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Nest choice in arboreal ants is an emergent consequence of network creation under spatial constraints

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Abstract Biological transportation networks must balance competing functional priorities. The self-organizing mechanisms used to generate such networks have inspired scalable algorithms to construct and maintain low-cost and efficient human-designed transport networks. The pheromone-based trail networks of ants have been especially valuable in this regard. Here, we use turtle ants as our focal system: in contrast to the ant species usually used as models for self-organized networks, these ants live in a spatially constrained arboreal environment where both nesting options and connecting pathways are limited. Thus, they must solve a distinct set of challenges which resemble those faced by human transport engineers constrained by existing infrastructure. Here, we ask how turtle ant colonies' choice of which nests to include in a network may be influenced by their potential to create connections to other nests. In laboratory experiments with *Cephalotes varians* and *Cephalotes texanus*, we show that nest choice is influenced by spatial constraints, but in unexpected ways. Under one spatial configuration, colonies preferentially

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occupied more connected nest sites; however, under another spatial configuration, this preference disappeared. Comparing the results of these experiments to an agent-based model, we demonstrate that this apparently idiosyncratic relationship between nest connectivity and nest choice can emerge without nest preferences via a combination of self-reinforcing diffusion along constrained pathways and density-dependent aggregation at nests. While this mechanism does not consistently lead to the de-novo construction of low-cost, efficient transport networks, it may be an effective way to expand a network, when coupled with processes of pruning and restructuring.

Keywords Collective behavior · Transportation network · Self-organization · Agent-based model · Arboreal ants · Nest choice

Declarations

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Code availability Code for the model is available at `https://github.com/JoannaChang/TurtleAntSim`.

Authors' contributions All authors contributed to the study conception and design. J.C. and M.C.D.-M. designed and carried out the laboratory experiments with input and materials from S.P. The agent-based model was designed by J.C and M.C.D.-M. with input from E.J.H.R. The agent-based simulations implementing that model were written and run by J.C. Analysis of laboratory and simulation experiments was performed by J.C. and M.C.D.-M. with input from S.P. and E.J.H.R. The first draft of the manuscript was written by J.C. All authors contributed to subsequent versions of the manuscript, and read and approved the final manuscript.

1 Introduction

Biological transport networks are constructed by many organisms to collect and distribute vital nutrients. To perform well, a network must be able transport resources efficiently, cost little to construct and maintain, and still remain robust to disturbances. While biological networks are unable to perfectly optimize all network features, different biological systems may balance the trade-offs in distinct ways based on their functional priorities and ecological context. For example, leaf venation networks incorporate loops to prioritize dynamic efficiency and robustness over cost of construction (Katifori et al. 2010), while reconfigurable *Physarum polycephalum* slime mold networks prioritize low costs over robustness (Tero et al. 2010; Reid and Beekman 2013). Polydomous (multi-nest) ant colonies have become a model system for studying transportation networks because they frequently move adult ants, brood, and food between multiple spatially separated nests (Debout et al. 2007). Previous studies on the network structures of several polydomous ant species have shown that they are able to construct low-cost networks that nonetheless achieve relatively high efficiency (Cook et al. 2014; Cabanes et al. 2015). Because biological networks like these lack centralized control, studying the mechanisms used to build such networks has inspired scalable algorithms for constructing and improving human-designed networks that balance cost, efficiency and robustness in specific ways (reviewed in Perna and Latty 2014; Nakano 2011). However, these studies have focused on a small handful of biological systems whose transport networks can expand in two-dimensional space without spatial constraints.

Spatial constraints can affect the functionality of both biological and human-designed transport networks. By restricting where pathways can be built, spatial constraints can limit the possible connections within a network and affect its ability to efficiently transport resources and respond to disruptions. For example, leaf venation patterns are constrained by the 2D plane of a leaf so that veins cannot cross without intersecting, thereby limiting the routes for nutrient transport throughout the plant vascular system (Nelson and Dengler 1997). Ant foraging trails are similarly constrained to the terrain of the ecosystem, limiting the ways food can be transported back to a colony (Fewell 1988; Cook et al. 2014). Many human-designed networks also operate under spatial constraints; for example, public transit networks and power grids need to be built around existing city infrastructure. Currently, much of the design of human-designed transport networks rely on approaches based on heuristic algorithms to optimize and balance competing network properties (Farahani et al. 2013). However, the heuristics need to be constantly improved, especially in response to changing patterns of demand, and determining the optimal heuristics proves to be an ongoing challenge (Kepaptsoglou and Karlaftis 2009). Studying biological networks which operate under varying degrees of spatial constraint and translating their local rules into mathematical and computational models could thus provide useful heuristics to inform the construction of human-designed networks without the need for centralized planning.

Polydomous ant species are found in a wide range of ecological contexts, providing an opportunity to study inter-nest transport networks subject to varying degrees of spatial constraint. While inter-nest transport networks have been studied in a variety of distantly related polydomous ant species—including Argentine ants, Australian meat ants, and European wood ants—they all have large ground-

nesting colonies (Cook et al. 2014; Cabanes et al. 2015). However, polydomy is also prevalent among arboreal-nesting ants, which are diverse, abundant, and ecologically dominant in tropical canopies (Longino et al. 2002; Powell et al. 2011). Compared to their terrestrial counterparts, polydomous arboreal ants face much stronger spatial constraints. They are restricted by the topology of the trees they inhabit, which limits the possible structures of the networks that they construct. While terrestrial ants can potentially build new trails and nests almost anywhere, arboreal ants must establish trails along existing tree branches and often only occupy existing cavities instead of constructing their own nest sites (Carroll 1979; Powell et al. 2011; Powell 2008). Many arboreal ants never descend to the ground, and must rely on connecting vegetation to travel beyond a single tree (Adams et al. 2019). In arboreal networks, decay and strong winds may frequently cause branches or connecting vines to break, destroying both pathways and nests—which themselves are already a limited resource (Philpott and Foster 2005; Powell et al. 2011; Gordon 2012). The high risk of these disturbances thus requires arboreal ants to respond to dynamic environments (Gordon 2017). Conversely, localized disturbances in terrestrial networks are less disruptive because terrestrial ants are not constrained to certain physical routes and can more easily re-route around the disturbances (Oberhauser et al. 2019; Burns et al. 2020). These differences between the ecological conditions for terrestrial and arboreal ants may lead them to construct networks which balance trade-offs between cost, efficiency and robustness in different ways. As such, studying arboreal ant networks can provide insight into the design of transport systems which must continually adapt to changing conditions, while subject to spatial constraints on both the location of nodes (e.g. transit stations or nests) and the pathways between them.

In this study, we examined how spatial constraints affect the inter-nest network formation of two arboreal-nesting turtle ant species: *Cephalotes varians* and *Cephalotes texanus*. *C. varians* are found throughout the mangrove and Hammock forests of Southern Florida, and especially the Florida Keys (Wilson 1976). *C. texanus* are typically found in oak trees in southern Texas and northeastern Mexico (Creighton and Gregg 1954). For *Cephalotes*, as for many other arboreal ants, viable nest cavities are a limited resource. *Cephalotes* rely on pre-existing cavities made by wood-boring beetles (Powell 2008), and differentiate between nests based on cavity volume and entrance size (Powell 2009; Powell et al. 2017; Powell and Dornhaus 2013). *Cephalotes* species that have a soldier caste with a specialized disc head shape, including *C. varians* and *C. texanus*, also tend to occupy cavities with entrance areas that are close to the size of the soldiers' heads (Powell 2008; Powell et al. 2020). Moreover, *Cephalotes* colonies tend to occupy nests only within one tree (Powell 2009), meaning that they are constrained to the nests and pathways in a single tree. Given that limited nests and pathways impose spatial constraints on turtle ant networks, this study aims to examine how turtle ants choose which nests to occupy in constrained spaces where their movement and options are limited.

Since turtle ant colonies can choose among nests based on intrinsic properties of the nests themselves, we hypothesized that turtle ant colonies might choose which nests to occupy based on how they contribute to properties of the network. First, we conducted two sets of laboratory experiments to determine whether spatial constraints on pathways between nests affect which nests a colony chooses to occupy. In each set of experiments, we presented turtle ant colonies with an

environment that had two sections with different spatial constraints: one section was linearly connected with just a single path connecting the cavities in sequence, and the other was fully connected with all possible paths between each pair of cavities (Fig. 1). The ants were given the opportunity to explore both sections and to move from their original nests into the new cavities in these sections. The fully-connected section has the potential to form a network with greater efficiency, greater robustness, and lower cost than the linearly-connected section, so we predicted that the ants would move into the cavities in the fully-connected section if spatial constraints influenced nest choice.

Spatial constraints could also affect nest choice indirectly: not as a result of preference for specific network properties, but as an emergent consequence of the process of network creation within the spatial constraints of the environment. To examine this hypothesis, we constructed an agent-based simulation as a null model to demonstrate how a colony of ants might behave without basing nest preferences on network properties or making comparisons between nests. Prior models of ant movement have shown that random walks reinforced with unconditionally laid trail pheromone allow ant colonies to coordinate movement along specific trails and choose efficient pathways between existing nests and food sources in a self-organizing, emergent fashion (Goss et al. 1989; Aron et al. 1990; Dussutour et al. 2004; Ma et al. 2013). However, to our knowledge, the impacts of such a process on nest choice have not yet been modelled. To model nest choice emerging from spatial properties alone, we also included a self-reinforcing aggregation rule depending only on the number of individuals already present. Our model thus explores how the process of random diffusion coupled with positive feedback loops along paths and at nests could interact with the spatial constraints of the environment to affect which nests are occupied.

2 Materials and Methods

2.1 Laboratory Experiments

2.1.1 Study species

Queenright colonies of *Cephalotes varians* were collected from state-managed Hammock forest in Key Largo, Florida, and queenright colonies of *Cephalotes texanus* were collected from live oaks on private property near the city of Gonzalez, Texas. The first set of experiments, performed in June to July 2017, used three colonies of *C. varians* (V1, V2, and V3) and three colonies of *C. texanus* (T1, T2, and T3). The second set of experiments, performed in October to November 2017, used four colonies of *C. varians* (V4, V5, V6, and V7). The colony sizes (comprising workers, soldiers, and queens) at the start of each experiment for V1 to V7 and T1 to T3 were 190, 100, 140, 184, 64, 137, 56, 43, 55, and 82, respectively.

2.1.2 Experimental setup

To examine how spatial constraints affect turtle ant nest choice, we constructed arenas that had two sections with different structural features and levels of constraint (Fig. 1). One section had cavities that were fully connected to one another

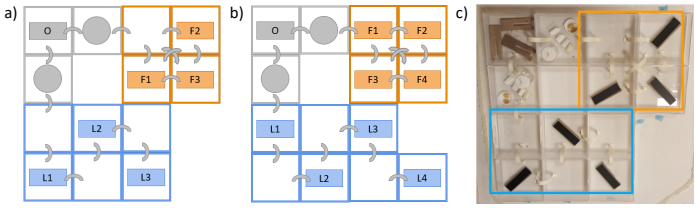

Fig. 1 Arena setups for laboratory experiments. Arenas were made of boxes connected by arched bridges. Rectangles within the boxes represent nest cavities. Each arena had 2 sections: one with fully connected cavities (F, orange) and one with linearly connected cavities (L, blue). Original cavities were put in at (O), equidistant from the closest cavities in F and L. Circles represent food and water. a) Diagram of the limited-cavity setup; b) Diagram of the additional-cavity setup; c) Picture of the limited-cavity setup with outlines drawn in for the F and L sections.

(F), while the other section had cavities that were linearly connected in sequence (L), with greater distances between the cavities. The F section had cavities that were closer to each other with more possible pathways between them, so it was less constrained than the L section. The arenas were made with boxes (dimensions: 11 x 11 x 3.75 cm high) in a grid arrangement as shown in Fig. 1. Boxes were connected with arched paper bridges which went from the floor of one box to the floor of another, over their adjacent walls. Fluon was applied to the sides of each box to prevent ants from escaping. The artificial nest cavities all had the same entrance size and volume and were made as outlined in Powell and Dornhaus (2013). In the first set of experiments (June to July 2017), there were three nest cavities in each section for a total of six cavities while in the second set of experiments (October to November 2017), there were four nest cavities in each section for a total of eight cavities (Fig. 1). Additional cavities were added in the second set of experiments to allow us to assess potential nest preferences in larger colonies that may be finding and occupying all of the cavities. For the rest of this paper, the two sets of experiments will be referred to as the *limited-cavity* and *additional-cavity* experiments, respectively.

2.1.3 Nest Choice Experiments

At the beginning of each experiment, we placed original cavities containing a single turtle ant colony in the box labeled O, equidistant from the closest cavities in the F and L sections (Fig. 1). We then opened the original cavities to force the ants to move and occupy new cavities in the arena. Colony movement was filmed for the first 12 hours and cavity occupation was checked 4 times a day at 8:00, 12:00, 16:00, and 20:00. Cavity occupation was measured by lifting the outer cover of the cavities and counting the number of workers inside with minimal disturbance. Both workers and soldiers moved between cavities, but workers were counted for simplicity and because they were much more numerous. The presence of brood was also noted. Turtle ants rapidly allocate workers and brood to new cavities and differentiate between different cavity properties (Powell and Dornhaus 2013), so both the number of workers occupying a cavity and the presence of brood can be used as indications of their preference for the cavity. The limited-cavity experiments lasted 5 days and showed that colonies occupied new cavities within

the first 12 hours, with the proportions of ants in each cavity remaining stable after the second day. Thus, the additional-cavity experiments lasted only 3 days.

2.2 Simulation Modeling

2.2.1 Model Description

The model description follows the ODD (Overview, Design concepts, Details) protocol, a standardized structure for describing agent-based models (Grimm et al. 2006, 2010).

Purpose This agent-based model simulates the movement and cavity occupation of an ant colony within a constrained space that can be designed by the user. The space (or arena) may have different structural features based on the spatial arrangement of the cavities and the bridges between them. This model is designed to explore the effects of structural constraints on turtle ant cavity occupation when the ant agents act under simple rules of movement driven by diffusion and pheromone feedback loops on trails and at nests, excluding preference or memory. Specifically, we used this model to examine the cavity occupation in simulated arenas based upon the two arenas used in the laboratory experiments described above. Within each arena, we compared the cavity occupation between two sections with different spatial features. Between the two arenas, we examined how the proportional occupation of these two sections differed.

Entities, State Variables, and Scales The agent-based model has two kinds of entities: ant agents and square cells. The ant agents represent the individuals of an ant colony that participate in exploration for new cavities, and there are 100 agents in each simulation. Each agent has a unique ID used to track its individual movement and two state variables to track its orientation and location (described as the cell that it is on). A 2D grid represents the floor of the arena and is divided into square cells. Arched bridges exist outside of the grid and are also made up of square cells. The length of a cell corresponds to the length of a worker ant, which is about 4.5 mm for the turtle ant species we used (*C. varians* and *C. texanus*). Each cell can represent either a wall, a cavity, a bridge, or an empty space (Fig. 2). The type of each cell is determined by the user based on the design of the arena. Each cell has two state variables that track the amount of pheromone and the number of ant agents in the cell. Empty cells within the arena may also have access to a bridge; such cells, called *bridge accessor cells*, represent the ends of the bridge where agents can get onto the bridge. Each bridge is made of an array of bridge cells and two bridge accessor cells at the ends of the array; this array is flanked on both sides by arrays of wall cells (representing the boundaries of the bridge) (Fig. 2c).

Initialization The structure of the arena, designated by the positions of each cell type, is generated when the simulation starts. The structure depends on user input: in this study, we ran simulations with two different structures modeled after arenas from laboratory experiments (Fig. 2). All of the cells are initialized without any pheromones. One hundred ant agents, each facing a random *direction*,

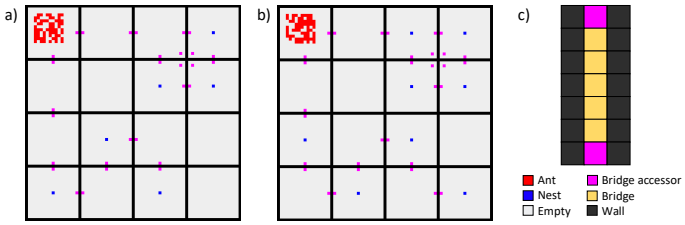

Fig. 2 Arena structures for the agent-based model. Cells in the arena can represent a wall, a nest cavity, a bridge, or an empty space; they make up the 2D grid representing the floor of the arena and the bridges that exist outside of the grid. Empty spaces that have access to a bridge are bridge accessor cells. Ant agents are generated within a random area designated by the starting location. a) Floor of the arena structure (excluding the bridges) modeled after the limited-cavity setup; b) Floor of the arena structure (excluding the bridges) modeled after the additional-cavity setup; c) A bridge of length 5 consisting of two bridge accessor cells and 5 bridge cells, flanked on both sides by wall cells.

are generated in random cells within a 10 x 10 grid of cells surrounding a *starting location.*

Process Overview and Scheduling Each time step represents the amount of time an ant takes to traverse the length of a cell (i.e. its own body length) and is approximately equal to 1 second of real time. During each time step, each ant agent has a probability of turning and a probability of moving into a new cell (the details of movement are outlined under "Movement Submodel"). Agents that move into a new cell or stay in a cavity deposit pheromone into the cell (details under "Pheromone Submodel"). The movements for each agent are tracked by recording each time it enters or exits a cavity or crosses a bridge. The order of ant agent movement is randomized within each time step so that the effect of an agent's movement on subsequent agents is randomized. After all of the agents have moved within the time step, the amount of pheromone in each cell is decreased. Each simulation lasts for 50,000 time steps, which is approximately equal to 14 hours and encompasses the initial stages of exploration according to the empirical experiments. At the end of each simulation, the number of agents in each cavity is recorded.

Design Concepts The *basic principle* addressed by this model is the concept of spatial constraints and how they may affect ant occupation in nest cavities by limiting possible network structures. In particular, the model examines how apparent nest preferences—examined as ant occupation in different cavities—can *emerge* from the movement of ant agents through cells that make up a constrained space (the arena). This behavior is modeled *dynamically* as the ant agents *sense* and react to changes in the amount of pheromone in adjacent cells, and *interact* with the cells by depositing pheromones. While this behavior is consistent with an adaptive response—ants tend to follow pheromone trails that can increase their fitness by leading to resources like food and nest cavities—ant agents in the simulation have no defined goals and lay pheromones unconditionally; the model thus explores how ants behave when they are solely driven by pheromones, and not by other factors that may maximize fitness (Goss et al. 1989; Deneubourg et al. 1990).

Stochasticity is used to represent variability in ant movement. Ant agents usually move in a forward direction and follow stronger pheromone trails, but they also sometimes turn or explore new paths (Garnier et al. 2009; Chandrasekhar et al. 2018). Ant agents aggregate in cavities according to a positive feedback loop, where the chance of an ant agent leaving a cavity decreases exponentially as the number of ants within the cavity increases (Deneubourg et al. 2002). In this study, we used pheromones to model local positive feedback loops at nest cavities, but such feedback loops could take different forms for real ant colonies (Pratt 2005). Additional details about movement and pheromones are outlined in "Movement Submodel" and "Pheromone Submodel", respectively.

Throughout the simulations, agent movement is *observed* by recording entries into and exits from cavities, as well as crossings over bridges. At the end of the simulations, cavity occupation is observed as the total number of agents in each cavity.

Movement Submodel The *movement submodel* defines how ant agents move within the arena according to a diffusion process and pheromone-mediated positive feedback loops. Many species of real ants, including turtle ants, deposit chemical pheromones which can be detected by other ants within a colony (Wilson 1976). Ants following a trail of pheromones can also deposit their own pheromones, creating a positive feedback loop along the trail. Turtle ants usually move in a forward direction and presumably follow stronger pheromone trails, but they also have high rates of movement and exploration on new paths (Gordon 2017).

Ant agent movement is summarized in Fig. 3. If an agent is in a cavity at the beginning of its move, it has a probability of leaving the cavity calculated by $q_{exit}/2^{(p_n+a_n)/p_y}$. The parameter p_n is the amount of pheromone in the nest cavity; a_n is the parameter *nest cavity attractiveness*, which is used to model the greater likelihood that an ant will explore a cavity compared to an empty space. The probability of leaving a cavity decreases with more pheromone in the cavity; the parameter p_y (the *staying factor*) refers to the amount of pheromone that decreases this probability by half. The value of the parameter q_{exit} is 0.5, meaning that the agent has an equal probability of staying or leaving the cavity in the absence of pheromone and when cavity attractiveness is zero. If the agent leaves the cavity (or if it is not in a cavity to begin with), it has a probability of turning determined by the parameter q_{turn}. If it turns, it does so within a uniform, symmetric range of degrees (e.g. -90 to 90 degrees) determined by the parameter *turning range*. From the new direction it is facing, the agent can perceive any adjacent non-wall cells within its field of vision, determined by the parameter *vision range*. Agents on bridge accessor cells can also perceive the first empty cell on a bridge, regardless of the direction they are facing. The agent then stays in its current cell or moves to any of the cells it can perceive based on a weighted random walk. The weight of any adjacent cavity cell, if present, is $a_c + a_n + p_c$, where ac is the parameter *cell attractiveness*, a_n is the parameter *nest cavity attractiveness*, and p_c is the amount of pheromone in the cell. The weight of non-cavity adjacent cells is $a_c + p_c$ and the weight of the current cell is a_c because an agent is not following a pheromone trail by staying in place. *Cell attractiveness* refers to the intrinsic attractiveness of each cell and allows neighboring cells with no pheromone to be considered in the weighted random walk. If an agent moves onto a bridge

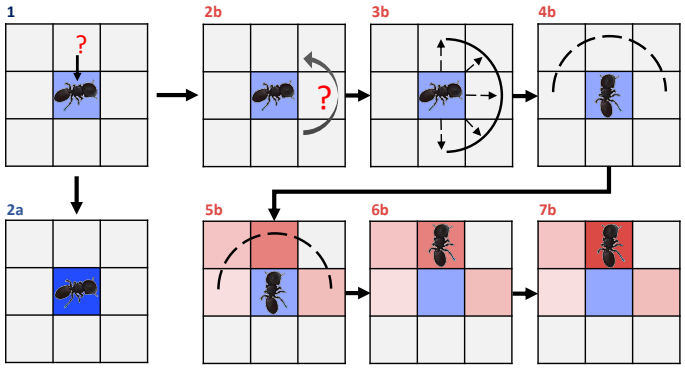

Fig. 3 Ant agent movement. 1) Ant agents in a cavity (*blue*) have a probability of leaving. 2a) If they stay, they deposit pheromones in the cavity. 2b) If they leave a cavity or if they were originally not in a cavity, they have a probability of turning. 3b) If they turn, they randomly turn within a turning range. 4b) After turning, they can perceive adjacent cells within a vision range. They can move into any cell within their range of vision or remain in their current cell. 5b) They take their next step based on a weighted random walk, where each adjacent cell is weighted by the amount of pheromone (*pink*) it contains. Cavity, non-cavity, and current cells are weighted differently. If they move into a new cell (6b), they deposit pheromone into it (7b).

cell, it traverses the cells of the bridge according to the same rules of movement as those in the rest of the arena.

Pheromone Submodel The *pheromone submodel* defines how the amount of pheromone is updated as a state variable for each cell. Each time an agent enters a new cell, it increases the pheromone value by depositing an amount of pheromone determined by the parameter *pheromone strength* (p_s). Agents that remain in cavities also deposit pheromone in each step. The amount of pheromone in each cell is saturated at the parameter *max pheromone* (p_m). After each time step, the pheromone in each cell is decreased exponentially by the rate q_{decay} to model the decay of real pheromones over time.

Simulation Experiments and Data Collection The model was implemented in Java 8 and each experiment had 100 simulations (Table 1). Each simulation ran for 50,000 time steps, with each time step equal to 1 second. To examine how spatial constraints might have affected turtle cavity occupation in our laboratory experiments via limited diffusion and pheromone feedback loops, we ran experiments with arena structures based on the limited-cavity and additional-cavity arenas (Figs. 1 & 2). We performed preliminary analyses to determine and validate the parameters that modeled ant movement (Online Resource 1). To further examine the effects of pheromones on ant movement, additional simulations were run that 1) removed all pheromones from the model and 2) modeled pheromones only within cavity cells (Fig. 7). Apart from varying the arena structure and pheromone presence, all of the experiments used the parameters outlined in Table 1. During each simulation, the time step and ant ID for each bridge crossing, cavity entrance, and cavity exit were recorded. At the end of each simulation, the number of ant agents in each cavity was recorded.

Table 1 Model Parameters

Description	Parameter	Value	Rationale/notes
Arena Structure: includes locations of each type of cell, locations of bridges, and bridge lengths	–	varied (Fig. 2)	based on laboratory experiments
Starting position	–	middle of original box	agents are generated within 5 cells of this location
Number of ant agents	–	100	approximate size of colonies in laboratory experiments
Number of time steps	–	50,000	equal to 14 hours real time
Max pheromone in a cell	p_m	550	validated in Supplemental Materials
Pheromone strength: amount of pheromone deposited by an agent	p_s	4	validated in Supplemental Materials
Staying factor: amount of pheromone that decreases the probability an ant agent will leave a cavity by half	p_y	50	validated in Supplemental Materials
Nest cavity attractiveness: additional attractiveness of a cavity compared to an empty cell	a_n	8	validated in Supplemental Materials, represents the greater likelihood an agent will explore a nest cavity over an empty space
Cell attractiveness: intrinsic attractiveness of a cell	a_c	12	allows all potential cells to be considered within a move
Probability of turning	q_{turn}	0.2	consistent with Chandrasekhar et al. (2018), validated in Supplementary Materials
Baseline probability of exiting a cavity without accounting for pheromones or attractiveness	q_{exit}	0.5	no bias for staying or leaving a cavity without pheromones or attractiveness
Pheromone decay per time step (%)	q_{decay}	0.05	consistent with Chandrasekhar et al. (2018)
Turning range: maximum possible turn (degrees)	–	-90 to 90	prevents agents from going backwards in one step; consistent with Sendova-Franks and Lent (2001) and Perna et al (2012)
Vision range: field of vision (degrees)	–	-90 to 90	prevents agents from going backwards in one step, determines where agents can move

2.3 Statistical analyses

We used generalized linear mixed models to examine turtle ant occupation across the different cavities at the end of each laboratory experiment. We used a Poisson distribution to model the number of worker ants in each cavity, and a binomial distribution for the presence of brood in each cavity. Within each model, the colony was included as a random effect to account for consistent differences between colonies. The observation identifier (a unique identifier assigned each time occupation was counted for each cavity) was used as an additional observation-level random effect to account for overdispersion caused by the possibility that ants aggregate non-independently in cavities (Harrison 2014). The cavity connectivity (whether a cavity was in section F or L) was included as a fixed effect since we were interested in the effects of structural features on cavity choice. For the model of number of worker ants per cavity, we also included species (*C. varians* or *C. texanus*) as a fixed effect, to account for consistent differences in colony size between species.

We also used randomization tests to examine whether the observed effects of structural features on cavity occupation could have been due to chance. First, we chose just to consider the observation in the afternoon of the third day as being representative of the colony decision. The number of ants was averaged across all cavities in each section (F and L) for each colony, and the test statistic was calculated as the difference between the two sections, averaged across all colonies in each experiment. In each randomization, the section label for each cavity (F or L) was randomly shuffled within each colony, and the test statistic was recalculated. For each experiment, 5000 randomizations were performed to calculate the proportion of randomizations with test statistics more extreme than the observed test statistic.

3 Results

3.1 How do spatial constraints affect turtle ant nest choice?

We examined turtle ant cavity occupation in the laboratory experiments by observing the numbers of workers and the presence of brood in each section (the fully-connected section or the linearly-connected section) at the end of each experiment (Fig. 4). In the limited-cavity experiments, there was significantly greater occupation of the fully-connected section than the linearly-connected section based on the total number of workers (Poisson GLMM, effect $= 1.12 \pm 0.44$, $p = 0.01$) and the presence of brood (Binomial GLMM, effect $= 3.66 \pm 1.49$, $p = 0.01$) in each cavity. On average, colonies had 11.27 more ants per occupied cavity in the fully connected section than in the linearly connected section. Out of 5000 randomizations, none yielded such a large difference between the sections. However, there was no significant difference in cavity occupation between the two sections in the additional-cavity experiments, neither based on the number of workers (Poisson GLMM, effect $= 0.14 \pm 0.55$, $p = 0.80$) nor the presence of brood (Binomial GLMM, effect $= -6 \times 10^{-7} \pm 4.6$, $p = 1.0$). The randomization test also showed no significant effect: the experimental colonies had just 1.06 more ants per cavity in the fully connected section on average, and over a third (1941 out of 5000) of

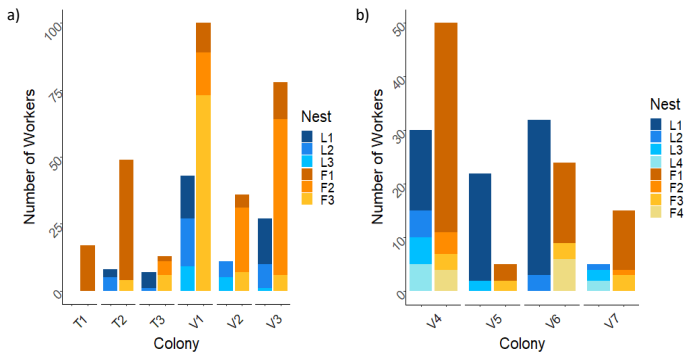

Fig. 4 Final cavity occupation is affected by spatial constraints. The number of workers per cavity was observed at the end of each empirical experiment for each colony in the a) limited-cavity setup and b) additional-cavity setup. In the limited-cavity setup, there were always more workers in the fully connected (F) cavities, while in the additional-cavity setup only half the colonies had more workers in F cavities.

the randomizations yielded a difference between sections that was greater. While colonies in the two sets of experiments had different patterns of cavity occupation, they had similar levels of activity, with the same number of cavities found and occupied within the first 8 hours (Fig. 5).

Each colony typically occupied most of the cavities; however, instead of distributing workers evenly across the cavities, all colonies except for T3 (the smallest colony) either concentrated most of their workers into just one cavity, or split most of their workers between two cavities within the first day of the experiments. These cavities had at least 2.5 times as many ants as any other cavity at the end of the experiments, and they typically had most, if not all, of the brood and soldiers. We thus take these criteria as an indicator of cavity choice. In the limited-cavity experiments, all of the colonies except for T3 (Fig. 5c) chose to aggregate in one cavity, and it was always in the F section (e.g. Fig. 5a & 5b). In the additional-cavity experiments, all of the colonies chose to aggregate in F1, L1, or both (e.g. Fig. 5d, 5e and 5f). All of the chosen cavities were among the closest available cavities to the original cavities (limited-cavity experiment: F1, F2, F3 and L1; additional-cavity experiment: F1 and L1) (see Fig. 1).

3.2 Could spatial constraints indirectly affect nest choice?

While the empirical results for the limited-cavity setup seem to suggest a preference for well-connected nests, the empirical results for the additional-cavity setup do not. As an alternative, we hypothesized that nest choice could be indirectly influenced by spatial constraints, emerging from movement patterns within those constraints, even in the absence of preference. To test this hypothesis, we created a model for ant movement through arena structures based on the experimental setups. The model simulates ant movement based on simple diffusion, self-reinforcing movement, and density-dependent aggregation at nests, without preferential recruitment to specific nests. By varying the parameters controlling how many ant agents are needed to induce others to stay at a nest, the model can generate a

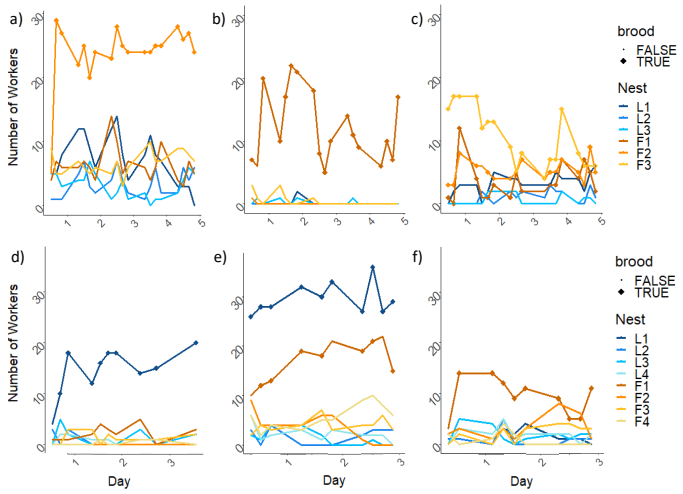

Fig. 5 Ants were concentrated in one or two nest cavities. Within the first day of the empirical experiments, all colonies had concentrated most of their workers and brood into just one or two nest cavities and the trends in occupation remained the same after the first day (except for T3). Colonies in the limited-cavity experiments typically chose to aggregate in one cavity in F. Two examples are shown: a) Colony V2, b) Colony T1. An exception was c) Colony T3. Colonies in the additional-cavity experiments chose to aggregate in F1, L1, or both. Three examples are shown: d) Colony V5, e) Colony V6, f) Colony V7.

variety of results, ranging from consensus choice of one nest to dispersion across all of them (see Online Resource 1). We chose parameter values to produce levels of aggregation similar to those observed in the laboratory experiments: simulated colonies typically occupied one or two cavities (i.e., they aggregated in one or two nests, containing at least 2.5 times as many ants as any other nest). Under these conditions, as observed empirically, the cavities closest to the starting positions (L1 and F1-3 for the limited-cavity experiments and L1 and F1 for the additional cavity experiments) were more likely to be occupied (Fig. 6). Thus, the majority of simulations fell into one of three categories: (1) most ant agents aggregated in one nest in F, (2) most ant agents aggregated in one nest in L, or (3) the group split between two nests, one in each section (Fig. 6).

The simulations showed that patterns of cavity occupation similar to those observed in the laboratory experiments could emerge without being driven by preference. Like the laboratory results, the simulation results showed greater usage of nests in the fully-connected section for the limited-cavity experiments, but not in the additional-cavity experiments. In the limited-cavity experiments, simulations were 5.9 times more likely to fall in the 'Single nest in F' category than in the 'Single nest in L' category, and there were few cases of splitting between F and L (Single nest in F: 59, Single nest in L: 10, Split between F and L: 9, out of 100 simulations). In contrast, in the additional-cavity experiments, simulations were 1.5 times more likely to fall in the 'Single nest in L' category than in the 'Single nest in F' category, and the majority of simulations had splitting between F and L (Single nest in F: 16, Single nest in L: 25, Split between F and L: 52, out of 100

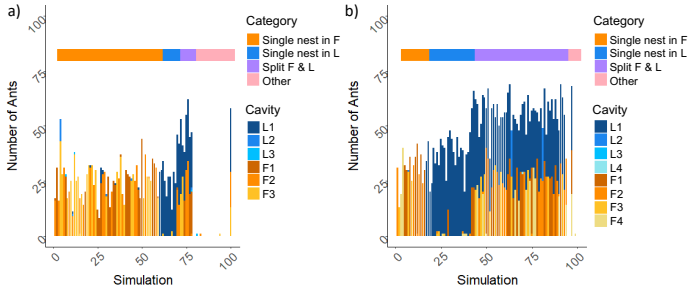

Fig. 6 Cavity occupation patterns were different under different spatial constraints. Cavity occupation was recorded at the end of each simulation for the a) limited-cavity arena structure and b) additional-cavity arena structure. Each simulation was assigned to one of 4 categories according to where most ant agents aggregated at the end of the simulation: (1) Single nest in F; (2) Single nest in L; (3) Split between F and L; and (4) Other if the simulation did not fit into any of those categories.

simulations). These patterns remained robust across a range of suitable parameter values (Online Resource 1).

3.3 How do spatial constraints mechanistically drive patterns in cavity occupation?

To understand the mechanisms that drive patterns in cavity occupation, we examined the distribution and movement of the simulated ants within the spatial structures. In both the additional-cavity and limited-cavity experiments, the proportions of ant agents in the boxes of each section were about 50-50, but the proportions of ant agents in the cavities of each section differed between the experimental setups (Fig. 7a). This difference suggested that the agents diffused equally into the boxes of the linearly-connected and fully-connected sections, but moved into the cavities in proportions which differed between the experiments.

To parse out the effects of diffusion and pheromone feedback loops on movement, we ran two additional sets of experiments: one without any pheromones to model the effects of diffusion alone, and one with pheromones deposited only within nest cavity cells to model the effects of diffusion plus local pheromone feedback loops at cavity cells. In the set without any pheromones, the rate of ant agents encountering each cavity reflected cavity occupation distribution patterns observed in both the laboratory and simulation experiments. Encounter rate was highest for the three F cavities in the limited-cavity experiments while it was highest for the L1 cavity, then the F1 cavity, in the additional-cavity experiments (Fig. 7b); these were the most populated nests in the respective laboratory experiments (Fig. 5) and simulation experiments (Fig. 8c & 8f). Thus, diffusion alone can explain the overall distribution of ants in the experiments. However, pheromones are still necessary for ants to accumulate in cavities. In the set of simulations with pheromones only within cavity cells, the limited-cavity and additional-cavity experiments showed similar proportions of ant agents in the boxes of each section but dissimilar proportions of agents in the cavities of each section, just as in the experiments with pheromones in all cells (Fig. 7a). Therefore, the observed patterns in

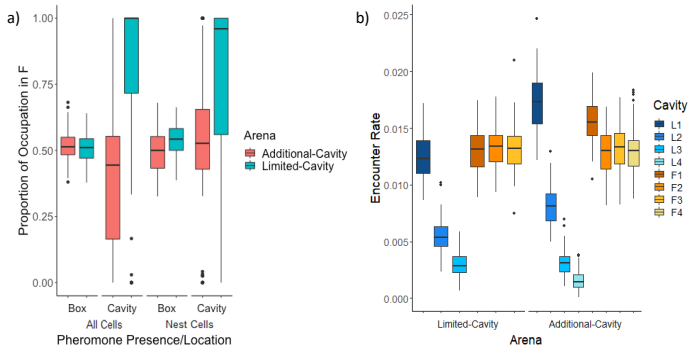

Fig. 7 Simulation results showing cavity occupation depends on cavity encounter rates driven by diffusion and local pheromone feedback loops at cavity cells. a) Between the additional-cavity and limited-cavity experiments, the proportions of ant agents in the cavities of each section were similar, but the proportions of agents in the boxes of each section were dissimilar. b) In diffusion-only (no pheromone) experiments, patterns in encounter rates for each cavity reflect patterns of cavity occupation, with higher rates corresponding to greater occupation.

cavity occupation can be achieved with diffusion driving ant movement outside of cavity cells and with local pheromone feedback loops driving ant movement within cavity cells.

Proximity to the cavity cells is required for ant agents to be affected by local pheromone feedback loops, so we examined how spatial features can lead agents to encounter or bypass cavity cells through diffusion. Specifically, we examined the behavior of the ant agents when they first enter the two structurally different sections through the boxes closest to the original cavity: L-Box 1 and F-Box 1 (Fig. 8a & 8d). The paths leading to these two boxes from the original cavity are exactly equivalent, but the paths leading onward are different, so this was a good place to look for sources of asymmetry between the two sections. Also, the only difference between the F sections in the limited-cavity and additional-cavity arena structures was the addition of a cavity in F-Box 1, making that box of particular interest. We thus inferred that the spatial structure surrounding F-Box 1 likely contributed to the differences observed between the experiments, and we focused on how ant agents moved at F-Box 1 and its equivalent in the other section, L-Box 1. Specifically, we documented the movement of ant agents after they entered F-Box 1 or L-Box 1 and categorized their next steps as 'backward' (moving back towards the original nest), 'forward' (moving forwards into the section), or 'nest' (going into a nest cavity in the box) (Fig. 8).

In both the limited-cavity and the additional-cavity experiments, additional forward paths in F-Box 1 compared to L-Box 1 caused greater forward movement into the fully-connected section compared to the linearly-connected section. In both setups, there were three forward paths from F-Box 1, compared to one forward path in L-Box 1. As such, there was a greater or equal proportion of ant agents moving forwards than backwards from F-Box 1, compared to a smaller proportion of ants moving forwards than backwards from L-Box 1 (see Fig. 8b & 8e). While these patterns of movement are similar between the limited-cavity and additional-cavity experiments, they have different effects on cavity occupation. In

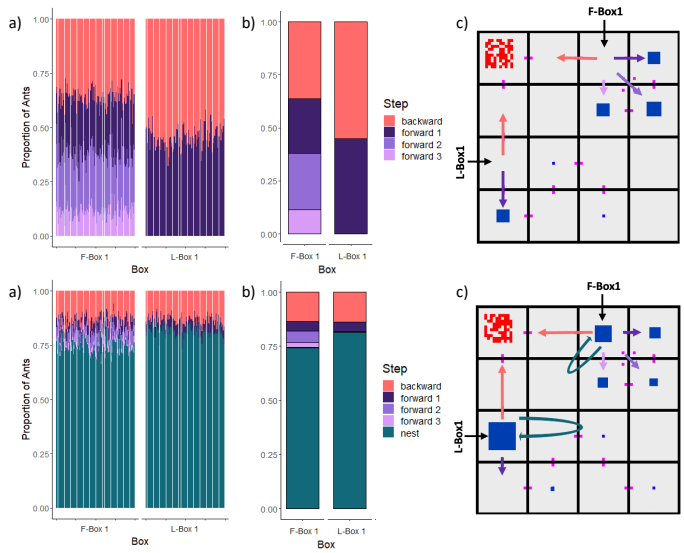

Fig. 8 Simulation results showing greater forward movement from F-Box 1 compared to L-Box 1. The movement of ant agents once they entered the first box of each fully-connected (F) or linearly-connected (L) section was examined and their next steps were categorized as 'backward' (moving back to the original cavity), 'forward' (moving forward into the section), or 'nest' (going into a nest cavity in the box). Proportion of agents that took each type of step for all simulations in the a) limited-cavity arena structure and d) additional-cavity arena structure. Average proportion of agents that took each step for the b) limited-cavity arena and e) additional-cavity arena. Summary diagram of movement in the c) limited-cavity arena and f) additional-cavity arena. Size of blue cavities is proportional to average number of agents in the cavity at the end of all simulations, and length of arrows indicates relative proportion of agents that take the step.

the limited-cavity experiments, greater forward movement from F-Box 1 results in less backward movement, compared to L-Box 1 (Fig. 8b). This led to greater occupation in the fully-connected section, likely by allowing more agents to encounter the three F cavities that are equidistant from the original cavity (Fig. 8c). However, in the additional-cavity experiments, greater forward movement from F-Box 1 causes agents to miss the closest F nest in F-Box 1 without affecting the rate of backward movement, compared to L-Box 1 (Fig. 8e). This led to less occupation in the fully-connected section, likely by reducing the rate of encounter at the closest F nest (Fig. 8f).

4 Discussion

Our empirical results show that spatial constraints can affect turtle ant nest choice and thus shape the formation of their transport networks. In two sets of experiments designed to test whether colonies would preferentially occupy different physically equivalent nests based on network characteristics, we observed apparently conflicting results. The experiment with fewer cavities suggested a preference for nests with close connections to other nests, but the experiment with additional cavities did not. Taken alone, these empirical results might suggest that turtle ant

colonies preferentially target well-connected nests, but only under specific conditions. One explanation for the observed differences could be changes in activity level or motivation during the different seasons in which the two sets of experiments were performed, which have been observed in other species (Heller and Gordon 2006; Stroeymeyt et al. 2014). However, colonies in the two sets of experiments showed similar patterns of exploration and occupation, both in terms of numbers of active ants and nests occupied. More importantly, simulations of ant movement based on the two sets of experiments show that the observed patterns can in fact be explained as an emergent consequence of simple rules of diffusion and pheromone feedback loops, interacting with subtle differences in the layouts of the two experimental set-ups. Since the computational simulations do not model preference or memory, the results demonstrate that the empirically observed patterns of nest choice could emerge from the imposed spatial constraints, even without individual preference for nests that improve network characteristics of efficiency and robustness.

Our model of nest choice focuses on emergent effects of spatial constraints by including only quality-independent feedback processes: continuous trail-laying outside the nest, and density-dependent aggregation inside the nest. Classic models of nest choice in social insect colonies utilize quality-dependent recruitment coupled with a quorum threshold rule to balance three objectives: speed, accuracy and group cohesion (Sumpter and Pratt 2009). In the two best-studied examples, rock ants and honey bees, individuals assess site quality directly, judging characteristics like cavity volume and entrance size; quality-dependent recruitment then amplifies traffic to the best site more quickly than to other sites, allowing the group to integrate information collected by many individuals and make accurate consensus decisions (reviewed in Franks et al. 2002). We know that turtle ant colonies also choose to occupy cavities based on physical nest properties like entrance size (Powell 2009; Powell et al. 2020) and cavity volume (Powell and Dornhaus 2013). Besides quality-dependent recruitment, such preferences could emerge from quality-dependent resting time at a nest, as in cockroaches aggregating at a shelter (Jeanson et al. 2007), or even a combination of the two, as observed in the ant *Messor barbarus* (Jeanson et al. 2004). While our work does not rule out the possibility that nest choice is influenced by individual ants assessing the spatial characteristics of physically equivalent nests, it demonstrates that nest choice can be influenced by spatial characteristics in an emergent fashion, even without such assessment. How the interactions play out between the emergent spatial influences on nest choice and the demonstrated preferences for certain physical nest properties remains to be explored.

Of the two quality-independent feedback processes we included, trail-laying outside the nest might seem a natural candidate to produce indirect spatial effects on nest choice. Argentine ants use continuous trail-laying to choose shorter paths, leading to efficient and low-cost networks of trails linking multiple pre-established nests (Goss et al. 1989; Aron et al. 1990; Latty et al. 2011). Although nothing is known about pheromone use in *C. varians* or *C. texanus* specifically, it has been suggested that *Cephalotes goniodontus* may also lay pheromone continuously, allowing colonies to improve efficiency of foraging trails (Gordon 2017; Chandrasekhar et al. 2018). If so, we might expect this process to impact turtle nest choice during colony expansion into new cavities, potentially leading to the construction of efficient and low-cost networks. However, we found that simulated

colonies, like real turtle ant colonies, did not always choose sets of nests leading to an efficient, low-cost network. Furthermore, since qualitatively similar results were observed with and without pheromones outside the nest, we can conclude that positive feedback along trails is not necessary to explain the qualitative patterns of nest choice we observed.

Instead, the patterns of nest choice we observed in the simulations seem to be driven primarily by the second positive-feedback loop—aggregation at the nest—interacting with the diffusive flow of ant agents along constrained pathways. To induce aggregation at the nest, we included a quality-independent positive feedback rule based only on the number of individuals already present, as has been suggested for other gregarious invertebrates choosing a shelter without spatial constraints (e.g. Ame et al. 2004; Broly et al. 2016). This induces a quorum-type response, allowing us to represent a continuum of strategies—ranging from perfect consensus to dispersion across all nests—by varying the parameters controlling how many ant agents are needed to induce others to stay at a nest (Sumpter and Pratt 2009). Turtle ants seem to lie somewhere in between: a strategy of broad exploration coupled with consolidation of most workers along with soldiers and brood into a subset of nests may allow colonies to monitor a larger set of cavities without spreading their defenses too thin (Powell and Dornhaus 2013; Powell et al. 2017). It was under such conditions, where simulated colonies showed substantial cohesion without requiring complete consensus, that we observed the strongest emergent effects of spatial constraints.

While an apparent preference for closer nests could emerge naturally from quality-independent recruitment, we show that the spatial constraints of an arboreal environment could also influence nest choice via diffusion and aggregation in more complex ways. In both our laboratory experiments and simulations, we found that the closest nests were those most likely to be occupied. Similarly, colonies of ground-nesting rock ants consistently choose the closer of two equivalent nests, likely because they are discovered more quickly and the recruitment process amplifies more quickly (Franks et al. 2008). The quality-independent recruitment process we included in our model could lead to an apparent preference for closer nests in just the same way. Even without recruitment, closer nests may be encountered at a higher rate due to diffusion, so that density-dependent aggregation can proceed more quickly. However, distance is not the whole story: nests that were equidistant in our simulation experiments were not always equally likely to be chosen. This occurs because the encounter rate decreases when there are more paths leading away from a cavity, since ants that miss encountering a cavity the first time are more likely to move away from it and encounter other cavities further away. Observations of the foraging networks of *C. goniodontus* suggest that foraging ants take longer to find new food sources that require travel through many junctions, and that new foraging trails are made more efficient over time by reducing the number of junctions, not the total distance along the trail (Gordon 2017). Our work further supports the idea that, within arboreal transport networks, the efficiency of travel between two points is strongly influenced by the number of junctions en route to and even beyond the destination. In turn, it also shows that nest choice can be shaped by these spatial constraints.

While turtle ant colonies did not always choose new nests in a way that would lead to low-cost and efficient transport networks, it could still be the case that they utilize a process which usually leads to low-cost and efficient networks under

conditions that they are likely to encounter in nature. The process of diffusion coupled with aggregation at cavities with high encounter rates would typically lead ants to choose nests that are easily accessible from their starting point. Such a strategy might often lead to low-cost and efficient transport networks, particularly if the colony preferentially expands from nests that are strategically placed in the network, as observed in European wood ants (Ellis et al. 2017). In the additional-cavity experiments, however, this fundamentally myopic strategy may have caused ants within a colony to split between two cavities that were easily accessible from the original nest but less easily accessible from one another. Because the original nest was destroyed and no longer a node in the network, this resulted in a network that was less efficient and higher cost, compared to the choice of two cavities further from the original nest but close to each other. However, this initial acceptance may simply reflect the first stage in a longer-term process of network expansion, followed by nest abandonment and network restructuring, as observed in wood ants (Ellis and Robinson 2015). A related process of adding new connections, followed by selective pruning of trails, has been shown to shape the construction of low-cost, efficient trail networks between nests in Argentine ants (Latty et al. 2011) and has also been proposed to explain the dynamic structure of foraging networks in *C. goniodontus* (Gordon 2017; Chandrasekhar et al. 2018). Our model focuses just on the initial choice of nests needed to start building a network of nests, not on how the resulting network functions to transport goods. However, it could serve as the initialization step for a dynamic model that explores how ants distribute or transport resources between nests over time, and how they may change their nest occupation in response to that flow of resources.

By focusing on nest choice in a network context, this study adds a new perspective to the problem of transport network design. Like their human-designed counterparts, biological transport networks must balance competing priorities of cost, efficiency and robustness (Bebber et al. 2007; Tero et al. 2010; Latty et al. 2011; Cook et al. 2014; Lecheval et al. 2020). Studying biological transport networks and translating their local rules into mathematical and computational models has already begun to provide heuristics to inform the construction of human-designed transport networks without the need for centralized planning (reviewed in Teodorović 2008; Nakano 2011). In particular, ant pheromone models demonstrate how collective path selection can allow the emergent construction of low-cost, efficient networks (Goss et al. 1989; Aron et al. 1990; Latty et al. 2011; Reid and Beekman 2013), leading to popular ant-inspired algorithms for routing and scheduling, among other optimization problems (reviewed in Dorigo et al. 2006). Yet transportation networks consist not just of paths but also nodes: sources and sinks for the goods and individuals being transported. In situations where potential nodes are limited and the potential pathways between them are highly constrained, a network's cost and efficiency may be strongly shaped by the choice of which nodes to include in the network. In contrast to path selection, the study of collective resource selection—for example, making a choice between alternative nests or food sources—typically focuses on the integration of quality information collected by many individuals (Seeley et al. 1991; Sumpter and Pratt 2009; Jeanson et al. 2007). In this study, we show how resource selection can shape network characteristics even without individual preferences, as a byproduct of spatial constraints shaping diffusive flow and aggregation. Recent work on resource selection in robot swarms has shown that quality-dependent positive feedback can be used to optimize the

rate of resource collection, by effectively balancing the trade-off between selecting high-quality versus nearby resources (Font Llenas et al. 2018; Talamali et al. 2020). Bringing all three processes together—quality-dependent positive feedback, aggregation, and diffusion within constrained spaces—into a dynamic model of transport networks could be a powerful way to design efficient and low-cost networks for transporting resources under spatial constraints.

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Conflict of interest

The authors declare that they have no conflict of interest.

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