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HOW ANTS TURN INFORMATION INTO FOOD

by

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DISSERTATION

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DEDICATION

To my husband, Mike

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HOW ANTS TURN INFORMATION INTO FOOD

by

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ABSTRACT

Animals constantly process information from their environment. In social organisms, information exchange among individuals allows for behaviors to be finely tuned to local environmental cues. Such is the case of foraging in ants, where sharing information about the distribution of resources can drive adaptive behaviors to exploit those resources. In a first study, we quantified how clustering of experimental seed baits significantly increased foraging rates of seed harvester ants. That study found that species with larger colonies were no better than species with smaller colonies at collecting clumped seeds. In a second study, we integrated computer simulations, information science and computational analysis to re-analyze data. We found that seed intake patterns from larger colonies were more consistent with foraging patterns generated by behaviors that use information, such as recruitment and site fidelity, particularly for foraging on clustered distributions of resources. Finally, we studied recruitment behavior in large colonies of Argentine ants. Our results indicate that Argentine ants recruit nestmates to food directly

from persistent nearby trails. Once ants find a new food source, they walk back and forth between the bait and sometimes share food by trophallaxis with nestmates on the trail. Recruiting ants from nearby persistent trails creates a dynamic circuit, like those found in other distributed systems, which facilitates a quick response to changes in available resources. These studies quantify how remembering and communicating information in a range of colony sizes increase foraging rates.

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CHAPTER 1

INTRODUCTION

Information streams continuously from the environment to animals, which in turn alter the environment. In social organisms, there exist many simultaneous information feedback cycles, where the behavior of each individual gives rise to group-level properties. Thus, information cues collected by each individual produce collective behavioral strategies that allow the colony to be finely tuned to local environments. Such is the case of foraging in ants, where individual foraging strategies may consist of one or more foraging behaviors which depend on information obtained from the environment. From individual responses to each other and the environment emerges the behavioral response of the colony. The result of information use is successful foraging through behavioral strategies adapted to the spatial distribution of resources.

In ants, information drives behaviors based on memory, movement and communication. The mechanisms for storing, transporting and sharing information are expected to change in larger colonies, due to larger territories and larger numbers of interactions among ants. Behavioral strategies of large colonies are expected to adapt to the challenge of vast territories, the difficult coordination of simultaneous efforts of thousands of individuals and the diversity of resource distributions in space and time.

Past studies have investigated ant foraging and the effect of colony size and distribution of resources on their success. However, less effort has been made to explicitly quantify the use of information and its effects, and the feedback cycle between information, behavior and environment. This work develops a quantitative framework to integrate fieldwork, statistical methods, and computer science theory and techniques, to

reveal how ants of different colony sizes use information from distinct spatial distributions of resources.

Chapter 2 of this dissertation quantifies how seed harvesters exploit the spatial distribution of seeds to improve their rate of seed collection. We found that the clustering of experimental seed baits significantly increases foraging rates. We developed a method to compare foraging rates on clustered versus random seeds across three *Pogonomyrmex* species that differ substantially in forager population size. We found that species with larger colonies are no better than species with smaller colonies at collecting clumped seeds. These findings contradict the theoretical expectation that larger groups are more efficient at exploiting clumped resources, thus contributing to our understanding of the importance of the spatial distribution of food sources and colony size for communication and organization in social insects.

Chapter 3 examines how ants use information from their environment to improve collective foraging. We analyzed resource intake patterns to test whether species with larger colony sizes use more information-based behaviors than species with smaller colony sizes. Our approach integrates data (from Chapter 1) obtained in the field from three harvester ant species with distinct colony sizes, and computer simulations that model foraging behaviors. We used a fuzzy pattern-matching algorithm with idealized behaviors to infer behaviors from field data. Seed intake patterns from larger colonies were more consistent with foraging patterns generated by behaviors that use information, such as recruitment and site fidelity. Seed intake patterns from smaller colonies were more consistent with patterns produced by behaviors that do not use information, such as correlated random walks.

Finally, in Chapter 4, we studied information use in very large colonies of Argentine ants. We investigated whether some ants recruit directly from established, persistent trails to food sources, thus accelerating food collection. Our results indicate that Argentine ants recruit nestmates to food directly from persistent trails, and that the exponential increase in the arrival rate of ants at baits is faster than would be possible if recruited ants traveled from distant nests. Once ants find a new food source, they walk back and forth between the bait and sometimes share food by trophallaxis with nestmates on the trail. Recruiting ants from nearby persistent trails creates a dynamic circuit, like those found in other distributed systems, which facilitates a quick response to changes in available resources.

This work makes important interdisciplinary contributions through the integrated use of fieldwork, simulation data and computer science. It builds toward an explicit understanding of information by quantifying its content and its effect in ant behavior. There is need for further investigation of how social organisms process, share and use information, including field studies of animal behavior that explicitly characterize information flow. This work is an example of such a study, and its approach can ultimately be extended more generally towards the study of information use in collective animal behavior.

CHAPTER 2

QUANTIFYING THE EFFECT OF COLONY SIZE AND FOOD DISTRIBUTION ON HARVESTER ANT FORAGING

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Abstract

Desert seed-harvester ants, genus *Pogonomyrmex*, are central place foragers that search for resources collectively. We quantify how seed harvesters exploit the spatial distribution of seeds to improve their rate of seed collection. We find that foraging rates are significantly influenced by the clumpiness of experimental seed baits. Colonies collected seeds from larger piles faster than randomly distributed seeds. We developed a method to compare foraging rates on clumped versus random seeds across three *Pogonomyrmex* species that differ substantially in forager population size. The increase in foraging rate when food was clumped in larger piles was indistinguishable across the three species, suggesting that species with larger colonies are no better than species with smaller colonies at collecting clumped seeds. These findings contradict the theoretical expectation that larger groups are more efficient at exploiting clumped resources, thus contributing to our understanding of the importance of the spatial distribution of food sources and colony size for communication and organization in social insects.

Introduction

Seed harvester ants, *Pogonomyrmex* spp., are ideal for testing hypotheses about how food distribution and group size favor different foraging strategies. *Pogonomyrmex* are relatively large ants found mostly in arid regions of South, Central, and North America (Cole 1968). They are well studied, monodomous central-place foragers whose primary diet is local seeds found on the top of the soil (Bernstein 1975; Carroll and Janzen 1973; Davidson 1977; Gordon 1991; Holldobler and Wilson 2008; Taniello 1989). Although all harvester ants eat seeds and often occur in sympatry, with colonies of several species often found within a few meters of each other, individual species differ in average body size, the size of seeds eaten, and average mature colony size (Bernstein 1975; Davidson 1977). The spatial distribution of seeds eaten by harvesters ranges from highly clumped to randomly dispersed. Reichman (1984) found extreme variability in the density of seeds eaten by *Pogonomyrmex* in the Sonoran Desert, with a 78-fold difference in seed density across space, including a 25-fold difference within microhabitats. Edeleman (2010) found three-fold increases of seeds surrounding kangaroo rat mounds in the Chihuahuan desert.

Although *Pogonomyrmex* individuals communicate and coordinate tasks in their underground nests, it is not clear whether foragers communicate information, mediated for example, by pheromone trails. They are able to use pheromone trails to recruit foragers to large piles of seeds, as when supplied experimentally (Holldobler and Wilson 1970), but it is not clear that they commonly use pheromone recruitment under natural conditions. While some authors found evidence of recruitment (Davidson 1977; Hölldobler 1976; Whitford 1978), others found that foraging is regulated by other

behaviors (Gordon 1991; Schafer et al. 2006). For example, *Pogonomyrmex* foragers exhibit strong “directional fidelity,” returning to search for food in the same general direction as they successfully foraged before (Beverly et al. 2009; De Vita 1979; Hölldobler 1976).

We expected harvester ant foragers to preferentially harvest dense seed cashes, maximizing their efficiency by minimizing their search time. When a forager leaves its nest in search of food, it will travel in a general direction (Fewell 1990), presumably established by a pheromone trail or by directional fidelity. The time it takes for an ant to arrive at a general area it expects to find food is the *travel time*. Once at the destination, the ant engages in a more localized search. The time it takes to find a patch of food in this general area is the *search time*. Once a patch of food is discovered, each ant that returns to that pile will still take the same travel time, but its search time will be shorter. Beverly et al. (2009) showed that search time has a much stronger effect on total trip duration than travel time. Thus, we assume clumps of seeds can be collected significantly faster because the search time component of foraging time is reduced when an ant already knows the location of a pile of seeds.

We test colonies from three related, sympatric *Pogonomyrmex* species that vary substantially in forager population size and ask how forager population size affects foraging rates for seeds in different spatial distributions. In turn, we posit that the foraging patterns we observed reflect underlying behavioral mechanisms.

Our two key variables were average forager population size and the spatial distribution of seeds. We estimated average forager population size in each species,

experimentally manipulate seed distribution, and measure how these differences affect foraging efficiency.

The three species of harvester ants we studied, *Pogonomyrmex rugosus*, *P. maricopa*, and *P. desertorum*, vary substantially in total colony population size. Forager population size also varies substantially between species, between colonies of the same species, and over time for any particular colony. Johnson (2000) estimated total colony population sizes in the Chihuahuan Desert of New Mexico as thousands for *P. rugosus*, a few hundred for *P. maricopa* and fewer than 100 for *P. desertorum*. Whitford and Ettershank (1975) estimated colony forager populations of dozens in *P. desertorum* and thousands in *P. rugosus*. Since not all members of the colony actively forage, total colony population is an upper bound on forager population size.

We manipulated the distribution of seeds by providing each colony with seeds dispersed over a broad range of pile sizes, ranging from 1 to 256 seeds, to establish a quantitative relationship between the distribution of seeds and the foraging rate. We then compared the relationship between food dispersion and foraging rate across these species, with their different forager numbers, to determine whether larger colonies concentrate relatively more foraging effort on clumped seeds when compared to smaller colonies.

We tested two specific hypotheses. First, we tested whether rates of seed intake are faster when the same numbers of seeds are concentrated in fewer, larger piles. Second, we tested whether there is a positive relationship between colony size and the ability to harvest dense food resources.

Materials and Methods

We studied three sympatric species of desert seed-harvester ants in the genus *Pogonomyrmex* in the high desert of central New Mexico: *P. desertorum*, *P. maricopa* and *P. rugosus*. According to national guidelines, no permits were required for the described field studies. We carried out this fieldwork in the summer of 2008 and 2009 in a mid-succession lot of approximately 13 hectares in central Albuquerque, New Mexico, in the Chihuahuan desert of the southwestern U.S. No permissions were required for the locations of these activities.

Estimating active forager population size

We relied on data and methods from an earlier study (Moses 2005) to estimate the average number of active foragers for each species. Preliminary estimates of forager numbers per colony and per-ant foraging distances and times characterizing each species were based on observation of colonies in the McKenzie Flats area of the Sevilleta Long Term Ecological Research site in central New Mexico. These observations were carried out in the summers of 2003 and 2004, where we tracked 63 individual ants from 13 colonies.

We made the following observations for each forager under natural field conditions. Individual foragers were followed as they left the nest, traveled to a search location, searched for and acquired a seed, and returned to the nest. We marked some foragers either with paint (DecoColor opaque paint ® Uchida of America) or colored chalk powder; others were followed and left unmarked. For each forager we measured the time to complete a foraging trip (T_f) from nest to seed and back to the nest, the linear

distance from nest to seed (d_s) and travel velocity (v_t) of each forager returning with the seed to the nest. The measurements are reported in Table 1.

Variable/Spp	N	Mean	SE	Lower Bound	Upper Bound
Tf Total time of round trip from the time an ant leaves the nest to the time it returns with a seed [minutes]					
<i>P. desertorum</i>	15	7.25	2.73	1.84	12.67
<i>P. maricopa</i>	16	17.96	2.85	12.29	23.62
<i>P. rugosus</i>	32	13.56	2.24	9.11	18.01
dt Measured distance between seed and nest [meters]					
<i>P. desertorum</i>	15	3.86	1.04	1.8	5.92
<i>P. maricopa</i>	16	8.18	1.09	6.02	10.34
<i>P. rugosus</i>	32	7.83	0.85	6.14	9.53
vt Travel velocity. Calculuted as dt/return time [meters/minute]					
<i>P. desertorum</i>	15	2.96	0.49	1.97	3.95
<i>P. maricopa</i>	16	2.25	0.48	1.29	3.21
<i>P. rugosus</i>	32	3.10	0.34	2.42	3.77
R Rate of foragers returning to the nest measured at equilibrium [foragers/minute]					
<i>P. desertorum</i>	15	8.73	3.08	2.61	14.86
<i>P. maricopa</i>	16	12.50	2.99	6.57	18.43
<i>P. rugosus</i>	32	107.94	2.11	103.74	112.13
F Number of active foragers (calculated from foraging trip time multiplied by mean seed intake rate)					
<i>P. desertorum</i>	15	77.88	196.49	-312.37	468.13
<i>P. maricopa</i>	16	208.52	190.25	-169.34	568.38
<i>P. rugosus</i>	32	1712.61	134.53	1445.43	1979.8

*Based on modified population marginal means. N is the number of experiments conducted to measure each variable.
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Table 1. Means* for characteristic variables of each species estimated at the Sevilleta LTER in 2003–2004.

One way to estimate the number of active foragers size is to multiply the average time of a foraging trip (T_f) by the rate that ants return to (and leave from) the nest when the rates of leaving and returning ants are at equilibrium. At equilibrium the number of foraging ants (F) is constant. The equilibrium rate of ants leaving (which is equivalent to the rate ants return) multiplied by T_f provides an estimate of active forager population at a particular time: the forager population (F) equals the time of a foraging trip (T_f) multiplied by the rate that ants leave the nest. We estimated the number of foragers per

species at the Sevilleta in 2004 using this method. We calculated the equilibrium rate by counting each ant leaving the nest for three minutes and each ant returning for 3 minutes. When these numbers differed by less than 10 percent, we considered that an equilibrium flux of ants (Table 1). We multiplied that number by average foraging trip time (T_f) to get the active forager population for that day (F , Table 1).

Manipulative Seed Studies

In order to measure the effect of seed dispersion on foraging rates, we conducted manipulative field experiments on the three *Pogonomyrmex* species in the summers of 2008 and 2009. We began observations each morning to coincide with the start of daily foraging activity. We account for daily variations in colony activity, which may affect forager numbers (Gordon 1991), by using the distribution of randomly scattered bait seeds to normalize our observed foraging rates. (see *Data analysis* section for more details). The normalized foraging rate also allowed us to make comparisons across species and conditions that varied widely.

We selected an active colony and baited it with dyed seeds arranged in a wide ring around the colony entrance (Figure 1). We placed dyed seeds in four distributions of different colors, equal in number but varying in degree of dispersion: one pile of red seeds, four piles of purple seeds, sixteen piles of green seeds and a random scattering of blue seeds. Regardless of the pile size, we distributed the seeds in every pile evenly over a $10 \times 10 \text{ cm}^2$ area. As soon as the first seed was placed, a starting time for the observation was marked. We immediately began observing the arrival of seeds at the nest entrance,

recording the color – and thus the distribution from which each seed was collected – and the time of arrival.

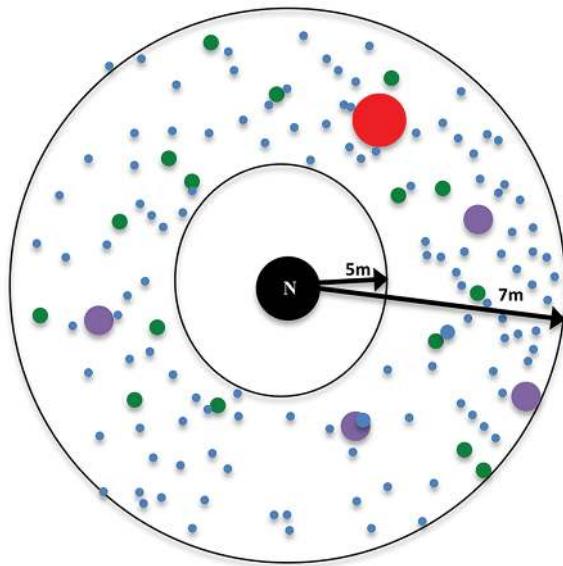


Figure 1. Experimental seed distribution around the nest entrance of a *P.rugosus* colony. Each colored circle is a pile of millet seeds dyed to that color. The size of each circle represents the relative number of seeds in that pile: red = 1-pile of 256 seeds, purple = 4-piles of 64 seeds, green = 16-piles of 16 seeds, and blue = 256 individual seeds distributed randomly.

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

We dyed bait seeds using food coloring. We tested for bias in the collection or observation of bait seeds of different color by observing colonies of each species foraging in piles of bait seeds of mixed colors, with equal numbers of the four colors in a single pile.

We arranged our experimental seed distributions so as not to disadvantage small colonies. By placing fewer seeds closer to smaller colonies with smaller average foraging distances, we attempted to provide an equal chance for an individual forager to encounter one of our experimental seeds whether that individual was in a large or small colony (Table 1). We chose a number of seeds roughly proportional to the forager population size: 1024 seeds for *P. rugosus* and 128 seeds each for *P. desertorum* and *P. maricopa*. We adjusted the distances of baits from the nest entrances in order to obtain a similar density of seeds patches in each treatment, placing the baits in a ring 5-7m from each *P. rugosus* colony, 2-4m from each *P. maricopa* colony and 1-3m from each *P. desertorum* colony (Table 2). Because the distance that a forager typically travels does not increase linearly with the number of foragers in a colony, it was not possible to simultaneously keep the density of seeds constant and the distance from nest to seed precisely proportional to typical forager travel distance.

P. desertorum foragers, with the smallest body size, frequently had difficulty handling the hulled millet with which we baited the other species. Because recruitment responses may be reduced with excessive handling times of large grains (Hölldobler 1976), we baited *P. desertorum* colonies with sesame seeds. All three species readily collected experimental seeds whenever they encountered them, suggesting that any difference in seed preference was not a significant factor.

After placing the experimental baits, an observer recorded the color of each seed brought into the nest with a time stamp using a computer program we created. For each experimental observation, we generated a time series for each distribution (a set of cumulative curves representing four time series in one observation is shown in Figure 2).

Species	Distance from nest	Distribution	Color	Number of seeds per pile
<i>P. desertorum</i> (8 colonies)	2–4 m	1 pile	Red	32
		4 piles	Purple	8
		16 piles	Green	2
		Random	Blue	1
		Total		128
<i>P. maricopa</i> (4 colonies)	2–4 m	1 pile	Red	32
		4 piles	Purple	8
		16 piles	Green	2
		Random	Blue	1
		Total		128
<i>P. rugosus</i> (9 colonies)	5–7 m	1 pile	Red	256
		4 piles	Purple	64
		16 piles	Green	16
		Random	Blue	1
		Total		1024

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Table 2. Experimental seed distribution.

We concluded observations when a focal colony ceased foraging or when ants had collected all experimental baits, usually between 60 and 90 minutes after the start-time of the observation.

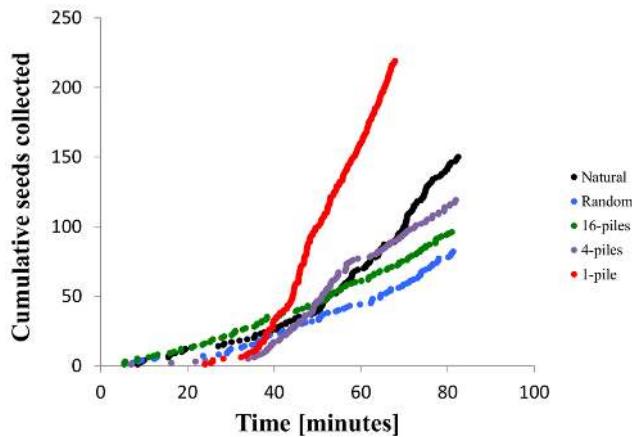


Figure 2. Seed intake rates from one field observation of a colony of *P. Rugosus*. The y-axis shows the cumulative number of seeds collected by the time specified on the x axis. Red = 1 pile of 256 seeds, purple = 4 piles of 64 seeds, green = 16 piles of 16 seeds, blue = 256 piles of 1 seed (randomly scattered seeds).

Data Analysis

We produced five time series from each observation, one each for seeds from each experimental seed distribution (color) and one for naturally occurring seeds. We calculated how much faster seeds from each clumped distribution were collected compared to those in the random distribution.

We measured seed collection rates in two time periods. The first time period was measured from the placement of seeds (the start of the experiment) to the time that the

first seed from each distribution was collected. This *discovery time* measures the amount of time for an ant to find a seed from each distribution. The second time period was measured from the discovery of the first seed of a distribution to the last seed collected from that distribution. We call the rate at which seeds were collected once a distribution was discovered *foraging rate*. In Table 3 we report, for each species, the discovery times and the foraging rates for each distribution.

Species	Distribution	Discovery Times	
		Mean	SE
<i>P. desertorum</i> N=9	Natural	9.578	3.361
	1 pile	25.99	5.842
	4 piles	20.393	5.688
	16 piles	16.571	3.821
	Random	11.551	3.365
<i>P. maricopa</i> N=9	Natural	13.035	3.881
	1 pile	21.942	6.746
	4 piles	27.55	6.568
	16 piles	16.187	4.412
	Random	15.772	3.885
<i>P. rugosus</i> N=9	Natural	9.238	3.229
	1 pile	20.547	5.613
	4 piles	19.829	5.465
	16 piles	9.813	3.671
	Random	11.669	3.233
Combined species	Natural	10.617	2.022
	1 pile	22.827	3.514
	4 piles	22.591	3.422
	16 piles	14.190	2.299
	Random	12.998	2.024

*Based on modified population marginal means. Discovery times are calculated as the total time in minutes from the start of the observation to the retrieval of the first seed for each distribution.
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Table 3. Mean* discovery times.

We focus our analysis on the foraging rate, which measures the foraging efficiency once an ant knows the location of one seed from a distribution. We calculated

the foraging rate for each distribution by dividing the number of seeds collected from that distribution by the time elapsed between the collection of the first and last seeds of that distribution.

The foraging rate on randomly scattered bait seeds served as a baseline seed collection rate for each colony during each foraging period. We therefore calculated a *normalized rate* by dividing the foraging rate of each piled distribution by the foraging rate of randomly scattered seeds for each observation. This ratio allowed us to quantify how much faster clumped seeds were collected relative to randomly scattered seeds and to compare foraging rates across variable colony activity levels, conditions and colony sizes. In order to correct for skew in our field data, we log₂-transformed the normalized rates to obtain a normal distribution.

We analyzed both foraging rates and log₂-transformed normalized rates using repeated measures general linear model (SPSS PASW Statistics,R.18.0.1). Repeated measures analysis accounted for the non-independence of multiple measures taken of a single focal colony. Repeated measures also provide greater statistical power in this case by controlling for variation in activity level among our focal colonies, allowing us to distinguish within- and between-subject effects. We included species as a between-subject factor in these analyses. We use the resulting estimated marginal means to account for the influence of the independent variables (species and seed distribution) on our dependent variable (log₂-transformed normalized rate).

Results

We estimated an active forager population (mean \pm standard error) of 71 ± 341 for *P. desertorum*, 269 ± 185 for *P. maricopa*, and 356 ± 211 *P. rugosus* in our 2009 study. The *P. maricopa* and *P. desertorum* estimates are similar to those estimated in earlier years at the Sevilleta NWR (Table 1), but the *P. rugosus* estimates are significantly lower in our experimental study in Albuquerque in 2009.

The test for bias in the collection or observation of bait seeds of different color showed no bias by color in the order of arrival of seeds at the focal nests (Kruskal-Wallis test: $n=802$ seeds; $p=0.59$).

Figure 2 shows the cumulative number of seeds collected over time for each distribution in one field experiment. The graph depicts a single typical experiment in which dispersed (blue and green) seeds are discovered faster than clumped (red and purple seeds). The x-intercept measures the time it took for each distribution to be found. These discovery times were unaffected by species identity ($p > 0.05$), but not surprisingly, were longer in the more clumped distributions across all species ($p = 0.002$, Table 3).

Averaged over all species, discovery times for blue (13.00 ± 2.02 minutes) and green seeds (14.19 ± 2.23 minutes) were indistinguishable, and discovery times for red (22.83 ± 3.51 minutes) and purple seeds (22.59 ± 3.42 minutes) were indistinguishable.

Once an ant discovers the location of an experimental pile, the time for a forager to search for additional seeds from that pile is negligible. Our analysis focused on the foraging rate: the rate at which ants collect seeds from a distribution once they have discovered a pile in that distribution. We measured foraging rates of naturally occurring

seeds as well as rates for each colored seed distribution (Table 4). The mean foraging rates for natural seeds are similar to those for our baits, indicating that our measured rates are not an artifact of baiting the ants with extraordinary amounts of food. Figure 3 shows the foraging rate for the piled, randomly distributed, and naturally occurring seeds collected during our field observations.

Repeated measures analysis shows a significant difference in foraging rates between species ($p<0.001$) indicating that species with larger colonies have greater absolute foraging rates 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 (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 high variation, foraging rates are not significantly different between distributions for *P. maricopa*.

The colored bars in Figure 4 show the normalized rates: the foraging rate from each of the three piled distributions divided by the foraging rate for randomly distributed seeds. Data were log-transformed to obtain normal distributions (Shapiro-Wilk test: $p>0.102$ after transformation). After log₂-transformation, a value of 0.0 for normalized rates 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. Repeated measures analysis of the log-transformed normalized foraging rates revealed no effect of species ($p = 0.463$), but a significant effect of distribution on normalized rates

within species ($p < 0.003$). According to paired t-tests, normalized rates for 4-pile (purple) and 16-pile (green) distributions are significantly different from the 1-pile (red) distribution for *P. rugosus* ($p = 0.028$ and 0.021 , respectively) and for *P. desertorum* ($p=0.001$ and 0.15 , respectively). As is the case with foraging rates, normalized rates are not significantly different between distributions for *P. maricopa*.

Because we found no effect of species on the normalized foraging rates, we combined data from all three species and found that the normalized foraging rates declined significantly from the largest (red) piles to the more dispersed (purple) piles ($p = 0.004$) and green piles ($p < 0.001$). The combined marginal means \pm standard error of log₂-transformed normalized rates are 1.2 ± 0.2 , 0.5 ± 0.2 and 0.3 ± 0.1 for 1-pile, 4-pile and 16-pile distributions of seeds respectively. These log₂-transformed rates indicate that foraging rates decrease as seeds are more clumped such that seeds are collected roughly twice as fast from piles that are 4 times bigger. Pairwise comparisons between distributions for combined species show a significant difference (paired t-tests: $p < 0.004$) between 1-pile (red) and the more dispersed distributions. Table 4 summarizes the marginal means for foraging rates and normalized foraging rates for all species and distributions.

Species	Distribution	First seed to Last Seed		Start-time to Last Seed	
		Mean	SE	Mean	SE
<i>P. desertorum</i>	Natural	0.610	1.292	0.569	0.826
N=9	1 pile	0.683	0.485	N=15	0.249
	4 piles	0.316	0.266		0.138
	16 piles	0.350	0.123		0.173
	Random	0.314	0.095		0.235
	Total	2.273			
<i>P. maricopa</i>	Natural	3.286	1.218	3.025	1.066
N=9	1 pile	1.018	0.457	N=9	0.650
	4 piles	0.842	0.251		0.367
	16 piles	0.485	0.116		0.383
	Random	0.429	0.090		0.328
	Total	6.060			
<i>P. rugosus</i>	Natural	3.696	1.218	3.591	0.887
N=9	1 pile	3.436	0.457	N=13	2.340
	4 piles	1.726	0.251		1.438
	16 piles	1.490	0.116		1.345
	Random	1.005	0.090		1.080
	Total	11.353			
<i>Measure: Normalized foraging rates</i>					
<i>P. desertorum</i>	Natural	2.555	8.142	4.289	5.858
N=9	1 pile	2.491	1.352	N=15	1.325
	4 piles	1.175	0.426		0.638
	16 piles	1.177	0.195		0.868
<i>P. maricopa</i>	Natural	17.041	8.142	18.654	7.562
N=9	1 pile	4.072	1.352	N=9	3.182
	4 piles	2.361	0.426		1.392
	16 piles	1.320	0.195		1.328
<i>P. rugosus</i>	Natural	4.190	8.142	4.102	6.292
N=9	1 pile	3.614	1.352	N=13	2.550
	4 piles	1.790	0.426		1.373
	16 piles	1.582	0.195		1.494
Combined species	Natural	7.929	4.701	9.015	3.817
N=27	1 pile	3.392	0.781	N=37	2.352
	4 piles	1.775	0.246		1.135
	16 piles	1.360	0.112		1.230
	Total	11.353			

*Based on modified population marginal means. Total collection time used to calculate the rates is measured from first seed to last seed of each distribution and from the time the observation starts to last seed of each distribution.

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Table 4. Mean* foraging rates and normalized rates for each seed distribution.

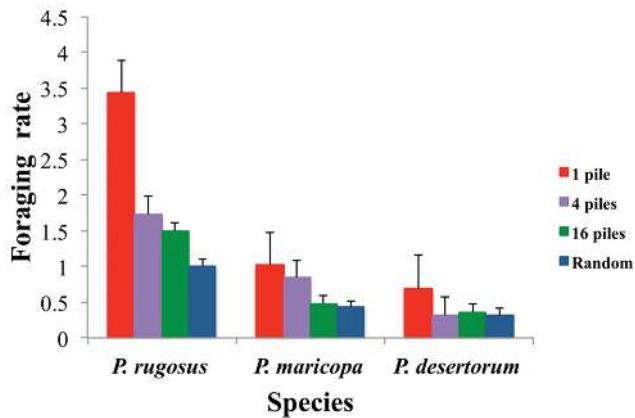


Figure 4. Normalized foraging rates. Bars indicate *normalized rates* (foraging rate on piled seeds divided by foraging rate on random seeds) for three distributions for three species depicted separately and combined. A value of 1 indicates that seeds from a piled distribution are collected at the same rate as randomly distributed seeds. Asterisks indicate significant differences of the single pile distribution rates with all other rates within the same species. Error bars are standard errors.

Discussion

We observed foraging by three sympatric species of *Pogonomyrmex* on experimentally manipulated seed distributions and quantified the effect of seed distribution and forager population size on foraging rate. Not surprisingly, more-clumped distributions were collected faster by all ant species (Figure 4), suggesting that all species reduced foraging times on clumped distributions, minimizing the cost of searching for seeds. However, given theoretical differences in foraging strategies in larger colonies

(Anderson and McShea 2001; Beckers et al. 1989; Bourke 1999; Sumpter 2006; Wilson and Osborne 1971), we were surprised to find no evidence that colonies with large forager populations collected clumped seeds relatively faster than smaller colonies.

All ant species systematically increased foraging rates on seeds in more clumped distributions. Foraging ratios for each piled distribution increase from 0.3 to 0.5 to 1.2 as the clumpiness of the distribution decreases from 1 pile, to 4 piles and to 16 piles. Seeds are collected roughly twice as fast from piles that are 4 times bigger. So, the ants exploit the distributions that are more clumped to improve whole colony foraging intake. However the increase in foraging rate with pile size is slower than we expected — piles that are much bigger are collected only slightly faster.

The rate at which ants collect seeds is a function of two processes — the time for the ants to discover seeds from a distribution and the time it takes to collect a distribution once it is found. For all species, the time to discover more dispersed (green and blue) seeds was faster than the time to discover more clumped (red and purple) seeds. However, once those piles were discovered, clumped seeds were collected significantly faster than the dispersed seeds. We analyzed the rate at which ants collected seeds from each piled distribution relative to randomly scattered seeds and this normalized foraging rate indicated how much faster foraging occurs once a colony knows the location of one seed from a distribution. The normalized foraging rate also accounts for differences in the number of active foragers in a given day and allowed us to make comparisons across species and conditions that varied widely.

Not surprisingly, colonies with more foragers collected a larger total number of seeds (Figure 3). However, repeated measures analysis showed no effect of species

(which vary significantly in forager population size; see Table 1) on normalized foraging rates. Because prior work suggests that larger colonies are more likely to use some form of group recruitment, we expected that large colonies might be disproportionately good at collecting seeds from large piles. However, colonies collected seeds from large piles faster than seeds from small piles, regardless of colony size. This study suggests that large and small colonies of *Pogonomyrmex* allocate relatively similar numbers of foragers to large piles to collect them faster. Figure 4 shows that the increase in foraging rate with pile size is indistinguishable for large and small colonies. However, these results should be interpreted in the context of our study design.

We controlled for colony territory size and for the distance that foragers travel to look for food by placing seeds closer to smaller colonies, giving large and small colonies equal opportunity to access the seed piles. However, this resulted in a higher density of piles in the territories of species with small colonies compared to the density of piles for larger colonies. In natural settings, it is possible that large colonies more often exploit large piles because their larger territories contain more large piles.

Our study does not reveal the specific foraging behaviors that these ants employ to collect clumped seeds faster, but we do suggest that two strategies are plausible. Clumped seeds in our study could have been collected faster by group recruitment, or they may be collected faster as a result of a behavior called site fidelity.

Bigger piles are collected faster with group recruitment because more ants are attracted via pheromones to forage from bigger piles. If the ants in our study were using group foraging, it would be surprising that larger colonies do not recruit more ants to the larger piles, since previous work on other ant species that shows that large colonies with

large numbers of ants and sophisticated communication networks recruit more effectively (Anderson and McShea 2001; Beckers et al. 1989; Beverly et al. 2009). It is possible that the ants in our study do use some sort of group recruitment, but allocate only a small number of additional foragers to collect from even very large piles. If large and small colonies each allocate a similar small number of foragers to collect from large piles, this could explain why large and small colonies forage equally fast on large piles.

Some have hypothesized that seed harvesters rarely recruit in nature because seeds are distributed heterogeneously over time rather than over space (Fewell 1990; Gordon 1991). Further, *Pogonomyrmex* use a site fidelity behavior--foragers repeatedly return to the last place that they found a seed (Beverly et al. 2009; Crist and MacMahon 1991). This foraging behavior allows ants to exploit large piles faster because a single ant repeatedly returning to the same pile reduces its search time. Site fidelity may be sufficient to collect piles of seeds quickly (Beverly et al. 2009; Buchkremer and Reinhold 2008). 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. If ants primarily use site fidelity and not recruitment, then we would expect large and small colonies to be equally capable of collecting large piles faster, as we saw in our field study. However, in the case of a pile so large that the seeds cannot be collected by a single ant in a foraging period, or when seeds might be taken by competitors if they are not collected rapidly, recruitment of other ants to the site may be much more beneficial.

In other work, Letendre and Moses Letendre and Moses (2013) use an agent-based model to show that pheromone recruitment results in increased foraging rates on

more clumped distributions, although that study suggests that pheromone recruitment alone results in lower normalized foraging rates on piles than we observed in our field study. Site fidelity may provide an alternative explanation for how these seed harvesters collect large piles faster. In future modeling work we will explore how the processes of site fidelity and pheromone recruitment may each contribute to the ants' exploitation of seeds in different distributions.

While our findings suggest no differences in foraging strategy among these species, this stands in contrast to descriptions of interspecific variation within *Pogonomyrmex* in foraging strategy in the literature (e.g. Johnson 2000). It is possible that smaller colonies are capable of the foraging strategies that allow them to exploit more densely distributed foods when given the opportunity to do so, even though larger colonies more often have opportunity by virtue of their larger territory size, given random placement of patches of food in the environment.

Further studies specifically designed to measure foraging rate given the same distribution of seeds for all colonies are warranted, particularly since native seed distributions are not adjusted so that more small piles occur closer to small colonies. The effect of colony size might be very different given the same distribution of food for all colonies or given competition for food between colonies of different sizes. Since colony size has profound effects on colony life history (Hou et al. 2010; Shik 2008) and foraging strategy (Anderson and McShea 2001; Jun et al. 2003) this should be a fruitful area for further study.

Our study shows that ants from three *Pogonomyrmex* species systematically increase foraging rates as seeds are clumped into fewer large piles. The species differ

substantially in colony size and forager population, but the increase in foraging rate with colony size is consistent across all three species. The increase in foraging rate on more dispersed distributions is surprisingly slow—roughly doubling as seeds are clumped in 1 versus 4 vs. 16 piles. Other foraging studies, for example Deneubourg et al. (1990), suggest that foragers of heavily recruiting ants converge very quickly on rich resources. This may suggest that seed harvesters, which forage on resources that remain relatively static over the course of a foraging period, spend more time exploring for new seeds rather than exploiting known piles of seeds. Understanding how different species of ants balance the trade-off between exploiting known resources versus exploring for new ones may improve understanding of foraging behavior in other animals that forage collectively.

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CHAPTER 3

USING INFORMATION TO IMPROVE COLLECTIVE FORAGING

Abstract

Organisms constantly process information from their environments. Behaviors that communicate or store information necessarily shape the result of their activities. Communication of information is fundamental for large colonies of social insects to integrate information and organize large numbers of foragers, thus colony size should produce distinct effects on choice of foraging behaviors and the corresponding resource intake patterns. In this study, we analyzed resource intake patterns to test whether species with larger colony sizes use more information-based behaviors than species with smaller colony sizes. Our approach integrates data obtained in the field from three *Pogonomyrmex* seed harvester ant species with distinct colony sizes, and computer simulations that model foraging behaviors. We examined foraging patterns generated by idealized behaviors that rely on recruitment, individual ant memory or a random walk without memory or recruitment. We inferred the likely behaviors used by three species of harvester ants that vary in size. We found evidence for recruitment, but only to large piles by large colonies. Mid size colony foraging was more consistent with site fidelity; and the smallest colonies used random walks even for largest piles.

Introduction

Behavior is a result of the interaction between an organism and information from its environment. Using information is key to adaptive behavior (Danchin et al. 2004), as organisms that acquire information reduce uncertainty about their environment and increase their chance of choosing appropriate behavioral strategies (Schmidt et al. 2010). However, ecological features are constantly changing; therefore, animals must continually gather information when it is available (Dall and Johnstone 2002). Animals can acquire information by interacting with the environment (private information) or through interactions with others (social information) (Danchin et al. 2004). Finally, the continuous interactions between information and resulting individual behaviors in social insects produce a response that is finely tuned to environmental cues.

Ants are known to engage in foraging behaviors that use social and private information, such as site fidelity (Fresneau 1985; Rosengren and Fortelius 1986) or recruitment (Hölldobler 1976). By decreasing the uncertainty of their environment, these well-known foraging behaviors necessarily shape food intake rates by reducing search time when resources are predictable. It is important to note that recruitment by pheromones is not the only form of recruitment. For example, in *Pogonomyrmex* seed harvesters, foragers are stimulated to leave the nest by the return of successful foragers. This positive feedback mediated by the simple encounter rate among ants enables the colony to increase foraging activity in response to currently available food (Schafer et al. 2006).

Colony size has profound effects on foraging strategy (Anderson and McShea 2001). In large groups of animals, the successful coordination of many individuals

depends on their coordination. However, foraging presents a particular challenge to scalability due to substantial travel costs for each ant in large foraging territories. As ants transport resources between a central place and the space of the territory, the work a colony must do to acquire food increases faster than the number of foragers (Moses 2005). To address diminishing returns, communication of information is characteristic of large colonies of social insects, necessary to organize and optimize foraging with larger numbers of foragers (Beckers et al. 1989; Kendal et al. 2005). Due to these increased interactions, larger groups are better than small ones at tracking their environment (Pacala et al. 1996). Therefore, in addition to individual behaviors, a second predictor of foraging patterns is colony size, which we expect will in turn produce distinct effects on choice of foraging behaviors.

Ants increase seed intake rates as seeds are clumped into fewer large piles and raw intake rates vary significantly between species. However, when we compared normalized foraging rates (foraging rates from piled seeds relative to randomly dispersed seeds), we found no significant difference between species (Flanagan et al. 2012). This stands in contrast to descriptions of interspecific variation within *Pogonomyrmex* in foraging strategy (e.g. Davidson 1977; Johnson 2000), and in contrast with the hypothesis that larger colonies must use more communication to organize foraging with larger numbers of foragers (Beckers et al. 1989). Further, the study did not reveal the specific foraging behaviors that ants use to collect clumped seeds faster, but suggested that two strategies are plausible: clumped seeds may be collected faster than dispersed seeds by ants sharing information through forager recruitment, or as a result of site fidelity. It is

also possible that a combination of the two behaviors leads to faster collection of clumped seeds.

We asked whether species with large colony sizes use more information-based behaviors than species with smaller colony sizes. Since colonies with a larger number of foragers are expected to communicate more than colonies with a smaller number of foragers (Beckers et al. 1989), and we know that seed intake from clustered spatial distributions is faster (Flanagan et al. 2012), we expected larger colonies to use information-based behaviors, in particular, when resources are spatially clustered.. Integrating data from computer simulations and natural field data, we examined the effect of colony size and spatial distribution of resources on seed intake rates, in simulated data, and from field data obtained from three *Pogonomyrmex* species.

In the first part of this study we examined the variation in seed intake patterns over time. If ants were communicating information about the location of food, we expected seed intake rates to increase exponentially over time, and thus, the corresponding time between arrivals to exhibit an exponential decay (Flanagan et al. 2013). In simulations, we compared the fits of linear and exponential regressions to time between arrivals from simulated behaviors to test our hypothesis that exponential patterns represent seed intake rates obtained with recruitment. We additionally tested the arrival time distributions generated by other behaviors, we examined the arrival time patterns in field data and determined which behaviors are consistent with those observed patterns. Additionally, we used a half-life model to examine between-species variation in the rate of decay of time between arrivals.

In a second part of the study, we inferred behaviors in the field from idealized behavior patterns based on how foraging rates changed across spatial distributions of food. We first quantified the information contained in each spatial distribution. We used exponential regressions to model how seed intake rates change with respect to entropy in spatial distributions, and used distinct idealized behaviors to determine the shape of patterns generated by the use of information. We used these idealized patterns to train a machine-learning algorithm implemented specifically for this study. We then inferred behaviors in the field by assessing the similarity of field resource intake patterns to patterns from simulated data.

Characterizing foraging behavior

Throughout the study, we used exponential models to examine the relationship patterns between seed intake rates, behavior and colony size. We then use the parameters from those models to train a machine-learning algorithm to relate seed intake rates to different behaviors and colony sizes.

We chose to model changes in foraging rates using exponential models because they represent the underlying foraging process well. Forager recruitment involves a process where each ant increases productivity by engaging the work of other nestmates. Thus, exponential decay in ant arrival times suggests a positive feedback loop (Flanagan et al. 2013). Any process of recruitment, for example pheromone recruitment, recruitment through nest interactions (Gordon 2010), or tandem running (Wilson 1959) would exponentially increase the rate of seed intake and decrease the time between each successive seed arrival. If ants were using private information (i.e., memory based

foraging strategies such as site fidelity) to remember the location of food, we expected seed intake rates to increase linearly over time. If ants arrived at the baits by chance (without relying on remembered or communicated information) the time between successive arrivals to the nest with seeds would remain the same throughout the experiment.

Foraging patterns are typically shaped by complex interactions among individuals and by external factors. Although humans are uniquely gifted at recognizing patterns, it is in fact a very complex process (Duda et al. 2012), often exacerbated by noisy and sparse data. These methodological difficulties often lessen our ability to analyze identify all variables involved in complex system interactions and impede our ability to recognize underlying mechanisms (Nathan et al. 2008; Spiegel et al. 2015). Such is the case with foraging patterns from ants in the field. Fuzzy logic, which originated from fuzzy set theory (Zadeh 1965), is used to predict the probability of data similarity with non-exact matches. Here, we addressed this challenge by implementing a well-known machine-learning algorithm based on fuzzy logic for pattern recognition. Fuzzy Pattern Matching (Mouchaweh 2004; Mouchaweh et al. 2002) allowed us to leverage the speed of computers, and the law of large numbers to learn from many examples of idealized simulated behaviors and compare learned representative patterns to patterns from noisy and sparse data from field studies.

Materials and Methods

Field data

We used field data from 21 colonies from three *Pogonomyrmex* species, with known average colony sizes. Johnson (2000) estimated total colony population sizes as thousands for *P. rugosus*, a few hundred for *P. Maricopa*, and fewer than 100 for *P. desertorum*. In our field study we estimated forager populations (not total colony size) from these same species as (mean \pm standard error) of 71 ± 341 for *P. desertorum*, 269 ± 185 for *P. maricopa*, and 356 ± 211 *P. rugosus*. Ants foraged on a distribution of seed baits arranged as a power-law distribution. Table 1a describes the experimental setup. See Chapter 2 of this dissertation (Flanagan et al. 2012) for further explanation on experimental setup and methodological details.

Simulated data

To generate data for idealized behaviors, we used software developed by Hecker et al. (2012) that simulates foraging using a set of agent-based models (ABMs) of 80 foragers on a 280 x 280 grid, with parameters optimized by a genetic algorithm (GA). The parameters specify how ants travel from the nest, search, and use site fidelity and communication. The simulation model was designed based on foraging behaviors obtained in the field, described in Chapter 2 of this dissertation (Flanagan et al. 2012). Foraging rates obtained with this model were similar to foraging rates in our field study (Letendre and Moses 2013).

We generated data from simulations optimized for distributions that consist of piles, each pile with equal number of seeds, and pile number determined by dividing the

total number of seeds into piles of some specified size (see Fig. 1a for examples). We generated a second kind of distribution, a power-law distribution, which consisted of several piles, many small piles and a few large piles (see Fig. 1b for an example).

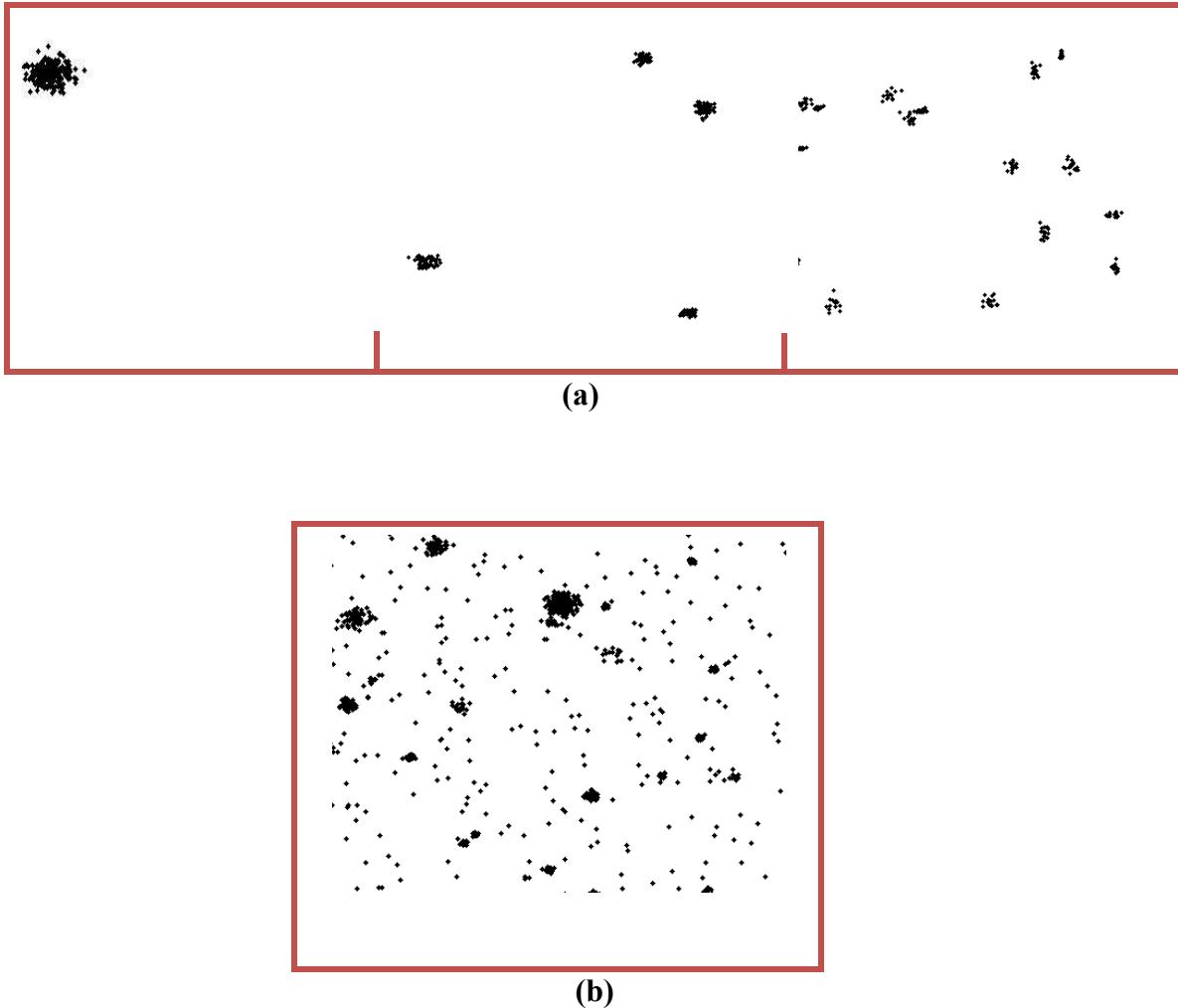


Figure 1. (a) Three examples of distributions with piles that contain the same number of seeds. From left to right, 1-pile distribution, 4-pile distribution, and 16-pile distribution.
(b) An example of a power-law distribution of seeds. The piles in a power-law distribution have different numbers of seeds. Power-law distributions contain a large number of piles with few seeds and few piles with a large number of seeds.

We repeated the simulation using each one of four behaviors. The behaviors simulate a correlated random walk (CRW), where ants walk randomly on the grid but exchange no information. The remaining three behaviors add features to the CRW: site fidelity (SF), where foragers remember the position where they last found a resource, and return to it; forager recruitment (PH) in the model is implemented as virtual communication that is not actually used by ants. Food locations are communicated as an x- y- coordinate location in space to ants as they leave the nest. This could represent any kind of recruitment in which one forager guides another to a location in space (for example, pheromone recruitment, or tandem running). The fourth foraging behavior used both SF and PH together. We parameterized each behavior based on optimizations for seven different distributions of seeds (Table 1b), following methods described in (Hecker and Moses 2015).

Variation between spatial distributions

Using simulated and natural data, we verified that our data sets were not randomly distributed. We used a Chi-square test to evaluate the goodness of fit of a Poisson curve to the frequencies of time between arrivals. The tests rejected the hypothesis of data being consistent with Poisson distributions ($p < 0.001$), suggesting that arrival rates have a pattern different than would be generated by a random process. We used exponential and linear regressions to examine how time between arrivals changed over time. The time between arrivals at the nest was the dependent variable and the cumulative number of new arrivals at the nest was the independent variable.

(a) *Field setup. Power-law distribution of seeds.*

Total seeds per experiment = 256,128; N=37

	<i>P. rugosus</i>			<i>P. maricopa</i> and <i>P. desertorum</i>		
Number of seeds	256	256	256	128	128	128
Number of piles	1	4	16	1	4	16
Number of seeds in each pile	256	64	16	128	32	8
Shannon entropy	0	2	4	0	2	4

(b) *Simulation setup. Distributions of seeds with piles of equal size.*

Total seeds per experiment = 1280; N=400

Number of seeds	1280	1280	1280	1280	1280	1280
Number of piles	1	4	16	32	80	320
Number of seeds in each pile	1280	320	80	40	16	4
Shannon entropy	0	2	4	5	6.3219	8.3219
						10.3219

(c) *Simulation setup. Power law distribution of seeds.*

Total seeds per experiment = 1280; N=4000

Number of seeds	256	256	256	256	256
Number of piles	1	4	16	64	256
Number of seeds in each pile	256	64	16	4	2

Table 1. Experimental setup for simulations and field experiments. Experiments use four behaviors, correlated random walk (CRW), site fidelity (SF), forager recruitment (FR) and a combination of site fidelity and forager recruitment (SF+FR). We used each behavior once on each of (a) seven distributions of seeds and once on (b) one power-law distribution, obtained by dividing 1280 seeds into five distributions with piles of different sizes, placed simultaneously. Field experiments were conducted on a power-law distribution of seeds. Section (c) shows the distribution for each species of ant.

We examined the time between successive arrivals to the nest, for each spatial distribution, for simulated and natural data. We knew the behaviors that generated

simulated data, and the colony size of natural data. For each combination of behavior and spatial distribution in simulated data, we examined the time between arrivals over time. To compare linear and exponential regressions, we used the average model performance error, root-mean-square error (RMSE) as a measure of goodness of fit. Since RMSE measures an average error, lower values indicate a better fit. RMSE values have the same units as the dependent variable; therefore, the values should be interpreted accordingly.

Variation between species

We repeated the process for each combination of species (with different characteristic colony sizes) and spatial distribution on natural data. From results for simulated data with known behavior, and results for natural data with known colony size, we inferred behaviors in the field.

Half-life model

Our previous analyses showed that time between arrivals of successive seeds, as a function of cumulative seed arrivals, followed an exponential relationship. Cumulative number of seeds was our independent variable, and time between seed arrivals was our dependent variable. To study the change in seed intake rate from a different perspective, we used a half-life model to describe the change in time between arrivals of seeds as a function of time, instead of cumulative seed arrivals. Time between arrivals of seeds continued to be our dependent variable, but now *time* was our independent variable. To analyze between-species variance, we compared half-life values calculated for each species using a non-parametric two-sample Kolmogorov-Smirnov test.

In exponential models, half-life ($t_{1/2}$) is the period of time required for an initial quantity to decrease to half its initial value. This period is independent of initial quantity or initial time, and it represents a rate of decay.

Let $Y=Ae^{-Bt}$ represent the exponential decay of Y over time t . If we calculate the time at which an initial value Y_0 will decay to half of its value, we have

$$\frac{Y_0}{2} = Y_0 e^{-Bt}$$

Solving for t , we obtain the half-life for Y , $t_{1/2} = \frac{\log 2}{B}$, which is independent of time, and independent of initial value Y_0 .

The period of time between when the dependent variable has a value V_0 and when it decreases to half $V_0/2$ remains constant. For example, if at an intial time $T_0=10$ minutes, the time between arrivals was $V_0=50$ seconds, and at $T_f=20$ minutes, the time between arrivals was $V_f=25$ seconds, we can expect that after another similar period of time, $T_f - T_0=10$ minutes, the time between arrivals will halve again to $V_f/2=25/2=12.5$ seconds. This constant time period $T_f - T_0$, the time between T_0 , when the value of the independent variable is V_0 , and T_f , the time when that value of the independent variable is $V_0/2$, is what we call half-life ($t_{1/2}$). If we count the number N of times any value V_0 halves during a certain amount of time T , and divide that time into N parts T/N , we can obtain the half-life of that variable (Fig. 2).

Large half-life periods represent exponential models with slow decay and small half-life periods represent exponential models with fast decay. The advantage of the half-life metric is that it is a single number averaged over multiple experiments which allows the rate of exponential decay can be compared across colony sizes and seed distributions.

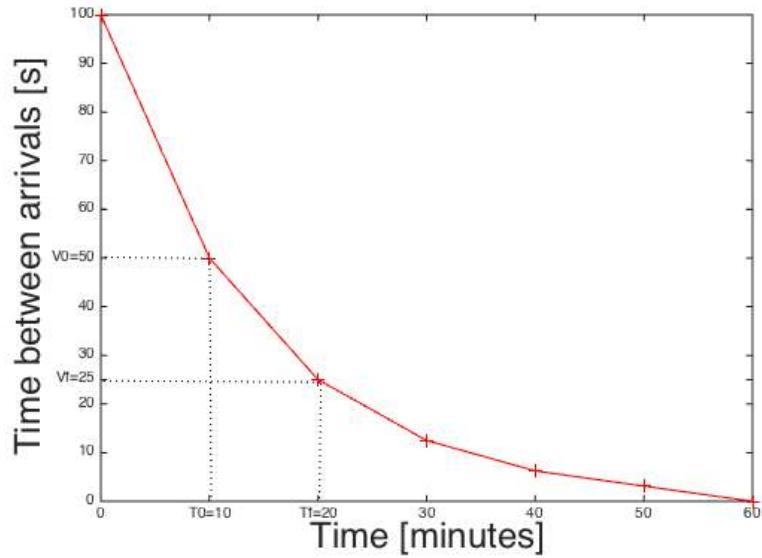


Figure 2. Example of a half-life model with half life = 10 minutes. As the time between arrivals (dependent variable) halves from $V_0=50$ to $V_f=25$, the period on the independent variable during which this happens $T_f-T_0 = 10$ remains constant. For example, when the time between arrivals halves from 50 to 25, the period of time during which this happens is 10 minutes, from minute 10 to minute 20. When the time between arrivals halves again from 25 to 12.5 the period during which this happens is again 10 minutes, from minute 20 to minute 30. This constant period of time is what we call half-life. To calculate the half-life value, we can count the number of times a value is halved N and then divide the total time T by this number. For example, 100 is halved 4 times before it reaches a value of 6.25 at 40 minutes. $T/N=40/4=10$. The half-life value for this model is 10.

To calculate the half-life of each distribution we followed these steps:

- a. We defined initial activity as the time between the first and second arrival of seeds. The time between the first and second arrivals will be, on average, the longest interval between seed arrivals.
- b. We divided the initial activity by two, and successively halved that result until the value equaled the minimum time between two successive arrivals in that distribution. We keep count of the number of times we divided the initial activity.
- c. By dividing the total collection time by the number of divisions, we obtained the half-life value that represents the exponential decay of time between arrivals for that distribution.

Use of spatial information

Each seed pile in a distribution contains information. Once an ant discovers a pile, that ant knows the location of seeds in that pile. That location information can be shared (in recruitment) or remembered (in site fidelity), which eliminates search time in subsequent foraging trips. To determine how information in spatial distributions shapes seed intake rates, we characterized information in the spatial distribution of seeds by using Shannon information theory, following the concept used in Flanagan et al. (2011).

We modeled the relationship between spatial distribution and average intake rate through exponential regressions. To uncover behavior patterns, characteristic of different colony sizes, we used these exponential models to train a Fuzzy Pattern Matching

algorithm (Mouchaweh 2004; Mouchaweh et al. 2002). We implemented the algorithm in Matlab R2015b and compared natural behavior patterns to simulated foraging patterns by assessing pattern similarity to one or more behaviors

Information in spatial distributions

To characterize information in spatial distributions, we used Shannon entropy, which provides a metric that relates the clustering in spatial distributions with information available in that distribution. We used Shannon entropy to measure the number of bits of information the ants obtain once they find one pile from a distribution. We calculated the Shannon entropy of spatial distributions as

$$H(p) = - \sum_i p_i \log_2 p_i$$

where p_i is the probability of a single resource being in the i^{th} pile. Once a pile is found, the location of all seeds in that pile is known.

Entropy also measures the amount of uncertainty in a distribution (Cover and Thomas 2012). The uncertainty left about the position of the remaining seeds in the distribution increases as the seeds are scattered in a larger number of piles. For example, in a distribution with one pile, the location of all resources is known once the pile is found, so the entropy of the distribution is zero. When all resources are randomly distributed, finding one seed does not decrease the uncertainty of the location of other seeds. In this case, the entropy or uncertainty of the distribution is at its maximum.

Clustered distributions offer information about the location of more seeds to the ant that discovers the pile. We expected that communication of information about the location of resources would produce an exponential increase in foraging rates as ants

exploit that information in clustered distributions. On the other hand, discovery of the location of one seed in a random distribution offers no information about the location of other seeds; thus, we expected random distributions to produce no exponential increase in foraging rates. To examine the relationship between foraging rates and clustering, measured as Shannon entropy, we calculated the percent improvement of intake rates for each distribution over intake rates for a random distribution. We obtained the percent improvement by dividing all seed intake rates by the intake rate from randomly distributed seeds in the same experiment. We then modeled the change in foraging rates versus Shannon entropy using exponential regressions.

Information use and colony size

A pattern is a set of features, individual measurable properties that describe a phenomenon (Bishop 2006). Therefore, a foraging pattern is a set of variables that describe the foraging dynamics of the system that we are studying. We chose seed intake rates to describe the foraging patterns in our study, and modeled the change in seed intake rates with respect to Shannon entropy with exponential regressions. We defined these models as foraging patterns and the parameters that describe them as features.

Fuzzy pattern matching is the implementation of fuzzy set logic (Zadeh 1965), which allows us to score the likelihood of a pattern being similar to another. Fuzzy logic is useful to predict the probability of similarity in patterns with non-exact matches. In this study, we seek to compare simulated and natural foraging patterns. We modeled the change in seed collection rates as exponential regressions using time between seed arrivals as the dependent variable, and entropy as the independent variable. For field

data, we have only four data points (4 different pile sizes with 4 different entropy values) with which to calculate each regression. While this is a small number of data points for each regression, Fuzzy Pattern Matching allowed us to leverage the large number of simulated regressions to obtain representative models and assign similarity scores to the patterns we obtain from natural data.

We used the fuzzy pattern-matching algorithm to compare patterns generated by behaviors in simulations to natural foraging patterns. Fuzzy pattern matching involves three steps. First, we selected features that best describe our data; second, we trained the algorithm by constructing model classes with those features, and third, we compared features in natural data with our model features, and assigned scores from 0 to 1 to each natural experiment according to its similarity to each model class. See Mouchaweh et al. (2002) for a detailed description of the approach.

We measured average seed intake rates from simulations on a power-law distribution of seeds, similar to the field setup. We used the simulation model with each of four behaviors, correlated random walk (CRW), site fidelity (SF), forager recruitment (FR) and a combination of site fidelity and forager recruitment (SF+FR). We generated data for each behavior in combination with parameters optimized for seven different distributions of seeds (Table 1c).

To construct behavior classes for pattern matching, we modeled the relationship between seed intake rates and spatial distributions with exponential regressions of the type $Y = Ae^{Bx}$, where y is the time between arrivals and x is the Shannon entropy calculated for each distribution. We conducted a total of 1000 simulations for each of four behaviors, for a total of 4000 simulations. We selected the exponential parameters A

and B as features representative of each behavior class. Thus, the learning set for each parameter contained four behavior classes: correlated random walk (CRW), site fidelity (SF), forager recruitment (FR) and the combination of site fidelity and forager recruitment (SF+FR), characterized by the distribution of values for A and for B . The larger the frequency of a parameter value, the more representative that parameter is of that class.

We calculated our model patterns by constructing histograms, one histogram for feature A and one histogram for feature B . To compute the histograms, we divided the complete interval of feature values into b bins of equal width w as $b = \frac{f_m - f_0}{w}$ where f_m is the maximum value of the feature value interval, f_0 is the minimum value of the same interval and w is the width of the bin. The height of each bin is the number of occurrences within that interval. To normalize the histograms, we divided the height of each bin by the maximum value in the same bin, so the largest bin will have a value equal to one. Each histogram represents a class. We then created a membership function f for each class by joining histogram bin point centers; these are the membership functions for each class.

To classify natural patterns, we calculated membership scores by using interpolation to evaluate each membership function f at every new point p that we wish to classify. We interpret a membership score $s=f(p)$ as the degree of compatibility of the new sample with the most representative examples of a class. The membership score is a linear weighting between competing classes based on its distance to the most likely features, represented by the bin with a height of one. To calculate global membership scores for each experiment, we average all scores for each behavior class, so each

experiment has four final scores. Each score describes how close the evaluated pattern is to the most representative models of one of four classes. Small numbers represent a very unlikely match, while large numbers represent a very close match. We defined each score as a weight proportional to the value of the score. Using this reasoning, we calculated the sum of membership scores for each behavior within a species, and visualized them in bar plots, one bar for the added weights of one behavior. The height of each bar is the weight that supports the hypothesis that a behavior is used by that species.

Results

We asked whether species with large colony sizes use more information-based behaviors than species with smaller colony sizes. The results below suggest that information-based strategies are used more by larger colonies in clustered resource distributions, consistent with our initial hypothesis.

Variation between spatial distributions

In simulations, recruitment provided a decrease in time between arrivals when seeds were clustered in few piles but not when those seeds were distributed randomly (Fig. 3a, Fig 3b, rows 1,2). Both site fidelity (SF) and recruitment (PH) have declines in arrival rates. However, recruitment is best modeled by an exponential decline, suggested by lower RMSE in distributions of 1 and 4 piles (Fig. 3a, col. 2, rows 1,2); and site fidelity (SF) is best modeled by a linear decline, as suggested by negative linear slopes in distributions of 1, 4 16 and 32 piles (Fig. 3a, col 3, rows 1,2). See Supplemental Table 1

for exponential regression parameters, Supplemental Table 2 for linear regression parameters, and Supplemental Table 3 for goodness of fit values (RMSE).

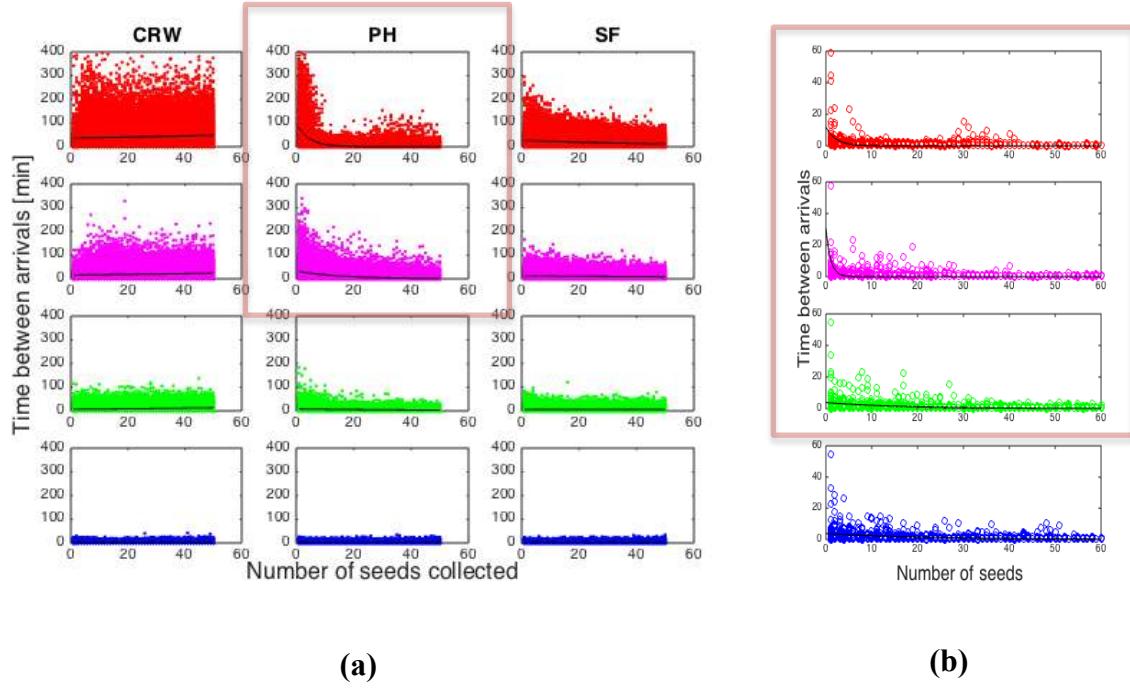


Figure 3. Exponential regressions (black curves) show time between arrivals versus number of seeds collected for spatial distributions obtained with (a) three known, simulated behaviors, and from (b) field data from three species of ants. Each column in (a) shows plots for one of three behaviors, correlated random walk (CRW), pheromone recruitment (PH), and site fidelity (SF). Red colored markers represent a one-pile distribution, purple represents a 4-pile distribution, green represents a 32-pile distribution, and blue represents randomly scattered seeds. Regressions show exponential declines in clustered distributions for both simulated (a) and natural data (b). Exponential declines occur only with recruitment in simulated data; linear declines occur when using site fidelity.

In the case of distributions that are not clustered, seed intake rates over time showed no between-behavior variation. Exponential regressions in these distributions showed no significant decline in time between arrivals; RMSE for exponential regression was not significantly different than RMSE for linear regressions. (Fig. 3a, rows 3,4; see also Supplemental Table 3 for goodness of fit values).

When we combined field data for all species, our results suggested that the exponential decline in arrivals, characteristic of recruitment, occurs only when distributions are clustered. Times between arrivals declined exponentially over time for distributions with 1 and 4 piles of seeds (Fig. 3b). Exponential regressions for natural data yielded better goodness of fit values (Table 2) when compared to linear regressions in clustered distributions, suggesting recruitment. As the distributions increase in entropy (i.e. in distributions with increasing number of piles and decreasing pile sizes), the difference in goodness of fit becomes insignificant. Exponential regressions for all distributions resulted in a better goodness of fit, since RMSE was lower for all exponential regressions compared to RMSE of linear regressions fit (see Supplemental Table 6 for RMSE values of regressions on natural data). However, in distributions with 32 piles and randomly distributed seeds, the difference in goodness of fit between exponential and linear models is less than 0.1 minutes, which makes the regressions indistinguishable considering the accuracy of measurements in the field.

A further examination of regression parameters for simulated data suggests that A and b parameter values for exponential regressions show a large difference only in clustered distributions (Supplemental Fig. 1). Parameter A is larger and parameter B is

smaller when using pheromone recruitment than when using site fidelity or correlated random walks in clustered distributions, suggesting a vertical stretch and thus steeper exponential curves. However, the parameter values asymptote towards the same value as the number of piles increases, suggesting no contribution of information-based behaviors to seed intake rate in random distributions.

(a) Natural data. Exponential regressions $Y=Ae^{Bx}$			
	A	B	RMSE
1	11.9400 (10.2000, 13.6800)	-0.4508 (-0.5242, -0.3774)	2.2192
4	30.9700 (22.4000, 39.5000)	-0.9668 (-1.1900, -0.7436)	3.6476
16	3.8150 (3.2960, 4.3330)	-0.0594 (-0.0731, -0.0457)	2.7408
RND	3.7530 (3.2740, 4.2330)	-0.0457 (-0.0568, -0.0347)	2.8711

(b) Natural data. Linear regressions $y=p1*x + p2$			
	p1	p2	RMSE
1	-0.0088 (-0.0105, -0.0071)	1.3190 (1.1600, 1.4780)	2.3830
4	-0.0157 (-0.0199, -0.0115)	2.026 (1.7140, 2.3390)	3.9133
16	-0.0132 (-0.0168, -0.0097)	1.849 (1.6330, 2.0640)	2.8025
RND	-0.0146 (-0.0179, -0.0112)	2.131 (1.91100, 2.3520)	2.9416

Table 2. Parameters and goodness of fit (RMSE) for exponential (a) and linear (b) regressions of time between arrivals versus number of seeds for natural experiments, all species grouped. Confidence intervals are shown in parenthesis.

Variation between species

We compared exponential regressions to linear regressions to assess between-species variation in times between arrivals of seeds in natural data. The independent variable was number of seeds collected and the dependent variable was time between arrivals. Lower RMSE for linear regressions (see Supplemental Table 6) indicated that they were a better fit to the data (see Supplemental Fig. 2 for plots of exponential regressions, Supplemental Table 4 for exponential regression parameters, and Supplemental Table 5 for linear regression parameters). These results suggested that the decline in time between arrivals was linear. We found that *P.maricopa* and *P.desertorum* had significantly lower slope values, suggesting behaviors more consistent with site fidelity for species with medium and smaller colony sizes (Fig. 4).

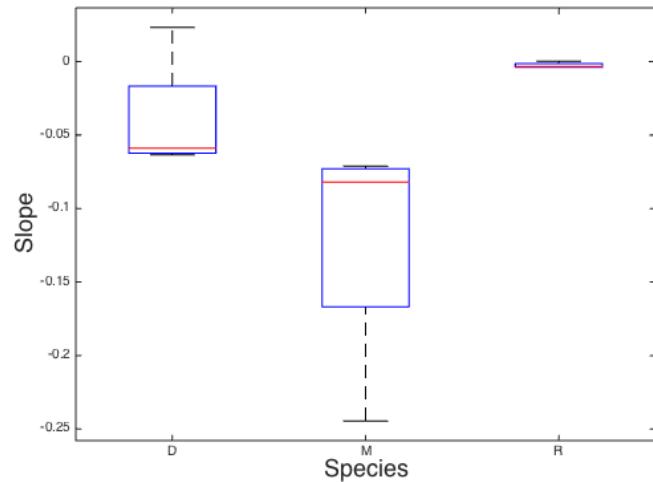


Figure 4. Slopes of linear regressions of time between arrivals versus number of seeds collected for three species, *P.desertorum* (D), *P.maricopa* (M) and *P.rugosus* (R). *P.maricopa* and *P.desertorum* show significant lower slope values than *P.rugosus*, suggesting use of site fidelity.

The linear fit for *P.rugosus* is flat, suggesting that site fidelity does not explain decreases in arrival rates, while the exponential fit is negative, suggesting recruitment can explain decreases in arrival rates, even though the RMSE is lower for the linear fit.

Site fidelity has an impact in seed collection rates only in clustered distributions. This result is demonstrated by slope parameter values that differ when the distributions are clustered, but asymptote towards zero as distributions increase in number of piles, showing that the decline in time between arrivals is insignificant in distributions that are not clustered (Supplemental Fig. 3).

Half-life model

We used a half-life model of times between arrivals to test for between-species variation in times between seed arrivals. Different half-life values represent different rates of decay in times between arrivals as a function of time. We expected larger species to have smaller half-life values, representing faster rates of decline in time between arrivals. We found significant between-species variation in half-lives only in clustered distributions of 1 and 4 piles (Fig. 5), where the half-life for times between arrivals in 1- and 4-pile distributions were significantly lower for the species with largest colony size, *P.rugosus* (2-sample Kolmogorov Smirnoff test, $p < 0.05$). This result provides support for between-species variation in seed collection rates.

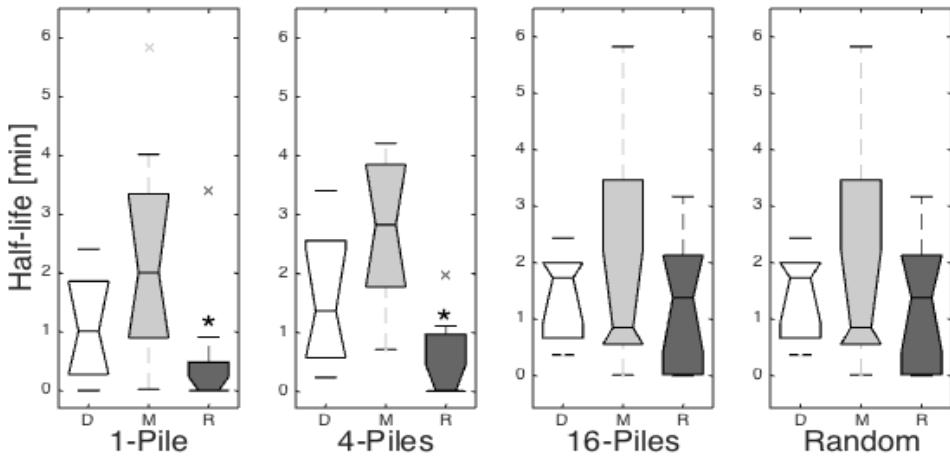


Figure 5. Half-life of time between arrivals. Boxes grouped by spatial distribution: 1 pile, 4 piles, 16 piles and random, and three species. White boxes represent *P.desertorum* (D), gray boxes represent *P.maricopa* (M), and black boxes represent *P.rugosus* (R). Each box represents the interquartile range; the line shows the median. Notches represent 95% confidence intervals around the median. Non-overlapping notches show significant differences between medians. Asterisks show significant differences between *P.rugosus* (large colony size) and the species with medium and small colony sizes, *P.maricopa* and *P.desertorum* in distributions with 1 and 4 piles.

Use of spatial information

Information in spatial distributions

We asked how foraging behaviors affect seed collection rate. We measured seed collection rates for different spatial distributions, quantified by Shannon entropy. For

simulated data, we found that exponential increases in seed collection rates are characteristic of foraging using either of two information-based behaviors, site fidelity and recruitment, when foraging on clustered distributions. On the other hand, using a correlated random walk becomes less efficient as the distribution is more clustered, since finding a pile by chance more difficult.

We used exponential regressions to measure the change in normalized seed intake rates versus Shannon entropy for all combinations of four behaviors and seven spatial distributions. Each distribution was composed of piles with the same number of seeds (distribution described on Table 1b; also see Table 3 for parameter results and regression statistics).

Exponential Regression $Y=Ae^{Bx}$			
	SF	FR	SF+FR
<i>A</i>	5.068	8.212	8.179
(CI)	(4.908, 5.228)	(7.993, 8.43)	(7.968, 8.39)
<i>B</i>	-0.2646	-0.3583	-0.3521
(CI)	(-0.2793, -0.2499)	(-0.3756, -0.341)	(-0.3685, -0.3357)
R^2	0.7428	0.8366	0.8437

Table 3. Parameters and regression statistics for exponential regressions. Time between arrivals generated with information-based behaviors, with respect to correlated random walk. Experiments were conducted on seven spatial distributions (Table 1b), with piles of the same size. Each column represents a behavior. 95% confidence intervals are in parenthesis below the values for each of two parameters, *A* and *B*.

Normalized intake rate obtained by using information-based behaviors decreases exponentially as entropy increases (Fig. 6). Site fidelity shows an exponential increase in efficiency over intake rates from correlated random walk. This difference is at its largest when foraging from clustered distributions. Recruitment shows a greater increase in parameter A, steepening the slope of the curve, an thus increasing seed intake rates as the entropy of the distribution decreases. This result provides evidence that both information based behaviors, recruitment and site fidelity, provide an exponential increase in seed collection rate as the predictability of seed location increases (entropy/uncertainty decreases).

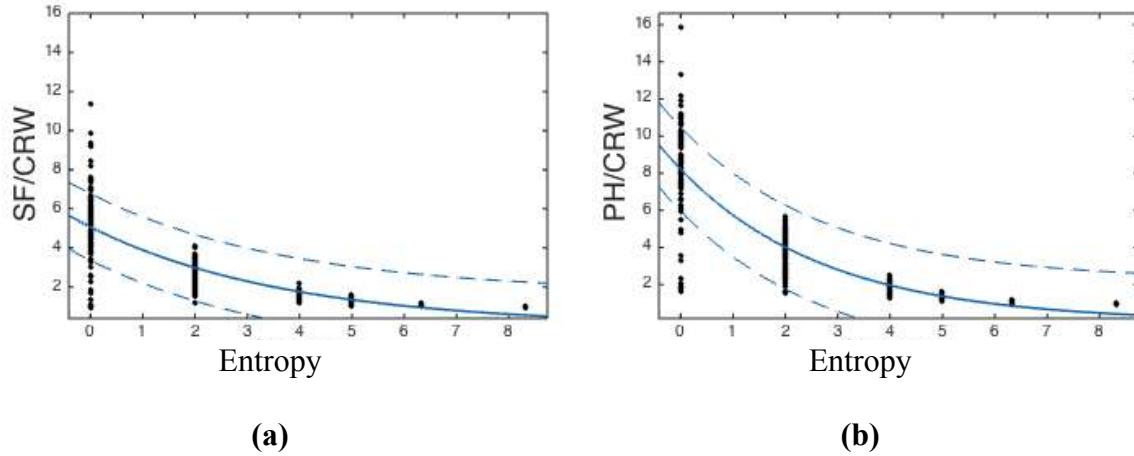


Figure 6. Exponential regressions in the form $Y=Ae^{xB}$ show the percent change in foraging rate versus Shannon entropy compared to that of a correlated random walk for two behaviors, (a) site fidelity (SF) and (b) pheromone recruitment (PH). Simulations were conducted on a power-law seed distribution. Regression is shown as a solid blue line. Dotted lines represent 95% confidence bounds. We do not show the regression plot for site fidelity combined with forager recruitment because there is no significant difference between its regression parameters and those of pheromone recruitment.

Information use and colony size

To match field collection rates from natural data, with known colony sizes, with simulated collection rates from known behaviors, we use Fuzzy Pattern Matching (FPM).

To construct our membership functions, we exponential regression models of the form

$Y = Ae^{Bx}$, where y represents foraging rates and x represents Shannon entropy, for 4000 experiments, 1000 for each behavior. The exponential regressions yielded values for two parameters, A and B . We constructed histograms and membership functions for each exponential parameter (Fig. 7). The membership functions for A show a clear separation between classes that use recruitment, forager recruitment (FR) and the combination of recruitment and site fidelity (SF+FR), and the two classes that do not communicate information, correlated random walk (CRW) and site fidelity (SF). In the same manner, the classes constructed with B only show a clear separation between classes that communicate information and those that do not. Due to numerous intersections between classes, we expect multiple memberships per experiment.

To better examine the details of experiment memberships, we chose to calculate scores for each membership instead of merging the closest classes. We counted the number of memberships scored by each field experiment, calculated the sum of membership scores, and grouped them by species (Fig. 8). We found that the behavior patterns of larger colonies, *P. rugosus* and *P. maricopa*, are consistent with patterns generated by the use of information-based behaviors, site fidelity, recruitment and the combination of recruitment and site fidelity. In contrast, the behavior patterns of *P. desertorum* are consistent with patterns generated by correlated random walks, a behavior that does not store or share information.

Our findings support the hypothesis that larger colonies make more use of information-based behaviors, than smaller colonies. Our study provides support for the use of information-based behaviors, that include site fidelity, recruitment and a combination of both.

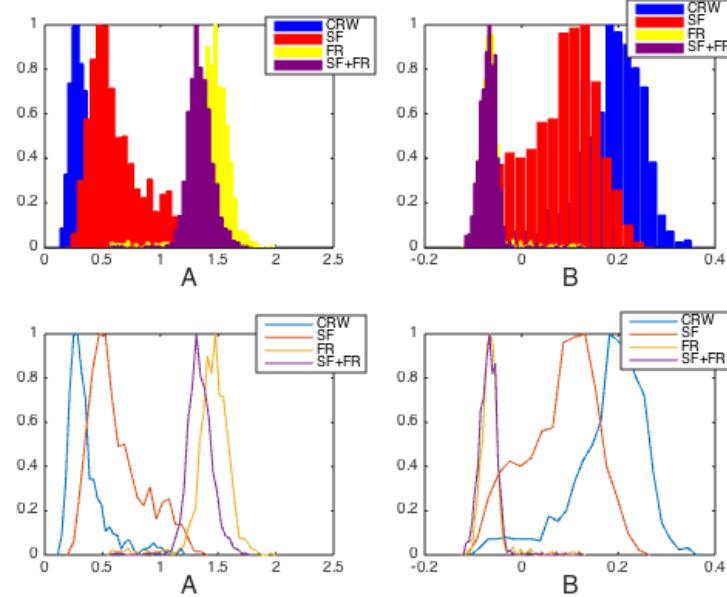


Figure 7. Class histograms and membership functions normalized by dividing each bin by the maximum number of counts. All experiments were conducted on a power-law seed distribution, to mimic field experimental setups. We constructed four behavior classes: correlated random walk (CRW), site fidelity (SF), forager recruitment (FR), and a combination of site fidelity and forager recruitment (SF+FR). The top two panels show the normalized histograms for two features. Histograms for feature *A* are in the left top panel and the histograms for feature *B* are in the right top panel. Each behavior class is color-coded. The bottom two panels show the corresponding membership functions, calculated from the top histograms.

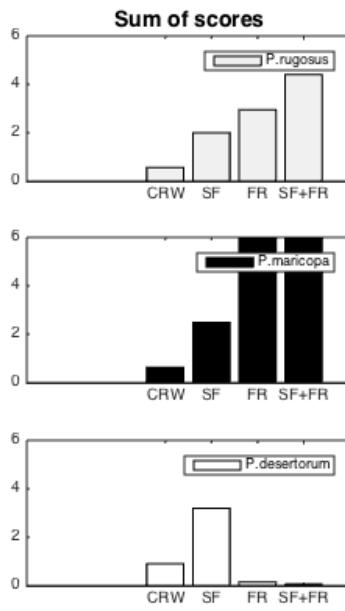


Figure 8. Sum of membership scores for each behavior class, grouped by species.

The species name is noted in the legend. The bars represent the sums of membership scores for each behavior. CRW=sum of membership scores for correlated random walk, SF=sum of membership scores for fidelity, FR=sum of membership scores for forager recruitment, SF+FR=sum of membership scores for site fidelity and recruitment.

Discussion

We asked whether ants from larger colonies use information. We provided evidence that supports the hypothesis that larger colonies use more information-based behaviors.

We determined that recruitment produces exponential decay patterns and that site fidelity produces linear decay patterns in time between arrivals by analyzing patterns from simulated data, generated with known behaviors. When we combined natural data from all species, we found evidence for recruitment by larger colonies in clustered

distributions and evidence for use of site fidelity by smaller colonies. In our analysis, time between seed arrivals decayed when seeds were clustered in only a few piles.

We determined that significant between-species differences exist by comparing exponential decay rate of time between arrivals. We calculated the decay rate for each experiment using a half-life model. Half-life values for time between arrivals were lower for the largest species, *P.rugosus*, in distributions with 1 and 4 piles.

We modeled simulated foraging rates, generated with known behaviors, as an exponential decay of time between arrivals with respect to the Shannon entropy of the spatial distribution of seeds. We quantified the information contained in each spatial distribution using Shannon information theory. Using fuzzy pattern matching, we determined that foraging patterns from larger colonies were more consistent with foraging patterns generated with information-based behaviors, such as site fidelity or recruitment. Computer simulations provided us with data generated with known behaviors and natural data provided us with data from known average colony sizes. Integrating patterns of seed intake rates generated by idealized behaviors with field data, we were able to uncover subtle behavioral patterns from the field, which we couldn't have achieved using either one alone.

Although we knew average colony sizes per species, the variance in field data is enormous and difficult to account for. In our study, some *P.maricopa* colonies seemed at least as large as some of the *P.rugosus* colonies, which accounts for a very large variation in our results, with patterns that align with those for *P.rugosus* in some cases and with *P.desertorum* in others. Further field studies that include more colonies of *P.maricopa* are necessary to reduce variance in the data.

The choice of tools to complex data is fundamental to our ability to detect patterns. Similar to the problem of facial recognition, comparing curves and patterns is a difficult problem; approaches to detect curve similarity are varied and can be complicated. The probabilistic flexibility of a well known machine-learning algorithm, Fuzzy Pattern Matching, allowed us to compare curve shapes non-deterministically and detect behavioral patterns in the field by matching models of seed intake rates from natural data and comparing them to idealized behavior patterns by assigning a score to their likeness. Further, there may be interactions among behaviors, and different behaviors may be used in combination in different environments, making it difficult to identify and classify foraging strategies in field studies. Using computer models and data from field studies we gained insights that can be only obtained with the integration of computer models and field data. Thus, we were able to uncover subtle behavioral patterns in field data that we were unable to see in a previous study (Flanagan et al. 2012).

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CHAPTER 4

FAST AND FLEXIBLE: ARGENTINE ANTS

RECRUIT FROM NEARBY TRAILS

Flanagan, T. P., Pinter-Wollman, N. M., Moses, M. E., & Gordon, D. M. (2013). Fast and flexible: Argentine ants recruit from nearby trails. *PLoS one*, 8(8), e70888.

Abstract

Argentine ants (*Linepithema humile*) live in groups of nests connected by trails to each other and to stable food sources. In a field study, we investigated whether some ants recruit directly from established, persistent trails to food sources, thus accelerating food collection. Our results indicate that Argentine ants recruit nestmates to food directly from persistent trails, and that the exponential increase in the arrival rate of ants at baits is faster than would be possible if recruited ants traveled from distant nests. Once ants find a new food source, they walk back and forth between the bait and sometimes share food by trophallaxis with nestmates on the trail. Recruiting ants from nearby persistent trails creates a dynamic circuit, like those found in other distributed systems, which facilitates a quick response to changes in available resources.

Introduction

Ant colonies operate without central control. The foraging behavior of an ant colony is a collective process (Traniello 1989) with dynamics that vary among species (Beckers et al. 1989). The dynamics that lead to the formation and maintenance of trails determine how well the colony selects and exploits available food sources (Camazine et al. 2001).

Recruitment to food by ants has been studied for many decades (see e.g. Wilson 1962). Early work on recruitment showed that ants accumulate over time at food baits in response to direct and indirect social cues (Detrain and Deneubourg 2009; Gordon 2010), such as pheromone trails (Hölldobler and Lumsden 1980), tandem running (Fernandez and Deneubourg 2011; Franks and Richardson 2006), and interactions among foragers, initiated by the ants that first encountered the food source. Diversity in recruitment strategies is probably related to the diverse ecological conditions in which colonies search for and retrieve food.

The Argentine ant *Linepithema humile* is an invasive species that has spread throughout the world (Carpintero et al. 2005; Rowles and Silverman 2009; Suarez et al. 2001), including northern California (Holway and Suarez 1999; Knight and Rust 1990; Sanders et al. 2001). Colonies are polydomous, occupying at least two spatially distinct nests (Debout et al. 2007). The network of separate nests, connected by persistent trails (Markin 1968; Markin 1970; Newell and Barber 1913), spans up to 200 m² in the summer and contracts to a few large aggregations in the winter (Heller and Gordon 2006). As in many polydomous ant species (Cherix and Bourne 1980), food (Heller et al. 2008; Markin 1968), and brood (Fernandez and Deneubourg 2011) are transported from one

nest to another along the trails (Latty et al. 2011). Argentine ants explore using a search process that links individual path shape to density (Gordon 1995), and lay pheromone trail as they move (Aron et al. 1989). Rapid recruitment to food sources appears to provide Argentine ants with an ecological competitive advantage in its exotic range, because native species tend to retreat from food sources occupied by Argentine ants (Human and Gordon 1999).

Many ant species exhibit central place foraging (Hölldobler and Wilson 1990; Traniello 1989), which may incur substantial travel costs when the foraging area is large, because each ant must travel back to a central nest (Moses 2005). Urban road networks, like ant trails, form branching structures to move individuals and resources. Cities often reduce per capita travel distances by using distributed transportation networks between dispersed locations without reliance on a single central transportation hub, reducing the costs of resource transport (Samaniego and Moses 2008). Similarly, in Argentine ants, recruitment from the pool of workers on nearby persistent trails could reduce travel costs, and increase the speed with which ants accumulate at a new food source. Here we investigate whether Argentine ants recruit nestmates directly from nearby trails. Our field trials test whether Argentine ants recruit workers to new food sources from persistent trails. We observe the recruitment behavior of ants at bait and examine whether recruited ants come from the pool of workers already available on a nearby persistent trail or from a nearby nest (Fig. 1).

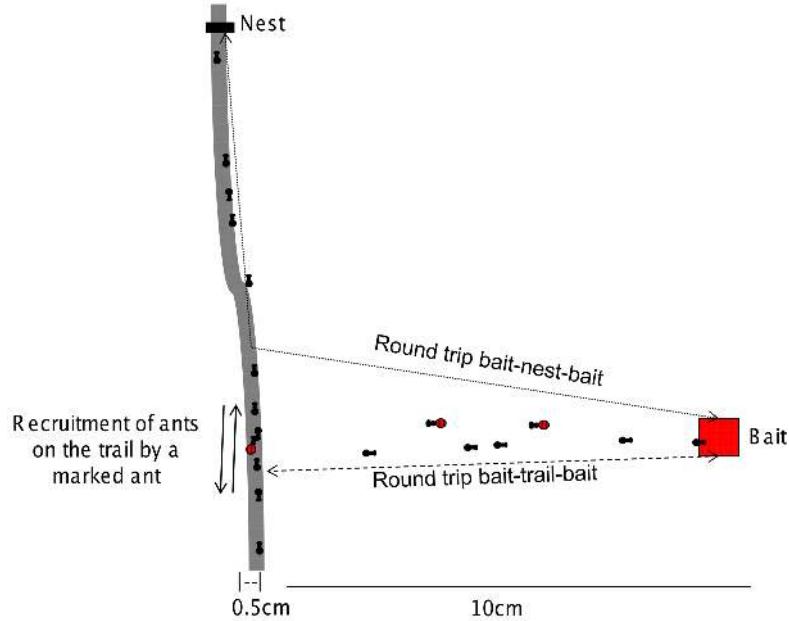


Figure 1. Experimental setup. The sketch represents our experimental setup. The thick gray line represents the persistent trail. The dotted line represents round trips taken by ants from the bait to the nest. The dashed line represents round trips taken from the bait to the trail. Marked ants that drank sugar water form the bait are shown with red, striped abdomens. Note the marked ant on the trail that goes back and forth recruiting nestmates.

Materials and Methods

We studied the foraging behavior of Argentine ants on the Stanford University campus near Palo Alto, California, from May 16–26, 2011. In spring and summer, the mean distance between Argentine ant nests linked by trails is about 15 m (Heller and Gordon 2006). We performed 13 baiting trials on two persistent trails, on opposite sides of a building, with 5 trials for the trail on the West and 8 trials for the trail on the East side of the building. The trails were confined to tight spaces between concrete blocks and

were never wider than 0.5 cm. Here we examine a) whether Argentine ants recruit from the trail and b) demonstrate (quantitatively) how fast this recruitment occurs.

Experimental Setup

Trails were visible in the cracks between large paving stones. For each trial, baits were placed for 90 minutes approximately 10 cm from a persistent trail (Fig. 1). The distance between trail and baits was an experimental constraint imposed by the ants' behavior. We observed that the ants do not reliably find a bait that is more than 0.3 m away from the trail in less than a day. Thus, we chose this distance because ants appeared at the baits at this distance within 12 hours. We recorded all activity during this period. The bait consisted of sugar water in a concentration of 25% sugar to water volume. We saturated a $2 \times 2 \text{ cm}^2$ square piece of cotton in sugar water and placed it on top of a paper towel of approximately the same size. To mark the ants that visited the bait, we added four drops of food coloring (Americolor Soft Gel Paste) to the solution, as in Heller and Gordon (2006).

We filmed the bait for the 90-min duration of each trial using a JVC GZ-HM670 HD Everio Camcorder. An ant was considered to have arrived at the bait when it started drinking from the cotton or paper towel. When an Argentine ant ingests colored water its abdomen swells, making the colored water visible between abdominal segments. We distinguished between arrivals of unmarked ants that had not yet ingested the bait, and arrivals of ants with a colored abdomen that had previously ingested the bait during that trial.

Data were recorded using an iPad app that we wrote called EventLog.

Origin of new arrivals

To investigate whether recruitment occurred from the pool of available workers on the persistent trail or from workers at the nest we followed individual ants as they left the bait. We haphazardly selected 2–7 ants in each trial that were ingesting the bait, and observed the ants as they returned to the trail and then went back to the bait. Only few marked ants were present simultaneously in the area between the bait and the trail, thus there was little chance of confusing the identity of marked ants. We recorded the time it took each ant to reach the trail, the time it spent at the trail, and the time it took to return to the bait.

We defined a ‘bait-trail-bait’ round trip as the time for an ant to go from the bait to the trail and back, and compared this time to the ‘bait-nest-bait’ round trip, the time for an ant to go from the bait to the nearest possible nest location and back to the bait (Fig. 1). We obtained a direct measure of individual ‘bait-trail-bait’ round trip times by following individual ants as they walked from the bait to the trail and back. We call this measure ‘observed’ bait-trail-bait round trip time.

To calculate the ‘bait-nest-bait’ round trip time, we first measured the speed of ants walking on the trail by selecting 2–6 ants during each trial and measuring the time it took each ant to walk one meter. We estimated the mean time to the nest as distance divided by velocity. To locate the nearest possible nest location we followed trails until we found ants disappearing under paving stones. The concrete was light colored, contrasting well with the dark color of the ants, making it easy to see the ants. To calculate a minimum time to return to and from the nest, we considered the nearest point

where the persistent trail disappeared and the ants could have been entering a nest. Our ‘bait-nest-bait’ round trip times may be underestimated because a nest could have been located further from the location where the ants disappeared under the paving stones.

To test whether ants returned to the bait without first returning to the nest, we compared bait-trail-bait round trip times with bait-nest-bait round trip times using ANOVA. We additionally measured the round trip time for the first marked ant that returned in each trial and defined it as ‘estimated’ bait-trail-bait round trip time. We compared that time to the ‘observed’ bait-trail-bait time and to the bait-nest-bait time.

Recruitment

We tested for recruitment in two ways. First, following (Pratt et al. 2002) and (Hölldobler 1976), we measured the change in the number of ants at the bait over time. To test whether arrival at the bait was due to recruitment rather than to chance, we examined the relationship of the flow of ants on the trail with the number of ants on the bait. Second, to test whether the rate at which new ants arrived at the bait increased, we used a regression. We tested whether the increase in arrival rates was due to recruitment by comparing it with the rate discovery by chance.

To determine if the number of ants at the bait increased over time, we recorded the time of arrival of each ant at the bait, and subsequently counted the number of ants on the cotton and the paper towel throughout the trial, approximately every 5 minutes.

We measured the flow of ants on the trail by counting the number of ants passing an invisible line on the trail, in both directions, for one minute, 3–9 times for each trial. If ants arrive at a bait alongside a persistent trail by chance alone, then the rate of arrival of

ants at the bait should be correlated with the rate of flow of ants on the persistent trail; more ants moving along the persistent trail would lead more ants to discover the bait. However, if ants actively recruit nestmates from the trail, then the rate of arrival at the bait would not necessarily be correlated with the rate at which ants are moving along the persistent trail.

We examined the relationship between the number of ants at the bait and the flow of ants on the persistent trail in several ways. First we used a linear regression to directly compare the flow of ants on the persistent trail as the dependent variable to the number of ants at the bait as the independent variable. To allow for a comparison between the number of ants on the bait and the flow of ants on the persistent trail, we used a one-dimensional data interpolation to produce continuous data points for the flow variable. We then examined how the relationship between the number of ants on the bait and the flow of ants on the persistent trail depended on time. We tested for positive slopes in the linear regression of each of these two variables versus time. We then normalized the number of ants on the bait by dividing it by the flow on the persistent trail and calculated a linear regression of this ratio against time. We used the False Discovery Rate (FDR) (Benjamini et al. 2001) to correct for multiple testing.

We defined rate of arrival as the time between new arrivals to the bait and the time to discover the bait by chance as the time it took the first ant to discover the bait in each trial. We examined increasing arrival rates by using an exponential regression with the time between arrivals at the bait of new, unmarked ants, as the dependent variable and the cumulative number of new ants that had arrived at the bait as the independent variable. We used an exponential regression instead of a linear regression because it

provided a better fit to the data when comparing the two models using the Akaike Information Criterion (AIC) (Akaike 1974).

To test whether the rate of arrival at the bait was faster than random discovery, we compared the time between arrivals at the bait with the time it took for the first ant to discover the bait. We expected recruitment to cause ants to arrive at the bait faster than the time it took the first ant to discover the bait. We define ‘discovery time’ as the time it took the first unmarked ant to discover the bait and used it to estimate how long it would take an ant to arrive at the bait by chance. Recruitment should decrease the time between successive arrivals of new ants at the bait.

All means are reported \pm standard deviations. Analysis was conducted using Matlab (7.12.0.635 R2011a, Mathworks, MA) and IBM SPSS Statistics (Version 20, NY).

Results

Ants are recruited from the persistent trail. Of the 47 ants followed as they left the bait and returned to the trail, we observed that 40% (19 ants: 5 of 15 followed on the East trail and 14 of 32 followed in the West trail) completed a second trip, returning from the trail to the bait and back to the trail again. Once on the trail, the recruiting ants spent 0.87 ± 0.67 minutes interacting with nestmates on the persistent trail, via trophallaxis, before returning to the bait. The mean round trip time from the bait to the trail and back again for the 19 ants that were followed for the entire round trip was 1.78 ± 1.46 minutes (East

trail: 1.38 ± 0.67 , West trail: 1.92 ± 1.66 minutes). We lost visual contact with the remaining ants (60%) once they arrived at the trail.

Recruitment from the persistent trail is faster than recruitment from the nest. The minimum distance to the nest for the East trail was 17.88 meters; and for the West trail, 12.19 meters. We estimated the mean speed of ants on the trail as 1.07 ± 0.45 meters per minute for the East trail and 1.06 ± 0.49 meters per minute for the West trail. Thus, ants from the East trail required at least 30.52 ± 18.91 minutes to travel from the bait to the nest and back, and ants from the West trail could complete this round trip in 18.91 ± 13.77 minutes. In all trials, observed and estimated bait-trail-bait round trip times were significantly shorter than the mean bait–nest-bait trip times (East trail ANOVA $F = 20.82$ $N = 7$, $p < 0.001$; West trail ANOVA $F = 18.48$ $N = 17$ $p < 0.001$) (Fig. 2).

The number of ants at the bait increased significantly over the course of the trial. Ten of the thirteen trials showed a positive and significant ($p < 0.01$) slope and three were not significant ($p > 0.05$) (Fig. 3, Table 1). Both trails exhibited an increase in the number of ants at the bait over time. The slopes of linear regressions on values from all trials were both significantly positive (0.13 East and 0.08 West, $p < 0.05$).

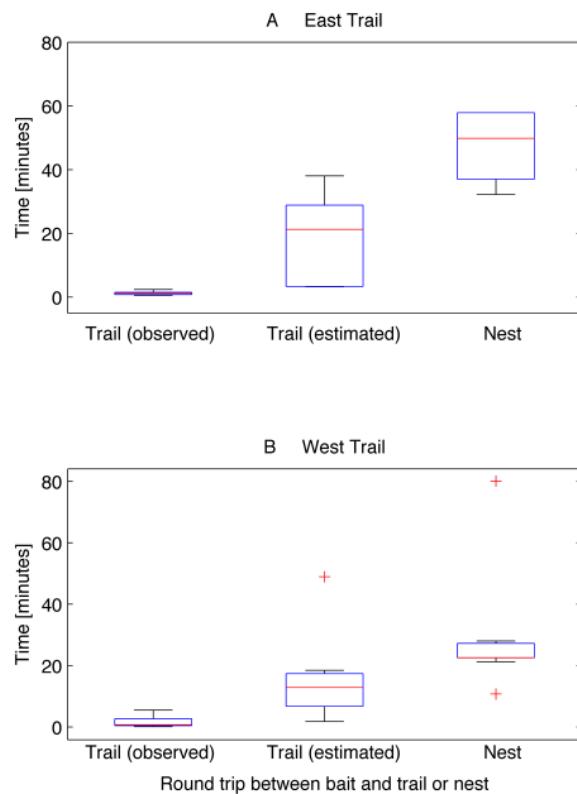


Figure 2. Round trip ‘bait-trail-bait’ and ‘bait-nest-bait’ durations. The time to complete a round trip from the bait to the nest and back is significantly longer ($p<0.001$) than the observed and estimated bait-trail-bait time for both East and West trails. Box plots represent the duration for (A) seven measurements on the East trail, and (B) seventeen measurements on the West trail. The central line on each box is the median. The box edges are the 25th and 75th percentiles. The whiskers extend to the most extreme data points that are not considered outliers which are plotted individually as “+”.

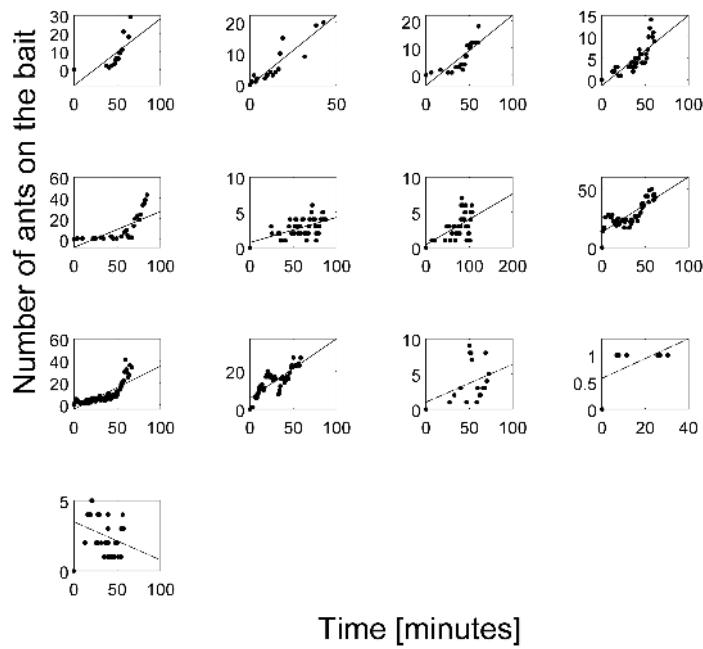


Figure 3. Number of ants on the bait over time. Each plot represents one trial. Ten of thirteen trials have a significant positive slope (first two rows, Table 1). The regressions for the last three trials are not significant. Solid lines represent significant linear regressions ($p < 0.01$). Dashed lines represent linear regressions that are not significant ($p \geq 0.05$).

Trail	Trial	# Ants on bait vs. time			Flow on trail vs. time			# Ants on bait/flow on trail vs. time			# Ants on bait vs. flow on trail			Inter arrival time vs. # ants on bait		
		R ²	P	Slope	R ²	P	Slope	R ²	P	Slope	R ²	P	Slope	R ²	P	Slope
East	1	0.46	<0.001	0.13	0.22	0.200	0.13	0.84	<0.001	0.02	0.57	0.003	-1.11	0.13	<0.001	<0.01
East	2	0.82	<0.001	0.03	0.01	0.888	0.03	0.78	<0.001	0.01	0.02	0.640	0.17	0.04	0.058	-0.01
East	3	0.70	<0.001	0.28	0.10	0.601	0.28	0.67	<0.001	<0.01	0.50	<0.001	0.25	0.36	0.019	-0.51
East	4	0.62	<0.001	0.18	<0.01	0.460	0.18	<0.01	0.847	<0.01	0.01	0.587	0.01	0.06	0.497	-0.40
West	5	0.50	<0.001	0.01	<0.01	0.961	0.01	0.36	<0.001	0.01	0.03	0.369	-0.29	0.18	<0.001	-0.02
West	6	0.28	<0.001	0.12	0.11	0.378	0.12	0.18	0.004	<0.01	0.02	0.405	0.03	0.17	0.026	-0.11
West	7	0.26	0.001	0.23	0.58	0.047	0.23	0.15	0.014	<0.01	<0.01	0.842	0.01	0.26	<0.001	-0.08
West	8	0.66	<0.001	0.37	0.35	0.042	0.37	0.08	0.027	<0.01	0.24	<0.001	0.42	0.02	0.001	<0.01
West	9	0.64	<0.001	0.08	0.01	0.845	0.08	0.76	<0.001	<0.01	0.33	<0.001	0.23	<0.01	0.812	-0.01
West	10	0.70	<0.001	0.08	<0.01	0.905	0.08	0.48	<0.001	0.01	<0.01	0.718	0.01	0.14	0.402	-0.40
West	11	0.12	0.147	0.14	0.13	0.428	0.14	0.06	0.331	<0.01	0.19	0.066	-0.13	0.12	0.018	-0.04
West	12	0.33	0.174	0.45	0.68	0.087	0.45	0.02	0.772	<0.01	0.22	0.345	0.02	1.00	<0.001	-12.1
West	13	0.08	0.068	-0.14	0.13	0.491	-0.13	0.20	0.008	<0.01	0.06	0.164	0.07	0.09	0.400	-0.57

Statistical indicators for goodness of fit and slopes for linear regressions for number of ants on the bait, flow of ants on the trail and time between arrivals. Bold numbers indicate statistically significant values after FDR-corrected for multiple comparisons.
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Table 1. Statistics for linear regressions.

The increase in the number of ants on the bait appears to be the result of active recruitment of nestmates from the persistent trail, not random arrivals due to an increased flow on the persistent trail. The flow of ants on the persistent trail did not change over time, none of the regressions showed a significant relationship between number of ants at the bait and flow on persistent trail (Table 1). When we divided the number of ants at the bait by the flow of ants on the persistent trail, 10 of 13 trials showed a significant ($p<0.05$) increase against time (Table 1).

Arrival at the bait provides positive feedback that leads to more arrivals at the bait. As the number of new arrivals at the bait increases, the time between successive arrivals decreases exponentially (Fig. 4), $\text{SSE} = 2299$, $R^2 = 0.35$, $\text{RMSE} = 1.26$). In 8 of 13 trials, the time between arrivals of new ants at the bait decreases significantly ($p<0.05$) as the number of ants that visit the bait increases (Table 1).

Arrival at the bait occurs more rapidly than it would if the bait were discovered by chance (Fig. 2). The time between new arrivals is substantially shorter than the time between bait placement and first bait discovery (two sided Wilcoxon Signed Ranks Test, $Z = 6.09$, $N_{\text{arrivals}} = 1467$, $N_{\text{discoveries}} = 13$, $p < 0.001$).

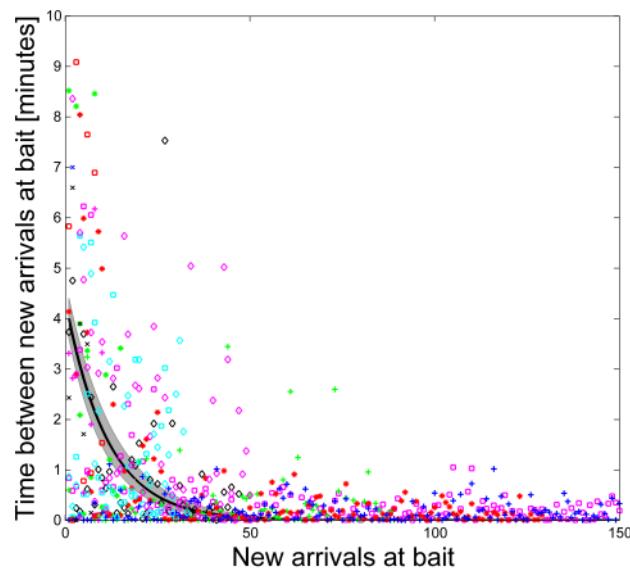


Figure 4. Time between ant arrivals at the bait versus cumulative number of new ants that have arrived at the bait. The exponential regression shows a rapid decrease in time between arrivals at the bait. As more ants arrive at the bait, the time between arrivals decreases. Data for each trial are represented by a symbol of a different color and shape. Exponential regression is shown as a thick black line. The shaded area represents the 95% confidence interval.

Discussion

We found that Argentine ants recruit nestmates to food bait from persistent trails. After locating a bait placed near a persistent trail, recruiting ants returned to the trail, and some shared food with nestmates on the trail. Activity at the bait, measured as the number of ants and the rate of arrival at the bait, increased as a result of recruitment, not as a result of an increase in the flow of ants on the persistent trail.

We directly observed 40% of marked ants going from the bait to the trail and back to the bait. This may be an underestimate because we do not know what fraction of the ants we did not directly follow went only to the trail or returned to the nest. Further, the time it takes an ant to complete a round trip from the bait to the nest and back is significantly longer than the durations of round trips that we estimated for the first ants to appear at the bait.

The increase in number of ants at the bait over time was not due to an increase in the flow of ants on the persistent trail. The time between arrivals at the bait decreased exponentially, indicating positive feedback due to recruitment (Fig. 4). We found that the intervals between the arrivals of subsequent foragers at the bait were shorter than the time it took the first forager to discover the bait initially, indicating that recruitment, rather than chance discovery, accounts for the increase in number of ants at the bait. Further work is needed to learn what determines the intervals between arrivals at the bait, and how these lead to non-linear accumulations of ants at baits (Detrain and Deneubourg 2009).

Our findings are based on observations of ants that take up colored sugar water into their gaster. Previous work (Heller et al. 2008) showed that 80% of Argentine ants

that ingested colored dye remain visibly marked after 14 days even though they engaged in trophallaxis. Therefore, it seems unlikely that many marked ants lost the color through transfer to nestmates in our 1.5-hour trials, so the unmarked ants were probably new arrivals at the bait.

A high proportion (40%) of the ants that we followed, after they found and fed from the bait, went back and forth from the trail to the bait. These ants were probably depositing a pheromone trail, but this remains to be demonstrated. Some species use different pheromones to signal different types of trails. Nelson et al. (1991) discussed the possible use of different pheromones for main and side trails in *Paraponera clavata*. *Pheidole megacephala* use two different pheromones, a long-lasting pheromone to explore and a short-lasting pheromone to recruit to a food source (Dussutour et al. 2009). Similarly, *Anoplolepis gracilipes* (à l'Allemand and Witte 2010) and *Paratrechina longicornis* (Witte et al. 2007) use short- and long-lasting pheromone signals. Aron et al. (1989) showed that Argentine ants lay a chemical trail as they walk. Additional work to explore the use of multiple recruitment pheromones in Argentine ants could determine whether these ants use different pheromones for persistent versus ephemeral trails.

Further work is needed to determine which ants are more likely to leave a persistent trail for a new food source, whether the small trails formed by short-term recruitment later become larger, more persistent trails (Heller and Gordon 2006), and how these dynamics are related to the quality and duration of the food source. Forming branches from persistent trails to exploit an ephemeral food source may expedite foraging and increase colony efficiency in obtaining food. This previously undescribed behavior, recruitment from a persistent trail, uncouples information about the location of a food

source from the transport of the food to the nest. Further work is needed to determine how often, and under what conditions, Argentine ants employ recruitment from existing persistent trails. Additionally, because our study was limited to two trails that were 50 m from one another, close enough that they could conceivably have belonged to the same colony; future studies should examine differences in local recruitment behavior among multiple colonies and ecological conditions.

The flexible recruiting system we describe, allowing new trails to form from worker pools available in nearby persistent trails, may help account for this species' success as an invader (Holway and Suarez 1999; Tremper 1976). Recruitment from nearby trails accelerates recruitment and food collection by a factor of at least 9 (Fig. 2). Argentine ants are successful in competing with native species in many areas of their invasive range, in part because they arrive at food sources more quickly than native species (Heller et al. 2008; Human and Gordon 1999). Similar dynamics can be found in other mass recruiters. For example, the trail formation by means of local recruitment can be compared to the exploratory dynamics of *Monomorium pharaonis*, whose workers interact through the trail pheromone laid on the ground and lead to the emergence of a network of exploratory trails from which scouts coming back from a food source can recruit (Fourcassie and Deneubourg 1994). *Lasius niger*, use short-term exploratory trails to guide workers towards rich food sources (Beckers et al. 1992) and *Leptogenys ocellifera* use permanent and ephemeral routes that may change according to the food supply (Maschwitz and Muhlenberg 1975). While flexible, ephemeral trail formation has been observed in other species, the novelty of our findings is that we demonstrate recruitment directly from persistent trails rather than recruitment from the nest as in,

Paraponera clavata or from within a foraging area as in the Brazilian ant *Pheidole oxyops* (Czaczkes and Ratnieks 2012).

The Argentine ant strategy of recruitment from the trail suggests a solution to a common engineering problem, that of collecting or distributing resources in “the last mile.” At the last mile, infrastructure networks connect to individual consumers. The last mile can be wired, such as cables that connect individual homes to trunk lines, or wireless where a tower connects cell phones to a high-speed backbone. In biological and engineered networks, the dynamics in the last mile can set the pace of the entire system (Banavar et al. 2010). The last mile presents a challenge, because if a network delivers or collects resources in a large area, the majority of the network wires may be in the many short-distance low-capacity links that fill the last mile.

Just as virtual networks like cell phone towers make coverage of the last mile less difficult than constructing permanent wired networks, the ephemeral recruitment trails that appear in response to newly discovered food and connect to more established, persistent trails provide an efficient way of routing resources in Argentine ants. Ants that discover new food, and go to a persistent trail to communicate that discovery to other ants, act as relays that efficiently route ants to ephemeral food. Although trails between nests are always needed for movement between nests, the ephemeral relays to local baits provide a fast and flexible mechanism for routing ants from persistent trails to ephemeral food. The network exists only when it is needed, and when the resource is exhausted, the network can disappear so that effort can be invested elsewhere. Ants have evolved solutions to many searching and communication problems (Banavar et al. 2010;

Prabhakar et al. 2012) that mirror or inspire approaches used by engineers. The ability of Argentine ants to cover the last mile with ephemeral trails is yet another example.

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CHAPTER 5

CONCLUSIONS

We studied how ants use information to improve foraging. We found that the clustering of experimental seed baits significantly increases foraging rates in three species of harvester ants, but our initial study found that species with larger colonies were no better than species with smaller colonies at collecting seeds from clustered resources. The lack of an observed colony size effect could have resulted from variability in forager population size, and the difficulty of measuring it or unforeseen effects of our experimental setup. Our study did not reveal the specific foraging behaviors that these ants employ to collect clumped seeds faster, but we suggested recruitment and site fidelity, or a combination of both behaviors as possible underlying mechanisms.

In a second study, we asked whether ants from large colonies used more information-based behaviors. By integrating computer science simulations and techniques with data obtained from our previous fieldwork, we found that seed intake patterns from larger colonies were more consistent with foraging patterns generated by behaviors that use information, such as recruitment and site fidelity. Seed intake patterns from smaller colonies were more consistent with patterns produced by behaviors that do not use information, such as correlated random walks. Although variance in field data was difficult to account for, the use of computer models integrated with data from field studies allowed us to gain new insights into ant behavior. Thus, we were able to uncover subtle behavioral patterns in field data that we were unable to see in our previous study.

Finally, we studied how large colonies of Argentine ants transport information

locally, forming ephemeral networks of communication. Our results indicate that Argentine ants recruit nestmates to food directly from persistent trails, and that the exponential increase in the arrival rate of ants at baits is faster than would be possible if recruited ants traveled from distant nests. Once ants find a new food source, they walk back and forth between the bait and sometimes share food by trophallaxis with nestmates on the trail. Recruiting ants from nearby persistent trails creates a dynamic circuit, like those found in other distributed systems, which facilitates a quick response to changes in available resources. Further work is needed to understand the formation of trails and how these dynamics are related to the distribution, quality and duration of the food source.

Organization in foraging is influenced by colony size in ants, however little is known about how the use of information-based behaviors scale with colony size. Previous studies have examined the transition between disordered and ordered foraging at critical colony sizes (Beekman et al. 2001; Latty et al. 2011), providing evidence for variation in information use. Our study of Argentine ants provides another example of how large colony sizes chose distinct strategies that use distributed information transport (Flanagan et al. 2013). Further studies of how animals collectively use information use are warranted.

Ant colonies are examples of complex systems whose information processing structures emerge from the interaction of individual components. Organisms, societies and computer networks are other examples. The efficiency of each of these systems depends on integrating information from multiple individual components. The number and density of individual components has an important impact the productivity of the

whole system. We are only beginning to understand the relationship between information use and group-level effects. Ants demonstrate the feasibility of collective coherent behavior when faced with information, even when individuals have only a narrow local perspective, and so, can offer a model to study how other complex systems, such as human organizations utilize information to achieve more than the sum of its individuals (Moses et al. 2013).

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