Title

Habitat complexity and predictability effects on finding and collecting food when ants search as cooperative groups

Authors

Denton, Kaleda K
Nonacs, Peter

Publication Date

2018-07-01

DOI

10.1016/j.anbehav.2018.05.004

Peer reviewed

Animal Behaviour 141 (2018) 77–84

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Habitat complexity and predictability effects on finding and collecting food when ants search as cooperative groups

Kaleda K. Denton, Peter Nonacs*

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, U.S.A.

ARTICLE INFO

Article history:
Received 15 November 2017
Initial acceptance 15 January 2018
Final acceptance 20 April 2018
Available online 12 June 2018
MS. number: A17-00901R

Keywords:
Argentine ant
Bayesian
foraging behaviour
Linepithema humile
sampling

Cooperatively foraging groups have two sequential goals: to find food and thereafter efficiently exploit or retrieve it. Previous research has largely focused on searching behaviours of individuals or organization of food retrieval processes, rather than on how groups initially distribute themselves to find ephemeral food items that are unpredictable in time and space. In the present study, we examined how Argentine ants, *Linepithema humile*, search environments in anticipation of food appearing briefly in areas with differing spatial complexity. Nests were connected to three foraging arenas containing 1, 9 or 25 cells. Food appeared briefly in one cell each day, either randomly or more predictably in distant cells (but equally often in each arena). We recorded the number of ants in cells when food had not been recently present, and thereafter whether ants successfully located the food when presented. Surprisingly, as food location became more predictable, ants found it less frequently. Foragers were located more often in cells closer to the nest (i.e. at information 'choke points' that returning foragers needed to traverse), and in cells with higher connectivity and greater centralness within foraging arenas. Such distributions reduce search coverage area but likely increase information transmission. Thus, it appears that *L. humile* foragers distribute themselves to favour rapid recruitment when food is found rather than maximizing food encounter rates. Although the reduced foraging success with more predictably located food suggests that ants did not adjust expectations in a Bayesian manner within arenas towards individual cells, they did appear Bayesian across arenas. Because foragers missed food more often in higher-complexity arenas than in lower-complexity arenas, this could increase perceptions that the latter are more rewarding. Shifts in distributions were consistent with such biased perceptions. Future studies to determine whether other group-foraging species use analogous solutions would be highly useful.

Foragers often face a changing landscape in terms of resource location and availability. Food can be distributed heterogeneously across the habitat (Lima, 1984), and individual patches can be highly ephemeral and subject to dissipation or exploitation and depletion by competitors (Naug & Arathi, 2007). Given that a forager's first goal is to effectively encounter potential food items, it is expected that how animals search their environment will change depending on the abundance or type of food present, current hunger state, likelihood of encountering dangerous competitors and variability of patch quality over time and space. There are a number of such examples of behaviour tracking changing conditions. Thrushes alter the spatial distribution of their sampling depending on food density (Smith, 1974). Ants vary their sampling patterns, both spatially and temporally, depending on whether carbohydrates or protein are available (Traniello, Kozol, & Fournier, 1992). Houseflies increase their turning rate and reduce their speed after recently eating (Hassell & Southwood, 1978). In *Formica* ants, smaller foragers will avoid sites at which they risk being attacked and larger ones may spend more time at these sites in a defensive mode (Kay & Rissing, 2005; Tanner, 2008). Griffon vultures, *Gyps fulvus*, routinely forage in variable and unpredictable environments, but when given a choice, prefer more predictable environments (Monsarrat et al., 2013).

Intrinsic to adopting an effective search strategy, therefore, is learning about one's environment through balancing between past and present experiences (Stephens & Krebs, 1986). Combining older with newer information to alter expectations is known as Bayesian updating (Valone, 2006). Behaviour consistent with a Bayesian sampling and learning regime has been observed in a wide variety of taxonomic groups, including birds (Alonso, Alonso, Bautista, & Muñoz-Pulido, 1995; Lima, 1984, 1985; Olsson, Wiktander,

* Correspondence: P. Nonacs, Department of Ecology and Evolutionary Biology, University of California, 621 Young Dr. S, Los Angeles, CA 90095, U.S.A.
E-mail address: pnonacs@biology.ucla.edu (P. Nonacs).

https://doi.org/10.1016/j.anbehav.2018.05.004
0003-3472/

Holmgren, & Nilsson, 1999; Valone, 1991, 1992; van Gils, Schenk, Bos, Piersma, & Moore, 2003), mammals (Spencer, 2012; Valone & Brown, 1989) and social insects (Naug & Arathi, 2007; Nonacs & Soriano, 1998). The value of an updating scheme can depend on the environment. For example, black-chinned hummingbirds, *Archilochus alexandri*, do not gain from being Bayesian in highly variable environments and generally do not update. In low-variance environments, however, most birds appear to update, and Bayesian-like foragers are the most efficient (Valone, 1992).

Group-foraging animals such as ants add a second dimension to the search algorithm. Search entails not only how individual foragers move but also group processes, such as how individuals interact and distribute themselves. These dynamics are evident in some species of desert ants that forage individually when food is abundant but forage together in narrow columns and circular areas when food is scarce (Bernstein, 1975). In addition to how best to initially find food, social insect colonies often face another distinct organizational problem—how best to retrieve food to the nest. If successful foragers do not recruit others to the found location (e.g. *Polistes* paper wasps; Reeve, 1991), then optimal foraging models such as central place foraging are useful in predicting how individuals gather food (Azevedo, Medeiros, & Araújo, 2014), or where nests are located relative to food patches (Holway & Case, 2000).

In more behaviourally complex cooperatively foraging species, food discovery by an individual can lead to recruitment of many others to the discovery site. This presents an interesting discovery–dominance trade-off (Davidson, 1998). Dispersing a foraging contingent widely will cover more area and therefore increase discovery rates. However, this simultaneously makes it difficult to quickly recruit many foragers from nonproductive sites to dominate and control the rewarding area. An alternative strategy would be to clump potential recruits at key locations where they can be quickly encountered and summoned (Roulston & Silverman, 2002); such a strategy has been observed in *Lasius niger* ants (Depickère, Fresneau, & Deneubourg, 2004b). This tactically reduces the total amount of area that all the foragers can search, but if found food is indeed ephemeral in nature, or competitors can potentially purloin it, then being able to quickly acquire it may offset reduced encounter rates.

We focus on examining this one stage of the group-foraging process: how colonies of the cooperatively foraging Argentine ant, *Linepithema humile*, search their habitat in anticipation of finding a shifting and ephemeral food source. We experimentally varied the spatial complexity of the search areas and the predictability of the exact location where food appeared. We were particularly interested in determining whether the spatial distribution of foragers influences how rapidly they might be recruited and the degree to which spatial patterns adjust in a Bayesian-like manner relative to information available from the environment.

METHODS

We set up three replicate nests of Argentine ants (*L. humile*) containing approximately 10–15 queens and 300–500 worker ants collected from a large population in Westwood, California, U.S.A. The ants nested in an open plastic container in a covered depression of a floor made of plaster of Paris, which was kept moist for nest humidity (Fig. 1). The sides of each container were coated with Fluon (BioQuip, Gardena, CA, U.S.A.) to prevent the ants from escaping. Water was provided ad libitum. Although Argentine ants often occur in an interconnected network of nests with millions of workers, the situation replicated here would resemble a smaller nest at the margin or edge of a larger supercolony (Gordon & Heller, 2014).

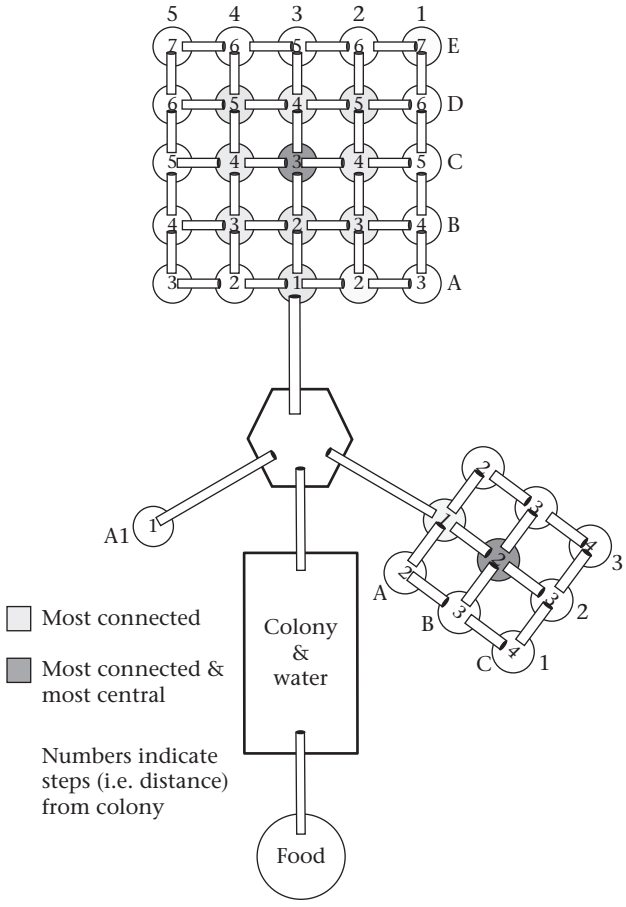

Figure 1. Diagram of the experimental foraging arenas. The location of arenas relative to the colony varied across the three replicates.

Each container was connected to a foraging arena with ad libitum protein-rich food items and to a central staging area. From the staging area, three additional tubes led to arenas that either contained 1, 9 or 25 individual cells (Fig. 1). The location of the arena types varied across replicate nests. Each cell was a small, inverted cup (diameter = 5 cm at the bottom), open at the top to facilitate observation of the ants and coated with Fluon to prevent escape. Any debris or dead ants that collected in the grids were removed, but the cells were not wiped or washed. Therefore, any pheromone marks left by the ants were not removed.

We conducted the experiment in three stages. First, we recorded by scan sampling the number of ants in each cell across the three arenas when no food was ever present in any of the cells (the 'control' period, 26 July – 8 September 2016: 45–67 scans per nest across 44 days). The number of samples varied across nests because they were not all set up simultaneously. On most days the arenas were scanned once, but on some days multiple scans were taken a minimum of 3 h apart.

In the second stage (8 September – 9 November, or across 64 days), we added a small vial of sugar water to one of the three arenas for each colony. Preferences determined before the experiment found that ants always recruited strongly to sugar water when provided. The choice of arena and cell within the arena's grid was randomly determined for each day, with the following constraints: (1) each arena had to receive the food approximately the same number of times, (2) no individual arena could receive food more than 2 days in a row and (3) no individual cell could receive food more than twice (for the 25-grid arena) or three times (for the

9-grid arena) over the testing period. During this 'random' treatment, we scan-sampled the grids 105–111 times across the three nests (the number varied because some scans had to be discarded when ants were observed escaping from an arena). The sugar water was generally added for 2 h in the morning and a scan sample always immediately preceded its placement. No additional scan samples were taken while the food was present or for at least 3 h after its removal. The ants did not have access to sugar water at any other time.

The third stage commenced 1 week after the second concluded (15 November – 18 January, or across 65 days). Food was again added to one of the randomly chosen arenas every day, but in the case of the 9-grid arena, it was always in either cell C1 or C3 (Fig. 1). In the 25-grid arena, it was always in E1 or E5. Thus, in this treatment ('distant'), food locations became more predictable, but always in the most distal cells within a grid. The choice of cells was constrained as above, differing only in that the four distal cells each had to contain the sugar reward equally often. We recorded 85–88 scan samples of the arenas under this treatment.

Across the three foraging arenas, the 1-grid arena would have food with a 33% probability on any given day. In comparison, cells in the 9-grid and 25-grid arenas would have daily probabilities of 0.037 and 0.013, respectively, of containing food in the random treatment. The probabilities rose to 0.167 for four cells in the 9-grid and 25-grid arenas in the distant treatment (and dropped to zero for all other cells).

Statistical Analyses

We analysed the relative level of exploration of grids across all three arenas in terms of both the absolute numbers of ants observed and the mean numbers of ants per cell. Also, the two arenas with multiple cells had four physical characters that could hypothetically influence ant distributions, as follows.

(1) Distance from the nest that a forager entered the arena: this could vary from the entry cell closest to nest (e.g. cell A2 in the 9-grid arena, or cell A3 in the 25-grid arena), to having to travel through a minimum of six other cells to reach cells E1 or E5 in the 25-grid arena (Fig. 1). Multiple cells were the same distance from the nest (i.e. level: Table 1), and we used the mean across all cells with the same level for the statistical analyses.

(2) Distance to food. Because food appeared only in the two most distant cells in the third treatment, foraging activity could be biased towards those cells. For example in the 25-grid arena, a forager stationed in E3 would be two steps away from where food might appear. A forager in E1 would be either zero steps away (if the food appeared there), or four steps away if it appeared in E5. Thus, its mean distance would also be two steps. Similarly calculated, a forager anywhere in row A would be, on average, six steps away from where food could appear. For the 9-grid arena, the means would range from one step to three steps for rows C to A, respectively. Thus, relative to the control (with no food present anywhere) and the random treatment (where food was equally likely to appear anywhere within an arena), a prediction would be for a proportional increase in foragers searching in the cells closest, on average, to where food might appear.

(3) Connectedness (similar to 'degree centrality' in network applications). In the arenas, individual cells can be connected with two to four other cells or directions of travel (Fig. 1). Ants in more connected cells would have more potential directions in which to travel or to meet returning successful foragers.

(4) Centralness. Cells in the centre of arenas minimize the mean number of steps that a forager needs to take to reach any other cell. We categorized the centralness of each cell by how many steps it would take for an ant to reach the most central cell (ranging from 0 for ants already in the most central cell, to 4 for the corner cells in the 25-grid arena).

We analysed distance from nest, connectedness and centralness by two-factor mixed-effects ANOVAs (in JMP, SAS Institute Inc., Cary, NC, U.S.A.) with ants/cell of specific level/number of observations as the dependent variable and treatment condition and cell level as fixed independent factors (and colony identity as a random variable). For distance to food, the dependent variable was the proportion of all ants observed at the defined distances from food (the ANOVA did not include colony as a random effect because the number of ants were standardized to a proportion). For the two distances and centralness, we analysed the data from the 9-grid and 25-grid arenas separately (and excluded the 1-grid arena) because the range of levels varied across the grids (Table 1). For connectedness, we included both 9-grid and 25-grid arenas into one analysis because the value ranges were identical (Table 1).

Finally, we analysed the ants' probability of finding the food in the random versus distant treatments by Fisher's exact tests for 2×2 contingency tables.

RESULTS

On a per-cell basis, the number of ants searching an arena was approximately proportional to the size of its grid in the control (Fig. 2a). When food was present, foraging on a per-cell basis became skewed towards smaller arenas, with the one-cell arena

Table 1
Characteristics of the two multicell arenas and the number of cells that shared the same level

Level	Distance from nest[a]		Distance to food[b]		Connections[c]		Centralness[d]	
	9-grid arena	25-grid arena	9-grid arena	25-grid arena	9-grid arena	25-grid arena	9-grid arena	25-grid arena
0	–	–	–	–	–	–	1	1
1	1	1	3	–	–	–	4	4
2	3	3	3	5	4	4	4	8
3	3	5	3	5	3	11	–	8
4	2	5	–	5	2	10	–	4
5	–	5	–	5	–	–	–	–
6	–	4	–	5	–	–	–	–
7	–	2	–	–	–	–	–	–

Where appropriate, levels were calculated relative to the shortest possible path that an ant could travel.
[a] Number of cells that had to be traversed to reach the arena.
[b] Mean number of cells that had to be traversed from a given cell to reach a cell where food might be available.
[c] Number of routes that foragers had available to enter or exit, when in a given cell.
[d] Number of cells that had to be traversed from a given cell to reach the most central cell in a grid.

drawing particularly strong relative attention. Statistically, both treatment ($F_{2,20} = 5.408$, $P = 0.0133$) and arena size ($F_{2,20} = 5.899$, $P = 0.0097$; Fig. 2a) had significant effects. A Fisher's post hoc test found that the 1-grid arena had a significantly higher rate of visits than the mean per-cell visit rate in either the 9-grid ($P = 0.0044$) or the 25-grid ($P = 0.0010$) arena.

When considering the overall number of ants, larger arenas had significantly more foragers searching in them ($F_{2,20} = 13.168$, $P = 0.0002$; Fig. 2b), but treatment did not have a significant effect. Fisher post hoc tests across the three arena sizes showed that the 1-grid arena had significantly fewer ants than either the 25-grid ($P = 0.0001$) or the 9-grid ($P = 0.0100$) arena. More ants searched in the 25-grid arena than in the 9-grid arena, but the difference was not significant ($P = 0.0603$).

Distance from the nest was a highly significant predictor of ant distribution, with the two cells closest to the nest (Fig. 1: A2 and A3) having much higher visit rates ($F_{3,28} = 6.201$, $P = 0.0023$; $F_{6,52} = 16.039$, $P < 0.0001$; Fig. 3a and b). The experimental treatment was not significant for foraging in the 9-grid arena but was significant in the 25-grid arena ($F_{2,52} = 4.433$, $P = 0.0167$), with the random treatment having the highest overall visit rate.

Foragers did not increase searching closer to where food would appear in the distant treatment (Fig. 4). There was no significant interaction effect of treatment and steps from food-bearing cells as would be expected if ants were responding to a more predictable location of food. The number of steps did have a significant effect ($F_{2,24} = 4.568$, $P = 0.0249$; $F_{4,42} = 5.678$, $P = 0.0016$; Fig. 4a and b), but in the same direction as above, where foragers minimized the distance to the nest rather than the distance to where food could appear.

The connectedness of cells also strongly predicted forager distributions (Fig. 5). Cells with a maximum of four connections had

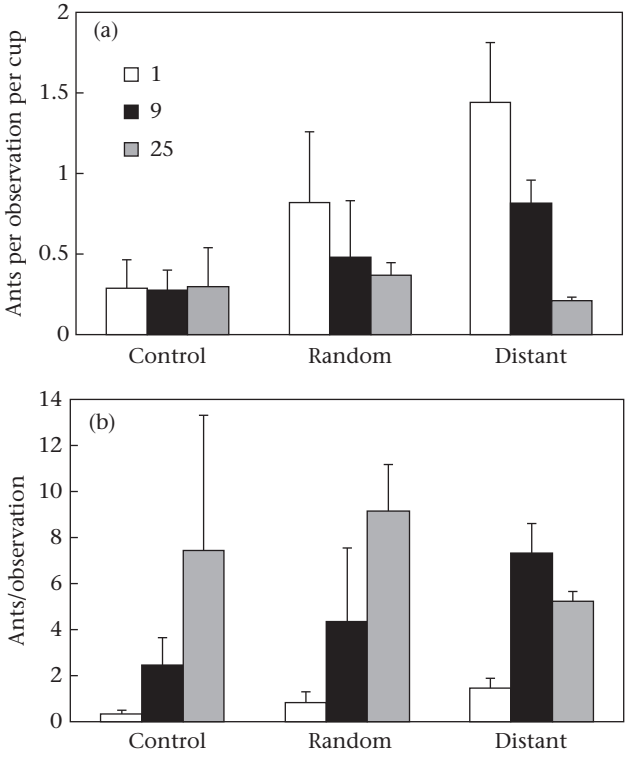

Figure 2. Mean (+SD) number of ants in the three arenas by treatment. (a) Ants in the entire arena averaged across scan samples. (b) Ants averaged across scan samples per cell in each arena. $N = 3$ for each bar.

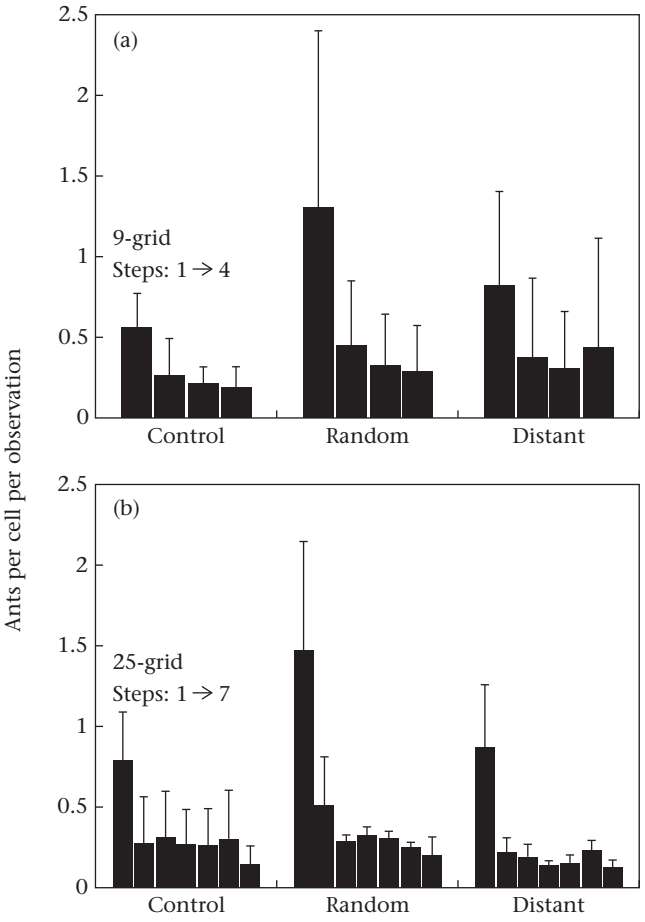

Figure 3. Mean (+SD) number of ants in each treatment that were 1–4 cells and 1–7 cells, respectively, from the nest in the (a) 9-grid arena and (b) 25-grid arena. $N = 3$ for each bar.

significantly higher visit rates ($F_{2,20} = 12.015$, $P = 0.0004$). The experimental treatment was significant for ants per observation per cell ($F_{2,20} = 12.751$, $P = 0.0003$), with the random treatment again exhibiting the highest overall visit rate.

Although forager visit rate was, on average, always higher for the most central cell in the 9-grid arena, the variance in the data was such that there was no statistically significant difference (Fig. 6a). There was also no significant main effect of treatment and no significant interaction term for visit rates in the 9-grid arena. In the 25-grid arena, ants showed significant partiality to be closer to centre of the arena ($F_{4,36} = 6.776$, $P = 0.0004$; Fig. 6b).

Foragers almost always found the sugar water when it was placed in the 1-grid arena (Fig. 7). The Fisher's test found that success rate, summed across all three replicates, was significantly higher for the 1-grid arena relative to the 9-grid and 25-grid arenas in both the random and distant treatments ($P < 0.0001$ for both comparisons). The summed values for the 9-grid and the 25-grid arenas did not significantly differ within treatment. The three nests varied individually in their use of arenas. Nest 1 always found the food in the 9-grid arena regardless of treatment, but nests 2 and 3 often failed to find the food (Table 2). Conversely, nests 2 and 3 were both more likely to find the food in the 25-grid arena than in the 9-grid arena, but nest 1 exhibited the reverse pattern. All three colonies showed a significant or nearly significant decline in foraging success in the 25-grid arena as food distribution shifted from random to distant. Nest 2 also showed a significant decline in success rate in the 9-grid arena (Table 2).

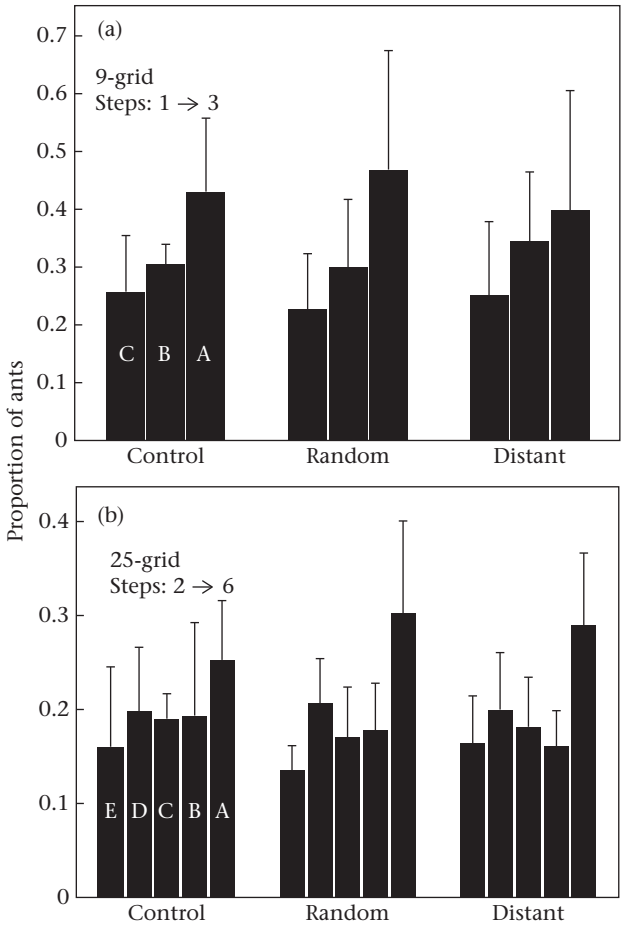

Figure 4. Mean proportion (+SD) of ants scan-sampled relative to their nearness to cells where food would appear: (a) 9-grid arena; (b) 25-grid arena. For both arenas, all cells in row A required the most steps, on average, to reach the location where food would appear; cells in rows C and E, respectively, required the least number of steps in the 9-grid and the 25-grid arena. $N = 3$ for each bar.

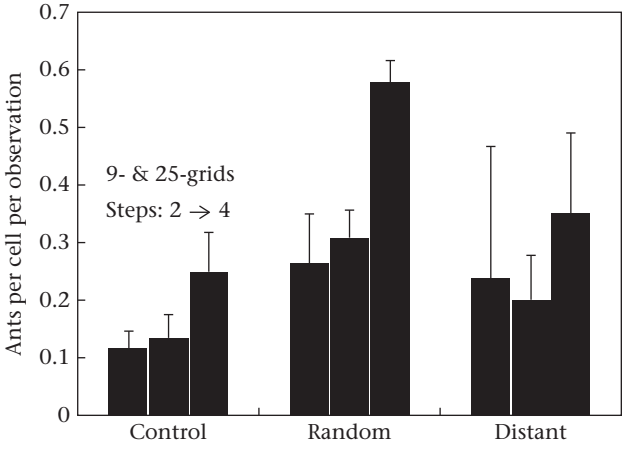

Figure 5. Mean (+SD) number of ants in cells that had two to four connections. $N = 3$ for each bar.

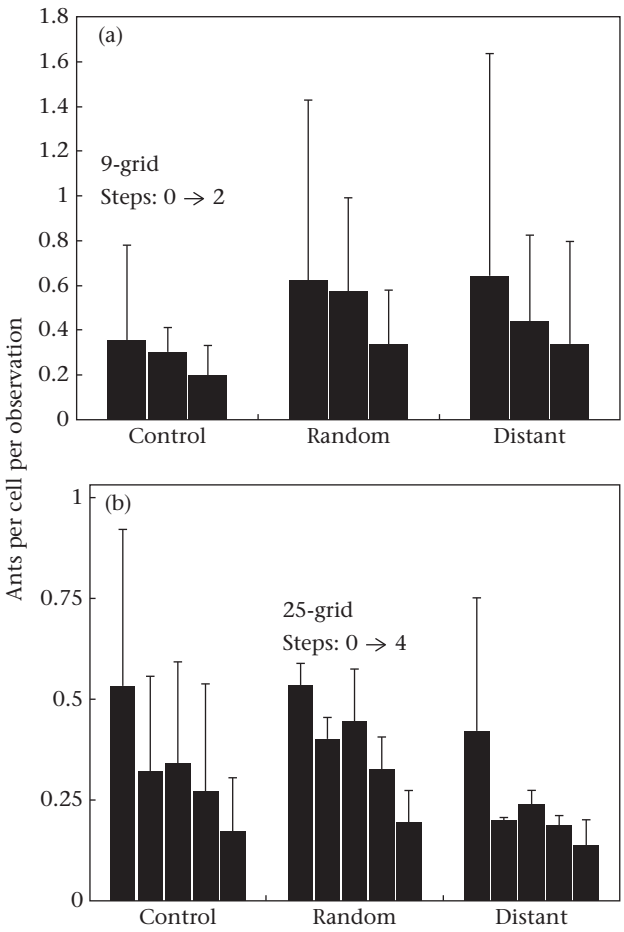

Figure 6. Mean (+SD) number of ants that were (a) 0–2 cells from the most central cell in the 9-grid arena and (b) 0–4 cells from the most central cell in the 25-grid arena. $N = 3$ for each bar.

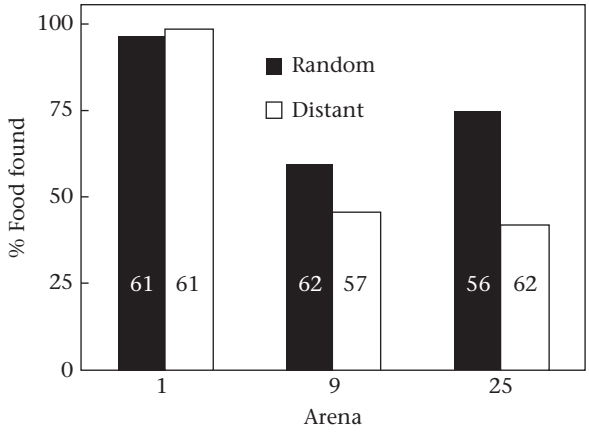

Figure 7. Percentage of food presentations that were found by the ants in the three arenas across the two food treatments. Numbers in bars are the total number of times (summed across $N = 3$ replicates) that food was presented in each arena.

Food-finding success was directly affected by the degree of coverage of arenas (i.e. the number of cells containing at least one ant, across all grids). By this metric, across all nest replicates and scan samples in the control period, 21.4% of the time the cell in the 1-grid arena had at least one ant in it, while 20.0% and 20.3% of the 9-grid and the 25-grid arenas had at least one ant in them. The comparable percentages for the 1-grid arena in the random and distant treatments were 46.1% and 62.9%, respectively. In contrast, for the 9-grid arena, the values were 27.4% and 22.6%. For the 25-grid arena, the values were 22.9% and 14.0%.

Table 2
Percentage of times that foragers in each arena were successful in the random and distant food treatments for each nest

	Random	Distant	*P*
1-grid arena			
Nest 1	95.2%	94.7%	NS
Nest 2	100%	100%	NS
Nest 3	95.0%	100%	NS
All nests	96.7%	98.4%	NS
9-grid arena			
Nest 1	100%	100%	NS
Nest 2	52.4%	17.6%	**0.0432**
Nest 3	28.6%	15.0%	NS
All nests	59.7%	45.6%	NS
25-grid arena			
Nest 1	83.3%	52.4%	0.0508
Nest 2	68.4%	38.1%	0.0673
Nest 3	73.7%	35.0%	**0.0248**
All nests	75.0%	41.9%	**0.0004**

Significant *P* values are shown in bold (Fisher's exact tests for 2×2 contingency tables comparing the random and distant treatments).

During the experiment we noticed that forager distributions were not randomly spread throughout the cells, as often multiple individuals would be found in the same cell. The tendency for ants to 'clump' was far more prevalent in the treatments with food (Fig. 8). In the random treatment, ants most often congregated in the entrances to the arenas (cells A2 and A3), while in the distant treatment, clumping became more prevalent in the 1-grid arena (Fig. 8).

DISCUSSION

Socially foraging insects are a biological model system for how cooperative groups achieve complex goals when the individual group members all have limited knowledge and cognitive capabilities. There are several steps or progressions that determine how such groups organize and function. The majority of previous research, however, has focused on two particular aspects: the methods that individuals use to search (Sakiyama & Gunji, 2016), or group assembly or activation relative to retrieving resources (Lanan, 2014; Pinter-Wollman et al., 2013). How groups organize their distributions to best initially encounter food sources has not been considered nearly as often. Here, we examine this phase of foraging in colonies of Argentine ants and find that they have several spatial proclivities or rules as relates to habitats of varying size and complexity.

An ant colony has two main objectives for effective food collection. The first is to find the food and the second is to retrieve it quickly to the nest before it is lost through degradation or to a competitor (Parr & Gibb, 2012). These objectives might not always be possible to simultaneously maximize (Cook, Franks, & Robinson, 2013; Davidson, 1998), and in our experiments, foragers distributed themselves in a manner that appeared more conducive to rapid recruitment than to maximizing encounter rates with ephemeral and unpredictable food locations. Foraging distributions also changed over time in a coarse-grained, Bayesian manner (Valone, 2006), whereby search activity became more biased towards general areas of higher experienced reward rates. The ants, however, did not adjust their distributions in a fine-grained manner to search closer to or in the specific locations in which food appeared. The result was that in more spatially complex arenas, food was more often missed. In a Bayesian sense, complex arenas (although potentially as rewarding as simpler ones) would become less valued, resulting in subsequent shifts in activity.

We draw the above conclusions from how group behaviour changed over the course of the experiments. Initially, in the control condition, there was nothing of value to be found. The larger arenas drew more attention in terms of overall number of searchers, but this increase appeared to be approximately proportional to differences in arena size (Fig. 2). Activity was relatively spread out and foragers did not strongly clump together at the same site (Fig. 8). In contrast, when food could have been present, searcher numbers increased (Fig. 2), but not uniformly, as ants tended to more often congregate in individual cells (Fig. 8). Thus, when food appeared in the larger arenas, it was found significantly less often (Fig. 7), although ants could have obtained equal rewards across all three arenas if they had searched every cell in the 9-grid and the 25-grid arenas as in the 1-grid arena. The increased clumping led to a loss in coverage area and the paradoxical result that as food location became universally more predictable, the ants became worse at finding it (Table 2).

We found no evidence that *L. humile* foragers use available information on specific food locations to target search on those individual sites. Instead, Bayesian updating appears consistent with respect to choices between arenas, and not within them. If we assume that a missed food item equates to a nonexistent reward from the perspective of a Bayesian forager, the cumulative probability of finding food in the 1-grid arena under the random treatment would be 0.322 (0.333×0.967 visit rate). The corresponding probability would be 0.199 (0.333×0.597) for the 9-grid arena and 0.250 (0.333×0.750) for the 25-grid arena. Hence, an expressed favouritism towards searching the 1-grid arena would be consistent with a changing Bayesian perception of that arena increasingly being the most rewarding one. Furthermore, the use of the two more complex arenas likely also showed the effects of stochastic events. One colony appears to have evaluated the 9-grid arena as the more fruitful area to search, while the other two colonies appeared to ignore it and searched more in the 25-grid arena. Such a pattern of favouritism could result from Bayesian estimates of quality on the arena-level scale. Argentine ants have previously been shown to exhibit coarse-grained approximation of habitat quality consistent with Bayesian updating, where they explore newly available novel areas at rates that correlate with their past territorial experience (Nonacs & Soriano, 1998).

We can attribute the lower visit rates in the more complex arenas, and particularly the increasing failure rate in the distant treatment, largely to the significant spatial tendencies as to where foragers located themselves. Ants did not distribute themselves equally or randomly within the arenas. Instead, they showed a significant tendency to favour cells (1) that were more centrally located within the grids (Figs. 6 and 8), (2) that had more connections to other cells (Fig. 5) and (3) that were closer to the nest. All three of these factors are likely to increase encounters with any successful forager returning towards the nest. Particularly significant was the number of ants found in cell A2 in the 9-grid arena and in cell A3 in the 25-grid arena (Figs. 1 and 3). These cells were critical informational 'choke points' that all foragers returning to the nest and all newly recruited foragers from the nest had to travel through; thus, these choke points likely increase communication across foragers. Clustering on paths that funnel into the nest will also create the straightest connections between the nest and the food location, which is consistent with Argentine ants preferring the most direct path with the fewest turns in reaching a food source (Yates & Nonacs, 2016). In naturally occurring Argentine ants, where local populations can number in the hundreds of thousands, foragers establish heavily travelled and persistent trails that provide a ready source of easily encountered and recruitable ants (Flanagan, Pinter-Wollman, Moses, & Gordon, 2013). This raises an interesting question as to how the patterns for searching in space

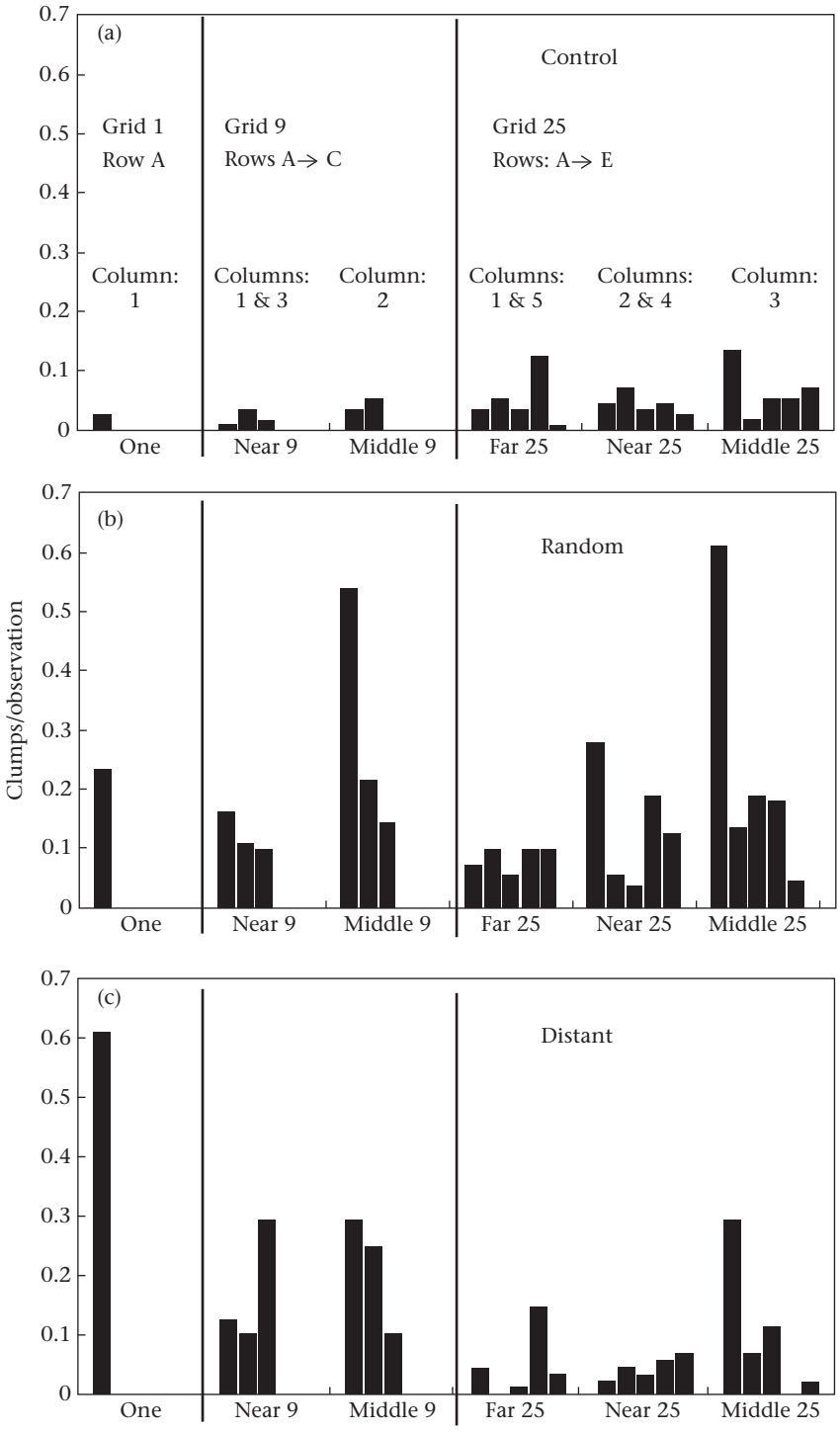

Figure 8. The frequency with which more than two ants were scan-sampled in the same cell in each of the three treatments. 'Middle' refers to the central column of the 9-grid and the 25-grid arenas; 'Near' includes the two columns adjacent to the Middle column; 'Far' (only possible in the 25-grid arena) includes the columns on the outside of the arena. For Near and Far columns, values are given as the mean of the cells to the left and right in the same row.

exhibited here might scale up or differ when thousands of foragers are available, as is often the case for Argentine ants in the field (Gordon & Heller, 2014).

Gains in increased communication also came with a cost, however: when food appeared either often or always in distant or peripheral cells, the efficacy of food discovery was reduced. Such trade-offs also appear to occur in natural ant populations. For example, *La. niger* ants may reduce the total amount of area explored by forming small clusters of foragers and aggregating near choke points (entrances of nests) to be available for recruitment by foragers (Depickère, Fresneau, & Deneubourg, 2004a).

In summary, cooperative group foragers face a trade-off. Foragers using a dispersed hunting strategy would likely encounter food more often, but it would be more difficult for them to pass this information to scattered group members quickly. Argentine ants solve this trade-off in favour of a rapidly recruiting foraging strategy that may

increase both harvest rates and response rates to intrusions by rivals. Whether these benefits actually offset lost opportunity costs remains to be explored. Also unknown is the degree to which other cooperatively foraging species face the same trade-offs as ants and whether their foraging strategies have converged to analogous solutions.

Acknowledgments

We thank David Babila for help in collecting the data and Noa Pinter-Wollman for helpful comments.

References

Alonso, J. C., Alonso, J. A., Bautista, L. M., & Muñoz-Pulido, R. (1995). Patch use in cranes: A field test of optimal foraging predictions. *Animal Behaviour, 49*, 1367–1379.

Azevedo, D. L. O., Medeiros, J. C., & Araújo, A. (2014). Adjustments in the time, distance, and direction of foraging *Dinoponera quadriceps* workers. *Journal of Insect Behavior, 27*, 177–191.

Bernstein, R. A. (1975). Foraging strategies of ants in response to variable food density. *Ecology, 56*, 213–219.

Cook, Z., Franks, D. W., & Robinson, E. J. H. (2013). Exploration versus exploitation in polydomous ant colonies. *Journal of Theoretical Biology, 323*, 49–56.

Davidson, D. W. (1998). Resource discovery versus resource domination in ants: A functional mechanism for breaking the trade-off. *Ecological Entomology, 23*, 484–490.

Depickère, S., Fresneau, D., & Deneubourg, J.-L. (2004a). A basis for spatial and social patterns in ant species: Dynamics and mechanisms of aggregation. *Journal of Insect Behavior, 17*, 81–97.

Depickère, S., Fresneau, D., & Deneubourg, J.-L. (2004b). Dynamics of aggregation in *Lasius niger* (Formicidae): Influence of polyethism. *Insectes Sociaux, 51*, 81–90.

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*, e70888. https://doi.org/10.1371/journal.pone.0070888.

van Gils, J. A., Schenk, I. W., Bos, O., Piersma, T., & Moore, A. J. (2003). Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. *American Naturalist, 161*, 777–793.

Gordon, D. M., & Heller, N. E. (2014). The invasive Argentine ant *Linepithema humile* (Hymenoptera: Formicidae) in northern California reserves: From foraging behavior to local spread. *Myrmecological News, 19*, 103–110.

Hassell, M. P., & Southwood, T. R. E. (1978). Foraging strategies of insects. *Annual Review of Ecology and Systematics, 9*, 75–98.

Holway, D. A., & Case, T. J. (2000). Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant. *Animal Behaviour, 59*, 433–441.

Kay, A., & Rissing, S. W. (2005). Division of foraging labor in ants can mediate demands for food and safety. *Behavioral Ecology and Sociobiology, 58*, 165–174.

Lanan, M. (2014). Spatiotemporal resource distribution and foraging strategies of ants (Hymenoptera: Formicidae). *Myrmecological News, 20*, 53–70.

Lima, S. L. (1984). Downy woodpecker foraging behaviour: Efficient sampling in simple stochastic environments. *Ecology, 65*, 166–174.

Lima, S. L. (1985). Sampling behaviour of starlings foraging in simple patchy environments. *Behavioral Ecology and Sociobiology, 16*, 135–142.

Monsarrat, S., Benhamou, S., Sarrazin, F., Bessa-Gomes, C., Bouten, W., & Duriez, O. (2013). How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PLoS One, 8*, e53077. https://doi.org/10.1371/journal.pone.0053077.

Naug, D., & Arathi, H. S. (2007). Sampling and decision rules used by honey bees in a foraging arena. *Animal Cognition, 10*, 117–124.

Nonacs, P. N., & Soriano, J. L. (1998). Patch sampling behaviour and future foraging expectations in Argentine ants, *Linepithema humile*. *Animal Behaviour, 55*, 519–527.

Olsson, O., Wiktander, U., Holmgren, N. M. A., & Nilsson, S. G. (1999). Gaining ecological information about Bayesian foragers through their behaviour. II: A field test with woodpeckers. *Oikos, 87*, 264–276.

Parr, C. L., & Gibb, H. (2012). The discovery–dominance trade-off is the exception, rather than the rule. *Journal of Animal Ecology, 81*, 233–241.

Pinter-Wollman, N., Bala, A., Merrell, A., Queirolo, J., Stumpe, M. C., Holmes, S., et al. (2013). Harvester ants use interactions to regulate forager activation and availability. *Animal Behaviour, 86*, 197–207.

Reeve, H. K. (1991). Polistes. In K. Ross, & R. Matthews (Eds.), *The social biology of wasps* (pp. 99–148). Ithaca, NY: Cornell University Press.

Roulston, T. H., & Silverman, J. (2002). The effect of food size and dispersion pattern on retrieval rate by the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). *Journal of Insect Behavior, 15*(5), 633–648.

Sakiyama, T., & Gunji, Y. P. (2016). Levy-like movements in Japanese carpenter ants: Experimental and theoretical approaches. *Ecological Complexity, 26*, 21–28.

Smith, J. N. M. (1974). The food searching behaviour of two European thrushes II: The adaptiveness of the search patterns. *Behaviour, 49*, 1–61.

Spencer, W. D. (2012). Home ranges and the value of spatial information. *Journal of Mammalogy, 93*, 929–947.

Stephens, D. W., & Krebs, J. R. (1996). *Foraging theory*. Princeton, NJ: Princeton University Press.

Tanner, C. J. (2008). Resource characteristics and competition affect colony and individual foraging strategies of the wood ant *Formica integroides*. *Ecological Entomology, 33*, 127–136.

Traniello, J. F. A., Kozol, A. J., & Fournier, M. A. (1992). Resource-related spatial patterns of search in the ant *Formica schaufussi*: A field study. *Psyche, 99*, 87–93.

Valone, T. J. (1991). Bayesian and prescient assessment: Foraging with pre-harvest information. *Animal Behaviour, 41*, 569–577.

Valone, T. J. (1992). Information for patch assessment: A field investigation with black-chinned hummingbirds. *Behavioral Ecology, 3*, 211–222.

Valone, T. J. (2006). Are animals capable of Bayesian updating? An empirical review. *Oikos, 112*, 252–259.

Valone, T. J., & Brown, J. S. (1989). Measuring patch assessment abilities of desert granivores. *Ecology, 70*, 1800–1810.

Yates, A. A., & Nonacs, P. N. (2016). Preference for straight-line paths in recruitment trail formation of the Argentine ant, *Linepithema humile*. *Insectes Sociaux, 63*, 501–505.