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EXAMINING THE SOCIAL BEHAVIOR OF ANT COLONIES USING COMPLEX NETWORKS

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ABSTRACT. This paper proposes the use of Complex Network Theory to model the interactions between ants and analyze their social behavior. Specifically, the study focuses on six colonies of ants to investigate whether their behavior is community-oriented or individual-oriented. The research employs various nodes properties that define nodes' importance to quantify the existence of a social or individual-oriented behavior. The results aim to provide insights into the social behavior of ants and may have implications for understanding other complex social systems.

1. INTRODUCTION

In nature, a variety of species exhibit a pronounced social behavior, whereby members of the same species tend to interact in order to increase their chances of survival. Such behavior is not restricted to mammals alone, but also found in insect colonies, schools of fish, and, to a lesser extent, reptiles. Certain species of lizards have been observed to display social behavior and organize themselves into complex social structures [6].

In species with smaller members, individual survival rates tend to be lower, leading to the formation of complex communities characterized by homogenity and defined roles. Ant colonies are a prime example of such communities, often comprising millions of members [17, 2]. These colonies exhibit remarkable synchronization in tasks such as food gathering, cleaning, and protection. Ant behavior has been widely studied in numerous experiments [10, 25, 19], although logistical challenges often pose a significant obstacle to researchers.

As the complexity of interactions between members within a system is difficult for human observation and measurement in real-time, researchers have

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sought frameworks to model the underlying dynamic system. Complex Network Theory (CNT) has emerged as an increasingly popular framework in recent years [7], as it enables the modeling of complex systems as topological spaces, specifically as graphs, where the members are represented as nodes and their interactions as edges.

By studying a modeled network, it is possible to gain insight into the behavior of the network's members using a range of properties. Some properties provide information at the level of individual nodes, such as node degree, assortativity degree, and centrality measurements [22, 4, 21]. Other properties are oriented towards characterizing the network as a whole, such as clustering coefficient [16], communities [9, 8], and network motifs [1, 13, 14].

Various studies have demonstrated the advantages of utilizing CNT to model ant colonies as intricate networks, enabling researchers to investigate ant social behavior and dynamic processes such as food collection and communication. However, most of these studies have focused on the colony as a whole rather than individual ants. Given the existence of well-defined structure and organization in ant colonies, the lack of research on individual behavior is notable. Therefore, the paper aims to explore whether individual ants prioritize their well being instead of their defined role in the organization or strive to exhibit purely altruistic behavior by acting for the benefit of the community without expecting anything in return.

A set of research inquiries will be developed to steer an experimental analysis of six ant colonies monitored for a duration of 41 days [18]. The objective is to employ properties at the node and network levels derived from CNT to measure and confirm the central query: do ants act altruistically or selfishly? The objective is to distinguish between selfish and altruistic behavior in ants by employing centrality measurements, which are commonly used to evaluate the significance of a node in complex networks. There will be utilized network properties that optimize the exchange of information within the colony, such as maintaining a low average shortest path, to identify altruistic behavior. Ultimately, a qualitative analysis will be conducted to compare the two methods of quantifying altruistic and selfish behavior.

The following sections aim to provide an overview and clarification on the challenges that arise when studying small-sized creatures, as well as how CNT can help overcome these challenges based on the existing state-of-the-art. Additionally, there will be detailed each of the metrics employed in the experiment, explaining their relevance and how they will be applied. There will be introduced the dataset and the research questions that will guide the experiment, with the results being validated against the network properties obtained.

Finally, the paper will conclude with a discussion that will confirm or reject the initial assumptions regarding the research questions posed.

1.1. **Problem definition.** From a logistical standpoint, studying ant colonies is challenging due to the small size of the ants, making them difficult to observe by the naked eye. Additionally, the high number of members that share a similar appearance can complicate the study of their behavior, as they move quickly and often exhibit chaotic movement patterns. Manually observing the behavior of ants in such a scenario would be time-consuming and exhaustive, requiring video recording and subsequent frame-by-frame tracking by one or more researchers [20, 26].

Following the logistical difficulties of studying ant colonies, there is a secondary issue that arises during the process of analyzing the interactions between ants. This issue is caused by the need for a framework to facilitate the entire process, starting from defining interactions and culminating with the impact a group of interactions has on the dynamic of the colony. One solution to this issue is to model ant colonies as systems that can be studied using mathematical and statistical approaches. This allows for the numerical quantification of ant behavior, leading to a feasible and valid way of answering research questions. However, even with a colony modeled as a system, it can be difficult to understand the apparent chaotic behavior between ant interactions. To address this challenge, a set of tools is required to extract properties from the system that may lead to paths not initially intended by the researchers. Complex Network Theory is one such framework that provides a wide range of tools to extract properties about the system modeled as a complex network. By modeling the colony's system as a network, where ants are nodes and their interactions are edges, it can be explicitly analyzed the interactions a given ant or group of ants have, defining statements about their social or individual behavior [24].

Complex Network Theory has emerged as a valuable analytical tool for studying the organizational dynamics of ant colonies. Its applications in this field are numerous, including investigations into the community structures of colonies [12] and the role of information flow in collective decision-making [5]. By modeling the networks underlying ant colonies, researchers aim to gain insights into the structural organization of the colonies, the development of modular structures, and the resilience and optimality of information flows among colony members. These studies also provide insights into the potential impact of member loss in the event of a disaster [3, 11].

In the subsequent section, there will be provided an overview of the fundamental properties existing in complex networks that are pertinent to the examination of social interactions among ants belonging to the same colony, accentuating the practical implementation of the theoretical aspects in the context of a real-world ant colony.

2. Theoretical insights

Any complex network is characterized by a collection of nodes and a set of edges that connect them. Although these two fundamental components are simple, they give rise to multidimensional complex topologies with unique properties that can be explored, underscoring the advantages of representing real-world systems as complex networks. One of the most widely researched concepts, particularly in social networks, is the definition of critical, important, or popular nodes. However, this is more of a philosophical question that has been debated extensively in the literature [15]. Nevertheless, the literature proposes a group of metrics known as centrality measures that aim to offer various ways of characterizing important nodes.

In this section, there will be provided detailed descriptions of the graphs and their respective nodes' centrality measures, as shown in Figure 1. The figures illustrate that different nodes are identified as "important" by each centrality measure, highlighting that each metric has a distinct approach to determining a node's significance.

Degree centrality (D_c) is one of the fundamental measures of centrality in complex networks. It quantifies the importance of a node based on the number of edges it has with other nodes in the network. Nodes with a high number of edges have higher degree centrality and are considered more important. The mathematical formula for degree centrality is as follows:

$$D_c(x) = \frac{d_x}{n-1}$$

where $D_c(x)$ is the degree centrality of node x, d_x is the degree of node x, and n is the total number of nodes in the network [22].

In addition to degree centrality, another centrality measure that takes into account the number of links and goes further in assessing a node's importance is *eigenvector centrality* (E_c) [22]. This property evaluates a node's influence in the network based on the degree centrality of its neighboring nodes. From a real-world perspective, a node with a high eigenvector centrality is connected to other nodes that are also important, meaning that being connected to popular nodes increases one's own popularity. The eigenvector centrality formula



FIGURE 1. Centrality measures in a Newman Watss Strogatz graph with 100 nodes. Light blue - low value, Dark blue - high value.

follows a recursive approach that calculates a value for a node by using the values computed for its neighboring nodes, as follows:

$$E_c(x) = \frac{1}{\lambda} \sum_{u \in N(v)} E_c(u)$$

where $E_c(x)$ is the eigenvector centrality of node x, N(x) is the set of nodes that are connected to node x, and λ is a constant called the leading eigenvalue of the adjacency matrix of the network [15].

A distinct perspective on defining node importance or popularity is based on the flow of information in the network, whereby nodes that enable the flow

of information in the network tend to be more important or popular to other nodes. In this regard, the next group of centrality measures uses the path between the nodes and their lengths to evaluate the significance of the nodes. *Betweenness centrality* (B_c) assesses the importance of a node by its ability to control the flow of information through the number of shortest paths between any two nodes that pass through it. Having more shortest paths passing through it means that the node is a hub facilitating the information flow in the most rapid manner through the shortest paths it is part of. The formula below depicts the quantification of this centrality measure:

$$B_c(x) = \sum_{s \neq x \neq t \neq x} \frac{\sigma_{st}(x)}{\sigma_{st}}$$

where x is the node for which there was computed the metric, σ_{st} is the total number of shortest paths from any node s to any node t and $\sigma_{st}(x)$ is the number of those paths that pass through x (not where x is an end point) [22].

Closeness centrality (C_c) is another measure that quantifies the importance of a node in a network. Unlike betweenness centrality, C_c considers how quickly a node can be reached by all other nodes in the network. A node with a high C_c is considered to be "close" to all other nodes in terms of its shortest paths, making it an important hub that facilitates the flow of information in the network:

$$C_c(x) = \frac{1}{\sum_{u \neq x} d(u, x)}$$

where $C_c(x)$ is the closeness centrality of node x, d(u, v) is the shortest path distance between nodes u and v, and the summation is taken over all nodes $u \neq v$ in the network [22].

In recent studies, a new approach to defining the significance of nodes has emerged, focusing on their role in maintaining network integrity. Articulation points (AP) are nodes that, when removed, divide the network into two or more connected components, acting as bridges between isolated groups of nodes (Figure 2). In social networks, an AP could be a social media influencer or politician, while in an ant colony, the queen can be an AP. This concept is gaining popularity as it provides insights into the structure of networks and can inform strategies for improving network efficiency and stability [23].

The centrality measures detailed earlier are indicative of macro-level characteristics of a node, which describes its role in influencing the overall dynamics



FIGURE 2. Example of Articulation Points (in red)

of the network. Conversely, there are other properties that are more relevant to micro-level behavior, which tend to be oriented towards the individual node itself. For instance, the local clustering coefficient (CC_l) is used to quantify the tendency of nodes to form communities with other nodes that share similar characteristics or interests (e.g., ants performing similar tasks). The following formula expresses CC_l as the ratio of the actual number of links (E_i) connecting the vertices within a node (i) neighbors to the maximum number of possible links that could exist among them $(k_i(k_i - 1)))$.

$$CC_{li} = \frac{2E_i}{k_i(k_i - 1)}$$

Assortativity degree (ρ) measures the tendency of nodes to connect with other nodes that share similar degrees (e.g., popular individuals preferring to associate with others who share a similar level of popularity). In this sense it can defined ρ as the correlation between the degrees of connected nodes in a network, with values in interval -1 to 1 computed with the following formula:

$$\rho = \frac{\sum_{jk} jk(e_{jk} - q_j q_k)}{\sigma_q^2}$$

where e_{jk} is the join probability between excess degree of j and k (excess degree, also known as remaining degree, is computed by subtracting one from the degree of a given node), $q_k = \frac{(k+1)p_{k+1}}{\sum_{j\geq 1} jp_j}$ is the normalized distribution of the excess degree of a randomly chosen node, respectively σ_q is standard deviation of q_k , used to normalize ρ in interval [-1, 1].

Positive values indicate nodes tend to connect with others with similar degrees, while negative values indicate nodes tend to connect with nodes with different degrees. An r value of 1 indicates perfect assortative mixing, 0 indicates non-assortative mixing, and -1 indicates completely disassortative mixing.

In the experiment described in the following section, the aim is to investigate the social behavior of ants in their colonies by analyzing their network properties. Specifically, it will be explored whether nodes with high values for centrality measures, such as degree centrality, eigenvector centrality, betweenness centrality, and closeness centrality, respectively local clustering coefficient and assortativity degree, but also existence of articulation points, are associated with the emergence of individual behavior among ants that is not aligned with the organization of the colony as a whole.

3. Experiment

The following section will overview the experiment proposed to analyze the social behaviour of ants, making use of a comprehesive dataset for which there were validated a series of research questions that will be evaluated using a defined methodology. The results of the extracted properties (detailed in Section 2) obtained in the experiment will be analyzed and a series of conclusions will be drawn to conclude the formulated research questions.

3.1. **Dataset.** To conduct a robust and meaningful experiment, it was deemed necessary to utilize a diverse dataset that is both horizontally and vertically scaled. To this end, there will be employed a complex dataset of complex networks that consist of six ant colonies that were completely isolated, as proposed by Mersch D. et al. in their research paper [18]. The complex networks were modeled by observing each ant colony over a timespan of 41 days, utilizing a video tracking system that was based on fiducial identification labels. Each ant's position was tracked twice per video frame, resulting in a vast amount of data - 2,433,250,580 ant positions and 9,363,100 social interactions. Social interactions were defined as instances where one ant's front end was within the trapezoidal shape representing another ant. From this data, a total of 246 networks were modeled, utilizing both the ant positions and the tracked interactions.

Table 1 provides a comprehensive summary of the modeled networks based on their nodes and edges - ants are represented as nodes, and the interactions between them are represented as undirected edges. The weight of each edge is determined by the number of interactions between the same ants. Since the ant colonies were observed for a period of 41 days, changes in the number

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colony id	metric	mean	95% percentile	Stdev
1	nodes	89.21	[82.35, 96.06]	± 21.15
	edges	2803.97	[2429.41, 3178.54]	\pm 1155.48
2	nodes	100.13	[91.47, 108.79]	\pm 26.71
	edges	3541.03	[2909.48, 4172.57]	\pm 1948.25
3	nodes	130.05	[122.01, 138.09]	± 24.80
	edges	6036.79	[5274.19, 6799.40]	\pm 2352.55
4	nodes	68.77	[60.73, 76.80]	± 24.79
	edges	2067.03	[1640.79, 2493.26]	± 1314.88
5	nodes	113.31	[102.26, 124.35]	± 34.07
	edges	4905.05	[4034.66, 5775.44]	\pm 2685.03
6	nodes	131.85	[123.07, 140.63]	\pm 27.09
	edges	6338.82	[5451.44, 7226.20]	± 2737.44

TABLE 1. General properties of the studied networks [18]

of individuals within each colony could occur, resulting in variations in the network's characteristics. These changes were captured by the mean, standard deviation, and 95% percentile values, enabling the dynamics of the colonies to be analyzed.

The metrics obtained from the modeled networks exhibit a significant degree of diversity with regards to the number of members in each colony, which is reflected in the number of edges present in each network. This phenomenon can be attributed to the fact that larger colonies tend to have more interactions among members, resulting in a higher number of edges.

3.2. Research questions. The experiment is designed to address two research questions, a primary one $(\mathbf{RQ1})$ and a secondary one $(\mathbf{RQ2})$:

- **RQ1** What is the extent of variation in individual behavior within ant colonies, and does this variation lead to the presence of outliers exhibiting selfish behavior or does the colony exhibit a predominantly homogeneous altruistic behavior?
- **RQ2** Does the dynamics of ant colonies optimize the flow of information through interactions among the ants?

3.3. Methodology. In accordance with the formulated research question, the methodology of the experiment will involve the extraction of centrality measures and articulation points from each network to investigate the occurrence

of nodes with abnormally high values for these metrics, indicating their inclination to strategically position themselves to maximize their valuable connections. In addition to the previously mentioned topological indicators, there will be also extracted two additional measures, namely CC_l and ρ , to gain a deeper understanding of the global social behaviour of ants and to investigate if any specific behaviour emerges. These measures will aid in addressing the research questions posed in this experiment.

By quantifying and validating **RQ1** through this approach, it can be employed the concept of popularity, which is defined in various ways as discussed in Section 2.

To investigate whether the networks and colonies aim to optimize the performance of the information flow among their members, there will be used two topological indicators: density and average shortest path. Density (d) is a measure of how close a network is to being fully connected, where all ants interact with one another. Networks with high density tend to optimize the information flow by ensuring that all members are easily reachable through a high density of edges. The average shortest path is a measure of the average number of steps needed to travel between any two ants in the network. There will be computed and used these indicators to demonstrate the colonies' dynamics and to answer the research question. The calculation of the average shortest path (AVG_{sp}) can aid in determining if ants strive to optimize the formation of valuable links within the context of an efficient information flow. A low average shortest path, which denotes the average number of links needed to create an optimal path between two members, suggests that ants can easily reach each other. By analyzing this metric, it can be provided a formal response to **RQ2**.

3.4. **Results.** In accordance with the methodology outlined in the preceding section, there were derived all the centrality measures outlined in Section 2 as well as other topological properties, including CC_l , d, AVG_{sp} , and ρ (Table 2). This was done to enable the quantification of the propositions that could potentially serve as answers to the formulated research questions.

Ants are social animals with highly organized behavior and specialized roles throughout their lifetime [18]. Their division into groups is strictly task-oriented, which may result in a large number of interconnections between ants within the same group. This behavior is well-reflected in the high values of CC_l observed in all the studied colonies.

It is well known that each of the examined ant colonies has a queen, whose exclusive responsibility is to lay eggs. Given its role as being one that it is unique in the structure of the colony (only one ant, namely the queen, lays eggs), it is reasonable to classify the queen as an articulation point (AP). However, the analysis showed that the queen is not often an articulation point in any of the modeled networks. This indicates that despite the queen's critical role, it is part of a well-connected community, and her death would not necessarily lead to the colony's disintegration.

At a macro level, the social behavior of ants does not exhibit a particular tendency to create links with new ants, as indicated by the value of ρ which is equal to 0. This suggests that the creation of links is not driven by individual preferences, but rather by the collective behavior of the group as a whole.

This hypothesis is strongly supported by all of the computed centrality measures, which do not identify any notable group of nodes that exhibit exceptional values for their centrality measures. By computing the 95% percentile interval and mean values, it can be observed the homogeneity of centrality measure values across all nodes, with insignificant standard deviation. Even though the standard deviation of the centrality measures' computed values is insignificant, the real-world implications of each metric should be taken into consideration while interpreting their mean values. It is noticeable that C_c has a substantially high value, reaching the maximum value of 1, which suggests that the colony's organization is optimized for efficient information flow, with every ant only a few connections away from any other ant. A similar observation can be made for D_c , which approaches a value of 1, indicating that all ants have nearly equal connectivity with each other. These findings reinforce the conclusions drawn regarding the ρ property.

The B_c value in the colony's centrality measures shows a relatively low value from the range of [0, 1]. Typically, a higher B_c value indicates that a network node has a greater ability to control information flow. This low value may, therefore, suggest that the colony is organized dynamically and oriented toward the collective benefit. Although members with high B_c values are essential to the network, they are also critical points whose loss could disrupt the system's functionality. This robust organization enables the colony to sustain itself even if some members are lost. Additionally, the centrality measure E_c shows a low value, suggesting that the ants' interactions are taskoriented, with little emphasis on creating new links based on other ants' links, resulting in an organization geared towards the benefit of the system as a whole.

Using these two observations it can be concluded the altruistic behaviour of the ants $(\mathbf{RQ1})$, meaning their interactions are ones established purely

on their role in the community they are part of and the only thing that is important to them is to succesfully complete their task.

TABLE 2. Network properties extracted for each of the six ant colonies

ID	Metric	Mean	95% percent.	Stdev	ID	Mean	95% percent.	Stdev
1	AVG_{sp}	1.31	[1.30, 1.33]	0.05	2	1.36	[1.34, 1.38]	0.07
	CC_l	0.79	[0.78, 0.80]	0.03		0.77	[0.76, 0.78]	0.03
	ρ	0.03	[0.02, 0.04]	0.03		0.09	[0.07, 0.11]	0.06
	d	0.69	[0.67, 0.70]	0.05		0.64	[0.62, 0.66]	0.06
	AP	0.08	[0.00, 0.16]	0.27		0.03	[0.03, 0.08]	0.16
	C_c	0.77	[0.74, 0.80]	0.08		0.75	[0.72, 0.77]	0.08
	B_c	0.0035	[0.003, 0.005]	0.0027		0.0041	[0.003, 0.006]	0.0038
	D_c	0.69	[0.64, 0.73]	0.15		0.64	[0.59, 0.70]	0.16
	E_c	0.11	[0.10, 0.12]	0.02		0.10	[0.09, 0.11]	0.03
3	AVG_{sp}	1.31	[1.30, 1.32]	0.04	4	1.20	[1.19, 1.21]	0.04
	CC_l	0.79	[0.78, 0.80]	0.03		0.86	[0.85, 0.87]	0.03
	ρ	0.01	[0.00, 0.02]	0.02		0.03	[0.00, 0.05]	0.04
	d	0.69	[0.68, 0.71]	0.04		0.80	[0.79, 0.82]	0.04
	AP	0.15	[0.04, 0.27]	0.37		0.00	[0.00, 0.00]	0.00
	C_c	0.77	[0.75, 0.80]	0.08		0.85	[0.82, 0.88]	0.08
	B_c	0.0025	[0.002, 0.003]	0.0015		0.0032	[0.002, 0.004]	0.0020
	D_c	0.69	[0.65, 0.73]	0.15		0.80	[0.76, 0.85]	0.14
	E_c	0.09	[0.08, 0.09]	0.02		0.13	[0.11, 0.14]	0.02
5	AVG_{sp}	1.29	[1.28, 1.30]	0.04	6	1.31	[1.29, 1.32]	0.05
	CC_l	0.80	[0.79, 0.81]	0.03		0.79	[0.78, 0.80]	0.03
	ρ	0.01	[0.00, 0.02]	0.05		0.03	[0.02, 0.03]	0.02
	d	0.71	[0.70, 0.72]	0.04		0.69	[0.68, 0.71]	0.05
	AP	0.00	[0.00, 0.00]	0.00		0.03	[0.00, 0.08]	0.16
	C_c	0.78	[0.76, 0.81]	0.08		0.78	[0.75, 0.80]	0.08
	B_c	0.0029	[0.002, 0.004]	0.0021		0.0025	[0.002, 0.003]	0.0015
	D_c	0.71	[0.67, 0.75]	0.15		0.69	[0.65, 0.74]	0.15
	E_c	0.10	[0.09, 0.11]	0.02		0.09	[0.08, 0.09]	0.02

The current findings strongly indicate the well-organized nature of ant colonies. The AVG_{sp} metric is another measure demonstrating that colonies are optimized not only in terms of creating specific groups for efficient task

completion, but also for the rapid flow of information among members. According to this metric, it takes approximately 1.30 edges for any ant to reach another ant using the shortest path in the modeled network. This value is remarkably low for any network, highlighting the communication efficiency present in ant colonies and confirming the answer to **RQ2**.

Another notable finding is that the ant colonies exhibit both a low AVG_{sp} and a high CC_l , which are characteristic features of small-world networks. These networks are commonly observed in various real-world systems, such as transportation networks, and have been the subject of many studies aimed at understanding their effective information flow and how to replicate it in other contexts. Given the well-organized structure of ant colonies, it is not surprising to find that the networks derived from observing them exhibit smallworld characteristics.

4. Conclusions

Ants have been a subject of fascination for the scientific community for a long time due to their ability to develop highly intricate social structures organically, which enables them to efficiently accomplish tasks such as foraging, cleaning, and defense. However, research on ants has largely focused on their collective behavior rather than individual behavior. While it is widely acknowledged that ants exhibit altruistic behavior at the group level, it remains to be seen whether this behavior is universal across all members of the colony or if some individuals display a more self-centered approach aimed at maximizing their own benefit.

Continuing this line of inquiry and utilizing a set of intricate network models based on observations of six distinct ant colonies over a span of 41 days, our research aimed to address two fundamental questions. These questions were formulated to resolve the previous uncertainties:

- **RQ1** What is the extent of variation in individual behavior within ant colonies, and does this variation lead to the presence of outliers exhibiting selfish behavior or does the colony exhibit a predominantly homogeneous altruistic behavior?
- **RQ2** Does the dynamics of ant colonies optimize the flow of information through interactions among the ants?

During the study experiment, there were obtained various topological properties and centrality measures of the examined networks. The analysis revealed that there is a considerable consistency among the centrality values of the individual nodes, with insignificant standard deviation. Furthermore, based on

the property ρ , it was observed that the ants do not have any macro-level inclination towards preferential attachment, but rather establish connections through their task-based activities. These two observations led us to confirm the altruistic behavior of ants as an answer to **RQ1**.

In addition to ants' ability to naturally and organically evolve complex groups that optimize task performance, the observations indicate that the information flow within their networks is highly efficient, confirming **RQ2**. The average shortest path between any two ants in the network is close to one edge, indicating that every ant is almost directly connected to every other ant. Furthermore, all studied networks show a high CC_l and exhibit characteristics of small-world networks, which optimize information flow performance and evolve strong and complex structures, as commonly observed in other realworld systems such as transportation networks.

The experiment corroborates the widely accepted behavior of ants as altruistic individuals that prioritize the collective good over individual interests, while also demonstrating their capacity to naturally develop sophisticated systems that optimize task performance for the group.

In future studies of this paper, a significant enhancement would entail exploring other network properties, including communities and network motifs, to gain a deeper understanding of the organization structure and how ants interact in small modules. Such an approach would provide further insights into the optimized interactions that drive task-oriented actions.

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