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Ant foraging: optimizing self-organization as a solution to a traveling salesman problem

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Abstract

Foraging ant colonies often face the challenge that food items can appear unpredictably across their territory. This is analogous to traveling salesman/salesperson problems (TSP), wherein solutions to visiting multiple possibly-rewarding sites can vary in cost, travel distance, or site revisits. However, TSP solutions for ants are likely also constrained by cognitive limitations. Rather than envisioning entire routes, ants probably determine their paths by individual-level responses to immediate stimuli, such as nestmate presence or avoiding revisiting an already explored site. Thus, complex group-level search and food retrieval patterns may self-organize from simple individual-level movement rules. Here we derive solutions through simulations that optimize net foraging gains across groups of ant-like agents. Agent search strategies evolve in three spatial networks that differ in travel distances to nests, connectivity, and modularity. We compare patterns from simulations to observed foraging of Argentine ants (*Linepithema humile*) in identical spatial networks. The simulations and ant experiments find foraging patterns are sensitive to both network characteristics and predictability of food appearance. Simulations are consistent in multiple ways with observed ant behavior, particularly in how network arrangements affect search effort, food encounters, and forager distributions (e.g., clustering in the more connected cells). In some distributions, however, ants find food more successfully than simulations predict. This may reflect a greater premium on encountering food in ants versus increasing find exploitation rates for agents. Overall, the results are encouraging that evolutionary optimization models incorporating relevant ant biology can successfully predict expression of complex group-level behavior.

Keywords Optimal foraging · Self-organization · Ants · Traveling salesman · Agent-based model

Introduction

Successful ant colonies often forage in two stages (Parr and Gibb 2012). First, workers need to locate food items that may appear stochastically and ephemerally in the colony's territory. Second, a find needs to be retrieved before competitors can appropriate it. The first stage involves search by individuals across the colony's territory. The second stage commences if found items are too large to be retrieved by one ant. The finder then must be able to also effectively recruit nestmates for retrieval (Nonacs and Dill 1988, 1990).

The foraging problem, thus, transforms across stages from an individual-level activity into a group-level activity.

Elements of this overall problem have been considered in three different ways: 1) What are individual-level effective search patterns when targets stochastically appear (e.g., Dorigo and Gambardella 1997)? 2) How can complex group-level retrieval behavior arise when individuals have limited cognitive ability (e.g., Bonabeau et al. 1997)? 3) Does the overall foraging strategy across both levels maximize colony-level success (e.g., Nonacs and Dill 1990)? In this study, we combine these three approaches to predict how Argentine ants (*Linepithema humile*) search their territory through evolutionary simulations that assume the goal is to maximize net overall energetic gain, but that individual agents are cognitively limited to using fairly simple decision rules while searching.

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The search problem

The initial searching stage by individual ants is a version of the “Traveling Salesman (Salesperson) Problem” (TSP; Robinson 1949). In this context, there are multiple places within a territory that may or may not have a food item. A priori, the forager does not know where food might be. It must physically visit the possible places. The TSP is to find the route that minimizes one or combination of travel metrics such as travel time, distance traveled, or site revisits (assuming sites never change state soon after a visit). When multiple foragers search simultaneously, TSP solutions could predict one optimal strategy for all, or that group success is maximized when individuals employ a variety of strategies.

Even if the TSP problem is quite spatially complex, there is always an optimal solution. However, prohibitively long computing times may preclude any current algorithm of being able to definitively identify a best path (Mele et al. 2021). It is, nevertheless, possible to compare a set of likely solutions and find the best one therein. In terms of foraging animals, such a solution can define a ‘trapline’; a path where sites are visited in a specific order that is more efficient than most or all of the alternatives (Thomson et al. 1982). Any trapline route visiting all the possible sites, without any revisits, is known as a Hamiltonian cycle (Gould 1991). A wide variety of species do exhibit movement sequences consistent with traplining, including: bumblebees, honey bees, hummingbirds, and pigeons (Ohashi et al. 2007, 2008; Sahel and Chittka 2007; Lihoreau et al. 2010, 2012; Baron et al. 2015; Tello-Ramos et al. 2015, 2022; Klein et al. 2017).

This approach emphasizes habitats as networks of nodes and connections, where exploitation patterns depend on a habitat’s site arrangement geometry. Thus, ant distributions can map relative to which physical aspects of the network predict the observed outcomes. For example, turtle ants’ (*Cephalotes goniodontus*) arboreal trail networks fit best with favoring highly trafficked nodes that reduce the possibility of getting lost, rather than minimizing travel distance (Chandrasekhar et al. 2021). In other species, sites predictably varying in reward can affect trapline paths and distribution of foraging effort across a network (Lihoreau et al. 2011).

Although the second stage of exploiting and retrieving a larger food find is no longer an explicit TSP, overall success requires that both stages are well executed. Thus, there is potential that strategies employed in one stage will affect the success of strategies in the other stage.

Cognitive ability

A forager could ‘solve’ TSP problems in two different ways. Cognitively, it could mentally construct the equivalent of a spatial map where the places to visit are a network of interconnected nodes. For example, a human traveling salesperson would know all the places and could plan out their route accordingly before embarking. Alternatively, foragers could use a set of internal decision rules that simply determine their next move, with little or no consideration on effects for subsequent decisions. For example, Dorigo and Gambardella (1997) modeled that a combination of ant forager redundancy and pheromone deposition could identify the shortest trapline across sets of traveled routes. If each forager distributed the same total amount of pheromone across their entire route, the shortest route would be the one with the highest per length concentration. Thereafter, all other foragers could choose the best trapline by simply following the most heavily marked route. This assumes, however, that all possible routes are initially equally traveled. Ants, however, deposit pheromone more stochastically, which can result in poorer paths initially receiving more signal. A feedback mechanism of preferring more heavily marked trails would then favor the less optimal path (Deneubourg et al. 1990).

Overall, evidence across ant species strongly suggests that individual behavior responds to surrounding environmental cues and interactions with others, rather than having global geographic knowledge as a detailed mental map (Stickland et al. 1995; Bonabeau et al. 1997; Detrain and Deneubourg 2006). Complexity arises through self-organization, whereby ants following simple behavioral rules with feedback create group-level phenomena. Such self-organization models have accurately predicted a variety of group-level phenomena, including: cluster formation (Theraulaz et al. 2002), prey retrieval (Detrain and Deneubourg 2002), brood tending (Gaubert et al. 2007), division of labor (Duarte et al. 2011), following pheromone trails (de Melo and Araújo 2011), patrolling versus foraging (Escario et al. 2015), soil excavation (Avinery et al. 2023), ant chains forming bridges (Carlesso et al. 2023), and swarm raids by army ants (Solé et al. 2000).

Optimal foraging theory (OFT)

The above two approaches suggest solutions to specific aspects of the ant foraging process. However, solutions to both encountering food and thereafter resource exploitation have to consider taxon-specific cognitive constraints in the behavioral abilities of ant foragers (Pratt et al. 2005). From an evolutionary perspective, the solutions

also are predicted to be adaptive and maximize colony growth, survival, and eventually reproduction (Nonacs and Dill 1990, 1993).

OFT assumes that efficiency and success in foraging will generally lead to greater eventual reproductive success (Stephens et al. 2007). This approach has been highly successful at predicting behavior (Nonacs and Dill 1993; Nonacs 2001; Stephens et al. 2007). Therefore, the third approach we employ is to model a series of TSP's where the goal is to maximize the net gain of foraging (i.e., food retrieved minus an energetic expenditure to find and collect it). This approach simulates a set of hypothetical agents whose behavioral repertoires are both relatively simple and evolvable. Thus, an agent's search path follows from its: 1) propensity to move; 2) how distance from the nest affects this propensity; and 3) inclination or disinclination to follow nestmates (e.g., Nonacs 1991; Mahavni et al. 2019). As in self-organization models, the agents are never prescient in knowing either the entire habitat map or which particular site is more likely to have food. The model mimics natural selection in that each character state can mutate. Mutations that improve foraging success are kept. Although modeled here as an allele value at a 'gene locus', each locus could represent a propensity for a certain type of behavior (e.g., an inclination or disinclination to follow other searchers—which can be learned and not genetic). The evolutionarily selective process may not necessarily find the single best solution, but will locate superior solutions relative to the defined objective. Such genetic algorithms have been successfully used to model group-level phenomena as facultative sociality in a bee (Kapheim et al. 2015), and worker movements and drifting between social insect nests (Nonacs 2017, 2023). Importantly, the optimization protocol can be restricted to using simple, individual-level behavioral rules that constrain evolution as found in self-organizing processes.

The OFT genetic algorithm simultaneously solves for both the first 'finding' stage of foraging and the second 'collecting' stage, accounting for any tradeoff between encountering food and maximizing exploitation. For example, at a group level, it may be optimal to bias or concentrate a stationary fraction of the foraging agents at locations where they are likely to meet successful agents returning to the nest (e.g., Denton and Nonacs 2018). This could, however, result in lowering encounter rates as fewer agents are searching more distant sites. Conversely, over-dispersing ants throughout the habitat may increase encounter rate, but at a cost of reducing the numbers that can be recruited to any found item as long distance communication of finds does not happen. Also, as the algorithm evolves toward efficient group-level strategies, it allows the possibility that not all foragers will employ the same strategy.

We evolved genetic algorithm OFT solutions separately across three habitat networks that differ in several

properties such as modularity, connectivity, and distance from nest, under the constraint that agents can only use local information. The OFT solutions are also evolved under two scenarios of food presentation that differ in spatial predictability (i.e., food appearing in any of twelve possible locations or in only two of them). The results from our simulations can then be compared to observed foraging of replicate Argentine ant nests (*L. humile*), under conditions as analogous as possible to the simulated TSP networks. Thus, we test the degree to which a model based on evolving optimized search strategies across differing spatial networks matches the search strategies exhibited by ant colonies.

Methods

Ant colony foraging

Argentine ants (*L. humile*) are often used for controlled foraging experiments in the lab (Deneubourg et al. 1990; Robinson et al. 2008; Yates and Nonacs 2016; Denton and Nonacs 2018; Page et al. 2018; Mahavni et al. 2019) and likely face foraging problems in nature similar to those presented here (Human and Gordon 1996; Holway and Case 2000; Fernandes and Rust 2003; Heller et al. 2008). Nine replicate nests were collected from the Los Angeles, CA, area in July, 2022, and established in the lab with one to several queens, 200–500 workers, and brood. The nests had continual access to water, but food was only provided in foraging networks. Each spatial network is composed of 12 cells (each cell 5 cm × 5 cm; total area = 300 cm²) and arranged in 4 adjacent columns with 3 rows each (Fig. 1; Supplement Fig. S1). Although *L. humile* has some species-typical movement predilections that may affect efficacy in exploring space (Yates and Nonacs 2016; Madrzyk & Pinter-Wollman 2023), cells are small and food placed in one is highly unlikely to be missed by any ant entering that same cell.

Network designs

The 24 cells are arranged into 3 different spatial networks that are analogs to natural situations. 1) Linear: sites mostly constrained to be searched in a sequential order, such as a trapline around the edge of a pond or some other impassable obstruction (Fig. 1A). 2) Uniform: an open plain with minimal obstructions between adjacent sites (Fig. 1B). 3) Modular: specific rewarding sites/paths (e.g., nectar-providing plants), but with the closest routes between sites requiring returning or passing by the nest (Fig. 1C).

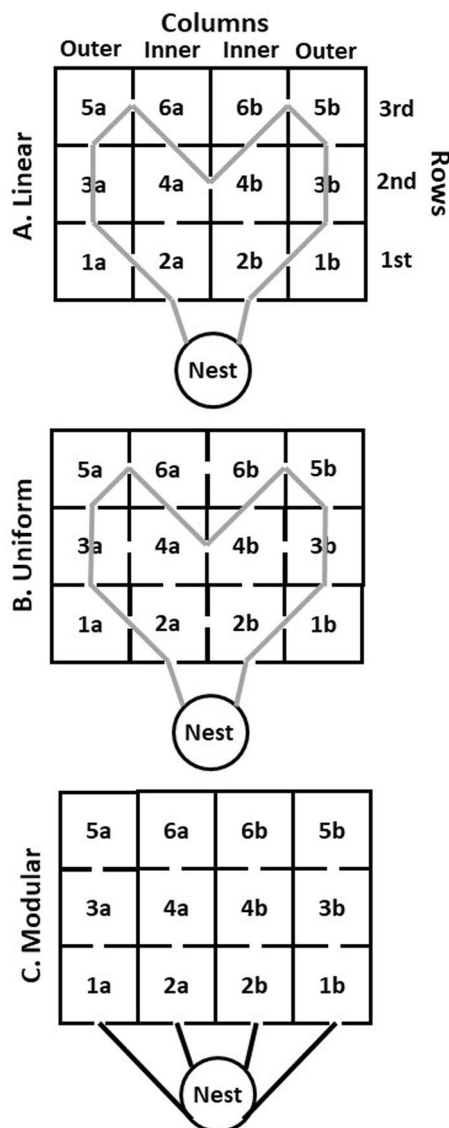


Fig. 1 Schematic of the three spatial foraging networks. **A** Linear. The cells are arranged in inner and outer columns with three rows of increasing distance from nest. The cells range from 1–4 transition steps from the nest. Eight cells connect to two other cells and four connect to three other cells (two of which connect to the nest). All cells with three connections are in the inner columns. Possible traplines (searches without revisits), are 4, 8, or 12 cells long. The gray path marks the 12-cell Hamiltonian track. **B** Uniform. Each cell is connected to every other adjacent cell, such that four cells connect to two others; four connect to three cells; and four connect to four others. Traplines of 2, 4, 6, 8, 10, and 12 cells are possible. Columns, rows, connections to nest, steps to nest and the Hamiltonian are as in the Linear spatial network. **C** Modular. The 12 cells are in 4 ‘modules’ of 3 cells. Each module is separately connected to the nest with no direct connections between them. No traplines without revisits or Hamiltonian cycle are possible. The cells range from 1–3 transition steps from the nest

Survey protocols

Foraging ant numbers and their cell locations were recorded by scan surveys when no food was present in the networks. We did not follow individual ants (i.e., the salespeople), but instead recorded how the ‘salesforce’ was distributed. Multiple scan surveys could occur in the same day, as long as they were separated by at least an hour. Every nest experienced all three networks in a randomized presentation order of three series (i.e., a given series had three nests foraging in each spatial network design). Ant presence is calculated per cell as the total number of ants observed in the cell during a given series, divided by the number of observations.

For the three series, nests were fed by semi-randomly placing food in 1 of the 12 cells, with constraints being that each cell had to experience approximately the same number of presentations and a food item could not appear sequentially in the same cell more than twice. No scan surveys were taken when food was present or within 2 h after its removal. The presented food varied and cycled between: scrambled eggs with meat, sugar water, ant protein jelly, or honey water. The day after a food presentation, no food was present in the networks to facilitate scan sampling.

After completion of the three series, each colony experienced a fourth series in which food continued to appear randomly and at the same frequency, but only in two cells and never more than three times in row in the same cell (locations 5a and 5b; Fig. 1). Data were collected across 50–83 days per series, and produced 51–68 location surveys across the nests, except for one nest, which in their initial Uniform presentation was set up late and had 25 surveys across 15 days. Food encounter data were collected both in the series where food could appear in any of the cells (50 timed encounters/nest) and in the series where food could appear only in the 2 most distant cells (25 timed encounters/nest). If no ant found the food within 60 min after being placed in a cell, the observation was terminated and recorded as 60 min. The food could remain until the following day, as this was the only food available to the nests. Before the first presentation and in between sequential ones, nests were allowed to acclimatize to the new network or pattern of food appearance for at least 2 weeks before data recording commenced.

OFT simulation model

Network designs

Agents foraged in 12-cell dimensionless networks, where the individual cells were connected to each other as described for the Linear, Uniform or Modular spatial arrangements. Depending on the simulation, food could appear randomly in any of the 12 cells (with the restriction that it could not appear more than twice sequentially in the same cell), or

randomly in one of two cells (cells 5a or 5b in Fig. 1; and no more than three sequential placements in the same cell). At any given time in the simulation, no more than one cell would contain food.

A food item would be present for 5–15 time units ('steps' in the model, mean = 10). When removed, food had a 5% probability of reappearing in the next step. Thus, food had 51% probability of having reappeared by the 14th time unit and a 92% probability by the 50th.

Agents in foraging networks leave 'footstep' marks. Each agent adds a score of one to the cell in which it resides at the end of a step. At the end of each time unit, all mark totals are decremented by 0.5 (with the minimal mark value being 0.05 in a given cell). Thus, a cell remains positively marked for at least one time unit after an agent passes through it. Mark intensity can accumulate in a cell by having multiple agents simultaneously pass through, or by agents entering the cell and then not moving for a number of steps.

Foraging agent behavior

A maximum of eight agents forage in a spatial network. Agents have three behavioral 'loci' that determine whether or not they move or remain at their present location in the next step. Agents also have three more 'loci' that determine movement preferences in choosing the next location (See Supplement Table S1 for the values used and the specific effects of the loci). Moves can be random, or positively or negatively affected by distance from the nest and the presence of other agents (i.e., the amount of footstep marks). Agents reaching the food location are 'laden' and return by the shortest path to the nest. They mark cells they traverse with a pheromone path to recruit and guide other recruits to the food cell. Searching agents that encounter either a laden agent or a pheromone trail immediately recruit. Recruits always move one cell closer to the food by following a pheromone trail in each time unit.

Foraging gains and costs

Every agent that reaches a cell where food is present brings back one unit of food to the nest. For each time unit, every agent incurs a metabolic cost of 0.01 independent of where it is. If the agent moves to a new cell, it incurs an additional cost of 0.01. The net gain rate from foraging for a nest is the total number of food units brought to the nest, minus the total metabolic costs incurred by all the agents, divided by the total number of time units. Laden or recruited agents move differently from searching agents. This makes the simulation's TSP an asymmetric problem (Odili et al. 2021), where the movement behavior, costs, and path choice differ before or after an event or move. Asymmetric TSPs add further complexity and it is not

known how well current TSP algorithms can predict their optimal solutions (Odili et al. 2021). Evolutionary simulations, however, are designed to find optimizing solutions in the simultaneous presence of all complicating factors.

Evolutionary simulations

Phase one: constructing agent libraries A simulation starts with one agent, assigned random values for each behavioral locus. The agent forages until 120 food items have been presented, after which its total net gain is calculated. Thereafter, one of its loci is randomly mutated and the agent once more forages for 120 food items. If the mutated behavioral repertoire creates a higher net gain, it is kept. If not, the previous repertoire is kept. This is repeated for 5000 mutations, at the end of which a more efficient forager has evolved.

At this point, a second agent (with randomly chosen loci values) is added to the nest and the process is repeated, but with mutations possible for both agents. Additional agents are similarly added until there are eight, in total. This entire process is replicated ten times each for the Linear, Uniform, and Modular spatial network arrangements, and where food can appear either in any cell or only two. Thus, at the end of this phase, there are 80 evolved agents from the 10 replicates in libraries with evolved behavioral repertoires for each network type and food distribution.

Phase two: optimizing foraging strategies A simulation starts with eight agents drawn from the run with the highest net energy gain rate. As before, they forage until food has been presented 120 times and net group gain is calculated. Afterwards, the agent population is modified in one of the following ways:

- A randomly chosen locus on a randomly selected agent is mutated or replaced by the locus value from another randomly chosen agent.
- The least productive agent of the eight is entirely replaced by another agent randomly drawn from the entire library.

Only modifications resulting in higher net gain are retained, otherwise they are discarded. This process is repeated 10,000 times, and then replicated ten times. Note that it is possible for combinations of behavioral repertoires to evolve that would bias agent distributions towards any given cell in a network. At the end of each of replicate, the evolved genotypes of the eight foraging agents are recorded (yielding 80 genotypes across the 10 replicates). From these optimized combinations of group-searching genotypes, the following data are recorded:

1. Agent distribution in the networks as calculated by the total number of agents observed in each of the 12 cells divided by the total number of time units.
2. Foraging efficiency as the proportion of food presentations which are encountered before disappearing ('hits' versus 'misses'), and the number of time units to first encounter for each found presentation. Food could appear in a cell where an agent is already present, yielding a time unit value of zero.
3. Agent search decisions as to movement between cells and the number of cells visited on each search trip. When the decision is between multiple cells, agents "follow" if the chosen cell has the greatest signal of previous agent presence; or "avoid" if the cell has the least signal; or a "random" if otherwise. Note that if the agent chooses randomly, it could still be logged as a follow or avoid. Also, if only one cell choice is available or all the available choices are identical in signal strength, then the choice is recorded as being random, even if the agent is strongly biased in behavior. Thus, strongly biased agents could still make mostly random choices. Decisions and paths are tracked until each agent in the group of eight has made at least 1000 trips. With thousands of decisions recorded, any bias in choosing would be statistically revealed.

Agent distributions are counted only in the time periods when food is either absent or not yet found, i.e., data are only recorded in the simulations when agents are searching and not while recruitment occurs. This matches when the observations are taken in the ant experiments.

Data analyses

The results from both the simulation models and ant experiments are analyzed by ANOVA, with the independent variables being habitat characteristics that are appropriate to the relationship being tested such as: the type of spatial network; the centrality of a cell (positioned on an inner or outer column); row number (first or closest to the nest to third and furthest away); and the pattern of food appearance (either equally likely in any cell or only appearing in two cells at the greatest distance: Fig. 1). Note that column and row are proxy measures for the effects of behavioral biases. It is not assumed that ants are cognizant of column alignment or row number, per se.

In each network setup, there are six distinct cell categories, each of which are defined by column and row locations. For distributions, the dependent variable is either the number of agents or ants in a given cell/number of times cells were observed. For ant search efficiency, the proportion of times a food item is encountered within an hour of its placement in the network, and the length of time until such

an encounter are examined. Agent search efficiency is the proportion of times a food item is encountered in the 5–15 time units it is present, and the number of time units until such an encounter occurs.

The results from the simulations are not intended to produce a quantitative match, given the unavoidable differences between a hypothetical agent and an actual ant. Instead, the intent of the statistical analyses is comparative. How similar are the statistical relationships that arise in foraging ant nests to the relationships to those evolved in an evolutionary simulation based on individual agents following simple decision rules?

Results

Simulation models: agent distribution

Patterns when food could appear in any cell

All three main effects (spatial network, inner or outer column location, and row distance from the nest) are significant, as are all two-way interactions (Table 1). Forager numbers are highest in the most connected spatial network (Uniform), and least in the Modular network (Fig. 2). Across spatial networks, agents more often occur in the inner column locations than the outer ones and in the first (closest to the nest) row (Fig. 2, and Supplement Fig. S2). In terms of interaction effects, agents are more biased towards the inner, more connected columns in the Linear and Uniform spatial networks than in the Modular one. Given that the three modules in the latter spatial network are only mutually connected at the nest (Fig. 1), the lack of any column bias is expected. With respect to row presence, foragers are equally present in both the first and second row of the Linear and Uniform spatial networks, but significantly biased towards the first row in Modular network. The attractiveness of cells 4a&b (Fig. 1) reflects their centrally connected location and results in a significant statistical interaction between column and row (Table 1).

Of the six behavioral loci, three evolved to similar mean values with relatively little variance (Supplement Fig. S3). Agents almost always recruit to a food signal, move often while searching, and do not backtrack. There is considerably more variation to spontaneously leaving the nest to search (particularly in Modular spatial networks), the propensity to follow or avoid other agents when moving, and the effect of distance. Although individual agents differ in their propensity to follow, summed across all agents, there is significantly more following than avoiding in the Linear and Uniform spatial networks (Fig. 3). In contrast, there is no significant bias for agents to either follow or avoid others in Modular spatial networks.

Table 1 ANOVA results for differences in agents or ants/cell in simulations and ant experiments across the spatial networks (Linear, Uniform, and Modular) under conditions where food can appear in any cell or just two cells

	Agents	Results	Ants	Results
Factor (food in any cell)				
Network	$F_{2,346} = 38.1; p < 0.0001$	Overall agent numbers: $U > L > M$	$F_{2,310} = 27.1; p < 0.0001$	Overall ant numbers: $U = L > M$
Column	$F_{1,346} = 464; p < 0.0001$	Overall agent numbers: Inner > outer columns	$F_{1,310} = 16.5; p < 0.0001$	Overall ant numbers: Inner > outer columns
Row	$F_{2,346} = 404; p < 0.0001$	Overall agent numbers: $2 > 1 > 3$	$F_{2,310} = 3.49; p = 0.0317$	Overall ant numbers: $2 > 1 = 3$
Network $\times$ column	$F_{2,346} = 136; p < 0.0001$	Bias toward inner column: $U > L > M$	$F_{2,310} = 2.19; p = 0.1321$	Bias toward inner column: $L = U = M$
Network $\times$ row	$F_{4,346} = 7.76; p < 0.0001$	Row: $1 > 2 > 3$; agent numbers: $U > L > M$	$F_{4,310} = 2.00; p = 0.0937$	In L and U: $2 = 1 = 3$, In M: $3 = 2 = 1$
Column $\times$ row	$F_{2,346} = 173; p < 0.0001$	Inner: $1 > 2 > 3$; Outer: $1 = 2 > 3$	$F_{2,310} = 3.15; p = 0.0441$	Inner: $2 > 1 > 3$; Outer: $3 = 2 > 1$
Factor (food in two cells)				
Network	$F_{2,346} = 522; p < 0.0001$	Overall agent numbers: $L = U > M$	$F_{2,94} = 2.14; p = 0.1239$	Overall ant numbers: $U = L = M$
Column	$F_{1,346} = 15.0; p < 0.0001$	Overall agent numbers: Inner > outer column	$F_{1,94} = 0.81; p = 0.3691$	Overall ant numbers: Outer = inner column
Row	$F_{2,346} = 88.0; p < 0.0001$	Overall agent numbers: $2 > 1 > 3$	$F_{2,94} = 11.2; p < 0.0001$	Overall ant numbers: $3 > 2 = 1$
Network $\times$ column	$F_{2,346} = 723; p < 0.0001$	Bias in L and U towards inner column; bias towards outer column in M	$F_{2,94} = 2.94; p = 0.0580$	Bias in L and U towards inner column; larger bias towards outer column in M
Network $\times$ row	$F_{4,346} = 4.30; p = 0.0021$	In all networks: $2 > 1 > 3$; agent numbers: $L = U > M$	$F_{4,94} = 0.39; p = 0.8142$	Similar bias L, U and M, where $3 = 2 = 1$
Column $\times$ row	$F_{2,346} = 32.0; p < 0.0001$	Inner: $2 = 1 > 3$; Outer: $2 > 3 = 1$	$F_{2,94} = 10.6; p < 0.0001$	Inner: $2 = 3 = 1$; Outer: $3 > 2 > 1$

For the main effects in results: > indicates that there is a significant difference between values (Fisher's least significant difference post hoc test, $p < 0.05$); = indicates which network has the higher mean, but the difference is not significant. For interaction effects, the symbols indicate differences in effect across networks

In each spatial network arrangement, a number of individual agents evolved to never spent more than one time unit in a cell, and thus experience no distance effect (i.e., 36, 57, and 46 out of 80 total agents, respectively, for Linear, Uniform, and Modular spatial networks). In the remaining agents, distance from the nest did have an effect on how likely they were to remain in a given cell (Fig. 4). However, because the propensity to move while searching (s) is high for most agents, the effect of distance (d) is minimal for Linear and Uniform spatial networks (Supplement Fig. S4), and only in Modular networks does distance contribute a bias in agents remaining closer to the nest (Fig. 4; Supplement Fig. S4: on average, 11.4% of the time agents stayed in the closest cells rather than moving further out).

Patterns when food could appear only in the two most distant cells

Similar to when food could appear anywhere, all the main and interaction effects for agent locations are significant

(Table 1). Likewise, significantly more agent searching activity occurs in the Uniform and Linear spatial networks than in the Modular one (Fig. 2a, b). Food appearing in only two cells (in the third row of the outer columns), however, does significantly change other patterns of agent distribution from the simulated results under the any-cell condition. Distributions shift from the inner columns to the outer ones and from the closer rows to furthest away third row (Fig. 2; Supplement Figs. S5 and S6).

The evolved foraging strategies differ from those when food can appear in all cells in the following ways:

- Agents in the Modular spatial network further increase the amount of time they spend in the nest not searching (Fig. 3; Supplement Fig. S3).
- Agents in Uniform and Modular spatial networks are significantly more likely to follow each other than to avoid each other (Fig. 3). This is the same as the pattern in the all-cell treatment for Uniform spatial networks, but there is no bias in the Modular. For Linear spatial networks,

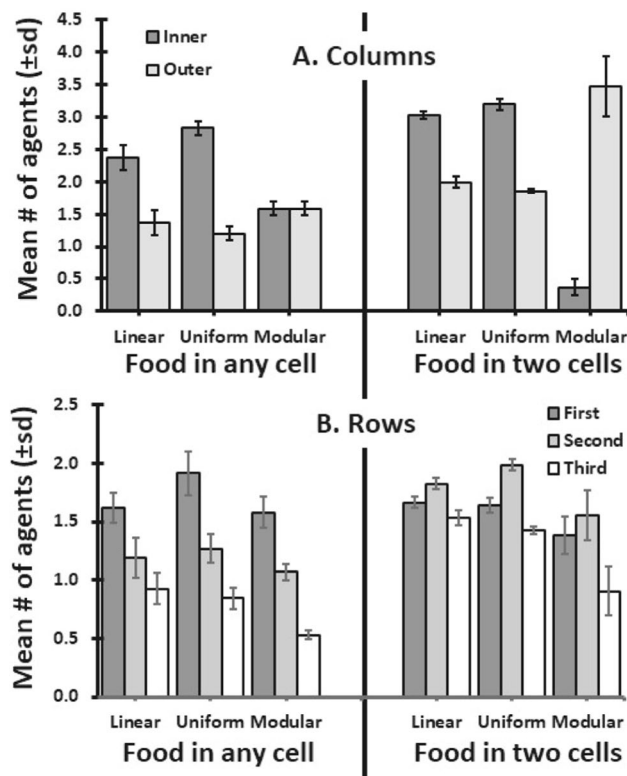


Fig. 2 Mean agent distributions in cells. **A** Agents/column/time units. **B** Agents/row/time units. Results are divided by the three spatial networks simulated and whether food can appear in any cell (left set of bars), or only the two most distant ones (right set)

there is a shift from significantly following to significantly avoiding.

- Both backtracking and the propensity to move less at distance increase in the two-cell treatment (Fig. 4; Supplement Fig. S4). Overall, more agents are sensitive to distance effects and the effects become more pronounced in Linear and Modular spatial networks.

Foraging efficiency

Efficiency (in terms of food encounters and time to encounter) is significantly higher in Linear and Uniform spatial networks than in Modular ones, and when food can appear in only two cells (Fig. 5). The mean foraging gain of groups is also significantly higher when food can appear in any cell than only two, but across groups, the net gain per time unit is significantly higher in Modular spatial networks than in Linear and Uniform ones (Fig. 6).

Short trapline paths (2 or 4 cells) are more common in the any-cell food treatment compared to the two-cell treatment (Fig. 7). The relationship reverses across path lengths of six or more cells. Traplines are more common in the Linear spatial network than in the Uniform one, as apparently

the higher connectedness makes revisits more likely, to the extent than very few agents complete a 12-cell Hamiltonian cycle.

Ant experiments: forager distribution

The data include only observations where eight or fewer ants were present in the foraging network to match the simulations of a maximum of eight foraging agents. Thus, out of 2,042 observations across all the nests, 50 (2.4%) are excluded.

Patterns when food could appear in any cell

All three main effects (network type, inner or outer column location, and row distance from the nest) are significant (Table 1). Overall, ant numbers are greatest in the most connected spatial network (Uniform), and least in the Modular spatial network arrangement (Fig. 8). Across networks, ants cluster more in the inner column locations than the outer ones and most in the second, which is the center row (Fig. 8, and Supplement Figs. S7 and S8). Interaction terms involving networks are not significant, but ants are more often in the cells that were most central and connected (i.e., the middle row of the inner column: Table 1).

Patterns when food could appear only in the two most distant cells

Differing from when food could appear anywhere, the only significant main effect is row; where the most distant row had the most ants (Fig. 8; Table 1). No interaction terms with spatial network type are significant, but there is a significant interaction between column and row as the inner columns (without food) are sampled relatively equally while the last row in the outer column (the only cells where food appeared) has many more ants (Supplement Fig. S8).

Differences in individual nest foraging behavior could also be compared by ANOVA (Table 2) across their third and last series of spatial network food distribution in any cell, and after the distribution was changed to only being in two cells (i.e., with network type held constant). Across the three spatial networks, all experience a degree of significant redistribution of search effort, although in none did the overall number of ants significantly change. The Linear spatial network was most affected, with foraging effort shifting generally from the inner columns and closer to nest rows to the outer columns and most distant row (Fig. 9), and particularly towards the two cells in which food could appear. In the Uniform and Modular spatial networks, none of the main effects are significant (Table 2), but significant interactions between column and row or food location are also reflective of a switch of search effort towards the rewarding two cells.

Fig. 3 Proportional distribution of activities by 80 simulated agents. The three spatial networks are split by either food can appear in all cells (**A**: left column of graphs) or only in the two most distant cells (**B**: right columns). When searching agents move they either follow, avoid or are random relative to presence of other agents. Non-searching agents are located in the nest. Two-sample t tests measured if following or avoiding occurred significantly more often

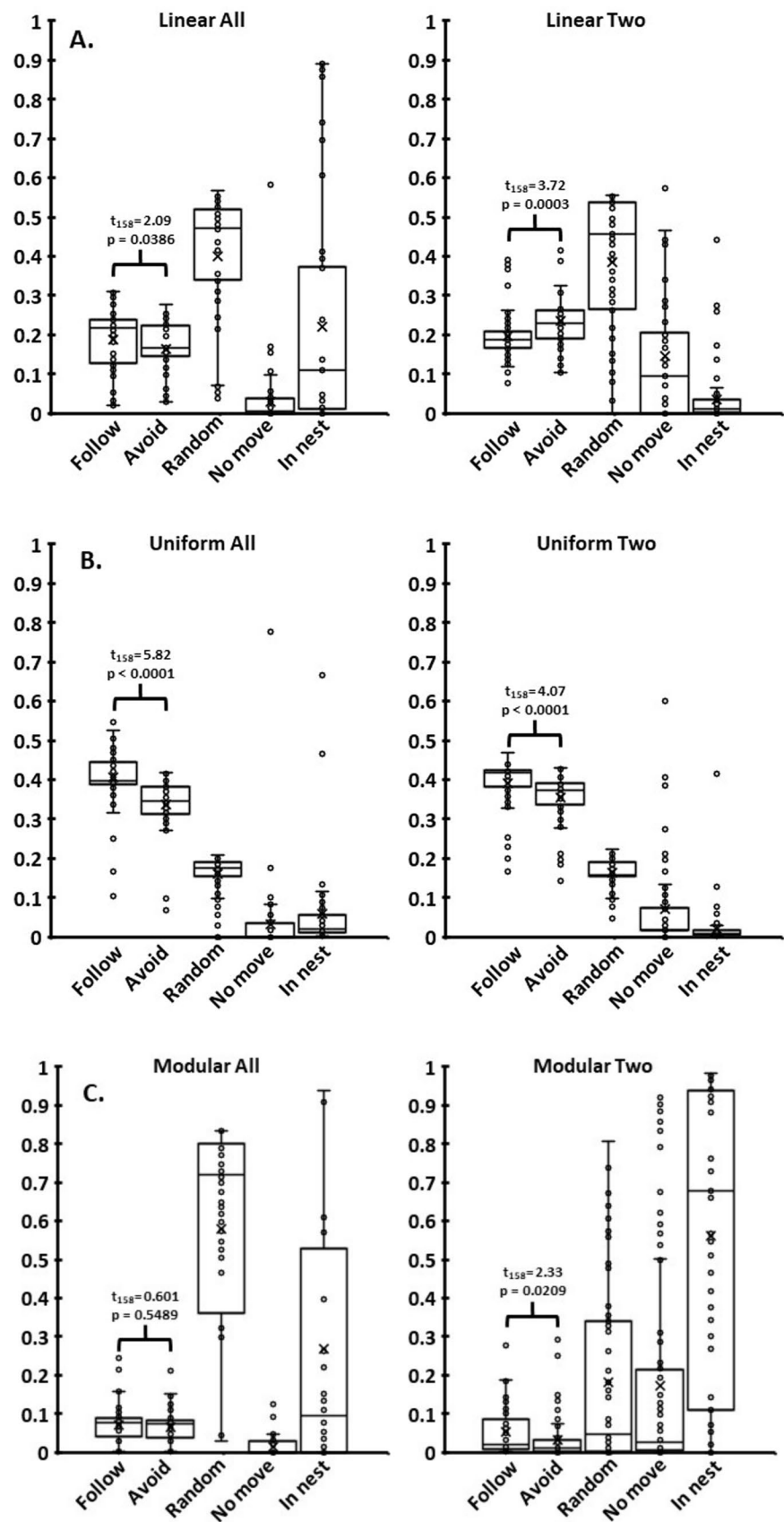
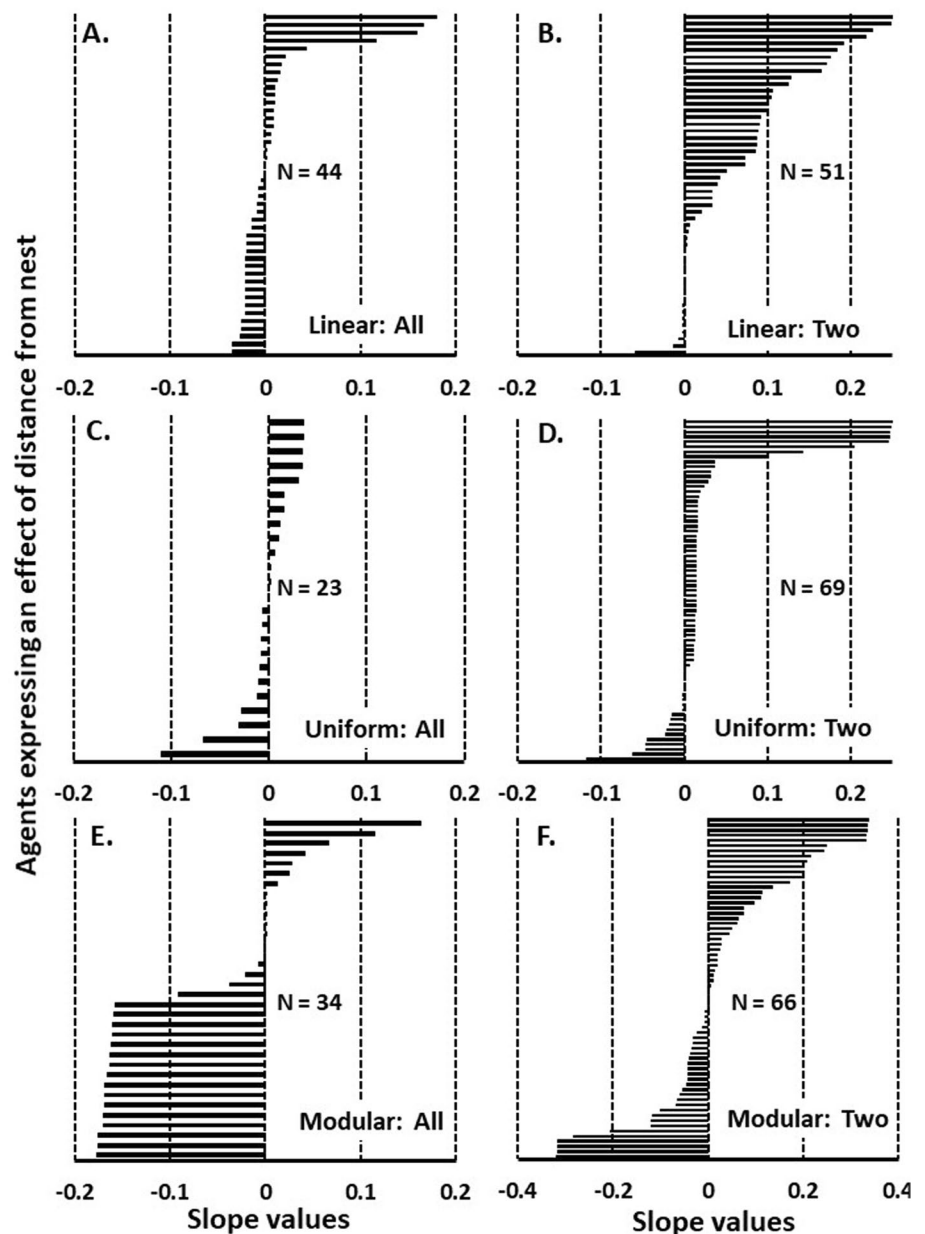


Fig. 4 Effect of distance from nest on the probability of searching agents moving. Agents with a positive distance (d) locus tend to move less and stay longer in the first row of cells. Negative loci values reverse the relationship. Therefore, positive slopes across distance (black bars) indicate an agent that moves less as distance to nest increases; negative bars indicate moving less when closer to nest. The agents are arrayed from the most positive to most negative slope. N = number of affected agents out of 80 possible. Results shown by spatial network and whether food appears in all cells (left column of graphs) or only in the two most distant (right column): Linear (A and B); Uniform (C and D); and Modular (E and F)



There is little evidence that foraging patterns changed over the time period in which observations were taken (i.e., that repeated presentation of food in only two cells caused foraging to become increasingly focused towards those two cells). Across the 12 cells, while the proportion of ants found in the outer columns or most distant rows is significantly greater in each network type, these distribution proportions are not significantly different across the first half of the observations compared to the second half (Supplement Table S2; Fig. S9).

Foraging efficiency

Spatial network type and where food can appear have significant effects on encountering food (Fig. 5). Efficiency (in terms of food encounters and time to encounter) is significantly higher in Linear and Uniform spatial networks than in Modular ones. Food appearing in only two cells also significantly increases hit rate, especially in the Modular spatial network. Given that the number of ants did not significantly change between the all- and two-food

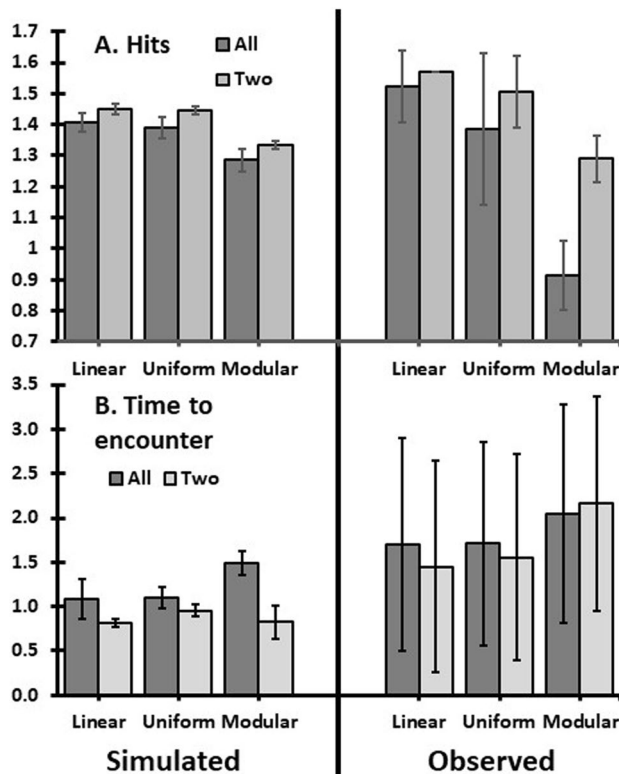


Fig. 5 Proportion of times food is found (hits) and encounter times by agents or observed for ants. In the simulations (values arcsine transformed, $\pm$ SD), hits significantly differ across the three spatial networks and when food appears only in two cells (A: left panel, main effect network $F_{2,54} = 80.3$, $p < 0.0001$; main effect food $F_{1,54} = 34.8$, $p < 0.0001$; two-way interaction $F_{2,54} = 0.275$, $p = 0.7608$). Mean time units ($\pm$ SD) to encounter food also significantly differ across spatial networks and when food appears only in two cells (B: left panel, network $F_{2,54} = 11.0$, $p < 0.0001$; food $F_{1,54} = 98.9$, $p < 0.0001$; two-way interaction $F_{2,54} = 18.4$, $p < 0.0001$ as the time reduction is most pronounced in Modular and least in Uniform). In the ant experiments, hits (ln transformed, $\pm$ SD) similarly significantly differ across spatial networks and when food appears only in two cells (A: right panel, network $F_{2,21} = 15.75$, $p < 0.0001$; food $F_{1,593} = 12.88$, $p = 0.0017$; two-way interaction $F_{2,21} = 6.410$, $p < 0.0067$ as the hit rate greatly increases in the Modular spatial network). Mean times to encounter food (ln transformed minutes, $\pm$ SD) only significantly differs across networks (B: right panel, network $F_{2,593} = 10.10$, $p < 0.0001$; food $F_{2,593} = 0.859$, $p = 0.3544$; two-way interaction $F_{2,21} = 1.084$, $p = 0.3389$)

presentations, the number of hits did increase in the latter, the nest-level efficiency was greater in terms of fewer foragers needed to be in spatial networks per food item found ($F_{1,21} = 4.400$, $p = 0.0482$).

Time to food encounter regressed against mean ants per observation across all spatial network types significantly decreases (Supplement Fig. S10). Thus, as more ants are searching, the faster they encounter food.

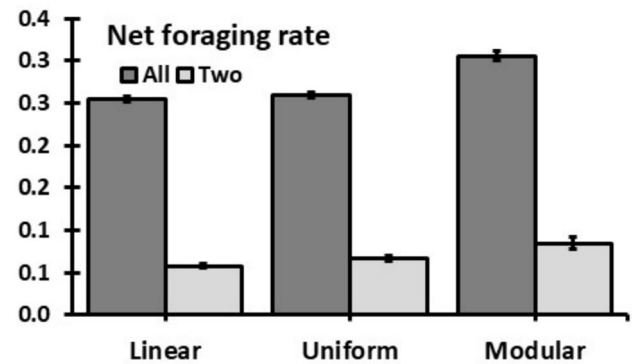


Fig. 6 Mean $\pm$ SD nest-level net foraging gain in simulations across the three spatial networks. Food in the three spatial networks could either appear randomly in all of the cells or only in the two most distant. ANOVA main effect network: $F_{2,54} = 404$, $p < 0.0001$; main effect food: $F_{1,54} = 28,432$, $p < 0.0001$; interaction: $F_{2,54} = 56.1$, $p < 0.0001$

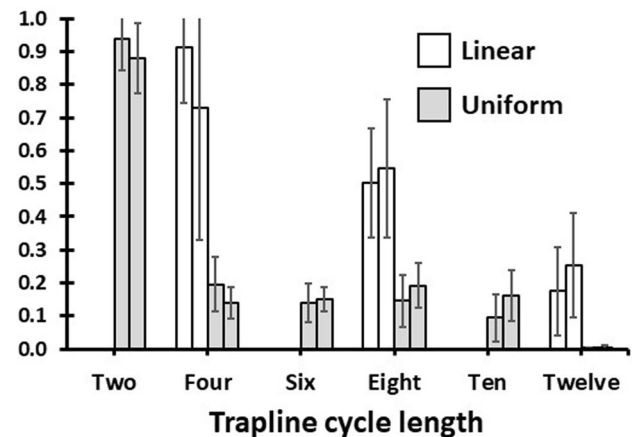


Fig. 7 Trapline cycles. Cycles are agent searches from point of entry to the spatial network to the point of returning to the nest after visiting multiple cells. Traplines are cycles in which no cell is visited more than once by the agent. They are only possible in the Linear (4-, 6- and 12-cell trapline cycles can occur) and Uniform spatial networks (can have 2-, 4-, 6-, 8-, 10-, and 12-cell trapline cycles). For each trapline cycle length, the first bar (proportion of trapline cycles for a given number of total cells visited, $\pm$ SD) is the spatial network when food appears in any cell, and second bar is where food appears in only the two most distant cells. Any 12-cell trapline cycle is also a Hamiltonian cycle (Fig. 1) as an agent visits all the network cells exactly once

Simulated versus observed outcomes

Overall, ant forager distributions are relatively consistent with those that arose in the simulations when considering the main effects of spatial network type and centrality of cells within a given network. The main difference is the simulations predict that ants should accumulate in central cells or those closest to the nest. This enhances recruitment speed as

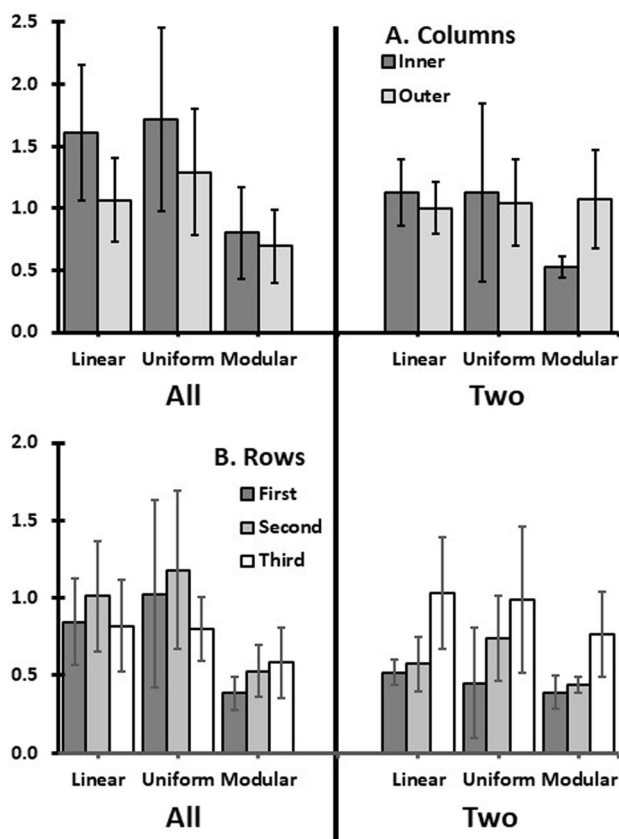


Fig. 8 Ant distributions in spatial networks. Values are the mean number ($\pm$ SD) of ants/number of cells in column or row/number of observations. The three spatial networks are split by either column (**A**; top panels) or row (**B**; lower panels). Food could appear in all cells (left column of graphs), or only in the two most distant cells (right column) in a network

ants residing in these cells could be quickly recruited by successful foragers returning to the nest. Instead, the ants adopt a more encounter-maximizing strategy. To favor clustering in the furthest cells does require traversing multiple cells to get there, and therefore making it possible to encounter food or successful foragers on their way.

The simulations correctly predicted that ants in the Linear and Uniform spatial networks would do better than in the Modular one in encountering newly placed food and finding it more quickly. The simulations also predicted that in Linear and Uniform spatial networks, food would be found more often and faster when it appeared in only two cells rather than in any of the twelve. The simulations, however, failed to predict the marked increase in encounters in the Modular spatial network when food presentation was shifted to only two cells.

The simulations find that in Modular spatial networks, the optimal strategy reduces agent search effort such that the net foraging gain per time step is higher than in the Linear and Uniform spatial networks, even though food is more often missed. A similar relationship is found in the ants where fewer are searching in the Modular spatial network and more often missing food items. When colony-level efficiency is equated to the mean number of ants searching in a network type per observation, divided by the number of times food items were found within 60 min, the ratios of searchers/hit are 0.110, 0.147, and 0.176, respectively, for the Modular, Linear, and Uniform spatial networks. The differences, however, are not statistically significant ($F_{2,15} = 1.012$, $p = 0.3868$).

Table 2 ANOVA results for differences in ants/cell in ant experiments when food changed from appearing in any cell or just two cells

Factor	Linear	Uniform	Modular	Effect
Food	$F_{1,62} = 0.38$; $p = 0.5386$	$F_{1,62} = 0.11$; $p = 0.7444$	$F_{1,62} = 1.11$; $p = 0.2965$	Same overall number of ants across both food treatments
Column	$F_{1,62} = 5.74$; $p = 0.0196$	$F_{1,62} = 0.55$; $p = 0.4598$	$F_{1,62} = 0.10$; $p = 0.7465$	In L, overall number of ants higher on inner column. Equal numbers in U and M
Row	$F_{2,62} = 4.75$; $p = 0.0120$	$F_{2,62} = 2.40$; $p = 0.0996$	$F_{2,62} = 1.21$; $p = 0.3061$	Overall ant numbers in L: 3 > 2 = 1 Same pattern in M: 3 = 2 = 1 In U: 2 = 3 = 1
Food $\times$ column	$F_{1,62} = 1.87$; $p = 0.1769$	$F_{1,62} = 0.052$; $p = 0.8210$	$F_{1,62} = 14.00$; $p = 0.0004$	In M, ants shift from inner to outer column. In L and U there is no similar significant shift
Food $\times$ row	$F_{2,62} = 4.09$; $p = 0.0215$	$F_{2,62} = 2.73$; $p = 0.0730$	$F_{2,62} = 2.35$; $p = 0.1041$	In all networks, activities shift from closer rows to 3rd row, but only significantly in L
Column $\times$ row	$F_{2,62} = 10.72$; $p = 0.0001$	$F_{2,62} = 3.91$; $p = 0.0252$	$F_{2,62} = 2.87$; $p = 0.0633$	In all networks, inner columns all rows are similarly searched, while there is a bias to the 3rd row in the outer columns

For the main effects in results: > indicates that there is a significant difference between values (Fisher's least significant difference post hoc test, $p < 0.05$); = indicates which network has the higher mean, but the difference is not significant

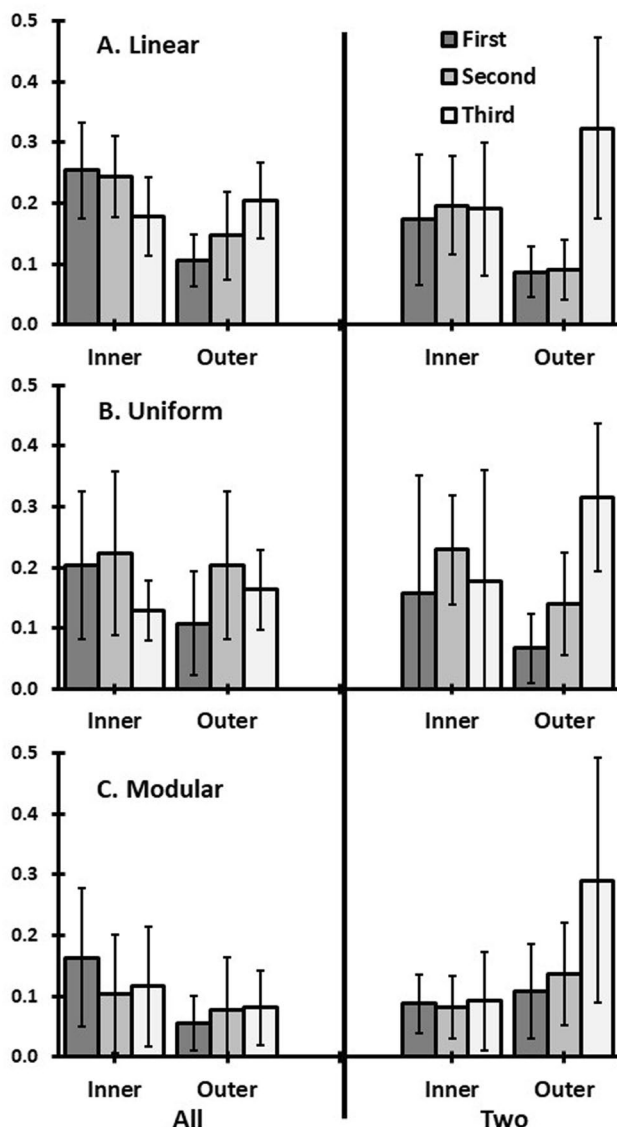


Fig. 9 Comparison of ant distributions. Values are the mean number ($\pm$ SD) of ants/number of cells in the row/number of observations across three spatial networks: Linear (A); Uniform (B); and Modular (C). Food could appear in all cells (left column of graphs), or only in the two most distant cells (right column) in a network

Discussion

In nature, ant colonies are likely to face the problem of finding and exploiting food sources that appear stochastically in territories varying in distances, connectivity, and modularity. For individual foragers, successfully finding food items fits the general paradigm of the traveling salesperson problem: How to visit a sequence of sites efficiently? Although a variety of algorithmic protocols for TSP solutions abound in the economic literature (Odili et al. 2021), they generally require considerable computational power to find the best TSP route in spatially complex arrangements. In essence,

the algorithms function as if they have a spatial map of the entire problem to which all possible solutions might be compared. In contrast, an ant may encounter a TSP situation, but: 1) will not recognize it as such; 2) is likely to base moves mostly or only on local information and experience; 3) will not be able to construct mental maps to compare alternative routes; and 4) if successful, will immediately transition to a second, non-TSP problem of how best to recruit nestmates to the found food. How such cognitively limited agents that may only ‘know’ their present circumstances solve a complex TSP has rarely been considered (Pop et al. 2024, but see Dorigo and Gambardella 1997).

In the modeling exercise here, we assume that ant-like agents in our TSPs cannot learn to predict where food is most likely to appear in space. Instead, evolved predispositions determine how often individual agents search and the effect of distance from the nest on movement rate. Each move may also reflect an agent’s biases in following or avoiding other agents, and for avoiding backtracking along the path just traveled. Thus, group-level search efficiency would arise as a self-organized process of multiple individuals following their own intrinsic set of simple rules. Evolutionary simulations generate solutions to this complex problem through setting a goal of maximizing net foraging gain across both stages of finding and exploiting encountered food. Simple rules adaptively evolve and are compared across three spatially different networks, that also vary in the predictability of where food might appear. The resulting distributions of individuals in the simulations and forager distributions observed in *L. humile* groups find that the spatial characteristics of networks do significantly affect the number, distribution, and searching success rate for both evolved agents and ant foragers.

When food can appear in any cell in a spatial network, both more agents and more ants search in the higher complexity and connected spatial networks (Linear and Uniform: Figs. 2 & 8), than in the simpler Modular spatial network. This leads to finding the food faster, with fewer missed opportunities (Fig. 5). Although all cells are identical in likelihood of reward, neither simulated agents nor observed ants are distributed equally across all cells. Instead searchers accumulate in the more connected cells in the center of the Linear and Uniform spatial networks, particularly favoring interior columns of cells over outer columns. These cells would also require the fewest turns to reach the most distant cells—a preferred feature in *L. humile* paths (Yates and Nonacs 2016). As expected because columns are unconnected in the Modular network, no such preference occurs either in the simulations or with the ants. Evolved agents are in the closest row to the nest across all three spatial networks (i.e., the cells most likely to encounter returning successful agents). The ants, in contrast, display a preference for the second row, interior

cells in Linear and Uniform spatial networks (i.e., the cells closest to every other cell). Both of these distributions of agents and ants would increase recruitment potential at some cost to encounter rate in comparison to a more even distribution across cells (e.g., Denton and Nonacs 2018). The tradeoff, however, appears more explicit for agents as they accumulate in the two ‘chokepoint’ cells; one of which every successful forager must traverse to enter the nest (Fig. 1). The behavior of ants did diverge from that of agents in the Modular spatial network, where only ants are significantly more often seen in the furthest row. This would also be more consistent with favoring encounter over recruitment as ants in the furthest row could only get, thereby passing through all the cells in a given module (Fig. 1).

A Linear spatial network contains 13 connections between cells within the 12-cell arena. This is intermediate between the Modular spatial network (8 connections) and the Uniform spatial network (17 connections). The results from both the simulations and ant experiments, however, are not intermediate—the Linear is much more similar in search patterns to the Uniform than it is to the Modular. This raises the possibility that the two networks similarly function as one complex module for ants, while the Modular spatial network functions as four simple networks. The results across spatial distributions in this study are not consistent, however, with Denton and Nonacs (2018) who found *L. humile* are relatively more successful at predicting and encountering food in simple arenas (i.e., 1 cell versus 9 or 25). What critical spatial differences produce these contrasting outcomes across studies merits future study.

When food could only appear in the two most distant cells, ants shift from the second to the third row (Fig. 8), but did not strongly bias distributions towards the two rewarding cells, which would have been consistent with spatially prescient knowledge (Fig. 9). Unlike bumblebees (Lihoreau et al. 2011), the ants do not prioritize visiting the most rewarding exact locations. Further, ant distributions do not change significantly over time between the first and second halves of the two-cell food treatment, as would be predicted if individuals were learning which spatial locations are rewarding (Supplement Fig. S9). The simulations also show that prescience is not required. Agents significantly follow each other and search effort shifts outward and directed towards the rewarding cells by reducing movement at greater distances from the nest, and in the case of Modular spatial networks, by having more agents remain in nests awaiting a recruitment signal (Fig. 4). Overall, the simulated and observed ant colony search patterns are more consistent with individual-level modulation of self-organizing behavior relative to the environment being experienced (Detrain and Deneubourg 2006), rather than suggestive of memorizing the location and

quality of specific food patches as exhibited by traplining bees (Lihoreau et al. 2011).

For both the simulated agents and foraging ants, the changes in search patterns as food appearance became more predictable, resulted in finding the food more often and generally finding it more quickly (Fig. 5). How this was accomplished, however, does differ in the simulations versus the ant colonies. The former predicted more effort and energy expenditure across the agents, resulting in significantly lower net energy gain when food became more predictable. Across all simulations, agents in the Modular spatial arrangement consistently had the highest net gain rate. Ant colonies, however, did not significantly increase foraging effort across the two food presentations. In terms of foraging efficiency (mean number of ants/cell/found food item), the same trend as in the simulations is observed, but it is not statistically significant.

In the simulations, we could record individual agent search paths. Where the spatial network made it possible, multiple agents followed a trapline, defined as multiple cells being visited without any revisits (Fig. 7). Indeed, most short searches (2–4 cells) were traplines. The results confirm that traplining search paths can arise through simple modification of a self-organizing rule, i.e., avoid backtracking. However, the physical network also had a strong influence. Traplining is significantly more common in the Linear spatial network than in the Uniform one. For example, an agent that did not backtrack in a Linear spatial network could often only move to one, previously unvisited cell (Fig. 1A). In the Uniform spatial network, more choices were often present, including cells that had been visited before (but not always in the previous time unit and, therefore, not a backtrack). Thus, over 15% of 12-cell search paths in Linear spatial networks are also Hamiltonian cycles, while less than 1% are Hamiltonian in the Uniform spatial network.

Arguably, only agents in the Linear and Uniform spatial networks where food could appear in any cell are faced with a true Traveling Salesperson problem. Our model results show that a solution (i.e., moving along the 12-cell Hamiltonian cycle) can result with agents that make step-by-step decisions rather than relying on spatial maps (see also: Dorigo and Gambardella 1997). Interestingly, longer traplines (8–12 cells) became more common when food could only appear in the two most distant cells (Fig. 7). Such search paths are more likely to take agents to food locations with minimal travel time. Nevertheless, most longer searches are not traplines. Having agents that search in a variety of ways may optimize net gain given that food could appear in already visited cells (thus, revisiting one’s path could be rewarding). Also, agents are not only seeking to encounter food, but to encounter either a successful laden agent or the pheromone trail left by such agents. These results are similar to behavior observed in turtle ants where trail use tends to

increase ant density and therefore the potential to interact and exchange information (Chandrasekhar et al. 2021).

Finally, the foraging simulations never evolved to the point that all agents used similar rules for search. For the majority of evolvable traits, considerable variance in trait value across agents exists at the end of simulations (Supplement Fig. S3). Agents regularly differed in their propensity to follow, avoid or move randomly with respect to the location of others (Fig. 3). This is consistent with general observations in *L. humile*. Exploratory behavior varies across individuals and negatively correlates with their expression of a gene (*Lhfor*) known to affect movement across multiple insect species (Page et al. 2018). At the group level, ants with a greater propensity for exploration are found relatively more frequently traveling to known food sources (Madrzyk and Pinter-Wollman 2023). Thus, a prediction for further testing is that TSP solutions in *L. humile* will also find that individual foragers consistently differ in their search and exploration strategies.

Conclusion

Ant foraging strategies in terms of finding and exploiting food sources have been selectively honed through many million years of natural selection (Detrain and Deneubourg 2006). Thus, it is encouraging that an evolvable genetic algorithm based on maximizing net foraging gain in a TSP and with relatively few simple individual-level rules for movement produces distribution patterns similar with respect to actual ants foraging. These results demonstrate the potential to study ant social behaviors using a synergistic approach addressing both ultimate questions (i.e., what is the fitness-maximizing objective?) and proximate ones (i.e., how might sensory or cognitive constraints limit the range of possible behavioral solutions?).

The fact that our simple model did not match every aspect of ant foraging does not necessarily mean that ants forage non-optimally. Ants may be non-optimal within the limits of a particular TSP, but ants have also likely evolved to balance multiple objectives in addition to optimizing food encounter and retrieval. Multiple objectives can cause significant and predictable deviations from OFT strategies that only maximize net food intake rate (Nonacs 2001). For ant colonies, some other objectives besides food gathering might be patrolling territory to protect against intrusion by competitors (Escario et al. 2015), or to minimize mortality rates (Nonacs and Dill 1990; Lessig and Nonacs 2021). No such complicating factors were present in the current study, but judicious incorporation of complementary objectives into both models and experiments may yield further insights into the organization of complex group-level behavior in ants and other social insects.

Author contribution statement PN designed the experiment and collected the ants. NP carried out the feeding trials. NP and WZ took observations of the ants and maintained the colonies. PN wrote the simulation model and performed the statistical analyses. All authors contributed to writing the first draft and to revisions.

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Data availability Data from the ant experiment will be uploaded to Dryad upon acceptance of the paper.

Code availability The code for the model (in TrueBasic) is available in the supplementary document.

Declarations

Conflict of interest None for any of the authors.

Ethical approval None needed.

Consent to participate Not applicable.

Consent for publication Not applicable.

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