Volatility and spatial distribution of resources determine ant foraging strategies

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Abstract

Social insect colonies have evolved collective foraging strategies that consist of many autonomous individuals operating without centralized control. The ant colony optimization (ACO) family of algorithms mimics this behavior to approximate solutions to computationally difficult problems. ACO algorithms focus on pheromone recruitment, which is only one of several known biological foraging strategies. Here, we use a spatial agent-based model to simulate three foraging strategies: pheromone recruitment, nest recruitment, and random search. We compare their performance across two environmental dimensions: spatial distribution of food resources and resource volatility. We find that pheromone recruitment performs only marginally better than the simpler nest recruitment strategy in most environments. Further, both strategies become progressively less efficient as resource dispersion and volatility increase. In the extreme, with highly dispersed or volatile resources, the simplest strategy of all, random search, outperforms the other two. Our results suggest that in many environments, pheromone-based strategies may not be required and that simpler methods like random search or nest recruitment may be sufficient, both for biological ants and computational methods.

Introduction

Social insects are notable for their ability to harness large populations of simple individuals without any apparent centralized control to solve complex problems, such as finding food and building nests (Hölldobler and Wilson, 1990). Computer scientists have long been interested in ant foraging behaviors, particularly as inspiration for *ant colony optimization* (ACO) search and optimization algorithms (Dorigo et al., 2006). These algorithms are based on one aspect of ant foraging called *stigmergy* (Theraulaz and Bonabeau, 1999). In this context, stigmergy refers to ants that alter their environment by depositing chemical markers called pheromones to indicate promising search directions. As they accumulate, the chemical markers form a trail leading from the ants' nest to a food source. ACO algorithms have been applied to many computational problems, including network routing (Di Caro and Dorigo, 1998), the Traveling Salesman Problem (Dorigo and Gambardella, 1997), and task scheduling (Merkle et al., 2002).

However, recent work has shown that chemical recruitment strategies in isolation may be suboptimal in the wrong environment. Evison et al. (2008) show that visual landmarks and pheromone contribute equally to an ant's ability to locate a previously encountered food source, and that the two may have a complementary function. Pheromone trails may also lead to suboptimal solutions, directing ants (or algorithms) to lower-quality resources before a richer location can be detected (Beckers et al., 1990; Robinson et al., 2008), although these traps may be avoided using repellent pheromone (Czaczkes, 2014). The drawbacks to chemical recruitment are not limited to ant foraging, nor to the problem of reinforcing the wrong path in a stable environment. Previous work has shown that T cells that rely on chemical gradients to locate sources of infection can become stuck when the infection spreads faster than the signal can diffuse (Levin et al., unpublished). The drawbacks of chemical recruitment strategies suggests that successful use of ACO requires an understanding of the appropriate domains where these algorithms are applied, and which other foraging strategies might be leveraged in different domains. There is relatively little work which investigates other ant foraging techniques or classifies which environments are most appropriate for which foraging strategies (Pratt, 2008; Schmolke, 2009; Pinter-Wollman et al., 2012).

There are many different foraging strategies employed by different ant species (Lanan, 2014). The desert ant, *Aphenogaster cockerelli*, forages individually with site fidelity (Sanders and Gordon, 2002). Site fidelity may be a more effective foraging strategy than pheromone recruitment in some contexts (Letendre and Moses, 2013). The acorn ant, *Temnothorax albipennis*, uses tandem running where informed ants that have located a food source lead naive ants to the food, without using any detectable pheromone trail (Franks and Richardson, 2006). Ants such as *Formica cinerea* establish long-term trunk trails, where massive numbers of ants follow one another to stable sources of food (Markó and Czechowski, 2012). The predatory *Pheidologeton diversus* raid smaller ant species and termites when colonies are discovered (Moffett, 1988).

In this paper, we explore the hypothesis that the best foraging strategy is determined in large part by the environ-

ment in which the ants live. We focus on how food resources are distributed and their temporal variability, which we call *volatility*. This hypothesis is supported by the observation that animal species use different strategies in different environments (Kacelnik and Bateson, 1996).

We investigate this hypothesis with an agent-based model of ant foraging. We model three different ant-based foraging strategies, which subsume most strategies observed in nature: solitary random walk, nest recruitment, and pheromone recruitment. We quantify the efficacy of each strategy across two environmental dimensions, the spatial layout of resources and the volatility of resources, and we evaluate the ability of each strategy to adapt to different environments.

We find that both pheromone and nest recruitment perform best in clustered stable environments, and their efficiency declines as food dispersion and volatility increase. To be effective, the recruitment strategies each require that the ants complete at least two round trips to a location before the food disappears (volatility). Because random search has no memory, volatility does not strongly affect its performance, and it performs well in environments where food is highly dispersed.

Recruitment strategies that have been optimized for one environment can be detrimental in other environments. For example, when we optimized the (nest and pheromone) recruitment strategies for stable environments, they performed poorly when volatility was increased, and in the extreme worse than random search. However, in environments with upredictable volatility, nest and pheromone recruitment strategies outperform random search, suggesting that recruitment is a powerful mechanism even in highly randomized environments. Finally, in environments where resource locations are sufficiently predictable, pheromone-based strategies are efficient, similar to Flanagan et al. (2011). In most cases, however, nest recruitment performs similarly to pheromones and requires a simpler mechanism (local interaction).

In addition to specific insights about ant foraging strategies, our results suggest that new approaches could be adapted into ACO algorithms. Since phereomone-based recruitment is nontrivial to implement in a fully distributed artificial system, nest recruitment could be an attractive alternative. Moreover, the modeling approach used here could be used to classify more generally which distributed search strategies perform best in which environments.

Model Description

We developed an agent-based model to study the effectiveness of various foraging strategies in different environments (Fig. 1), focusing on the spatial and temporal distribution of food resources on a flat surface. Our model extends the central-place foraging algorithm (CPFA) and swarm robotics platform studied in Hecker and Moses (2015), by including volatile resources and new foraging strategies.
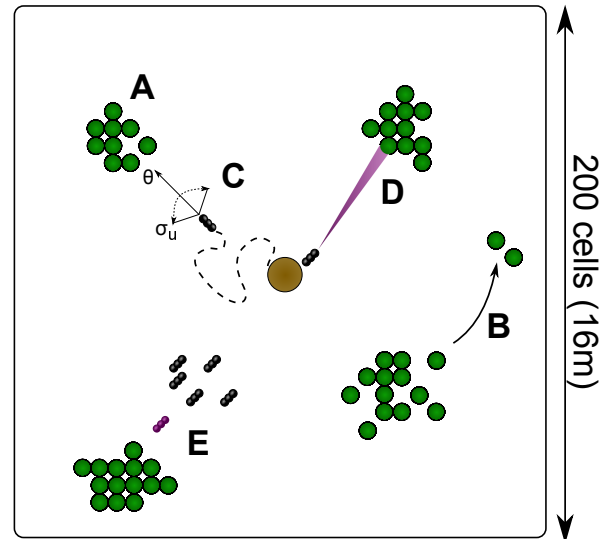

Figure 1: **Model Conceptualization.** The model is initialized on a square grid with the nest in the center. **A)** Food is randomly placed in patches a minimum distance from the nest. **B)** Food from a single patch moves at a constant rate to a new patch (volatility). **C)** Ants perform a random walk from the nest. An ant's angular trajectory θ is varied at each time step by choosing from a normal distribution: $N(\theta, \sigma_u)$. **D)** An ant lays a pheromone trail (decays exponentially) to a specific location if it detects enough food in its vicinity. **E)** Ants returning from a successful foraging search recruit ants resting at the nest.

The model consists of a two-dimensional grid with discrete food units (analogous to seeds) placed on the grid before the run begins. There is a single nest, where ants congregate, leave to search for food, return with food if successful, and possibly recruit other ants to follow them to a food source. Food sources can be arranged in different distributions (e.g., grouped together in a small number of clumps or dispersed randomly across the environment). Volatility is modeled as movement—food moves at a rate parameterized by the model. In the experiments for this paper, we varied the number of clustered food piles and the rate at which piles move, while holding the total amount of food constant (Fig. 1 A and B).

A recent paper by Lanan (2014) catalogs certain ant foraging strategies used by monodomous (single nest) ant species: random search, site fidelity, tandem running, pheromone recruitment, nest recruitment, and trunk trails. Two of these strategies, tandem running and trunk trails, closely resemble other strategies: nest recruitment is similar to tandem running and pheromone recruitment is similar to trunk trails. Therefore, we model three distinct foraging strategies: *random search*, *pheromone recruitment*, and *nest recruitment* (Fig 1 C-E), where each strategy is designed to mimic for-
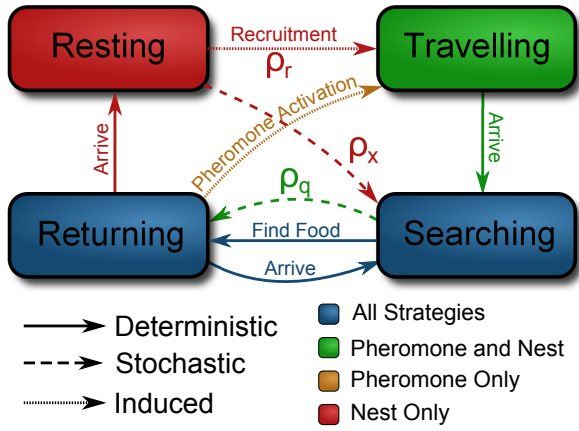
Figure 2: **Ant Foraging States.** Ants are initialized at the nest in either the `resting` (with nest recruitment) or `searching` state. Ants transition between behaviors based upon cues from the environment, random chance, and stimulation by other ants or pheromone.

aging strategies used by real ants (Moffett, 1988; Hölldobler and Wilson, 1990; Sanders and Gordon, 2002; Markó and Czechowski, 2012). We enable site fidelity in both recruitment strategies based on field observations.

- **Random Search:** Individual ants leave the nest all at once and perform a correlated random walk through the two-dimensional space. Ants continue searching until they encounter food. Ants that encounter food pick it up, return to the nest, and begin a new search. The correlated random walk works by choosing a new trajectory for each ant from a normal distribution $N(\theta, \sigma_u)$, centered on the ant's current trajectory θ. Ants using the random search strategy have no memory and perform no recruitment.

- **Pheromone Recruitment** is implemented following the central-place foraging algorithm (CPFA) detailed in Hecker and Moses (2015). Ants leave the nest and search randomly as described above. Ants may give up searching at any time with a probability ρ_q and return to the nest. However, if an ant finds food at any point it picks it up and immediately checks the neighboring 8 grid cells for more. Next, it decides to reinforce the location with probability $P(k; \lambda_p)$, where P represents the cumulative Poisson distribution and k is the amount of food found in the immediate neighborhood. The ant may also use site fidelity to return to the previously visited location with probability $P(k; \lambda_f)$. It then returns to the nest, creating the trail upon its arrival if $P(k; \lambda_p) > U(0, 1)$; the trail decays at a rate of σ_p. Subsequent ants may follow this trail to the same location before the trail evaporates. Recruited ants perform an informed correlated random walk upon arrival and may also lay a pheromone trail back to the nest.

Abbr.	Name	Distribution
σ_u	Uninformed Search Correlation	$U(0, 2\pi)$
δ_i	Informed Search Decay Rate	$E(5)$
ρ_q	Search Quit Probability	$E(30)$
λ_f	Site Fidelity Rate	$U(0, 20)$
λ_p	Reinforcement Rate	$U(0, 20)$
δ_p	Pheromone Decay Rate	$E(10)$
ρ_r	Recruit Probability	$E(10)$
ρ_x	Leave Nest Probability	$E(100)$

Table 1: Ant parameters tuned by the GA. Parameters were initialized randomly using either a uniform distribution (U) or an exponential distribution (E). σ_u and δ_i define turning parameters. ρ_q, ρ_x, and ρ_r are probability rates. λ_f and λ_p are Poisson probability parameters. δ_p is the pheromone decay rate. Parameters extend the model described in Hecker and Moses (2015). As in Figure 2: blue, σ_u, is used in by all three strategies, green parameters are used by the two recruitment strategies, yellow, δ_p, is used by pheromone only, and red parameters are used by nest recruitment only.

- **Nest Recruitment:** Ants probabilistically leave the nest and use random search to look for food. Ants that are not actively searching remain in the nest. As in pheromone recruitment, ants give up and return to the nest with probability ρ_q, and ants that find food pick up the food, survey the area, and if they find food above the threshold, they return directly to the nest and recruit more ants (otherwise they return to the nest and being a new solitary search). The number of ants recruited on a single return to the nest is a fraction of the ants currently in the nest, probabilistic determined by ρ_r. The original ant and the newly recruited ants then return directly to the previous location and perform an informed correlated random walk.

An informed random walk behaves as the uninformed random walk, but with a turning parameter of 4π that decays at a rate δ_i until it reaches σ_u.

These three strategies are well known in the ant literature, but the details can vary among individual species, and in some cases the exact parameters are simply unknown or difficult to measure accurately, such as the nest recruitment rate and the pheromone decay rate. Therefore we use a genetic algorithm (GA) to select each parameter for each environment. The GA-evolved parameters can significantly alter the outcome of a specific strategy. For example, in the pheromone recruitment strategy, if the decay rate of the pheromone is very high, it will dissipate before it is able to be utilized by other ants. This effectively reduces the pheromone recruitment strategy to random search.

Ants begin each simulation in the nest at the center of the grid. Ant behavior is governed by the eight parameters listed in Table 1. Behavior transitions among four possible states: `resting`, `traveling`, `searching`, and `returning` (Fig. 2) at rates determined by the evolved parameters.

To study the effects of different environments on optimal foraging strategies, we model two environmental dimensions: the spatial distribution of food and the volatility of food, where food is a discrete unit, analogous to a seed.

• **Spatial Distribution:** Food is placed randomly in space at one of one, four, or 16 piles, or distributed uniformly (Fig. 1A). These values were chosen to correspond to food distributions in known ant habitats (Hölldobler and Wilson, 1990; Sanders and Gordon, 2002; Markó and Czechowski, 2012). Piles were never placed within 20 grid cells of the nest.

• **Food Volatility:** Food piles are moved at a specified rate to new locations in the grid to simulate growth and decay of resources (Fig. 1B). The volatility rate corresponds to the number of times an ant can make a round trip from the nest to a food pile before the pile has moved. Food volatility was set to be either stable (no volatility), or it was moved at a rate of ten, five or 2.5 round trips. Rates of less than 2.5 round trips eliminated the value of recruitment, while rates above 10 round trips did not show behavioral difference from the stable scenario.

Experimental Design

We use the model to assess the performance of three different strategies across 16 different environments, using a GA to find good parameter values for each strategy/environment pair. This process mimics natural selection, which occurred over evolutionary time scales as each ant species evolved. Having tuned each strategy for a specific environment, we then compare their performance. Each run of the simulation evaluates a single colony of 64 ants foraging on a 200×200 two-dimensional grid over one simulated hour. Each cell in the grid represents an 8×8 cm patch, so the model simulates a 16×16 m area of flat land. The number of ants, spatial extent of the search, and its duration were each based on small desert seed-harvester ant colonies (Flanagan et al., 2012). Selected runs using 320 ants showed results consistent with the main model (data not shown). The simulated ants move through the grid one cell per time-step (Moore neighborhood), foraging for 1,280 food resources (*seeds*) where each cell can contain at most one seed.

We use a generational GA with population size of 25, runs of 50 generations, tournament selection (tournament size of 2), uniform crossover, 10% Gaussian mutation, and elitism, where the single best individual in each generation is retained unchanged. Full details of the algorithm are given in Hecker and Moses (2015). Each individual represents a single ant colony, and individuals are initialized using parameter values drawn from the distribution functions shown in Table 1, column 3. Because the strategies are non-deterministic, each individual's fitness is determined by summing up the number of seeds collected over 8 independent runs of the simulation, where each run lasts for 7,200
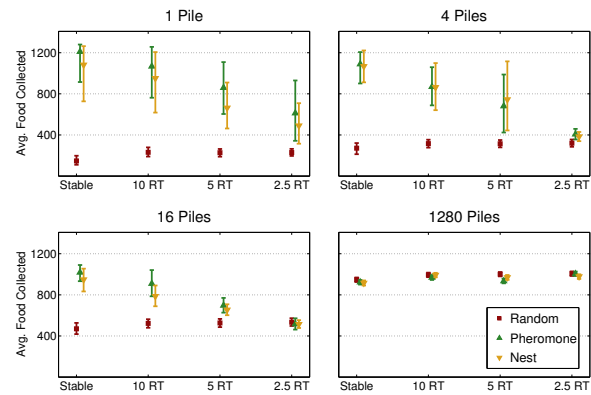

Figure 3: **Search Performance vs. Volatility and Spatial Distribution.** Random, pheromone, and nest recruitment evaluated over 16 environments (four pile counts by four volatility rates). Each bar represents the 95% credible interval resulting from 1,000 runs of the model after an optimal parameter set has been evolved for the specific environment-strategy pair. The two recruitment strategies show decreased performance both as the number of food piles increase and as the food volatility rate increases. The decrease in variance as pile count and volatility increases represents the dominant effect of finding and exploiting clustered piles quickly in the low pile, low volatility environments.

time steps. At the end of each GA run, the genomes of the final population of 25 are combined by averaging each gene's values. This combined genome constitutes the resulting colony of the evolutionary run. Finally, 1,000 additional simulations are run with these strategy parameters to assess variance of foraging performance for the strategy/environment pair.

Experimental Results

An optimal parameter set was evolved for each combination of strategy, food distribution, and food volatility. Because the model is stochastic, 1,000 runs of the model were then performed with these fixed parameters to generate 95% credible intervals [1] for each experiment (Fig. 3). Pheromone and nest recruitment perform well when food is stable and arranged in large piles. Random search performs the best in environments with highly dispersed food. This is to be expected as pheromone and nest recruitment leverage information about their environment to improve performance; increasing dispersal and volatility decreases the amount of information gained by finding food. In a majority of cases, nest recruitment performs as well as, or only slightly worse than pheromone recruitment.

The performance of all strategies equalizes when food is uniformly distributed in space (1,280 'piles' of single seeds).

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[1] Contains inner 95% of model outcomes.

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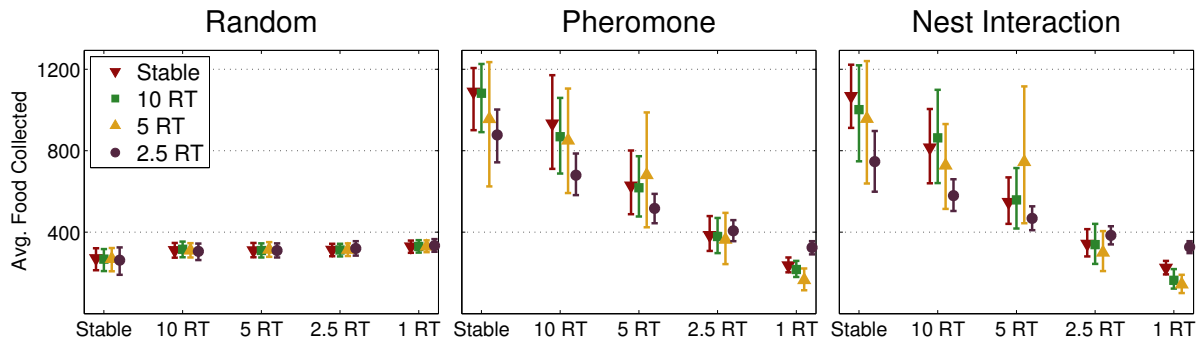
Figure 4: **Fixed Parameters Applied to Other Volatility Rates.** Four pile parameter sets evolved for a specific volatility rate applied to four pile environments with different volatility rates. The consistency of random search illustrates its independence from volatility rate. Pheromone strategy shows little difference between parameter sets evolved for different volatility rates, suggesting a level of robustness. Conversely, nest interaction shows increased performance by strategies evolved for the specific environment, suggesting environment specialization.

In this scenario, the collection of one food item gives no information regarding the location of any other, and the recruitment strategies cannot out-perform random search (as predicted by Flanagan et al. (2011)). Because each strategy uses an optimized parameter set for each experiment, and because random search outperforms both recruitment strategies for 1,280 piles, the recruitment strategies evolve parameters that eliminate information exchange among ants. This explains the similarity of the results in the 1,280 pile environment (Fig. 3). Similarly, information becomes less valuable in highly volatile environments. At volatility rates of 2.5 round trips, recruitment is only effective in the single pile scenario. In these cases of both maximum food piles and high volatility, recruitment strategies evolve away the use of any form of recruitment and behave as random search.

Because random search does not use any memory, food volatility has a minimal effect on its efficiency. Ant colonies using a random walk use similar parameter sets independent of volatility. Conversely, pile distribution does have an effect on random search efficiency. Tight clustering of food resources hinders random search even though total food quantity is held constant. There is also a positive relationship between pile size and overall variance (Fig. 3). Food spread evenly through space results in very consistent searches for all ants. Conversely, the distance from the nest to large piles of food will have a strong effect on the result of any given run. This effect is minimized as volatility increases because high volatility leads to multiple random pile sites.

Evolved values for the correlation in the random walk tend to be small: on the order of 0.1 radians. These values lead to relatively straight search vectors. Because ants return to the nest after finding food, and because their search paths are relatively straight, food hidden behind nearer patches will be found last. The number of straight trajectories from the nest that find food is proportional to the sum of the diameters of the food piles, which scale as the square root of the

size of the pile, not counting overlap. This means there are fewer straight trajectories from the nest that intersect food in clustered environments, and may explain why the random search strategy does worse there. Evolved values for the uninformed turning coefficient for the two recruitment strategies are generally higher than those of the random search: on the order of 0.15 radians. A larger turning coefficient corresponds to a random walk closer to the nest. This difference may indicate that the recruitment strategies more thoroughly exploit food resources close to the nest.

Fixed Parameters

Pheromone and nest recruitment are efficient strategies in the 1,280 pile environments and the 2.5 round trip volatility environments only because the optimal parameter sets for each reduce them to random search. We used fixed parameter sets that enforce the use of informed search to better evaluate the recruitment strategies in these environments.

Each strategy evolved unique parameter sets for each level of volatility. Here, parameter sets from specific volatilities were applied to each of the other volatility rates as well as the extremely volatile one round trip case for the four pile food spatial distribution (Fig. 4).

The results show a consistent decrease in performance by the two recruitment strategies as volatility is increased. Recruitment of ants to a localized pile works until the pile moves, at which point ants are recruited to an area that no longer contains food. The fixed parameter strategies are not outperformed by the random strategy in the 2.5 round trip environment, suggesting 2.5 round trips may be an approximate threshold beyond which recruitment does not work. This may be because while highly volatile, persistence of 2.5 round trips still offers ant colonies enough time to leverage information before the pile disappears. Recruitment strategies evolved for more stable environments perform worse than the effectively random search strategy in the extreme

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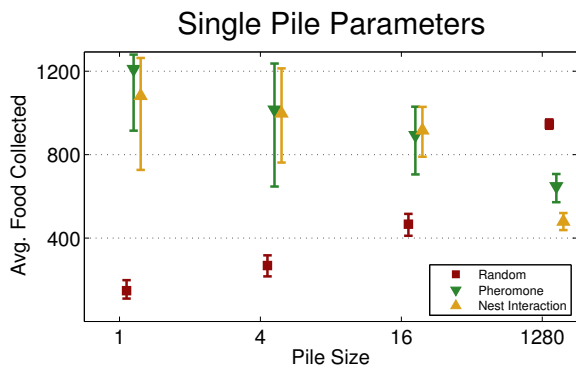
Figure 5: **Fixed Parameters Applied to Other Pile Sizes.**
Parameter sets evolved for the stable single pile environment applied to stable environments of all pile distributions. Recruitment strategies designed for a highly clustered environment do poorly as food becomes more distributed. Randomized search strategies evolved for a clustered environment perform well in distributed environments.

volatility case, showing that recruitment strategies can actively hinder search when used in the wrong environment.

Further analysis reveals that pheromone success is not dependent on whether the pheromone parameters were evolved for the proper volatility rate, except in the extreme case: specifically the parameters evolved for the 10 round trip volatility case perform *worse* for that environment than the parameters evolved for the stable case. Conversely, nest interaction performance is always highest by the parameter set evolved for that specific volatility rate. The best example of this in the five round trip environment, where the five round trip strategy improves on the others by over 33% (Fig. 5).

As explained in the previous section, the effectiveness of the random strategy is not strongly correlated with the volatility rate. The results of Figure 4 confirm this and also highlight the increase in performance as volatility increases.

Because each parameter set is evolved for a specific volatility rate, we expect that it should out-perform any parameter set evolved for a different volatility rate. This holds true except for the pheromone 10 round trip data point, where the parameters evolved for the stable environment perform the best. This is likely due to the similarity between the stable and 10 round trip environment, and the inability of the GA to evolve a globally optimal set of parameters for each environment due to computational limitations.

Similar to the fixed volatility parameter runs, results show that recruitment strategies evolved for clustered environments perform poorly in a spatially distributed environment (Fig. 5). In each case, recruitment of other ants to the location of a previously collected food source leads to a now empty area, actively hindering search. Conversely, a random strategy evolved for a clustered environment is able to perform well in more distributed environments as it does not get stuck looking for more food in the same location.
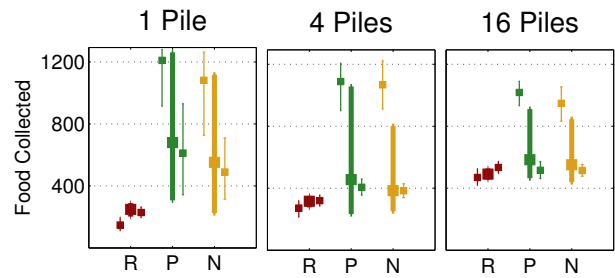

Figure 6: **Search Performance in Random Environments.**
Parameter sets were evolved for environments with variable volatility. Results are plotted as mean values inside their 95% credible intervals. Each result (thick middle) is plotted between results for the stable environment (left) and results for the 2.5 round trip environment (right). The results show a slight performance increase versus the 2.5 round trip scenario for the two recruitment strategies. The variance of the results for the recruitment strategies are large, suggesting the use of recruitment in random environments is helpful.

Variable Volatility

A consistent environment is not a reasonable assumption in the real world. To test the ability of each search strategy to cope with an uncertain level of volatility, we evolved new parameter sets in the 1, 4, and 16 pile cases where volatility was chosen uniformly at random to be between 1.25 round trips and stable for each iteration. Assuming 2.5 round trips is a reasonable threshold between environments where recruitment may be used beneficially and not, this produced a distribution of environments where half would benefit from recruitment and half would not (the functional volatility parameter is inversely proportional to the round trip unit). Similar to the original experiment, 1,000 runs were performed (each with a random volatility rate) once the parameters were set by the GA to generate credible intervals (Fig. 6).

Similar to previous results, the success of the random strategy is not strongly affected by volatility. A slight increase in performance versus the stable environment is consistent with results shown in Figures 3 and 4. Pheromone and nest recruitment strategies show slight improvements over the 2.5 round trip environments. Because random search results in low variance, the large variance of the recruitment strategies, as well as the general improvement in performance, shows that the recruitment strategies evolve parameter sets that make use of information, even when that information is short-lived.

Discussion

The fact that ants use different foraging strategies in different environments (Lanan, 2014) suggests that each strategy has been selected and tailored through evolution to perform well in that environment. We used a spatial computational model to study this hypothesis, simulating three general and

customizable strategies that subsume most known biological ant behavior. The results show that information-based strategies, such as pheromones and nest recruitment, perform worse as food becomes more spatially distributed and volatile. Success of random search, which does not rely on information, is not affected by food volatility, and performs better when food is widely dispersed. In extreme cases of dispersion and volatility, information-based searches perform worse than random search. Ants foraging in environments with unpredictable volatility are able to improve their performance only slightly using recruitment.

These results are consistent with previous findings (Hecker and Moses, 2015), which considered only food distribution: colonies that forage for clustered resources use recruitment-based strategies to exploit information, while colonies that forage for randomly distributed resources avoid recruiting and instead focus on efficient correlated random search. Further, colonies are most efficient when foraging on the distribution for which they are evolved, although some foraging strategies are sufficiently flexible to function well on different distributions. The study reported here extends this work to consider volatility and suggests that nest recruitment and random search may be better alternatives to pheromone recruitment in the right settings.

Implications For Robot Swarms

Chemical pheromones provide foraging ants with a stigmergic, mass recruitment method that is highly scalable, fully decentralized, and generally tolerant of environments with little or no volatility. Robot swarms that mimic ant pheromones, on the other hand, are restricted to foraging in tightly controlled environments that require complex, monolithic infrastructure. For example, swarm researchers have constructed elaborate stigmergic mechanisms using an always-on ink pen and white paper flooring (Svennebring and Koenig, 2004); a tightly-coupled video camera, video projector, and vision processing system (Garnier et al., 2007); and a phosphorescent-painted floor combined with ultraviolet light emitters (Mayet et al., 2010).

Ants also use simpler, more primitive recruitment strategies such as tandem running and group raids, which include a local recruitment display to stimulate nest mates to return to high-quality food patches (Cassill, 2003). Robot swarms mimic these short-range recruitment strategies using robot-to-robot physical connections (Krieger et al., 2000), nearest-neighbor local communication (Schmickl and Crailsheim, 2008), and robot-chain path formation (Nouyan et al., 2009). These swarms employ relatively simple communication schemes that do not require global coordination or preexisting infrastructure in order to collectively forage for resources or aggregate in target areas.

The results of this study demonstrate that nest recruitment strategies are at least as efficient as pheromone recruitment strategies for many environments. Nest recruitment is relatively simple to implement in robot swarms, while pheromone recruitment requires robot- and environment-specific infrastructure. Further, the foraging success of nest recruiters depends only on local, agent-to-agent communication, while pheromone recruiters often depend on global coordination with a single point of failure. We therefore suggest that research in swarm robotics should focus less on mimicking ant stigmergy, and more on designing and evaluating new decentralized information-sharing protocols that are more scalable and easier to implement in natural environments as foraging strategies for real robots.

Comparison To Biological Ants

Our results show that pheromone and nest recruitment work best in stable clustered environments and that random search works best in environments of high dispersal. We evaluate these statements by comparing them to a comprehensive review of physical ants and their habitats (Lanan, 2014). Lanan categorizes the use of ant search strategies over four environmental dimensions, one being spatial distribution of food and another being frequency of food occurrence, which is similar to volatility. Of the 402 species of ants examined in Lanan (2014), 58 were able to be classified completely into non-overlapping categories.

Of these 58, 13 forage in environments of high food dispersal: seven use random search to forage, three use long term trails. Of the three remaining species, two use a form of nest recruitment in what can be considered moderately volatile, which agrees with our model. The three species that use long term trails forage in a space of high food abundance, such that a trail to a specific location will not exhaust the resources located there. Our model did not explore the effects of high food abundance.

Of the rest of the 58 categorized ant species, 39 forage in environments of high spatial clustering of food. All but four of these use long term pheromone trails, as predicted by our model. Of those, one uses site fidelity in a resource rich area, one is listed as random although the author notes they visit the same location repeatedly, one harvests insects in a highly volatile environment, and one forages randomly and seems to be an exception worthy of future study.

Thus, of the physical ants able to be classified into categories defined by our model, our model immediately agrees with 80.7% of the observations, with an additional 9.6% consistent with the addition of site fidelity and food volatility. interesting case studies for future work.

Conclusions

The phrase 'ant foraging' is nearly synonymous with pheromone trails in computer science. However, field studies have shown that numerous ant species do not use pheromone recruitment. This suggests that there are environments for which alternative foraging strategies are at

least as efficient as the use of pheromone, or that pheromone based search can be detrimental to the nest.

Lanan (2014) cataloged hundreds of species of ants to create a classification of ant foraging strategies given their environment. Here we analyze three of these foraging strategies across two environmental dimensions: spatial distribution and volatility of food. We find that nest recruitment performs nearly as well as pheromone recruitment in all environments, and that simple random search is more efficient than either when resources are highly dispersed or volatile. Our results, coupled with observations by Lanan, suggest ant species have evolved the use of optimal foraging strategies for their environment.

Understanding how and why ants use different strategies in different environments is critical for biology-inspired algorithmic design. In many cases, an algorithm ill-suited to its environment will perform worse than a simpler naive strategy. Knowing when and how to use these simpler strategies may improve distributed search and swarm robotics.

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