model

In the density-dependent recruitment model, similar to the results of the simple recruitment model, we found significant, positive, main effects of both food heterogeneity and forager number on recruitment (GLM: Heterogeneity: $\beta = 0.507$, $p < 0.001$; Forager Number: $\beta = 0.166$, $p = 0.009$. $N = 137$ GA runs.) and a significant, negative interaction effect of forager number with food heterogeneity (GLM: $\beta = -.211$, $p = 0.003$).

Relative to the simple recruitment model (Fig. 3a), the intensity of recruitment behavior in the density-dependent recruitment model is more robust to decreasing heterogeneity in the distribution of food (Fig. 3b). Recruitment behavior remained relatively high even in the smallest colonies with as little as one quarter of the food distributed in dense piles; whereas in the simple recruitment model, recruitment behavior

declined steadily with decreases in food heterogeneity below heterogeneity 1. This is reflected in the relatively weak effect of forager number on recruitment behavior in the density-dependent recruitment model ($\beta = 0.166$, 95% CI 0.042 to 0.290; cf. $\beta = 0.373$, 95% CI 0.229 to 0.517 in the simple recruitment model).

In order to understand why and when ants use pheromone trails, we investigated the relationship between forager number, food heterogeneity, and the tendency of ants to leave pheromone trails on their return trip to the nest. The parameter λ , which describes ants' baseline probability of leaving a pheromone trail on the return trip with food, provides the clearest indicator of a colony's use of pheromone trails. We found no effect of forager number on λ (GLM: $p > 0.10$), but a significant quadratic effect of food heterogeneity (GLM: heterogeneity $\beta = -1.138$, $p < 0.001$; heterogeneity² $\beta = 0.947$, $p < 0.001$. $N = 137$.) These relationships are illustrated in Fig. 4.

Thus, colonies optimized on mixed distributions of food were most selective in their trail-laying behavior. We found that colonies evolved the most liberal trail-laying behavior when optimized on fully homogeneous food distributions; and that colonies evolved significantly more selective trail-laying behavior on fully heterogeneous distributions (two-sample t-test: heterogeneous mean $\lambda = -0.272$, SD = 0.674; homogeneous mean $\lambda = 0.448$, SD = 0.464. $p < 0.001$. $N = 53$ GA runs.) Therefore ants are significantly more likely to leave a pheromone trail each time they pick up food from a fully homogeneous food distribution than ants foraging on fully heterogeneous distributions. We believe this counter-intuitive result indicates selection for patch-switching behavior in heterogeneous environments, but is in part an artifact of our model. This is a subject we will return to in Discussion below.

Comparison to Field Data

Fig. 5 illustrates the cumulative collection of bait seeds placed in four distributions: one large pile of 256 seeds, represented by the red cumulative curve; four piles of 64 seeds each, represented by the orange curve; 16 piles of 16 seeds each, represented by the green curve; and 256 randomly scattered seeds, represented by the blue curve. Fig. 5a represents a typical field observation of *P. rugosus* foraging over an hour period. Fig. 5b represents a simulated observation of foraging by the simple recruitment model. Fig. 5c represents a simulated observation of foraging by the density-dependent recruitment model.

Qualitatively, the density-dependent model (Fig. 5c) provides a better match to the field data than the simple recruitment model. The field observation shows slow initial discovery of the single-pile and four-pile distributions, but the rate of collection of seeds from these distributions increases over the course of the observation. On the other hand, the simple recruitment model (Fig. 5b) produces a less satisfying match to the field observation: it is always the more homogeneous distributions that are collected more rapidly, and the rate of collection of each distribution falls off over time as the remaining seeds become fewer and harder to find. Because we found better fit of the density-dependent recruitment model to the field data, and because the density-dependent recruitment models had the capacity to evolve behavior identical to the simple recruitment models if that behavior were favored, we will focus the quantitative analysis below on the behavior of the density-dependent recruitment model.

We compared mean rate of collection of seeds from heterogeneous distributions relative to that of homogeneously distributed seeds, by ants in the field and by our

models. As in Paz et al. (In review), we analyzed the results of our simulated foraging observations using repeated measures ANOVA. In our field work, we (Paz et al. in review) found a significant effect of source seed distribution on the ratio of seeds collected from piled distributions relative to random seeds, but we found no effect of forager number. Similarly, our analysis (Repeated measures ANOVA. $N = 27$ simulated foraging observations) of the behavior of the density-dependent recruitment model found a significant within-subjects effect of seed distribution ($p < 0.001$), but no between-subjects effect of colony size ($p > .10$), nor a within-subjects distribution X colony size interaction ($p > .10$). These relative rates are illustrated for the field data collected by Paz et al. (In review) (Fig. 6a) and simulated foraging by the density-dependent recruitment model (Fig. 6b). Values for these ratios are \log_2 -transformed, so that a value of zero indicates that seeds were collected at the same rate as randomly distributed seeds, while a value of one indicates that seeds were collected twice as fast.

We analyzed field and simulation data together, including both species and data source as factors (Repeated measures ANOVA. $N = 54$, 27 field and 27 simulated foraging observations.) We found that ratios for the density-dependent recruitment model are generally lower than those for ants in the field (Between-subjects effect of data source: $p = 0.017$), perhaps indicating that ants in the field have a keener ability to exploit piled foods using additional behaviors to those we have modeled here (e.g. site fidelity, ability to smell or otherwise sense and move to nearby seeds when searching, etc). However the relative treatment of piles of different sizes follows much the same pattern in the model and in the field (Within-subjects effects of seed distribution X species and seed distribution X data source, both $p > 0.10$; Fig. 6).

DISCUSSION

We found a satisfying fit between the behavior of our density-dependent recruitment model and the foraging behavior of *Pogonomyrmex* harvester ants in the field. The simple recruitment model we developed based on common models of ant recruitment in the literature (Detrain & Deneubourg 2008) produced a less satisfying fit, as a result of its inability to converge foraging effort on high-quality patches in environments where seeds exist in a mixture of homogeneous and heterogeneous sources. We found that when optimized by GA, the density-dependent recruitment model tended to evolve relatively selective trail-laying behavior, instead of the behavior of the simple recruitment model. This allowed the model to decrease the noise in the pheromone system that resulted from trails leading to low quality patches in the simple recruitment model, and allowed colonies to adaptively converge their foraging effort on high quality patches given any degree of heterogeneity in the distribution of food. The density-dependent recruitment model allowed the evolution of intense recruiting behavior in colonies of all sizes, and in all environments except those completely devoid of heterogeneous food sources. Density-dependent recruitment behavior allows ants to exploit heterogeneity in the distribution of food when they encounter it, even if they encounter it only rarely.

Contrary to the expectation of the simple recruitment model, in which ants leave pheromone trails each and every time they pick up food, we found that for all forager numbers and for all degrees of heterogeneity in the distribution of food, the density-dependent recruitment model evolved mean values for λ less than 1; colonies always evolved a condition-dependent trail-laying behavior. The lowest values of λ tended to evolve in environments with mixed heterogeneous and homogeneous food sources, where

there is greatest advantage in basing the decision to leave a pheromone trail on the presence of other nearby foods, in order to distinguish randomly scattered foods from piled foods. We found a robust effect of increasing food heterogeneity on the evolution of increasing recruitment behavior in the simple recruitment model. In the density-dependent recruitment models, recruitment behavior remained high until essentially all heterogeneity was removed from the food distribution.

Although the results of our GA runs with the simple recruitment model revealed the hypothesized positive effect of forager number on recruitment behavior, this result was supported less strongly in our density-dependent recruitment model. Like the simple recruitment model, the density-dependent recruitment model evolved increasing recruitment behavior with increasing forager number in fully homogeneous food distributions. It is in these completely homogeneous environments, however, where we least expect to see the evolution of recruitment behavior. Therefore, this result indicates colonies' use of the pheromone trails to direct foraging effort an optimal distance away from the nest, rather than toward a particular food source. This is similar to the use of trunk trails by foragers to travel some distance from the nest before beginning to search. It is likely, however, that individual ants have the capacity to walk a distance from the nest entrance before beginning to search, without relying on pheromone trails to do so. While it may be that ants will often drop off a pheromone trail before reaching its end in order to explore for additional, nearby food sources, we think it unlikely that pheromone trails would be used solely for directing foragers away from the nest, given that, for *Pogonomyrmex* and other ant taxa that produce trail pheromone with a specialized gland (Hölldobler et al. 2004), producing pheromone presumably has some physiological cost.

In our models, we forced ants to follow pheromone trails from the nest, or else to begin searching immediately at the nest entrance, in order to force optimization on the use of the pheromone trails. The evolution of increased recruitment behavior with forager number in environments with completely homogeneously distributed foods may be an artifact of this aspect of our model. There may be other reasons that ants will use trunk trails to travel a distance from the nest before beginning to forage, e.g. avoidance of predators or management of conflict with neighboring nests; but we suspect it is unlikely that ants in nature use pheromone trails solely for the purpose of directing foraging effort away from the nest.

With the introduction of any piled foods to the environment, we found that the density-dependent recruitment model evolved relatively intense recruitment behavior even in the smallest colonies. Given some degree of heterogeneity in the environment, colonies that can exploit this heterogeneity when they encounter it are at a selective advantage over those that do not, even in species with small colonies that encounter piled foods relatively rarely. The density-dependent recruitment behavior allows colonies to exploit heterogeneity when and where they find it, even if they encounter piles of food infrequently, as for the small colonies modeled here (note the great variance in foraging success for the ten-ant colony in Fig. 2a).

We observed that the behavior of the simple recruitment model was similar to the behavior of the density-dependent recruitment model when evolved on fully heterogeneous food distributions. This is because in these environments, all available food is found in dense patches. Therefore if an ant finds a piece of food, that piece of food is necessarily coming from a dense patch and information about that location is of as

much value as for that of food found anywhere else. In these environments both models tend to produce well-defined pheromone trails and converge their foraging effort on nearby piles, as predicted by common models of ant recruitment and collective decision-making (Detrain & Deneubourg 2008). In addition, we found that the density-dependent recruitment model evolved significantly more selective use of the pheromones on fully heterogeneous food distributions than in fully homogeneous distributions. More selective trail-laying behavior allows ants to be sensitive to the depletion of dense piles, and allows the colony to more rapidly and adaptively switch to a new pile as the remaining seeds become fewer and harder to find. Wilson (1961) described the way in which the number of *Solenopsis* workers at a food source may be regulated by unsuccessful foragers returning to the nest without laying a trail. Similarly, Mailleux et al. (2004) found that *Lasius* workers require a threshold volume of nectar in their crops in order to lay a trail. This negative feedback has a lag of several minutes, however, resulting in an “overshoot” of the optimal number of workers arriving at a site (Wilson 1961). On the other hand, if even successful foragers are able to return from a dwindling food source without laying a trail, as we observed here, this “overshoot” may be minimized. Thus, even for species whose foods occur only in patches too large to be collected by a single forager, e.g. army ants specializing on raiding other social insect colonies (Franks et al. 1991, Solé et al. 2000) it may be adaptive to make relatively selective use of pheromone trails. Given that producing pheromone may bear some physiological cost – a cost we did not impose on the simulated colonies in our GA runs – we expect that for ants in the field, there is even greater advantage in using pheromone trails selectively.

When the simple recruitment model was evolved on increasingly homogeneous food distributions, recruitment behavior steadily fell off. We found that the addition of homogeneously distributed foods prevented the convergence of foraging effort on high quality patches. This was a surprising outcome, given the assumption that colonies will converge on high quality patches because of the increased ease of finding food in those patches (Detrain & Deneubourg 2008). We observed that pheromone trails being drawn back to the nest by ants that picked up homogeneously distributed foods created so much noise in the system that the colonies were unable to converge (see Fig. 1a); many ants that set out from the nest followed trails that led back to a site where no food was to be found, and therefore did not arrive in the high quality patches.

Instead of evolving less intense recruitment behavior with an increasing proportion of homogeneously distributed foods in the environment, the density-dependent recruitment models evolved increasingly selective use of the pheromones (see Fig. 1b). By becoming increasingly selective about drawing a pheromone trail on the return trip to the nest, the information value of the pheromone trails remained high enough that colonies continued to recruit heavily even when as little as one quarter of the available food was distributed in piles.

The binary decision making process surrounding the laying of a pheromone trail is analogous to the decision-making process by scouts of the species *Temnothorax albipennis* in nest-site selection. Scouts of this species evaluate potential nest sites and selectively recruit nestmates to preferred sites by tandem running, and a variety of nest-site properties relevant to this decision have been identified (Visscher 2007). Presumably each desired property is factored into a decision-making process such that each

contributes to the probability that a scout will begin recruiting to the site. Similarly, *Pogonomyrmex* foragers may incorporate a variety of additional factors into the decision to lay a pheromone trail, including, for example, the presence of other ants which may compete for a food source if it is not collected quickly. Over time, other foragers making the same evaluation cause reinforcement of paths to high value patches and convergence on the optimal colony-level behavior, without distraction by the noise of paths leading to sites of little or no value. This model of recruitment differs from that described by Beckers et al. (1993) for the black garden ant *Lasius niger*, in which workers modulate the weight of pheromone trails according to the concentration of sugar solutions they discover. Compared to *Lasius niger* which forages for nectars that may vary substantially in their concentration and value, there may be less variation in the quality and value of seeds returned to the nest by *Pogonomyrmex* foragers. Harvester ants select seeds within a range of sizes that are easy enough to handle given forager size and morphology of a species (Hölldobler 1976); within this range there may be less variation in nutrient value than that encountered by *Lasius niger* foraging on nectar. Therefore for *Pogonomyrmex* foragers, the qualities of individual seeds discovered may be less important to the colonies' foraging success than the presence of other nearby seeds, and this may be an important determinant of the optimal recruitment behavior in these taxa.

The decision-making process modeled by the density-dependent recruitment model may be valuable in the field of ACO's. We found that the simple recruitment model worked best when all available food was found in dense piles, and that its performance degraded with the addition of randomly distributed foods. This narrow set of favorable conditions (relative to the range of foraging ecologies of ants in the field) is

analogous to static ACO problem domains where it is known from the start which routes need to be optimized, e.g. in routing circuits, where a number of known connections must be routed (Arora & Moses, 2009). A decision-making process by individual ants in the laying of pheromone trails may improve ACO performance in dynamic problems in which the solutions to be routed are not known from the start, but must be determined during the process of optimization.

In many ACO's, agents lay pheromone in amounts proportional to the global quality of the solution they have found (Bonabeau et al. 2000). In contrast, ants in our density-dependent recruitment model make a binary decision based on local information, and lay pheromones in a constant amount. Such an approach may facilitate the use of ACO in problems where the global quality of a particular solution cannot be known, but must be estimated by sampling local information. A variety of kinds of local information can be incorporated into the binary decision process. The system can then converge on an optimal solution by allowing recruited ants to evaluate the site and reinforce pheromone trails based on the same decision. Such a decision-making process, and other aspects of the behavior of an ACO, can be optimized by GA for particular problems, as we have done here.

Johnson (2000) categorizes the foraging behavior of *Pogonomyrmex* species, ranging from solitary foraging to recruitment using persistent trunk trails. Our results and those of Paz et al. (In review) suggest that the individual behavioral components of recruitment may not differ so starkly and categorically across species. Rather, the tendency for harvester ant species to engage primarily in solitary foraging vs. trunk trail

recruitment may depend on the likelihood from one day to the next that a small vs. a large colony finds a high-density patch of seeds somewhere on its territory.

We wondered if differences in the ability to recruit to high quality food patches might cause the niche partitioning that allows the co-occurrence of the three sympatric *Pogonomyrmex* species examined in Paz et al. (In review). Our results suggest such a differential ability to recruit is not the answer to that question. Species with larger colony size may dominate high quality patches, however, by recruiting large numbers of foragers to these sites and overwhelming and excluding smaller colonies foraging there, while these smaller colonies are then forced to forage on randomly or less densely distributed foods. This suggests further research into interspecific competitive interactions may be fruitful in understanding how heterogeneity in the distribution of food causes niche partitioning among these ant species.

References

- Arora, T., and Moses, M. 2009. Using ant colony optimization for routing in VLSI chips. In *Proceedings of the 1st International Conference on Bio-Inspired Computational Methods Used for Difficult Problems Solving: Development of Intelligent and Complex Systems. AIP Conference Proceedings*, pages 145-156, 2009.
- Beckers, R. et al. 1989. Colony size, communication, and ant foraging strategy. – *Psyche: A Journal of Entomology* 96:239-256.
- Beckers, R. et al. 1990. Collective decision making through food recruitment. – *Insectes Soc.* 37: 258-267.
- Beckers, R. et al. 1993. Modulation of trail laying in the ant *Lasius niger* (Hymenoptera: Formicidae) and its role in the collective selection of a food source. – *J. Insect Behav.* 6: 751-759.
- Beverly, B. D. et al. 2009. How site fidelity leads to individual differences in the foraging activity of harvester ants. – *Behav. Ecol.* 20: 633-638.
- Bonabeau, E. et al. 2000. Inspiration for optimization from social insect behavior. – *Nature* 406: 39-42, 2000.
- Buchkremer, E. M. and Reinhold, K. 2008. Sector fidelity—an advantageous foraging behavior resulting from a heuristic search strategy. – *Behav. Ecol.* 19: 984-989.
- Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. – *Theor. Popul. Biol.* 9:129-136.
- Crist, T. O. and McMahon, J. A. 1991. Individual foraging components of harvester ants: movement patterns and seed patch fidelity. – *Insectes Soc.* 38:379-396.

- Crist, T.O. and Haefner, J. W. 1994. Spatial model of movement and foraging in harvester ants (*Pogonomyrmex*) (II): The roles of environment and seed dispersion. – J. Theor. Biol. 166: 315-323.
- Detrain, C. and Deneubourg, J. L. 2008. Collective decision-making and foraging patterns in ants and honeybees. – Adv. Insect Physiol. 35: 123-173.
- Fewell, J. H. 1988. Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. – Behav. Ecol. Sociobiol. 22: 401-408.
- Forrest, S. 1996. Genetic algorithms. – ACM Comput. Surv. 28: 77-80.
- Franks, N. R. et al. 1991. The blind leading the blind in army ant raid patterns: Testing a model of self-organization (Hymenoptera: Formicidae). – J. Insect Behav. 4: 583-607.
- Haefner, J. W. and Crist, T. O. 1994. Spatial model of movement and foraging in harvester ants (*Pogonomyrmex*) (I): The roles of memory and communication. – J. Theor. Biol. 166: 299-313.
- Hölldobler, B. et al. 2004. Dufour gland secretion in the harvester ant genus *Pogonomyrmex*. – Chemoecology 14: 101-106.
- Gordon, D. M. 1993. The spatial scale of seed collection by harvester ants. – Oecologia 95: 479-487.
- Hamilton, W. D. et al. 1990. Sexual reproduction as an adaptation to resist parasites (A review). – Proc. Nat. Acad. Sci. U.S.A. 87: 3566-3573.
- Hölldobler, B. 1976. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. – Behav. Ecol. Sociobiol. 1: 3-44.

- Johnson, R. A. 2000. Seed-harvester ants (Hymenoptera formicidae) of North America: An overview of ecology and biogeography. – *Sociobiol.* 36: 83-122.
- Mailleux, A.C., Detrain, C., and Deneubourg, J.L. 2005. Triggering and persistence of trail-laying in foragers of the ant *Lasius niger*. – *J. Insect Physiol.* 51: 297-304.
- Miller, B. L. and Goldberg, D. E. 1995. Genetic algorithms, tournament selection, and the effects of noise. – *Complex Systems* 9: 193-212.
- Mitchell, M. 1998. *An Introduction to Genetic Algorithms*. – MIT Press.
- Moses, M. 2005. *Metabolic Scaling in Individuals and Societies*. – Doctoral dissertation, The Univ. of New Mexico.
- Mull, J.F., and J.A. MacMahon. 1997. Spatial variation in rates of seed removal by harvester ants (*Pogonomyrmex occidentalis*) in a shrub-steppe ecosystem. *The American Midland Naturalist* 138: 1-13.
- Oster, G. and Wilson, E. 1979. *Caste and ecology in the social insects*. – Princeton Univ. Press.
- Paz, T. et al. Quantifying the effect of seed dispersion and colony size on foraging rates in three species of desert seed harvesting ants. In preparation.
- Reichmann, O. J. 1984. Spatial and temporal variation of seed distributions in Sonoran Desert soils. – *J. Biogeogr.* 11: 1-11.
- Ruxton, G. D. and Beauchamp, G. 2008. The application of genetic algorithms in behavioural ecology, illustrated with a model of anti-predator vigilance. – *J. Theor. Biol.* 250: 435-448.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. – *Science* 185:

27-39.

Solé , R. V. et al. 2000. Pattern formation and optimization in army ant raids. – *Artif. Life* 6:219-226.

Timmis, J. et al. 2006. Going back to our roots: Second generation biocomputing. – *Int. J. on Unconventional Comput.* 2: 349-382.

Trivers, R. L. and Hare, H. 1967. Haplodiploidy and the evolution of the social insects. – *Science* 191: 249-263.

Visscher, P. K. 2007. Group decision making in nest-site selection among social insects. *Annu. Rev. Entomol.* 52: 255-75.

Ward, P. and Zahavi, A. 1973. The importance of certain assemblages of birds as “information-centres” for food-finding. – *Ibis* 115: 517-534.

Weier, J. A. And Feener, D. H. 1995. Foraging in the seed-harvesting ant genus *Pogonomyrmex*: are energy costs important? – *Behavioral Ecology and Sociobiology* 36: 291-300.

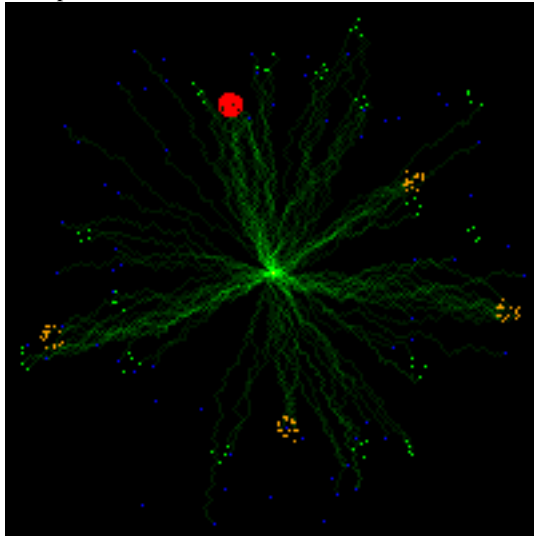
Wiens, J. A. 1976. Population responses to patchy environments. – *Annu. Rev. Ecol. Syst.* 7: 81-120.

Wilson, E. O. 1962. Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith) 1. The organization of mass foraging. – *Anim. Behav.* 10: 134-147.

Wilson, E. O. and Hölldobler, B. 1991. *The Ants*. – Belknap Press.

Parameter	Function
α	At model initialization, determines the probability each time step that an ant walking from the nest will stop walking and begin to search. For lower values, ants tend to walk farther from nest before beginning to search.
ω	For searching ants moving in a correlated random walk, determines the baseline degree of deviation in the direction an ant will move from one time step to the next. For low values, ants turn less, move in a straighter line, and cover more distance; for high values, ants movements are more random, they turn more, search more thoroughly in a local area, but cover less distance.
γ	For searching ants, determines the additional degree of deviation in turning early on in an ant's search, allows for more thorough, local searching at the end of a pheromone trail.
δ	For searching ants, this exponent term determines how quickly turning behavior approaches the baseline turning behavior determined by ω as time spent searching increases.
ε	For ants following a pheromone trail, determines the probability each time step that an ant will abandon the trail and begin searching before reaching its end. For lower values, ants tend to follow pheromone trails greater distances, and or more likely to follow trails to their end, where food was previously discovered.
η	Determines the rate at which pheromones evaporate. Higher values produce faster exponential decay of the pheromones from the grid.
λ	Determines the baseline probability that ants will leave a pheromone trail each time they pick up a piece of food. For values greater than or equal to one, ants leave pheromone trails each time they pick up food. Lower values correspond to decreased probability. For values below zero, the presence of other nearby food is required for ants to leave a pheromone trail. Density-dependent recruitment model only.
μ	Determines ants' sensitivity to the presence of other food when making a decision to leave a pheromone trail or not. With higher values, the presence of each additional piece of food in the neighborhood increases the probability of leaving a pheromone trail less. Density-dependent recruitment model only.

1a: Simple Recruitment Model



1b: Density-Dependent Recruitment Model

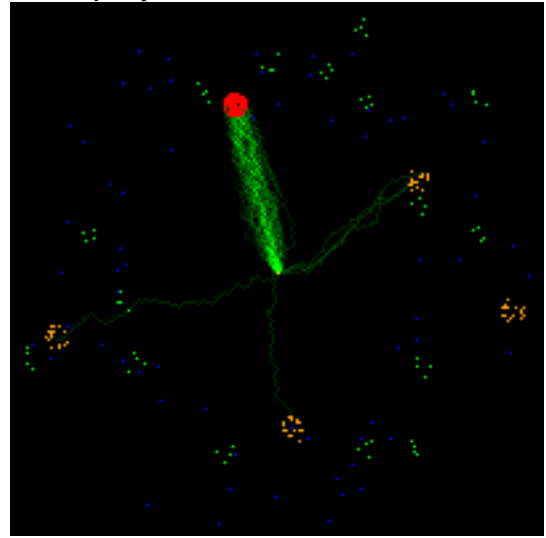
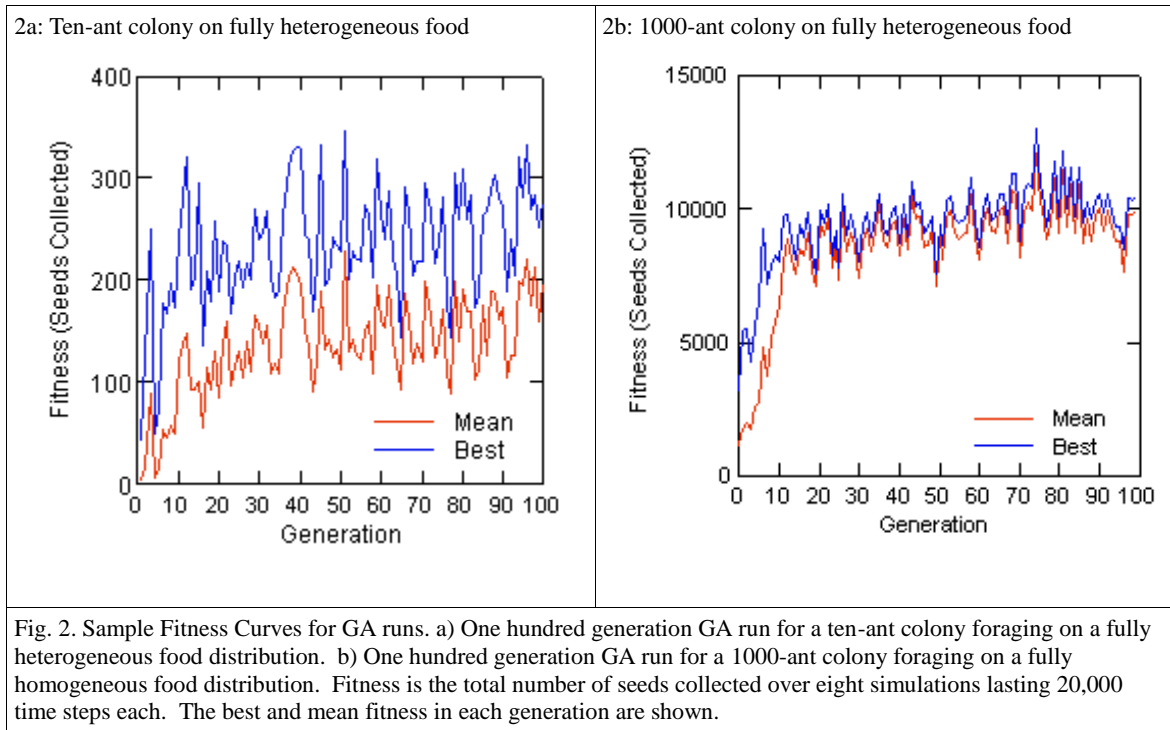
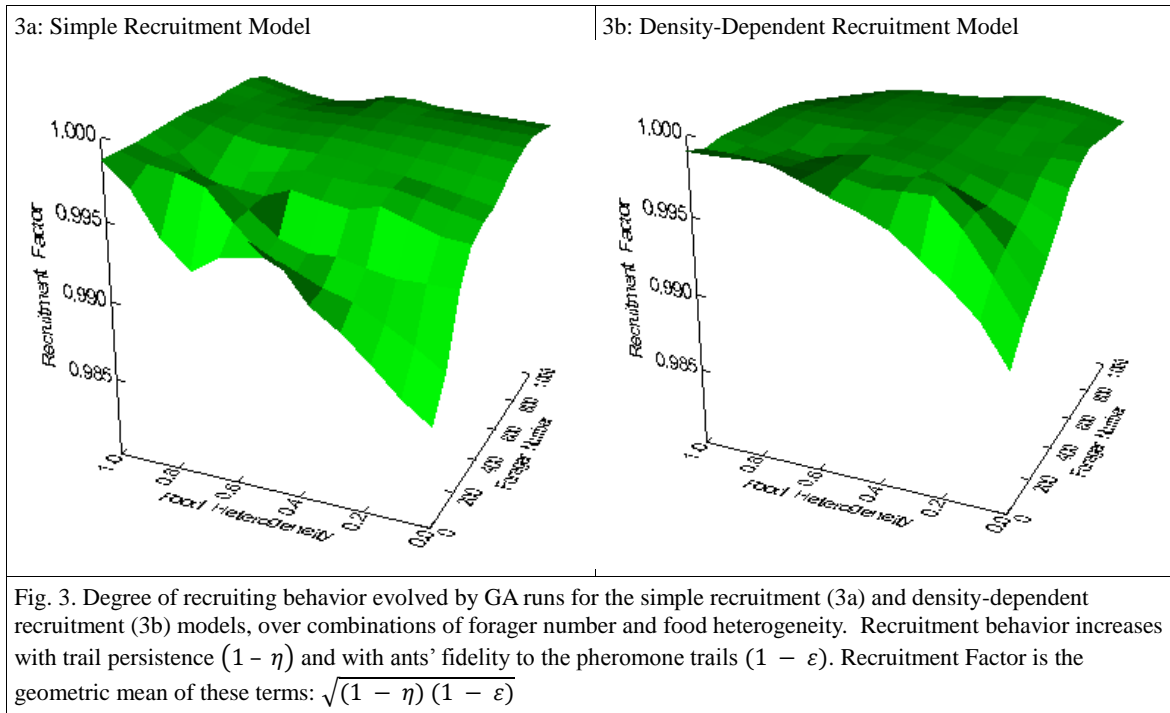


Fig. 1. 1a) Simple recruitment model running a simulated foraging observation. 1b) Density-dependent recruitment model running a simulated foraging observation on an identical bait distribution as in 1a. Pheromone trails radiate from the centrally located nest, overlaid on top of baits as they appeared at the beginning of the simulation before foraging began. For the sake of clarity, ants are not displayed, and bait piles have smaller numbers of seeds than reported in text.





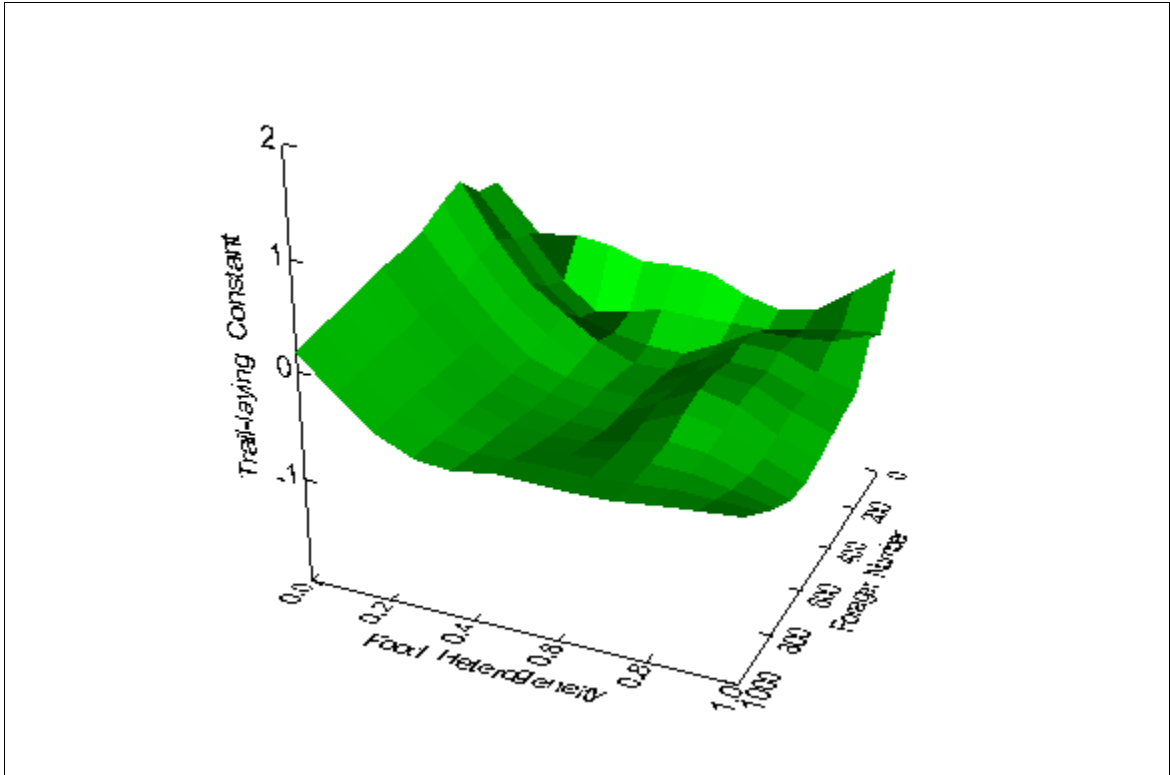


Fig. 4. The relationship between colony size, food heterogeneity, and λ , the baseline probability that ants will leave a pheromone trail on the return trip to the nest with food. Greater values for λ indicate greater probability of leaving a pheromone trail each time a piece of food is picked up. Note that this figure is rotated to allow a clearer view of the surface, such that the X and Y axes are reversed relative to Fig. 3.

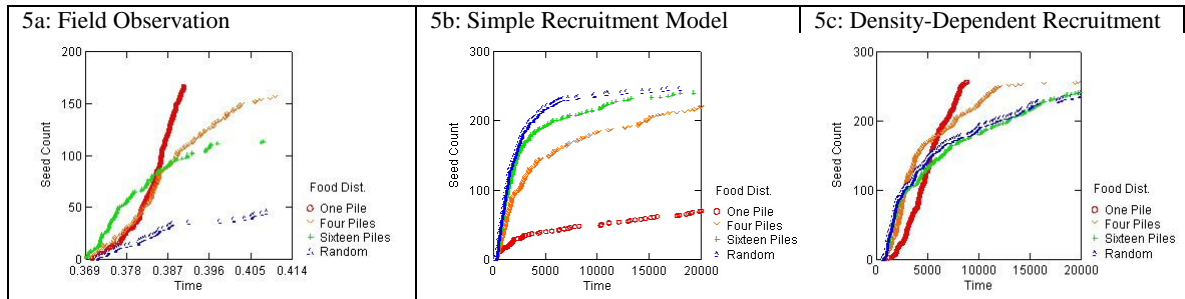


Fig. 5. Foraging observations of ants given seed baits in four distributions. Fig. 5a represents a field observation of a *P. rugosus* colony taken from Paz et al. [10]. 5b and 5c represent a simulated foraging observation of the simple recruitment model and density-dependent recruitment models, each parameterized with values optimized for a 50% homogeneous and 50% heterogeneous food distribution. For Fig. 5a, time is fraction of a day. For Figs. 5b and 5c, time is model time steps.

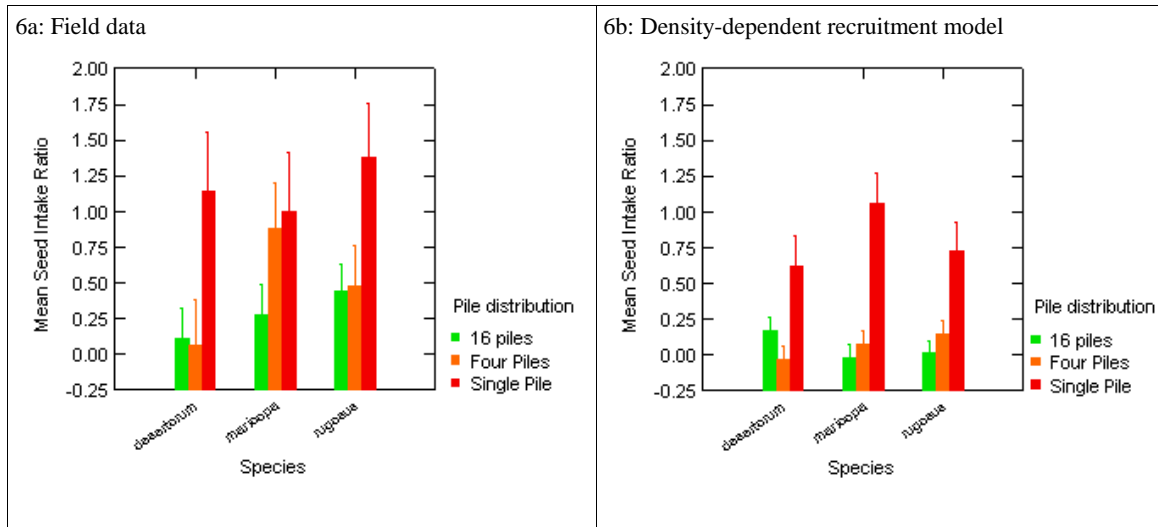


Fig. 6. Ratio of the rate of collection of seeds from piled distributions relative to randomly placed seeds. Fig. 6a illustrates the results of field observations by Paz et al. (In review) of *P. desertorum*, *P. maricopa*, and *P. rugosus*. Fig. 6b illustrates the results of simulated observations of the density-dependent recruit model, with colonies with comparable numbers of foragers to *P. desertorum*, *P. maricopa*, and *P. rugosus* colonies. These simulated colonies were parameterized by GA runs for a 50% homogeneous and 50% heterogeneous food distribution. Bars represent least squares means obtained by repeated-measures ANOVA. Error bars represent standard errors.