In-nest information flow analysis of social ant colonies

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Abstract

Physical interactions between social insects are critical in the transfer of information about food, nest construction, and other alarm signals within the colony. Analysis of time-aggregated interaction networks among ants can reveal key insights to the inner workings of these communication system and efficiencies. Previous studies measure empirical interactions and create models to observe these interactions in petri dishes, but little is known about the structure of these networks below ground. Restriction of movement through tunnels and chambers of an ant nest may have an impact on the efficiency of information flow. We propose an agent-based model to simulate ant behaviour within various nest topologies. We investigate the differences in above-ground and in-nest interaction network topologies and discuss the potentially beneficial and detrimental features of ant nests to the formation of these networks.

1 Introduction

Social insects rely on intricate communication systems to maintain a high-level of efficacy that is critical to the ant-colony super-organism. In social ant systems, complex behaviours such as efficient traffic flow based on density [1, 2], construction of organized nests [3], and rapid diffusion of information through a colony can emerge through simple local rules, and are byproducts of the organizational needs of the ants. One way ants will organize themselves is by dividing work into tasks and assigning workers to these tasks [4]. These tasks can and do change over time, and broadly inform the social hierarchy within the colony, making task allocation an ongoing need [5]. The nest itself contains different task zones that serve purposes such as food processing, brood care, and trash maintenance. Colonies can also have areas depending on species for unique behaviours such as growing fungus and an area at the entry of the nest that is designated for stationary workers. The structure of these nests impacts the colony's response to various stimuli [3] but not much is known about the specific interactions which occur to inspire these responses. The patterns and strategies that ants employ in order to operate successfully can provide useful insight for optimization of information spread in similar systems with applications being found in traffic management, supply chains, and human social networks [6].

Since these colonies function without an overarching controller, the diffusion of information through the colony relies on one-on-one contact between individuals. The decentralized nature of the social organization of ant colonies heightens the needs for efficient information travel throughout the entire nest to mobilize appropriate responses to threats and food sources. It has been observed that for some tasks, direct communication is not required but instead pheromones are used to inform workers of actions recently taken by others [7]. The use of pheromones is most common in nest construction and long-distance foraging. In other situations, we can observe the use of physical contact to convey information about food via trophallaxis and other alarming activity via antennation. These different forms of communication create an interesting contrast in information flow depending on the method employed by the ants.

Physical interactions typically have a dominance relation [8] with foragers receiving more dominance than their non-foraging counterparts. Amount of dominance is tied to the needs of the colony, apparent from the increased levels of dominance when a colony is starving and decreased levels when food is present in excess. We can extrapolate from this that dominance is not meant just to convey some internal social status but to convey information about colonies

needs. Due to the pointed nature of these interactions they are often modeled by directed networks. Recent studies of these networks include performing motif analysis of time-aggregated networks, measuring hamming distance between networks and random graphs over time to check for stability, counting motif clusters, and finding the distribution of node spins. These have revealed some interesting commonalities between ant interaction networks and other network types. For example, the feed-forward loop is abundant in ants but not commonly found in human social networks. Instead, it appears with similar distribution to biological regulatory systems such as signal transduction in mammalian cells and synaptic wiring in *C. elegans*.

Historically, much of the literature on eusocial insect species originated in relation to social ants [9]. However, there is a dearth of information regarding the social dynamics of ants inside the nest [3]. This presents a problem as much of the daily minutiae of colony upkeep happens within the nest, potentially without regard to all but the most extreme external disruptions. Hence a lack of understanding on internal nest dynamics presents a fundamental epistemological barrier to the collective understanding of ant social behavior [3]. This relative lack of understanding can be largely attributed to the difficulty associated with gathering reliable and complete interaction data within the labyrinthine structure of a nest [3]. However, new developments using tomographic imaging technology has begun to bridge this gap. It is in light of these recent developments that we develop our action plan.

By pulling together various models for ant interactions, task allocation, and nest structure, we hope to both build a new model that accurately delineates intra-colonial interactions and position ourselves to easily extend the model to the context of other social species or certain human economic applications [10]. With our model, we hope to shed light on the questions:

- How do social networks differ above and below ground?
- In what ways does nest structure affect the formation of social networks?
- Are there optimal nest features which promote efficient information travel?

In particular, we will use various metrics including informed population proportion, motif count of interaction networks, and contact rates between ants of different types to determine if certain architectural features of a nest affect the efficiency of information diffusion. By testing these on both novel features and comparing to the results of previous simulations in rectangular boundaries, we hope to gain an understanding of how ants may differ in the simpler above ground case and some of these more complex nest features.

2 Methodology

Our model is a discrete-time agent-based model which adapts the model in [4] to study various nest structures. The major differences include changes in the definition of nests, drifted walking style of ants, and information transfer. A colony is characterized by a connected set of grid cells X called a nest, a set of ants, and a set of spatial fidelity zones. An ant A at time t has five attributes: l(A,t), p(A,t), w(A,t), f(A,t), $\beta(A,t)$, and path(A,t) where l is the ants current location within the colony, p is the ants task, w is the ants walking style, f is the ants information status, β is probability of receiving information, and path is the current route the ant is following. We now discuss the details of each of these attributes along with some of their associated objects and metrics:

Location: Each ant has a unique $l(A,t) = (i,j) \in X \subset \mathbb{Z} \times \mathbb{Z}$. Each ant also has a von Neumann neighborhood NC(A,t) and a set of neighbors $N(A,t) = \{B : l(B,t) \in NC(A,t)\}$. Each update step, ants are able to move to an open grid cell with some probability depending on their walking style. By 'open grid cell' we mean an element $c \in NC(A,t)$ for which there is no ant with l(A,t) = c.

Tasks and Spatial Fidelity Zones: There are a total of P spatial fidelity zones (SFZs) within the colony represented by $S_p \subset X$ for $p \in \{1, ..., P\}$. Each S_p is connected and for $p \neq q, S_p \cap S_q = \emptyset$. These are meant to simulate task division amongst the ants and the relative isolation between task groups. Ants are initialized with some $p(A, t) \in \{1, ..., P\}$ and are assumed to maintain their task throughout the entire simulation. That is, p(A, t) = p(A, 0). We make this assumption since on small time scales, ants are unlikely to change tasks.

Walking Style, Ant Path, and Spatial Fidelity: Ants have a walking style $w(A, t) \in \{R, D\}$ where R represents a random walking style and D represents a drifted walking style. Similar to associated task, we assume w(A, t) = w(A, 0). With a random walking style, each time step an ant will move to a random open grid cell with uniform probability. With a drifted walking style, ants will attempt to follow an optimal path to reach their associated SFZ until another ant gets in the way. This was a necessary change to the previous model since with the allowance

of obstacles in the new definition of nest, ants would otherwise become stuck against the walls unrealistically. Our assumption is that ants are able to follow a near optimal path with the use of pheromone sensing back to their task zone. So now, ants use the A^{*} search algorithm [11] to calculate the optimal path from l(A, t) to $center(S_{p(A,t)})$ where we calculate the center of an SFZ as

$$center(S_p) = \lceil \frac{\sum_{x \in S_p} x}{|S_p|} \rceil$$

path(A, t) refers to this optimal path at time t. Each update step, ants with drifted walking style will attempt to move to the next cell in their path. If this cell is not open, the ant will instead move to an open cell which minimizes the L1-distance from l(A, t) to $center(S_{p(A,t)})$ with uniform probability. The ant will then recalculate its optimal path. In the case of ants with random walking style, this path doesn't matter so we skip its calculation to save some runtime. Ants with task p can move either randomly or drifted, so it is useful to keep track of the spatial fidelity of task p defined as

$$SF(p) = \frac{|\{A : p(A,t) = p, w(A,t) = D\}|}{|\{A : p(A,t) = p\}|}$$

which is just the proportion of ants with task p which have drifted walking style.

Information and Beta Value: All ants start with f(A, t) = 0 with the exception of a single randomly chosen ant which starts with f(A, t) = 1. 0 denotes a lack of information and 1 denotes the presence of information. Ants are able to become informed if an informed ant makes successful contact with them. These interactions are directed as in real scenarios with antennation and tropholaxis. Again, since the time window on the simulations will remain small, we make the assumption that once an ant becomes informed, they will keep that status for the remainder of the simulation. Other models consider the difference in characteristics, particularly movement style and speed, when an ant becomes informed, however our model does not take this into account because varying movement speed on a discrete grid will cause unrealistic behaviours such as ants jumping over each other or potentially jumping over walls. When an informed ant A decides to contact an uninformed ant B, information is transmitted with probability $\beta(B,t) = \beta(B,0)$. In the model ours is based on, β is assumed to be 1. Here, we change that to $\beta \sim Uni(0.3, 0.7)$ to better approximate variability in ants responses to contact as observed in [4].

After providing a nest X, spatial fidelity zones S_p , spatial fidelity sf, and a population density d, the grid is populated with $area(X) \times d$ many ants randomly distributed across all possible cells. Ants are generated with their appropriate attributes and have probability sf of having drifted walking style. Each simulation is run for a total of T time steps. Each time step, all ants are updated in a random order according to the update step in figure 1.



Fig. 1. Update step flow chart for our model.

Note that when an ant attempts to make contact with another worker, the ants switch locations. This is because we are simulating the ants coming close enough to contact each other and then walking past one another. Without this feature, small tunnels we are interested in studying would become impassable as ants collect inside. For each simulation we record several unique figures:

Information Proportion: Each time step we track the fraction of informed individuals within the colony. This is a useful metric for evaluating the 'efficiency' of information travel throughout a particular nest structure since we can determine on average how long it takes for random distributions to become fully informed or whether they reach this steady state at all in a reasonable time window.



Fig. 2. Informed ant proportion over time graphs for the 2-chain nest feature. On the left is 30 simulations in the same nest and on the right is their mean with two standard deviations.

Contact Rates (R_w and R_b): In addition to tracking the total number of unique contacts for the informed ant proportion, we also track two different contact types. These are the number of contacts within task groups each time step $C_w(t)$ and the number of contacts between different task groups $C_b(t)$. With these measurements, we can compute the contact rates within and between task groups with:

$$R_w(t) = \frac{dC_w}{dt} \approx \frac{C_w(t) - C_w(t - \Delta t)}{\Delta t}$$
$$R_b(t) = \frac{dC_b}{dt} \approx \frac{C_b(t) - C_b(t - \Delta t)}{\Delta t}$$

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Fig. 3. R_w and R_b averages over time for 30 simulations in a 2-chain nest. As we expect, these are inversely proportional as groups begin to isolate themselves from one another. The steady state is expected to be reached faster as spatial fidelity increases.

Spatial Heterogeneity Degree: Spatial heterogeneity degree (SHD) is a measure of the variance in ant distribution throughout the nest. It is calculated as:

$$SHD(t) = \frac{\sum_{x \in X} (P_x(t) - \frac{N}{A})^2}{A}$$

where $P_x(t)$ is the probability grid cell x has an att at time t and A = area(X) = |X|. SHD is minimized when ants move completely at random and maximized when ants are stationary or heavily clustered. We track this value because it gives us information about the spatial layout of the ants within the nest. As spatial fidelity increases, we can expect SHD to peak at a higher value since a higher proportion of ants will be attracted to their spatial fidelity zones. Note that we cannot explicitly calculate the values for each P_x . Instead, we estimate these values by storing a matrix of how many visits each grid cell has over the course of the simulation and divide by the number of time steps. Because of this, the first several time steps are a bad estimate of the actual value of P_x and we cut off the first 30 values when displaying the SHD figures.



Fig. 4. Spatial Heterogeneity Degree over time for 30 simulations in a square nest with low spatial fidelity. Most ants are moving randomly so we see the SHD drop to a lower value over time.

Motif Count: Motifs are triad subgraphs of a network which appear with some statistical significance compared to a random network. Previous results have seen high numbers of feed-forward loops present in the time-aggregated interaction networks of both empirical data and simulated networks [9, 12]. We store directed networks over time as an adjacency matrix and count the number of each of the sixteen motif types over time to see if similar patterns emerge. A high number of FFLs (motif 6) in our model could lead to similar conclusions as these previous papers.



Fig. 5. Motif count for a simulation run in a donut shaped nest. Note that we cut off the first couple motifs since these are uninteresting when studying interaction networks.

3 Results

We decided to run the model on four nest features including squares, chains, tunnels, and donuts. Each are meant to test simple examples of features which we hope will help us better understand their effect on nest information globally. For each nest feature, we determined three unique shape variations (s1, s2, s3), and ran 30 parallel simulations with each combination of shape variation, density (0.1, 0.2, 0.3), and spatial fidelity (0.2, 0.5, 0.8). With six figures for each of these combinations, we gathered a total of 648 figures to analyze for trends. In each section, the three shape variations for the given features are depicted in the appendix.

3.1 Squares

One of the nest structures that we ran simulations of was the square model. This feature represents free ant-movement within the nest, where ants are not inhibited by any walls besides the outer barriers of the nest, only the other ants. The unique shape variations of the square structured nests only differed in size, as we ran 10×10 , 20×20 , and 30×30 nests, all with 3x3 spatial fidelity zones in the bottom left and top right corners. The square nest was chosen to analyze how different density and spatial fidelity affect the efficacy of communication in ant colonies in open areas. Before running these simulations, we suspected that increasing the density of ants would uniformly increase the rate at which ant colonies become informed, due to information traveling faster in colonies where there was less space between ants. This result was observed in the majority of our data, and can be seen in figure 6. Here, the data of three separate 20x20 colonies which all have a spatial fidelity of 0.5 is displayed. The vertical axis shows the proportion of informed ants while the horizontal axis tracks the time steps. From left to right, the graphs display data of colonies of density 0.1, 0.2, and 0.3, with the proportion of ants that are informed in the colony after 300 time steps increasing with density. However, our prediction was not entirely true, as for the first 50 time steps, density has little to no effect on the efficacy of information flow. After returning to the model simulation and visually comparing information spread in these 3 colonies, we found that the similar proportion of informed ants regardless of density could be attributed to the drifted walking style of ants toward their respective spatial fidelity zones. In the nest with density 0.1, ants quickly spread information once the majority of those with a drifted walking style arrive in their spatial fidelity zone, as they are closer together and more likely to contact each other in the small 3x3 zone. But after these ants reach their fidelity zones, information drastically decreases, as the remaining randomly moving ants are less likely to contact each other with a low overall density of ants in the nest. Similarly, the colony of density 3x3 displayed quick diffusion of information as ants began to clump up in their fidelity zones. However, in the colony with higher density, the decrease in information spread was not nearly as drastic, due to the high density causing contacts between randomly moving ants to be more frequent. From the model it is apparent that even in colonies with low density, spatial fidelity allows for quick information flow within task groups. This is extremely beneficial for the success of the colony, as efficient communication between workers with the same task is of utmost priority. The decline in the rate of contact may also prevent the colony from being eradicated by a pathogen, as diseases may die out before the entire colony becomes infected.



Fig. 6. The proportion of ants that are informed through approximately 40 time steps is similar in all 3 graphs due to spatial fidelity causing ants to clump in their task zones, however, as the simulation proceeds, higher densities result in a higher contact rate of randomly moving ants, and thus more quickly inform all of the ants in the model

3.2 Donuts

The three variations of the donut nest structure we tested were 11x11, 17x17, and 23x23 holes in a 31x31 nest with 3x3 spatial fidelity zones in the bottom left and top right corners. These were meant to test whether loop structures in a nest would affect informed ant proportions in any way. An interesting result we saw was with a high spatial fidelity, there were more simulations which reached a steady state other than a fully saturated ant population. We suspect this is because the donut edges serve as two large alternative routes for ants to travel along towards their spatial fidelity zone. Because of this, increased spatial fidelity causes ants to reach their zones along one of these paths faster, potentially without passing information to ants of the other task. There is no bottleneck that all ants necessarily need to pass through to get this information so we get many graphs such as those in figure 8. We note that it was useful to have both mean ant proportion graphs and ant proportion graphs of all the individual colonies since on the mean graph, these lower steady states just look like higher variation. This high spatial fidelity effect on the steady states seems to be stronger with higher shape variations, that is, the donuts with larger holes. This is unintuitive as we would suppose that narrower tunnels between the spatial fidelity zones would encourage more interactions between the ants. What is likely causing these differences in number of simulations which have a low steady state is where the first informed ant is placed. When populating the nest with ants before the update steps begin, a single informed ant is randomly placed somewhere in the nest. With larger donut holes, there is a decreased probability this ant is placed within one of the tunnels. In these cases, the informed ant more likely starts near a spatial fidelity zone and waits around for those workers with the same task to come closer.



Fig. 7. With a high spatial fidelity as donut hole size increases, more simulations end with a lower steady state.



Donuts as Hole Size Increases (SF 0.2)

Fig. 8. With a low spatial fidelity, there is only a single steady state across all shape variations.

Since the presence of these low steady states seems to be relying on an informed ant starting around a spatial fidelity zone and waiting for other ants to arrive, a low spatial fidelity will probably remove them from the graphs. This is because few of the ants will actually make their way to the spatial fidelity zones and will become informed at a rate no faster or slower depending on donut hole size. In figure 8, we see this to be true.

3.3 Chains

Another nest structure we tested were chains of size 2, 3, and 4. By an n-chain, we mean a sequence of n-many 15x15 chambers connected by 7x2 tunnels with 3x3 spatial fidelity zones in the bottom left and top right corners. These were chosen for study because they resemble the vertical 'stem' seen commonly in ant nests [13]. The idea is to simulate how quickly a signal will pass deeper into a colony. Since the tunnels act as bottlenecks for ant movement, we suspected that increasing the density would actually make it more difficult for a signal to pass around. This is because although there would be more ants to cascade the signal, they would get in each others way and make the process slower as the depth of these connections increased. In figures 9 and 10, we see through the ant proportion over time that our prediction was true. In the case of the smaller 2-chain, there is certainly less of a difference in the time to reach the steady state as density varies, but for the larger 3 and 4-chains, there is certainly an advantage to having a more balanced population density.



Fig. 9. In 2-chains, there are some slight differences in variation, but the mean proportion of informed ants start just about the same across all densities.



Fig. 10. As chain depth increases to 3-chains, a low density promotes much faster information spread than higher densities.

We note that, just as in the case with donuts, this difference appears only when spatial fidelity is also high. That is, randomly moving ants are relatively unaffected by bottlenecks and will pass information effectively, but ants with a drifted walking style will attempt to move with purpose through a tunnel in opposite directions and ultimately impede ant (and therefore information) traffic. Also, it seemed that at the lowest density of 0.1, there were a few cases in which a second steady state seemed to be forming just as with donuts. We exclude these from our analysis however since in the cases they do occur, it was near the edge of the time window. To determine if these actually exist, we would need to rerun these simulations with a maximum time step of 500 or longer.

3.4 Tunnels

The last nest structure we simulated was that of the tunnel. Tunnels consisted of two 15x15 chambers connected by either 1, 2, or 3 7x2 tunnels. The purpose of this setup was to simulate how increasing connectivity between nest chambers could mediate the rate at which ants travel between them and therefore the rate at which information diffuses, especially in a high traffic scenario. Traffic makes for an effective analogy in the case of tunnels as the span of our parameters: density, spatial fidelity, and connectivity (s_1, s_2, s_3) can be understood as mediating a balance between effective dispersal and bottlenecking. Increased connectivity facilitates easier transport between the chambers, however this does not necessarily translate into more effective information diffusion. And moreover these effects are not always immediately clear. When density is low increased spatial fidelity almost always results in *decreased* speed of information diffusion for a fixed connectivity. This is likely because with few individuals around increased spatial fidelity encourages worker to congregate at task zones, which enhances within zone contact rates at the expense of global contact rates. It's worth noting in this scenario that increased connectivity tends to have little noticeable effect. This can be attributed, again, to the tendency for ants to congregate at task zones which necessarily leads to a decreased preference for between chamber transport.

At moderate densities (d = 0.2) There appears to be a trade-off between spatial fidelity and connectivity for optimizing information diffusion. Increasing either spatial fidelity or connectivity (but not both) improves both the speed and the saturation proportion of informed ants. It appears that at moderate densities slight increases to either within task contact rates or between task contact rates can both improve information diffusion. But when combined the effects appear to at least partially conflict, resulting in reduced mean proportions of informed ants and increased variance in this metric.



Fig. 11. In these plots we can note a decline in the average proportion of informed ants (or a longer time to peak colony information) as spatial fidelity increases.



Tunnels (s3) as Spatial Fidelity Increases

Fig. 12. Looking at individual plots of the graphs in figure 11, we can see this variance is caused by many different low steady states, likely due to a high number of options for route between the chambers.

3.5 Feature Comparison

Each of the nest features above had interesting results across various densities, spatial fidelities, and their own shape variations. Here, we discuss some of the similarities and differences between these results. The most noticeable similarity across squares, donuts, chains, and tunnels were the contact rates R_w and R_b . We expected these to change with spatial fidelity as in figures 12 and 13, but there were no other differences across density, shape variation, or feature. Higher spatial fidelities decrease the time in which these contact rates reach a steady state. As the ant population has a higher proportion of drifted walking styles, ants will separate into their task zones faster and the rates of within group contact will increase and between group contact will decrease.



Fig. 13. R_b over time and SF, but these trends are similar to all other shapes, features, and densities.



Fig. 14. R_w over time and SF, but these trends are similar to all other shapes, features, and densities.

For spatial heterogeneity degree, the same holds; spatial fidelity seems to be the only major factor in determining how SHD will change over time. At large spatial fidelities, SHD will increase as ants are drawn towards their spatial fidelity zones and at low spatial fidelities, SHD will drop and maintain a low value as ants move randomly. There is some variation across nest feature as bottlenecks in chains and tunnels can forcibly cause some clustering as ants move through them, but these don't cause changes in the SHD in the long term (since after sorting out the traffic in the connection, the clustering here no longer contributes to a higher SHD).

With the motif counts, the same patterns appeared across all a majority of the features and shape variations but they weren't what we expected. As discussed in the introduction and methodology, previous work saw a high number of feed-forward loops in both their simulations and in empirical data. However, in our model, this seems to be one of the lowest counts. Instead, there is consistently a very high number of motifs 7 and 8 and occasionally a high number of the later motifs as seen in figure 14. These later motifs are easily explainable by long runtimes. As time progresses, ants contact more, and do so at especially high rates when the spatial fidelity is 0.8. This causes the subgraphs of the interaction networks corresponding to the various tasks to rapidly become complete. This leaves a very high number of fully complete and nearly complete motifs which don't give us a lot of information. We suspect that the prevalence of these motifs is a result of the way the update step works in our model. In real world interactions, everything occurs simultaneously. In contrast, our model updates ants one at a time until all have been



Fig. 15. Here we see SHD over time for chambers with 3 tunnels. As spatial fidelity increases, so does the SHD.

attended to. Because of this, it is entirely possible (and perhaps quite common) for an ant to contact another and switch spots with it and for the other ant to immediately contact that ant and switch back. This would explain why motifs 7, 8, and 10 might be present in such high proportion; this type of asynchronous updating makes it easy for many two-way connections to be made among the ants. Another possible issue is the small nest size. We would have like to run the model on grids of sizes 100x100 but limited computational power forced us to use smaller nests. It could be that unrealistically small nest shapes led to unrealistic motif counts.



Final Motif Counts for Tunnels (s2)

Fig. 16. Across all features and shapes, motif counts looked like one of these two graphs. Either there was a high number of motifs 7 and 8 or a high number of 14 and/or 15.

4 Discussion

After running the model on various shapes and conditions, we analyzed the data in search of answers to the questions we first proposed. The main motivation of including the square feature in our simulations was to compare social networks of ant colonies above and below ground. This square is different from the other nest features we incorporated in that it is more analogous to an above ground system, as opposed to the chains and tunnels features that have separate compartments connected by narrow passages. Consequently, we expected a stark contrast between the motif frequencies of the square feature and the tunnel and chain features. After analyzing our results, we found that these motif counts didn't vary much between shape features, indicating that ants communicate in the same patterns regardless of their physical environment. However, the efficiency of the above and below ground models was more varied. In the square simulations, the amount of time steps that it took for the colony to become fully informed decreased as density increased, signaling that a high density increases the efficiency of a social network above ground. But increasing density in the square and tunnel features did not produce the same result, in fact, in some cases, the increase in density actually caused the colony to take longer to become fully informed. From these results it is apparent that above ground in open areas, network communication thrives with high density, while the narrow passages of under ground nests can cause high density to possibly have a detrimental effect on communication within the colony. The differing effects of density depending on shape feature revealed to us that different nests benefit from different variables. It was difficult to pinpoint general nest conditions that optimize information flow within the colony, as changing conditions often had effects that contrasted depending on the shape of the nest. For example, when viewing data on our 2-chains figure, we observed that an increase in spatial fidelity resulted in more efficient information flow, and supposed that other nests would be affected similarly. However, we were surprised to find that this trend failed to appear in the data of not only the other shape types, but also 3-chains and 4-chains variations. This leads us to conclude that colony communication networks can be affected differently by the same conditions, and that optimal nest structures depend on the density and spatial fidelity of the colony.

Future work on this topic would include studying interaction proportions and contact rates across combinations of these nest features. For example, what efficiency do we get when combining a large square with a large chain? Studying combined features like this will begin to narrow in on simulating and understanding nests in their entirety. Another route for future work is to incorporate additional task zones and more realistic ant movement (actually modeling the pheromones we assumed were present). For each of these, the code for our model is available on GitHub at https://github.com/CapSnCrunch/social-insects along with the results for our simulations. We strongly encourage additions to this code and further work on the grid based model theoretically.

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Appendix

Square Variations



10x10, 20x20, and 30x30 squares with 3x3 SFZs in either corner.

Donut Variations



31x31 square with 11x11, 17x17, and 23x23 holes with 3x3 SFZs in either corner.

Chain Variations



15x15 squares with 7x2 tunnels connecting them at lengths 2, 3, and 4 with 3x3 SFZs in either corner.

Tunnel Variations



15x15 squares with 7x2 tunnels connecting them with 1, 2, and 3 total tunnels and 3x3 SFZs in either corner.