

How Ants Turn Information into Food

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Abstract— Organisms that can more effectively exploit information about their environments to improve foraging success have a competitive and selective advantage over others. Thus, animals are expected to evolve strategies that use information to improve foraging success. We study how desert seed harvesters use information to improve the rate they collect seeds, which contributes to the colony's fitness. Through field studies and computer simulations, we manipulated the information available to the ants in the spatial distribution of seeds and measured the resulting foraging rates. In field observations, seeds were collected faster when seeds could be found with less information. The increase in foraging rate with clustering was indistinguishable across three related species that vary over an order of magnitude in colony size. Computer simulations show similar systematic increases in foraging rates when information about the food location is communicated among nestmates.

Keywords- information; ants, foraging; ant behavior; modeling

I. INTRODUCTION

According to optimal foraging theory, animals evolve behaviors that maximize energy gain and minimize foraging costs given the distribution of food in their environment [1, 2]. Group foraging can improve the efficiency of finding and exploiting food that is patchily distributed, densely concentrated, or difficult to acquire [3, 4]. Our goal is to quantify how much ant colonies improve foraging efficiency by communicating information to recruit nestmates to high-quality patches where search times are reduced.

Ants are a model system for studying how information exchange improves foraging [5, 6]. They are diverse, abundant, cosmopolitan, and easily observable and manipulated in the lab and field. They practice a range of foraging behaviors, from individual food gathering to mass recruitment of nestmates [5]. As eusocial animals, ants have a fitness incentive to maximize food intake for the colony. Communicating the location or quality of food can direct nestmates to resource-rich areas, reducing time and energy spent searching and helping a colony out-compete neighbors for rich food sources [7-10]. However, it is not clear to what extent the exchange of information among individuals, for example via pheromone trails [11-13], improves an entire colony's foraging success.

Ant recruitment behavior is of particular interest to computer scientists and artificial life researchers because it serves as the foundation for distributed problem-solving

systems like Ant Colony Optimization [14-16]. However, biologically inspired computation has not yet reached its full potential [17], as biocomputing techniques are based on only a small sample of natural behaviors, the diversity of which is still largely unexplored. Here we examine how variation in food distribution affects foraging in real and simulated ant colonies in different environments.

We investigated how the entropy of food distribution affects foraging rates in field studies and models of three sympatric species of *Pogonomyrmex* seed harvester ants. These well-studied central-place foragers can forage individually or use recruitment [4, 18-22]. There is a temporal and spatial heterogeneity in the distribution of seeds that make up the bulk of these ants' diet [23], which affects the costs and benefits of the solitary versus social foraging [4, 19]. For *Pogonomyrmex*, time costs dominate over energetic costs in foraging. Therefore, maximizing seed collection rates maximizes net energetic intake [24], an important contributor to colony fitness.

In field experiments, we placed dyed bait seeds in a spatial distribution around each ant nest, varying from a random scattering of seeds, to seeds placed in 16 piles, 4 piles, or a single large pile. The seeds concentrated in a single pile formed the distribution with the lowest entropy. An ant that found the single large pile thus gained information about the location of the largest number of seeds, and the ants could exploit that information to improve foraging. We calculated a foraging rate for each distribution by monitoring the seeds of each color as they were brought into the nest. Thus, we could measure how discovering piles that conveyed different amounts of information about seed locations, affected the rate that seeds were collected from each distribution. This allowed us to test our primary hypothesis, that foraging rates increase systematically as seeds are concentrated into larger piles.

Colony size could also influence how information affects foraging success. Many colony characteristics change systematically with size [5, 13, 25, 26]. Chemical communication should increase with colony size, reflecting the increasingly complex web of information in which an individual ant is embedded. Indeed, mass recruitment is more common in species with larger colonies [5, 27]. Our experiments and models were conducted on colonies whose forager population sizes at maturity range from fewer than 100 for *P. desertorum* to hundreds in *P. maricopa* to over 1000 in *P. rugosus* [28].

II. METHODS

A. Field Study

We refer to the forager population as *colony size*, although a colony may have many workers that do not forage. Forager population is the component of colony size that is relevant to questions about information sharing as food is collected. Our experimental design controlled for two effects of colony size: larger colonies with more foragers have larger territories; and larger colonies collect seeds at greater absolute rates. After controlling for these factors, we were able to test a second hypothesis, that the *relative* foraging rate for clumped seeds vs. dispersed seeds would increase with colony size, as a result of larger colonies' greater ability to share information.

Previous research has shown that the distribution of food [29] and the difficulty of finding food [30] affect the evolution and utility of communication. In [30], simulated hive-based foraging agents benefitted from memory and communication when food was sparse or clustered but not when it was distributed at random. In [17], communication evolved for ant-like agents only when food was difficult to find. Together, these studies suggest that randomly distributed or easily discovered food do not justify the use of communication, but for clustered foods, communication may provide substantial benefits. We also explore the hypothesis that the benefit of communication is dependent on the distribution of food. We do this for real and simulated ants, and we describe the distribution of food in terms of the information required to specify the locations of food piles.

We were interested in understanding how specific foraging behaviors generate different foraging patterns for seeds clustered in different pile sizes. Our goal was to quantify the benefit conferred to the colony, in terms of improved foraging rates, of communicating the information of the location of these piles to other nestmates. We used Shannon information theory to quantify information and an Agent Based Model (ABM) to simulate foraging with pheromone recruitment. We then compared model results to field data to assess the plausibility that pheromone recruitment explains the relationships we observed between seed distribution and foraging rates.

We replicated our field studies in simulated observations with our computer models. The field studies showed us how ants respond to particular food distributions in nature. The model allowed us to quantify how different behaviors of individual ants affect foraging rates of colonies under perfectly controlled conditions. The strong integration of models and field studies leads to insights that neither could achieve in isolation.

This study addresses two questions. First, do foraging rates increase as seeds are concentrated in fewer larger piles? Second, what is the effect of colony size on foraging rates of clumped seeds relative to dispersed seeds.

This paper is organized as follows: the next section describes the methods used in our field experiments and in our model. Section III describes and compares the results of field and model experiments. We discuss the results in section IV and finally, conclusions are presented in Section V.

We conducted manipulative field experiments on three sympatric species of *Pogonomyrmex* seed-harvesters in the summers of 2008 and 2009 in a mid-succession lot in Albuquerque, New Mexico.

We began observations each morning to coincide with the start of daily foraging activity. We selected an active colony and baited it with dyed seeds arranged in a doughnut-shaped ring around the colony entrance (Fig. 1). We placed seeds in four distributions equal in number but varying in the degree of heterogeneity as follows: one pile of red seeds; four piles of purple seeds; sixteen piles of green seeds; and a random scattering of blue seeds. The four distributions were laid out simultaneously. Observers at the nest entrance used the colors to identify the distribution of the pile from which a seed was collected. We tested for any bias in the rates of collection of different seed colors and we found no significant differences (Kruskal-Wallis test: $n=802$ seeds; $p=0.59$).

We conducted 38 experiments, 11 of which were excluded because the focal colony failed to find at least two seeds from at least one distribution during the observation period. This left us with nine observations with sufficient data from each species.

These three species vary by over an order of magnitude in colony size [31]. In a prior study [28], we estimated forager population (mean \pm standard error) of 77 ± 196 for *P. desertorum*, 208 ± 190 for *P. maricopa*, and 1712 ± 174 *P. rugosus*. Because foragers from small colonies do not travel as far as foragers from large colonies, we adjusted the distances of baits from the nest entrance to be roughly proportional to the square root of forager number per species to approximate the average distance a forager travels. Thus, seeds were distributed in a ring ranging from five to seven meters from each *P. rugosus* nest, two to four meters from each *P. maricopa* nest, and one to three meters from each *P. desertorum* nest. Since the seeds were closer to the smaller colonies, we required

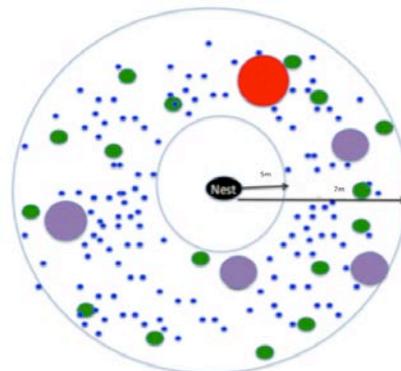


Figure 1. Experimental seed distribution around the nest entrance of a *P. rugosus* colony. Each colored circle is a pile of seeds, dyed to that color. The size of each circle represents the relative number of seeds in that pile; 1 pile of 256 seeds, 4 piles of 64 seeds, 16 piles of 16 seeds and 256 piles of 1 seed.

fewer seeds in order to maintain the same density of piles in the treatment area. Thus, we used 1024 seeds (256 of each color) for *P. rugosus*, and 128 seeds (32 of each color) for *P. maricopa* and for *P. desertorum*. Regardless of the pile size, we distributed the seeds in every pile evenly over a 10x10 cm² area.

After placing the baits, an observer recorded on a laptop the color of each seed brought into the nest with a time stamp using a Java computer program we created. For every observation we generated a set of cumulative seed collection curves, one for each distribution (one experiment is shown in Fig. 3a.) We concluded observations when the colony ceased foraging or when the experimental baits had been collected, usually between 60 to 90 minutes after the start time of the experiment.

B. Foraging Model

We developed an Agent Based Model (ABM) that simulates foraging using recruitment. We simulated our experimental field studies with ants foraging on seeds in one, four, and sixteen clumped piles and a random distribution of seeds. Colonies with 100, 250, and 1000 ants were simulated to approximate the number of foragers in each of the three species in the field study. The numbers of seeds and bait distances were adjusted to be proportional to those used in the field. Simulations were repeated 9 times each to replicate the sample size in the field study, and foraging rates were compared with those from the field.

For each model run, ants set out from the nest and walk in a random direction. While walking, ants have a small probability at each time step of slowing down to 1/4 their walking speed [32] and beginning to search. Searching ants move in a correlated random walk [32]. At each time step a searching ant draws from a normal distribution that determines the degree of deviation from the direction it moved in the previous time step. It then selects the neighboring grid cell that best satisfies that direction and moves to that cell. Searching ants that find themselves in a cell containing food pick it up and return to the nest (whose location is stored in memory). Ants treat all simulated food identically, without regard to source distribution.

Upon picking up food, an ant decides whether to leave a pheromone trail on the return trip to the nest. This decision is based on the number of other seeds in neighboring grid cells (as actual ants might use smell or briefly handle seeds nearby to gauge their density [33]). An ant laying a pheromone trail deposits an amount of pheromone on each cell it walks over during its trip back to the nest. This pheromone evaporates from the grid over time.

Returning ants move preferentially to grid cells that reduce their distance to the nest. Upon arrival at the nest, the ant drops the food; time and seed color (representing the source distribution) are recorded and the ant begins another foraging trip. Ants coming back out from the nest after successful foraging trips follow trails by moving preferentially to cells with the greatest amount of pheromone. At each time step, ants have a small probability of abandoning the trail to begin

searching; otherwise they begin searching when they reach the end of the pheromone trail. Fig. 2 shows one run of the model.

The ABM requires estimating eight parameters that are not known from field studies. We used genetic algorithms (GA), an optimization technique that simulates the process of evolution by natural selection [34], to find combinations of parameters that produced recruitment behavior that maximized seed intake for colonies of different sizes, given a mixture of homogeneously and heterogeneously distributed seeds. These 8 parameters control 5 behaviors (Table 1): degree of turning during the correlated random walk of a searching ant; ants' tendency to lay pheromone trails on the return trip to the nest; probability of laying a trail as a function of seed density; evaporation rate of the pheromone trails; and probability that ants abandon pheromone trails.

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. 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. We manipulated food heterogeneity 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 percent of seeds in 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 the same within each generation but varied between generations. Each colony was evaluated on each food configuration for 20,000 time steps per configuration. Fitness was measured as the total number of seeds collected by each

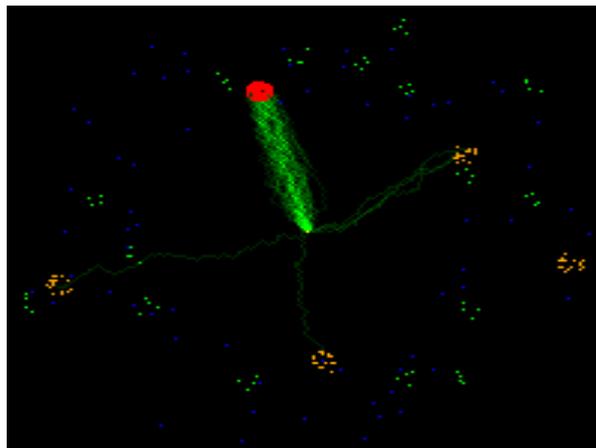


Figure 2. Foraging model running a simulated foraging observation on an identical bait distribution as in field observations. Pheromone trails radiate from the centrally located nest, overlaid on top of baits, as they appear. For sake of clarity, ants are not displayed.

TABLE 1. : SUMMARY OF PARAMETERS THAT INFLUENCE THE BEHAVIOR OF THE MODELS, AND WHICH ARE SELECTED BY GAS

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 are 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.

colony in the eight food configurations in each generation. The GA used tournament selection, with recombination rates of 10% and mutation with probability 0.05. The model is described in detail in Letendre and Moses, 2010 [35].

C. Defining Information

In order to relate foraging success to the distribution of seeds, we defined a single metric to describe each seed distribution that accounted for both the numbers of seeds per pile and the number of piles. We use Shannon Information Theory [36] to quantify the amount of entropy in each experimental seed distribution.

Entropy (H) is defined, in bits, as

$$H = \sum_i -p_i \log_2(p_i), \quad (1)$$

where p_i is the probability of a seed being in the i^{th} pile. In all of our experimental seed distributions, the total number of seeds was constant for a given species (e.g. 256 seeds for *P. rugosus*) and always distributed evenly among the specified number of piles, which simplifies calculating the entropy. For example, if seeds are distributed evenly in 4 piles, then $H = 4(-\frac{1}{4})\log_2(\frac{1}{4}) = 2$ bits. If seeds are evenly distributed in 16 piles, then 4 bits are needed to specify all 16 locations.

When an ant discovers a pile of seeds with a lower entropy distribution, it gives the ant information about a larger number of seeds. Every time the number of piles doubles, another bit is needed to specify the entropy of the distribution such that 1, 2,

or 4 bits are needed to specify the locations of 1, 4 and 16 piles, respectively.

There are different ways that we could define information in this system. Following [37], we measure information as reduction in uncertainty. More specifically, we define information gained when a seed is found as the reduction in uncertainty about the location of all seeds in that distribution. For example, when a blue seed (from the random distribution) is found it provides information about the location of only that seed. When a *P. rugosus* forager finds the 1 red pile containing 256 seeds, it gains information about the location of all 256 seeds of that distribution.

In the context of our field study, we used a random distribution (256 piles of 1 seed for *P. rugosus* and 128 piles of 1 seed for *P. maricopa* and *P. desertorum*) as a “null” distribution. We compared the rates of collection of all other distributions, as a ratio, to that of the “null” distribution of each observation. So, we compare the information (on a \log_2 scale) to a relative foraging metric (also on a \log_2 scale) (see below). The information measure is advantageous because it allows a single number to characterize the distributions.

D. Data Analysis

We produced four time series from each experimental observation, one from the collection of seeds from each experimental seed distribution. Our goal was to measure how much faster each clumped distribution was collected compared to the random distribution.

We calculated two foraging metrics for each distribution. A *seed rate* was calculated by dividing the number of seeds collected from a distribution by the total collection time (the

time between collection of the first and last seed of that color). A *foraging ratio* was calculated by dividing the seed rate for a distribution by the seed rate for random (blue) seeds. These three ratios, one each for red, purple, and green seeds, provided a normalized metric of how much faster clumped seeds are collected compared to randomly distributed (blue) seeds. The foraging ratios allowed us to make meaningful comparisons across variable colony sizes and activity levels, and to compare results from the field to those from the model, which are measured on different time scales (model time steps are not calibrated to seconds but time drops out in the calculation of foraging ratios). In order to correct for skew in our field data, we \log_2 -transformed the ratios to obtain normally distributed foraging ratios. We conducted our analysis on these \log_2 -transformed foraging ratios.

We analyzed seed rates and \log_2 -transformed foraging ratios using a General Linear Model with repeated measures analysis (SPSS). Repeated measures analysis accounts for the non-independence of multiple measures taken of a single focal colony, and it provides greater statistical power by allowing us to distinguish within- and between-subjects effects. In addition to the within-subject effect of seed distribution, we include species identity (as a proxy for colony size for field data) and forager population size (for model data) as a between-subject factor in these analyses. We use estimated marginal means in our analysis to account for different sample numbers and the influence of the independent variables (colony size and seed distribution) on our dependent variable (foraging ratio). All means presented in figures are estimated marginal means.

III. RESULTS

Fig. 3 shows cumulative seed collection over time for one field observation of *P. rugosus* and for one simulation of a colony with 1000 foragers. The field data depict an accelerated seed collection rate for the more clumped seeds (red) after an initial discovery period. The curves are flatter when seeds are distributed in more small piles. Not surprisingly, the rate of collection of randomly distributed seeds (blue) rises slowly and sometimes even decelerates.

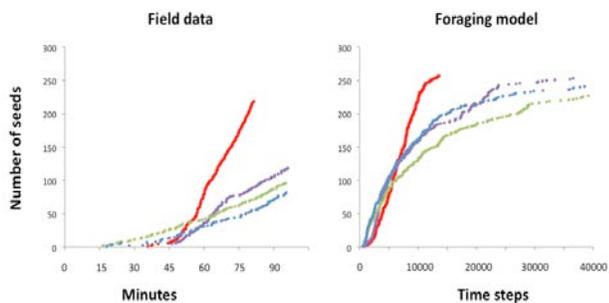


Figure 3. Cumulative seed counts from (a) one field observation and (b) one run of the foraging model. The cumulative seed count is the number of seeds collected after the specified time or number of time steps. The color of each curve represents the distribution from which the seed was collected: red=1 pile, purple=4pile, green=16 pile and blue=randomly distributed seeds.

Fig. 4 shows the seed rate (seeds collected per hour, not normalized) for the piled and randomly distributed seeds collected during our field observations. In all three species, the seed collection rate decreases as seeds are distributed across more piles: Repeated measures analysis shows a significant difference in foraging rates between species ($p < 0.001$) and a significant difference in foraging rates between pile sizes within species ($p < 0.001$). Within each of the three species there is a decreasing trend in foraging rate as seeds are dispersed across more piles. According to paired t-tests, foraging rates for 4-pile (purple), 16-pile (green) and random-scatter (blue) distributions are significantly different from the 1-pile (red) distribution for *P. rugosus* ($p = 0.008, 0.011$ and 0.009 respectively) and *P. desertorum* ($p = 0.004, 0.025$ and 0.012 respectively). Due to large standard errors, foraging rates are not significantly different between distributions for *P. maricopa*.

The bars in Fig. 5 show the foraging ratios, defined as the seed rate from each of the three piled distributions divided by the seed rate for randomly distributed seeds.

Data were \log -transformed to obtain normal distributions ($p > 0.102$ in Shapiro-Wilk test for normality after transformation.) After \log_2 -transformation, a value of 0.0 indicates that seeds from a piled distribution are collected at the same rate as randomly distributed seeds, and a value of 1.0 indicates that seeds are collected twice as fast. There was no effect of species on the normalized foraging ratios ($p = 0.463$) but a significant effect of distribution on foraging ratios within species ($p < 0.003$) again indicating that seeds were collected significantly more slowly when they were distributed among more piles.

Because there was no significant interaction between species identity and pile size in determining foraging ratios, we combined results for all three species for more statistical power to compare across distributions. Fig. 6 shows the foraging ratios (solid bars) for all species, emphasizing the decline in foraging rate as seeds are dispersed across more piles. Again,

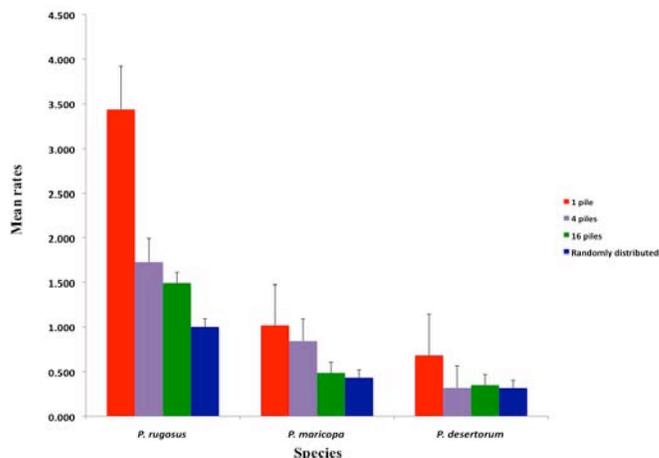


Figure 4. Mean seed rate per species. Colors represent the distribution from which the seeds were collected: red=1 pile, purple=4 piles, green=16 piles and blue=randomly distributed seeds. Error bars represent standard errors

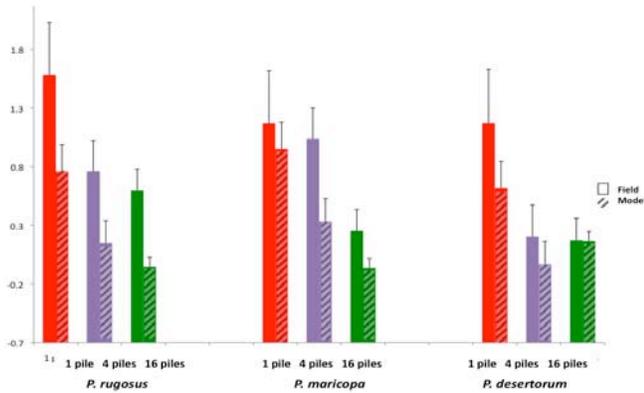


Figure 5. Bars represent mean ratios (rate of piled seeds divided by rate of random seeds) for three clumped distributions and three species. Solid bars are field ratios and pattern bars are model ratios. Colors represent the distribution that the seeds were collected from: red=1 pile, purple=4 pile and green=16 pile distributions. Error bars are std. errors. Ratios are log₂-transformed.

the within-subjects effect of seed distribution is highly significant ($p < 0.001$). In pair-wise comparisons, the single pile is collected significantly faster than the 4 piles and 16 piles ($p = 0.004$ and 0.000 , respectively), but the difference between foraging ratios for 4 piles vs. 16 piles is not significant.

Similar to the results of the analysis of our field data, foraging ratios in our foraging model are significantly influenced by seed distribution ($p < 0.001$) but not by colony size ($p > 0.10$). Mean foraging ratios in the ABM are significantly lower than those from our field data ($p = 0.017$), indicating a greater ability of ants in the field to exploit piled foods relative to their collection of randomly distributed foods; however, a non-significant within-subjects interaction of seed distribution and species relative treatment of foods from different size piles is similar, with the highest foraging ratios associated with seed distributions clustered in the smallest number of piles (Fig. 5).

Fig. 5 illustrates similar patterns for foraging ratios from field experiments and model when data from the three species are pooled. The ratios are smaller in the model, but the shape of the relationship is similar to the field: the single red piles are collected much faster than the 4 purple piles and the 16 green piles ($p = 0.004$ and 0.000 , respectively). The difference in foraging ratios between purple and green piles are not significant.

IV. DISCUSSION

A. Summary

Foraging rates increase as seeds are concentrated in fewer larger piles in the field and in our model, consistent with our primary hypothesis. In our recruitment ABM, information was communicated among ants and exploited using pheromone-mediated recruitment. This enabled the ants to collect seeds faster from bigger piles. We hypothesized that communication among ants is also relevant in determining foraging rates in the field, but perhaps by different or additional mechanisms.

In contrast to our second hypothesis, foraging ratios were not affected by species identity in the field (where species vary

substantially in size), or by colony size (ranging from 100 to 1000 foragers) in the foraging model.

B. Models Complement Field Studies

Our model and field studies were designed to quantify how much faster ants collect clumped seeds and how the rate of seed collection depends on colony size. We do not know which behaviors ants in the field use, and we have only very rough estimates of colony size based on species identity. In contrast, our ABM simulated foraging using pheromone-mediated recruitment for precisely specified colony sizes.

When we replicated our experimental seed distribution in the ABM, the relative increase in the foraging ratio as pile size increased was similar to our field data, with a non-significant increase in foraging ratio for 16 to four piles, and a large, significant increase between four piles and one pile. However, the foraging ratios in the model were lower than those from the field overall. ABM parameters were ‘evolved’ using genetic algorithms to maximize seed intake in a distribution of 50% of seeds in piles and 50% randomly scattered [35]. It is likely that evolving parameters for other seed distributions would change the recruitment behavior in the model, which may explain why recruitment ratios were lower than in the field.

Our foraging model should be interpreted as one of many possible foraging models. There may be other behaviors in addition to, or instead of, pheromone-mediated recruitment that ants employ to exchange information that might produce similar foraging results. Site fidelity is one such behavior: when *Pogonomyrmex* foragers find seeds, they often remember where that seed was found and repeatedly return to that location until the food source is depleted [38]. Other researchers have hypothesized that seed harvesters rarely recruit in nature and that site fidelity may be sufficient to collect piles of seeds quickly [21, 24, 32, 38]. For seed piles small enough that a single ant can collect all the seeds in a patch before the colony ceases foraging activity for the day, there may be no benefit in recruiting other foragers to that pile. The extent to which site fidelity and pheromone recruitment are used by harvester ants, and how effective each behavior is in increasing foraging on clumped resources remains a promising area for future ABMs to explore. Understanding how much memory and information exchange between agents can improve distributed search is relevant for artificial systems like robot swarms as well as biological systems.

C. Does Colony Size Matter?

Not surprisingly, colonies with more foragers collected a larger total number of seeds in the field and in our model (Fig. 4). However, we expected that large colonies would be particularly good at collecting seeds from large piles. We measure this effect with the foraging ratio, which normalizes the rate of collection of piled seeds by that of randomly distributed seeds. Our analysis indicates that large and small colonies collected seeds from large piles equally well; colony size had no effect on foraging ratio in the field or models (Fig. 5). However, these results should be interpreted in the context of our study design in which seed piles were placed closer to smaller colonies. We initially hypothesized that even

given equal foraging access to baits by foragers of colonies of different sizes, large colonies might take advantage of their collectively larger communication networks to collect seeds in large piles relatively faster. This hypothesis was not supported.

Natural seed distributions are not adjusted to favor more piles closer to small colonies, so the effect of colony size on foraging might be very different given a more natural seed distribution. Colony size has profound effects on life history[39] and foraging strategy [6, 27], thus more study of the affect of colony size on foraging is warranted.

D. The Value of Information

Information is a crucial currency for animals since informed individuals can adapt behavior to environmental conditions [40], but information is rarely measured in terms of its contributions to fitness [41, 42]. By quantifying how information improves foraging, we can begin to measure information in terms relevance to colony fitness or to performance metrics for artificial systems.

Fig. 6 shows that foraging ratios for each piled distribution increase (from 0.3 to 0.5 to 1.2) as the entropy of the distribution decreases from one bit (1 pile), two bits (4 piles) and four bits (16 piles). The time for ants to find the seeds increases roughly proportionally to the increase in the entropy of the distribution. So, these ants exploit the increased information available upon discovering a pile in lower-entropy distributions to improve whole colony foraging intake.

Intuitively, an ant colony needs more information to exploit seeds if those seeds are distributed in more piles. A forager that finds a large pile greatly reduces the entropy of that distribution. For example, if an ant finds a seed from a 1-pile distribution, the entropy of that distribution is reduced to zero; the ant colony has information about the location of all the seeds in that pile. Additionally, the ant can convey the location of these seeds to its nest mates and attract more foragers to the pile, resulting in a faster foraging rate.

Our results can also be interpreted in the context of a recent analysis of the fitness value of information [42]. Given an uncertain environment, the strategies that maximize fitness use effective bet hedging such that the probability of investing in any particular phenotype is proportional to the certainty that the environment will favor that phenotype. A cue that reduces uncertainty about the environment allows an organism to invest more in the appropriate phenotype. So, the cue has fitness value proportional to the amount of reduction in uncertainty, which is the information encoded in the cue. Since ant colonies do not know the distribution of the seeds, the colonies will “bet” on a strategy according to cues that reduce uncertainty about the location and availability of seeds in the environment. These cues are conveyed to the colony with the discovery of each pile of seeds, and the colony responds with a strategy appropriate to the average availability and distribution of seeds in that species’ evolutionary environment.

While [42] describes the fitness value of information over evolutionary time, the fitness value of information for the ants can be measured over the lifetime of an individual colony. In our ABM, the strength of a pheromone trail is a cue that reduces uncertainty about the location of seeds. When seeds are

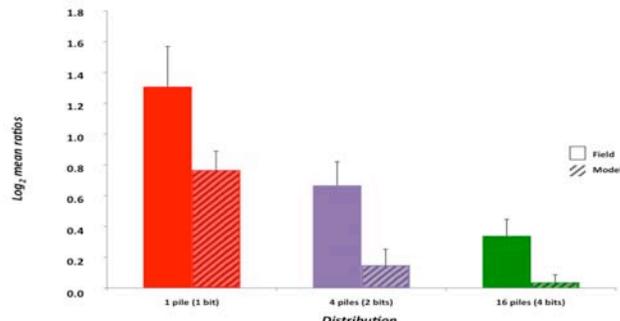


Figure 6. Bars represent mean foraging ratios for all species combined. Bars with solid colors represent field ratios and bars with diagonal pattern represent foraging model ratios. Colors represent the distribution from which the seeds were collected: red=1 pile, purple=4 pile and green=16 pile distributions. Error bars are standard errors.

clumped into larger piles, the cues encoded in the pheromone trail are more valuable, and the improvement in foraging is proportional to the information encoded in the cue. Thus, we suggest that the colony improves foraging rates in proportion to the information that an ant can convey upon finding a seed. The colony bet-hedges by allocating foragers to piles in proportion to the information about seed locations in that pile. Given that a colony faces an unknown distribution, this strategy maximizes seed intake rates over the life of the colony.

V. CONCLUSION

The spatial distribution of food available to foraging ants was manipulated in field studies and in an Agent Based Model. Like earlier Alife studies [29, 30], we found that the value of communication depends on the distribution of food in the environment. Our field study suggests that this is true not just for simulated ants, but also for real ants in the field. In both cases, seeds are collected significantly faster when they are clustered in fewer piles and therefore can be found with less information. The increase in foraging rate is indistinguishable across colonies ranging from 100 to 1000 foragers. Additionally, ants appear to effectively bet-hedge with their foraging strategy, optimizing the tradeoff between exploiting known locations of seeds and searching for new ones. Ants exhibited seed collection rates inversely proportional to the information cost of specifying the seed locations. Quantifying the value of information and its communication among social foragers may help us understand how animals use information more generally. It may also help us to assess the value of information exchange between components in engineered distributed systems. Exploring different mechanisms for turning information into fitness or performance is a fruitful area for Alife research.

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