

Bachelor's Thesis

Dynamik der Ressourcenverteilung in Interaktionsnetzwerken

Dynamics of Resource Dispersion in Interaction Networks

prepared by

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Submission: 6th July 2015

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1. Introduction

In colonies of social insects such as ants, wasps, and bees, no individual is in charge of everything. Instead, individuals take decisions based on local information and act without central control [15]. Nonetheless, colonies of social insects show an impressive grade of organization. Their behavior at group level is that complex that parts of scientific literature even call them “superorganisms” [22]. Since the large-scale properties of social insect colonies are thought to arise from an interplay of simple elements [4], they provide model systems for exploring self-organization: social insects can help us to understand how low-level rules give rise to higher-level attributes [3].

This thesis explores one aspect of the self-organization of social insects: the dispersion of resources within their colonies. Providing every individual in a colony with food and other resources is a logistical feat, which took nature millions of years to perfect. Probably being an evolutionary adaption, the rules governing the dispersion of resources are thought to be optimized for certain parameters. By learning more about these rules, we could learn from evolution in order to improve our own technical and social systems [3].

There is already research on the resource dispersion in social insect colonies [11, 15, 20, for example]. The existing experimental data on this process, however, are not yet precise enough to allow the detailed reconstruction of the rules governing their self-organization in this respect. Pending more detailed experimental data, this thesis therefore explores a number of theoretical models to contribute to the understanding of the system in question. It uses a simple simulation of social insects that exchange resources with each other to generate data – which are then analyzed using approaches from network theory.

Individuals that exchange a resource with each other interact so that, through more and more interactions over time, an interaction network is created. Analyzing such a network with approaches from network theory corresponds to having a bird’s-eye view of the interaction dynamics – one can zoom out from the details and focus on the big

1. Introduction

picture [7]. The approaches from network theory used in this thesis take into account at which points in time the interactions in a network took place. Incorporating the temporal information into the network structure allows to gain insights into the temporal dynamics of resource dispersion [3]. Through these approaches, this thesis hopes to generate understanding about the rules according to which resources are optimally dispersed in interaction networks.

More precisely, I investigate two questions in this thesis. First, which approaches from network theory can sensibly be used to describe interaction networks similar to the ones of social insects? To answer this question, various visualizations try to illustrate what happens during the resource dispersion in the simulated interaction networks. Second, how can the simulation itself contribute to the understanding of the resource dispersion? In this case, I investigate how variable parameters and other initial conditions of the simulation influence the generated data.

I expect the simulated data to be similar to the ones of real social insects. But even if the simulation cannot exactly reproduce the phenomena observed in nature, the generated and the real data should certainly lie within the same order of magnitude so that the approaches from network theory can still be tested for their usefulness. The comparison with detailed data from real social insect colonies, of course, could be realized in future research.

Many fields besides biology could profit from research on the self-organization of social insects. Engineers, for example, investigate how swarm robots can optimally exchange energy with each other. In this respect, it is a promising approach to use a strategy similar to one of social insects [6, 10, 16]. Another example is that, just like the networks of social insects, many human-made networks face multiple constraints at once. Here again, social insects could serve as model systems that teach us how to balance various constraints against each other. Through learning from evolution in this respect, applications in computer science and physics as well as social and economical networks could be improved [3].

In order to simplify the terminology, the rest of this thesis does not refer to the resource dispersion in interaction networks in general but only to the food dispersion in ant colonies. Every aspect of this thesis – the simulation, the generated data, and the discussion of the results – is formulated in terms of the exchanges of food between ants. Ants use a process called “trophallaxis” for the dispersion of food, but instead of trophallactic interactions, this thesis could also describe other exchanges of resources involving agents that move around and exchange a good with each other

that they can only carry in limited amounts. That is also why the title of this thesis is formulated that generally. Although not all networks are interaction networks, all interactions can be described as networks. Whether animals exchange resources, human beings exchange goods, or computers exchange information – the ubiquitous interaction systems in our world could learn from the natural experiment that has been taking place since the formation of the first life on earth.

The rest of this thesis consists of four more chapters, the appendix, some acknowledgements, and the bibliography. This introduction is followed by two theoretical chapters. Chapter 2 deals with the simulation that generates the data for the thesis, and chapter 3 goes into the network theory needed to understand the data. Then the data are analyzed. In chapter 4, three case studies examine the dynamics of the food dispersion within the simulated ant colony and the entailed structure of the interaction network. Chapter 5, finally, sums up the main results of this thesis and gives an outlook on future possibilities for research.

Preliminaries The following preliminaries are needed to understand this thesis.

- The word “average” refers to the arithmetic mean.
- The abbreviation “CU” stands for “code units”. In this thesis, code units are used as a unit of distance; their relation to other units of distance is irrelevant.

2. The Simulation

This chapter describes the simulation that generates the data for this thesis. First, section 2.1 gives an outline of the simulation and introduces the biological concept of trophallaxis. Section 2.2 goes into detail and explains the algorithmic steps that the simulation consists of. Section 2.3, finally, describes which aspects of the simulation are simplified in comparison with reality. I am very grateful to Johannes Gräwer who programmed the main parts of the simulation. Building on his work, I only had to implement some new features so that the simulation served the purpose of this thesis. The simulation is written in Python [14] and uses the packages Numpy [18] and NetworkX [5]; its source code is available on request.

2.1. Basics

In one sentence, the simulation consists of ants that move on a square grid, pick up food from a food source, and then exchange that food with each other. After the ants have been distributed randomly on the grid at the beginning of the simulation, they perform a random walk during which they walk from one grid point to any of the adjacent points or stay where they are. The food source is located on a grid point close to the border of the grid. At the beginning, the ants do not carry any food, but the food source contains some. This food is all that there is for the ants. Food is neither generated nor consumed so that the sum of the food in the food source and the food carried by the ants is constant during the whole simulation. An ant that is not yet full picks up food from the food source when it comes sufficiently close. Ants that carry food can exchange that food with any other ant they meet during their random walks. After such an exchange, both ants involved have to wait a short period during which they cannot do anything. After a pickup from the food source, an ant also has to wait. Through these interactions and pickups, the food is over time dispersed in the ants and in space.

2. The Simulation



Figure 2.1.: A trophallactic interaction between two ants.
(Copyright: Rakesh Kumar Dogra)

To underly this thesis with some biology, the process by which food is dispersed in an ant colony is called 'trophallaxis'. More precisely, trophallaxis is the regurgitation of food by one individual for another individual [13]. Ants realize trophallactic interactions through mouth-to-mouth contact, as figure 2.1 shows, but they are not the only animals that use trophallaxis. Besides other social insects, also larger animals like birds or wild dogs use trophallactic interactions to transfer food [13].

2.2. Algorithm

Before the actual simulation starts, the following steps are executed. The letters in this section denote the variable parameters of the simulation. Their exact meaning is explained in table 2.1.

1. The grid is created. It consists of $L * L$ points that are arranged in a square.
2. The food source is placed on a grid point near the border of the grid. The amount of food it contains is determined by the supply ratio.

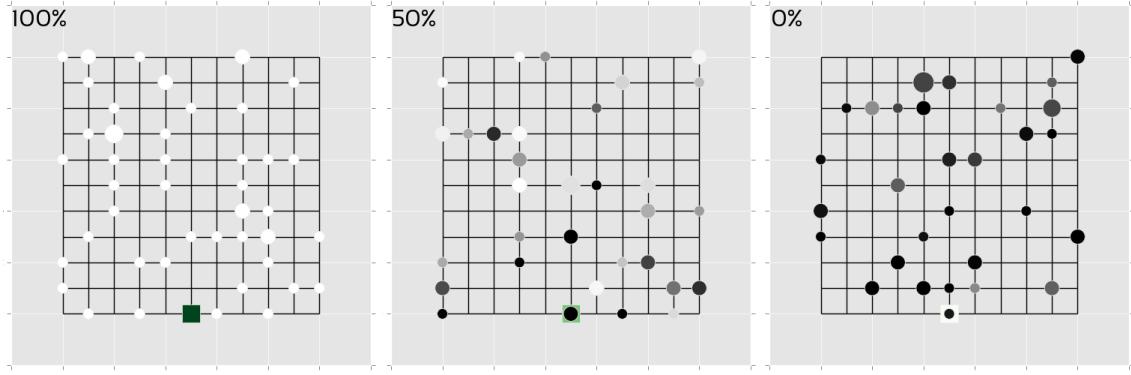


Figure 2.2.: Snapshots of a run of the simulation with 50 ants on an $11 * 11$ grid. The percentages give the filling level of the square food source at the bottom. The bigger a circle on a grid point, the more ants are on that grid point. The darker a circle on a grid point, the more food the ants on that grid point carry. In this run of the simulation, there was enough food to completely fill 90% of the ants.

3. N ants are created. Every ant can carry the same amount of food and has the same interaction time t_{int} , but none carries food at the beginning.
4. The ants are distributed randomly on the grid. Every ant is placed on any grid point with the same probability. Multiple ants can occupy the same grid point.

After these four steps have been executed, the simulation starts. From now on, time passes in discrete time steps until the end of the simulation is reached (which in this thesis always is the case as soon as the food source is empty.) At each time step, the following algorithmic steps are executed. Figure 2.2 visualizes a run of the simulation.

1. **Random walking.** Every ant takes f_{speed} random walk steps. There are two possibilities during a random walk step: an ant can move to any of the adjacent grid points, or it can stay where it is (somewhat counter-intuitively, taking a random walk step therefore could also result in no movement at all). An ant moves to any of the adjacent grid points with a probability of p_{walk} (for each of the f_{speed} times). In doing so, every adjacent grid point is chosen with the same probability. With a probability of $1 - p_{walk}$ (for each of the f_{speed} times), an ant stays where it is. An ant can thus move up to f_{speed} grid points from its original position at every time step.

2. The Simulation

2. **Picking up food.** All ants that are sufficiently close to the food source pick up food if the food source still contains some. An ant can pick up food if it is within a range of r_{int} from the food source. An interaction range of $r_{int} = 0$ CU, for example, means that an ant has to be directly on the food source. All ants that are sufficiently close to the food source pick up as much food as possible in random order. After an ant has picked up food, the ant is thus either completely full or the food source is empty (or both). Then the ant has to wait for t_{int} time steps. During this period, it can neither walk nor exchange food with other ants. (Of course, the ant cannot pick up further food as well because it is either full or there is no food left to pick up.)
3. **Exchanging food.** When an ant carries food, it can transfer that food to any other ant that is sufficiently close. A food transfer is possible if both ants involved are within a range of r_{int} from each other. An ant that carries food always transfers some food if there is any other ant sufficiently close that is not yet full. The amount that an ant transfers varies according to the probability density for the share ratio shown in figure 2.3. A share ratio of 0.5, for example, means that an ant transfers half of the food it carries (if the receiver has enough space in its stomach). If the receiver does not have enough space for the food, it accepts only as much food as it can carry; the rest remains in the other ant. If there is more than one potential receiver an ant can transfer food to, one of them is chosen randomly with the same probability. The order in which ants give food is also determined randomly. After a transfer, both the giving and the receiving ant have to wait for t_{int} time steps. During this period, they can neither walk nor pick up food from the food source nor exchange food with other ants.

2.3. Simplifications

Every simulation is an abstraction from reality. Some aspects of our complex real world indispensably have to be simplified when modeling them on a computer. In this respect, the simulation in this thesis is no exception: real ants do not perform a random walk on a square grid in order to exchange food that is never consumed with each other. What other simplifications are there apart from this obvious one?

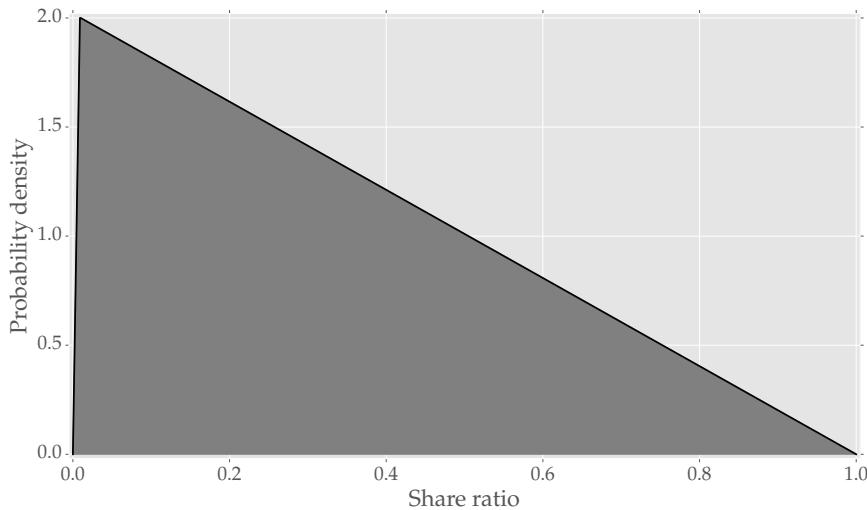


Figure 2.3.: The probability density for the share ratio, which determines what share of the food it carries a simulated ant transfers to another ant during a trophallactic interaction. Since the maximum is at 0.01, the ants exchange small amounts of food with a higher probability than large amounts.

One simplification in the simulation is the absence of variability among the ants. All ants are modeled as having exactly the same characteristics (apart from their initial position). This is not the case in real ant colonies. In nature, there is not only a range of biological diversity but also a substantial division of labor among ants. Not every ant can disperse food all of the time because tasks such as foraging, nest construction, and brood rearing have to be performed in an ant colony, too [11].

Two other simplifications concern the trophallactic interactions themselves. First, the probability density for the share ratio of real trophallactic interactions probably only resembles that of figure 2.3. It is plausible that real ants follow the rather selfish and conservative strategy of transferring small amounts of food with a higher probability than large amounts, but there is not yet experimental data regarding the real share ratio. That is why the exact triangular shape of the probability density was mainly chosen for its simplicity. Second, the duration of a real trophallactic interaction tends to correlate with the amount of food being transferred [3]. In the simulation, however, all trophallactic interactions take the same amount of time, regardless of how much food is transferred.

These are the main simplifications, but there are further points due to which the

2. The Simulation

simulation is an abstraction from reality.

- At first sight, one might wonder why there is the walk probability in the simulation. Why do the ants not move at every time step? Why can they also stay where they are? The answer is simple: Given an interaction range of $r_{int} = 0$ CU, a walk probability significantly smaller than one is necessary in order to avoid the forming of two subgroups of ants that only interact with ants from their own group. At the beginning of the simulation, some ants are placed on even grid points, and some are placed on odd grid points. If every ant moved one grid point at every time step, ants that are on an even grid point now would be on an odd one at the next time step, and ants that are on an odd grid point now would be on an even one at the next time step. But ants would never meet members of the other group so that there would be no interactions between the two groups.
- On a computer, a random walk on a grid can only be modeled using discrete time steps. This is also the case for the simulation in this thesis. How the duration of such a time step is related to the real and (probably) continuous time, however, is not relevant for this thesis because the simulated data are not compared with data of real ants. For the same reason, it does not matter how code units are related to real units of distance.
- A comment regarding the metric of the simulation: Without having mentioned it before, this thesis uses the euclidean metric for measuring distances because it allows a more flexible interaction range than other metrics. The taxicab metric, for example, limits the possible interaction ranges to fewer cases than the euclidean one, although it is another intuitive choice for a square grid. (The two metrics are defined as follows. If (x_1, y_1) and (x_2, y_2) are the coordinates of two points in two dimensions, then the euclidean distance between these two points is $d_{eu} = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}$, and the taxicab distance between these points is $d_{tc} = |x_1 - x_2| + |y_1 - y_2|$.)

All simplifications are incorporated in the simulation in order to keep it as simple as possible. Nonetheless, the hope is that the simulation still generates data that approximate the dynamics of a real ant colony. If this hope proves to be too optimistic, the simplifications mentioned in this section give a hint about which aspects of the simulation could be brought closer to reality.

Parameter	Symbol	Explanation
Grid length	L	Length of the sides of the square grid. The grid therefore consists of $L * L$ points.
Number of ants	N	The number of ants on the grid.
Supply ratio	R_{sup}	The supply ratio determines the amount of food that the food source contains at the beginning of the simulation. A supply ratio of $R_{sup} = 0.8$, for example, means that the food source contains exactly enough food to completely fill 80% of the ants while the other 20% of the ants are completely empty. (All ants can carry the same limited amount of food.)
Interaction time	t_{int}	The number of time steps during which an ant has to wait after it has picked up or exchanged food. During this period, an ant cannot do anything and stays where it is.
Interaction range	r_{int}	The range within which ants can pick up or exchange food. The distance between two adjacent grid points is 1 CU. For an interaction range of $r_{int} = 1$ CU, for example, an ant can interact with any other ant on the grid point where the ant itself is and with any other ant on the adjacent grid points.
Walk probability	p_{walk}	The probability with which an ant moves from its grid point to any of the adjacent points during a random walk step. For $p_{walk} < 1$, an ant therefore does not necessarily move at every time step.
Speed factor	f_{speed}	The speed factor determines the number of random walk steps that an ant takes per time step. Depending on the outcome of the random process determined by the walk probability, an ant can thus move up to f_{speed} grid points per time step from its original position.

Table 2.1.: Explanation of the parameters in the simulation.

3. Visualization of Networks

This chapter explains the fundamentals of network theory needed to understand the case studies in the following chapter and introduces various ways of visualizing networks. The visualizations are inspired by Blonder et al. [2] and were realized using the Python package NetworkX [5].

A network is a collection of nodes that are joined by edges [12]. In this thesis, the nodes represent the simulated ants, and the edges represent the trophallactic interactions between these ants. Two ants are joined by an edge if and only if the two ants have exchanged food with each other during the simulation. Ants that have interacted with each other several times are joined by several edges. The food source is not included in the network because it only serves the purpose of providing food for the ants. The edges do not only indicate that two ants have interacted, but they also incorporate further information. First, since trophallactic interactions are asymmetric, the edges are directed: an edge between two ants points from the ant that gave food towards the ant that received food. Second, in order to incorporate the temporal dimension, the edges are labeled according to the points in time at which the corresponding interaction occurred. (More precisely, an edge label gives the point in time at which the corresponding interaction ended. The duration of the interactions is neglected in this thesis because all ants in the simulation have the same interaction time.)

An example of a network with the described features is visualized in figure 3.1. This layout is called “time-aggregated layout” because all interactions that occurred during a certain time window are aggregated into the structure of the network [2]. This aggregation, however, results in a disadvantage: it makes it difficult to draw conclusions regarding the temporal dynamics of the interactions. Since all interactions are aggregated into only one network, temporal information is only conveyed by the labels and not by the structure of the visualized network itself. The so-called time-ordered layout in figure 3.2 resolves this problem [2]. This visualization

3. Visualization of Networks

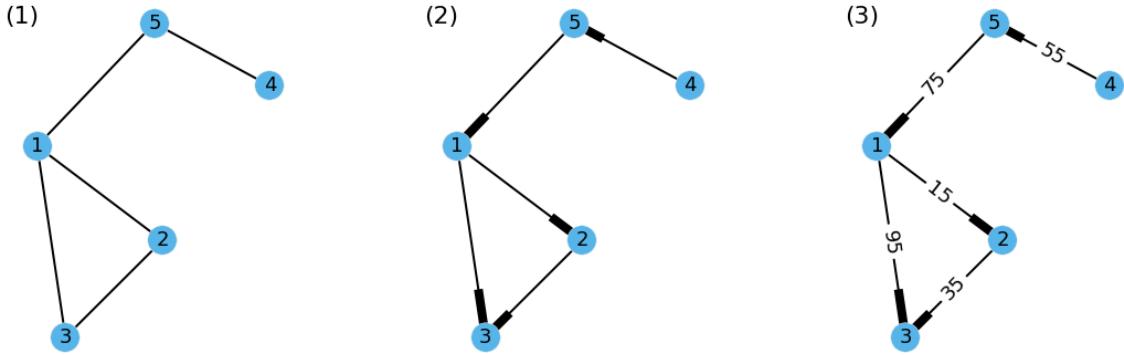


Figure 3.1.: The time-aggregated visualization of an interaction network of five ants. The blue nodes represent ants, and the black edges represent trophallactic interactions between the ants. (1): The edges are undirected. (2): The edges are directed: the thick part points towards the ant that received food. (3): The edges are labeled by the points in time at which the corresponding interactions occurred. The same network is visualized using the time-ordered layout in figure 3.2

makes it easier to discern which ants interacted with each other at which points in time. Furthermore, it allows to track the food flow between the ants by reading the visualization from the bottom to the top.

Unfortunately, the simple time-aggregated layout has another disadvantage: it is tricky to visualize ants that have interacted with each other at multiple points in time. Drawing multiple edges between two ants would require the bending of some of the edges so that they do not overlap each other. This problem is solved by the so-called weighted time-aggregated layout. In this visualization, the thickness of an edge corresponds to the number of interaction between two ants. The thicker the visualization of an edge between two ants is, the more interactions have occurred between the ants. An example using the weighted time-aggregated layout is shown in figure 3.3.

The three types of visualizations presented so far are influenced by the size of the time window that they show. A layout can visualize a complete run or only smaller parts of a run of the simulation. Choosing a time window that is shorter than a complete run can lead to a very different visual impression. For the time-ordered layout, a smaller time window would only result in a visual enlargement of a part of all interactions (if the size of the visualization remains constant). For the time-aggregated layouts, however, using different time windows could drastically change the structure of the visualized network. If some ants do interact with each other in

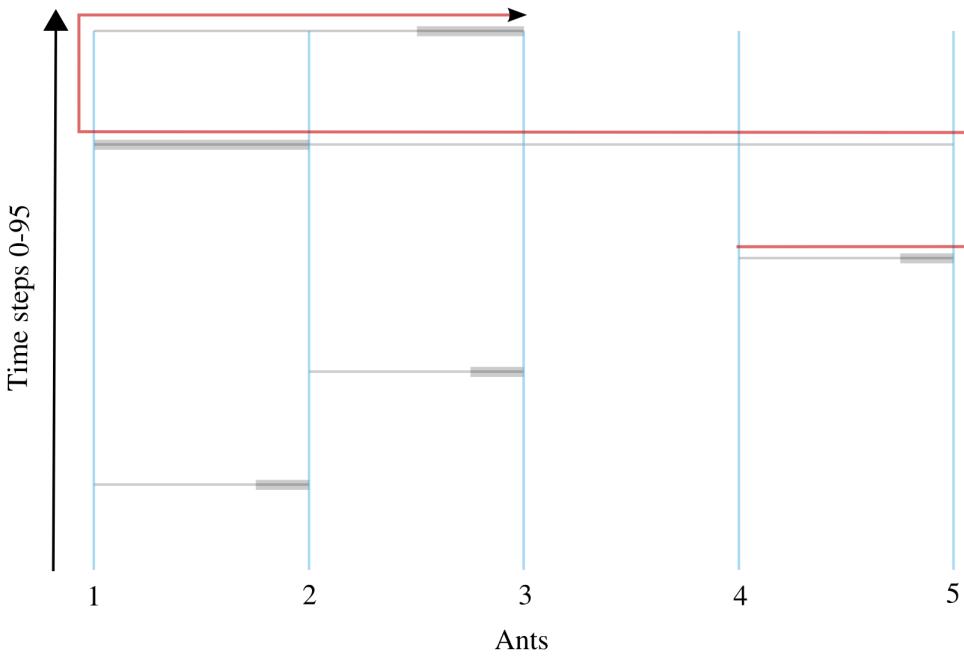


Figure 3.2.: The time-ordered visualization of an interaction network of five ants. The blue lines represent ants at different points in time, and the gray connections represent trophallactic interactions between the ants. The connections are directed: the thick part points towards the ant that received food. The red line gives an example of how the food flow can be tracked. The same network is visualized using the time-aggregated layout in figure 3.1

one time window but do not in another, an edge disappears when visualizing the second instead of the first time window. This chapter does not show such a situation. Instead, the first case study in the following chapter conveys the idea of how the visualizations are influenced by the size of the time window (figures A.13 and A.14).

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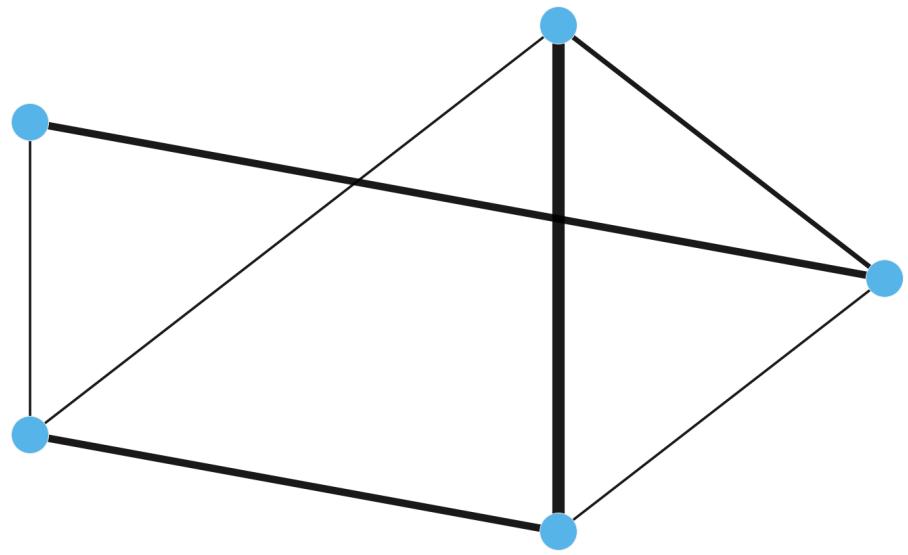


Figure 3.3.: The weighted time-aggregated visualization of an interaction network of five ants. The blue nodes represent ants, and the black edges represent trophallactic interactions between the ants. The thicker an edge is, the more interactions occurred between the two ants that are joined by that edge. Because this is just an example, no scale is given. This network is not the same as the one visualized in the two previous figures because the weighted layout requires a greater number of interactions to be useful.

4. Case Studies

In the simulation, there are only the parameters that are explained in table 2.1. But even given only these parameters, the possible parameter space of the simulation is far too large to explore it completely. Thus, in this chapter, only a few combinations of parameters are investigated. The following pages present three case studies, which deal with different scenarios of the simulation and discuss their results. The first case study simulates rather few ants on a small grid in order to establish first insights into the dynamics of the food dispersion. Furthermore, the visualizations introduced in the previous chapter are used in order to find out what they can teach us about the structure of the interaction network. In the second case study, the speed factor is varied in order to observe its influence on the outcome of the simulation. The last case study, finally, investigates a scenario in which stationary ants are distributed evenly on the grid and only exchange food with their neighbors. The plots in this chapter were realized using the Python package matplotlib [8]; due to their large number, they can be found in the appendix.

4.1. Case I: A Simple Case

In this case study, the simulation is run with the parameter values shown in table 4.1. Formulated in words, there are 60 ants on the 121 grid points of the 11×11 grid with an ant density of about 0.5 ants per grid point. Every ant performs exactly one random walk step per time step: with a probability of 80% an ant moves to one of the adjacent grid points, and with a probability of 20% an ant stays where it is. The food source contains enough food to completely fill every ant. Two ants have to be on the same grid point in order to be able to interact with each other. An interaction takes 10 time steps, during which the involved ants have to wait. The simulation stops as soon as the food source is empty and every ant is completely filled.

The purpose of this scenario is to find out what data a relatively simple run of the simulation produces. Therefore, the grid and the number of ants obviously have to be

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Parameter	Symbol	Value		
		Case I	Case II	Case III
Grid length	L	11	15	15
Number of ants	N	60	112	112
Supply ratio	R_{sup}	1.0	0.9	0.9
Interaction time	t_{int}	10	10	10
Interaction range [CU]	r_{int}	0	0	various
Walk probability	p_{walk}	0.8	0.8	0
Speed factor	f_{speed}	1	various	irrelevant

Table 4.1.: Values of the parameters in the three case studies. The meaning of the parameters is explained in table 2.1.

rather small. The other parameters were chosen on the basis of plausibility arguments. What are these arguments? The values of the supply ratio, the interaction range, and the speed factor are the simplest possible options because they each either take the smallest or greatest value possible. The walk probability of $p_{walk} = 0.8$ is a plausible choice because most grid points have four adjacent grid points. During a random walk step, an ant can thus choose among five options: moving to one of the four adjacent grid points or staying where it is. Assigning equal probabilities to these five options suggests a walk probability of $p_{walk} = 0.8$. The interaction time of $t_{int} = 10$, finally, is the least substantiated parameter value. A trophallactic interaction takes longer than taking a random walk step. But how much exactly? Without comparing the simulation with data from nature, it is impossible to answer this question. The choice of the interaction time therefore rather reflects the human preference for round numbers than compelling arguments. In general, due to the lack of data from nature, the parameter choices are to some degree arbitrary. Only future data from real ant colonies can prove that these parameter values result in a realistic simulation of the food dispersion in an ant colony. In the meantime, the simulation probably only produces data that lie within the same order of magnitude as the ones from nature. In what follows, thus, only their qualitative – but not their exact quantitative – discussion makes sense.

Results

In this section, I present the data that result from a run of the simulation with the above-mentioned parameter values. Most of the plots and visualizations are explained in their captions. The exact numbers I give in this section are, of course, subject to random processes in the simulation and would be different in a different run of the simulation even if it was initialized with the same parameter values.

The Food Source. Three figures visualize the interactions of the ants with the food source over time: figure A.1 the filling level of the food source, figure A.2 the number of pickups, and figure A.3 the amounts of food that were picked up.

The Trophallactic Interactions. Four figures visualize the trophallactic interactions between the ants over time: figure A.4 the total number of interactions, figure A.5 the number of ants that have already received food, figure A.6 the total amount of food exchanged, and figure A.7 the amount of food that was exchanged through each trophallactic interaction. Furthermore, figure A.8 shows the filling levels of the ants over time, and the histogram in figure A.9 visualizes the total number of interactions per ant.

Visualizations of the Interaction Network. Three figures use the layouts that were presented in the previous chapter to visualize the simulated interaction network: figure A.10 the time-ordered layout, figure A.11 the time-aggregated layout, and figure A.12 the weighted time-aggregated layout. Two further figures illustrate the effect of using different time windows: figure A.13 for the time-ordered layout and figure A.14 for the time-aggregated layout.

Further Visualizations. Two plots visualize more complex features of the interaction network over time. First, figure A.15 shows the number of unique outgoing trophallactic interactions per ant. In contrast to the total number of outgoing interactions per ant, the number of *unique* outgoing interactions of an ant only increases by one when the ant in question gives food to one of the other ants *for the first time*. Thus, this plot allows to discern how many of the other ants an ant has given food to during the simulation.

Second, figure A.16 shows the number of ants that an ant has reached directly and indirectly through trophallactic interactions. Some explanations are needed to

4. Case Studies

understand what this means. In one sentence, an ant *was* reached by another ant if the food in the first ant was in contact with the second ant at a previous point in time. Suppose, for example, that ant A transfers food to ant B at time step 15, and ant B transfers food to ant C at time step 35 (the first three ants in the figures 3.1 and 3.2 do exactly this). Then A has reached only B at time step 15. At time step 35, however, A has directly reached B and indirectly reached C: although A has never directly interacted with C until time step 35, the food in C was in contact with A because C received food from B after B had received food from A.

Given this definition, it is worth noting two points. First, this definition allows that an ant reaches itself: if C had transferred food to A at, for example, time step 45, A would have reached three ants because some of the food in A had been in contact with A before. That is also why the plot in figure A.16 reaches the maximum of 60 ants. Second, there is one hidden caveat in this definition: it assumes that the food that an ant receives is mixed with the food that the ant had received before in such a way that every amount of food it transfers to another ant always contains food from all the ants that the ant in question had received food from before (and from the ants that these ants had received food from before, and so on). Although there are no data from real ant colonies to prove it, this assumption is plausible because ants would need a quite ingenious mechanism to separate the different layers of food from each other.

Discussion

What can we draw from these results? The following points offer an overview of the most important conclusions.

- First, the simulated food dispersion seems to be very inefficient. In order to completely fill every ant with food, the 60 ants on the grid in total exchange almost 1200 times the food that one ant can carry with each other (figure A.6) through about 12000 interactions in about 12000 time steps (figure A.4). In comparison with the simplest imaginable scenario in which every ant just picks up the food it needs from the food source, this appears to be a very complicated mechanism. Of course, in an ant colony there is no entity that could order all ants to go the food source to pick up food; that is exactly why they have to resort to mechanisms of self-organization. It is hard to believe, however, that a real ant colony is that inefficient.

4.1. Case I: A Simple Case

- Second, a great part of the dynamics of the food dispersion takes place in a small part of the runtime of the simulation: 90% of the food has already been dispersed after a quarter of the runtime (figure A.1). In fact, towards the end of the simulation, the increases in the total number of pickups (figure A.2) and interactions (figure A.4) as well as the amounts of food that were picked up (figure A.3) and exchanged (figure A.7) become negligible because almost all ants are already full (figure A.8). The unrealistic wandering holes in figure A.7 explain at least a part of the mentioned inefficiency of the food dispersion.
- Third, the visualizations of the network (figures A.10, A.11, and A.12) are too complex to be a great help. Especially the time-aggregated visualizations rather resemble works of art than the results of scientific investigation. The visualizations manage to convey the complexity of the interaction network, but with regard to further useful information the other figures do a better job.

At least it is possible to improve the visualizations. Using three time windows (figures A.13 and A.14) already allows to obtain additional facts like the decreasing interaction rate in the case of the time-aggregated layout. Splitting the runtime of the simulation in more than three time windows would probably make the visualizations even more useful. Using more colors as in the case of the weighted time-aggregated layout could also help.

Another method of visualization, however, was not at all helpful: I also drew the time-aggregated network using the so-called spring layout for which the distance between two nodes is the shorter the more edges connect the nodes. The result, however, was that disappointing that I do not even include it in this thesis (most of the ants were clustered in the center and only a few ants were sticking out so that one could discern absolutely nothing).

- Fourth, the figures A.5, A.15, and A.16 allow to draw some conclusions about the spreading of diseases in the simulated ant colony. Such conclusions are important because the resistance to diseases could have influenced the evolutionary success of an ant colony [3].

Diseases can spread through trophallactic interactions either because of the direct contact they involve or because of the transferred food. If the food in the food source is contaminated, figure A.5 shows that at the latest after about 150 time steps every ant would be infected. If the food, however, has to

4. Case Studies

pass through a certain ant in order to be contagious, almost 700 time steps pass before every ant is infected for certain, as figure A.16 shows. The best option for the ants is the case in which the disease spreads only through direct contact. If the incubation period in this case is that long that ants that had mouth-to-mouth contact with an infected ant do not immediately become contagious, figure A.15 gives ground for a little hope for the ant colony: even after the whole runtime of the simulation there are still some ants that are not infected by the disease.

- Fifth, running the simulation only once produces too few data to determine what probability distribution underlies the interaction histogram in figure A.9. With some fantasy, it could be a Gaussian distribution, but more data are clearly needed.

To conclude, the case in this study is simple and yet already very complex. Although not all of its disadvantages can be changed for the better, some can: the facts that most of the dynamics take place in a small part of the total runtime of the simulation and that there are too few data to determine the probability distribution can be alleviated by changing the parameters of the simulation. This happens in the following two case studies.

4.2. Case II: Speeding up the Random Walk

The parameter values in this case study are again shown in table 4.1. In comparison with case study I, there are some changes. There are now 112 ants on the 225 grid points of the 15×15 grid with an ant density of about 0.5 ants per grid point. The greater number of ants and the bigger grid should lead to smoother data because statistical fluctuations and the effect due to the borders of the grid should be weaker. Additionally, the simulation is run 100 times with this parameter setting so that it is possible to obtain average values instead of only one statistically not very meaningful instance. Furthermore, in order to avoid most of the negligible interactions that led to the complexity of case study I, the food source now only contains enough food to completely fill 90% of the ants. The rest of the simulation – except the speed factor – remains the same as in case study I. The speed factor is varied between 1 and 50 in order to observe its influence on the generated data. The simulation stops again as soon as the food source is empty.

Results and Discussion

In what follows, I restrict my discussion to the two observables of the simulation that are most influenced by the variation of the speed factor: the interaction histograms and the efficiency of the food dispersion. Repeating the same analysis as in the previous case study would go beyond the scope of this thesis. Such an analysis would probably only provide similar conclusions as the ones I just discussed. It is likely that the most important new finding would be that the data are somewhat scaled up because there are more ants in this case study.

The Interaction Histograms. The figures A.17, A.18, and A.19 show the interaction histograms for several speed factors. The histograms for further speed factors that the simulation was run with are not included here for reasons of space. It was now possible to fit Gaussian functions to the histograms because the simulation was run 100 times for each speed factor. Figure A.20 shows these fits for speed factors between 1 and 15. Running the simulation with other speed factors up to 50 did not lead to a significantly different distribution. Apart from some fluctuations, the interaction histogram remained the same as for a speed factor of $f_{speed} = 15$.

What can we conclude from these data? First, running the simulation 100 times did generate enough data to determine the probability distributions that the interaction histograms are based on. Thus, it is highly likely that the histogram in the previous case study resulted from a Gaussian distribution, too. There were just not enough data to determine this fact with certainty. Second, the number of interactions obviously decreases when the speed factor increases. Until now it is impossible to decide why this is the case. The following paragraph about the efficiency of the food dispersion, however, explains this observation. Third, some of the interaction histograms show a tendency to be right-skewed. Especially in figure A.19 the Gaussian distribution has a tail of ants with many interactions. Other histograms like the one in figure A.18, however, almost perfectly resemble a Gaussian distribution. Unfortunately, the other histograms that are not included in this thesis are equally ambiguous: some of them are right-skewed, others are not. What these tails result from remains subject to further research. I do not know whether they arise because of statistical fluctuations or other reasons. That the simulation produces potentially right-skewed interaction histograms, however, is promising. There is some evidence that the interaction distributions of real ant colonies also follow a right-skewed – though not Gaussian – distribution [15].

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The Efficiency of the Food Dispersion How efficient is the food dispersion for the different speed factors? To answer this question, a metric for measuring efficiency is needed. The runtime of the simulation serves this purpose. Since the simulation stops when the food source is empty, the runtime gives the time at which the ants have managed to disperse all of the food in their colony – and colonies that do this faster are more efficient. Figure A.21 uses this metric by showing the average runtime of the simulation for different speed factors.

Why is the food dispersion faster for higher speed factors? An increased number of interactions cannot be the reason: it decreases when the speed factor increases (figure A.20). Instead, there are two other reasons, which can be inferred from the figures A.22 and A.23: for higher speed factors, the ants both pick up and exchange more food per pickup or interaction. Mathematically speaking, these observables are highly anti-correlated with the runtime: the Pearson correlation coefficient between the average runtime and the average amount of food picked up from the food source is $r = -0.97$ (with a 2-tailed p-value of $p = 4.2 \cdot 10^{-8}$), and between the average runtime and the average amount of food exchanged per interaction it is $r = -0.91$ ($p = 1.2 \cdot 10^{-5}$).

Correlation does not imply causation, but with some additional thought the causal connection between these observables appears plausible, too. Why are the pickups and the interactions more efficient for higher speed factors? The ants ignore both the food source and other ants when they perform their f_{speed} random walk steps. Thus, no matter what value the speed factor has, on average, the same number of ants is on one and the same grid point (but not necessarily on two different grid points because the random walk of the ants is restricted by the border of the grid). This is also the case for the food source so that there is on average always the same number of ants on the food source.

Given this fact, why does the efficiency of the pickups change at all? Because it does not only matter how many ants there are on the food source but also which ants. An ant that reaches the food source picks up as much food as it can carry so that it cannot pick up further food until it has passed on some of it to other ants. Ants that are farther away from the food source, however, potentially have more space left for food – and for higher speed factors these ants have a higher chance of reaching the food source. On average, the ants therefore pick up more food so that the food source is empty more quickly.

The argument regarding the more efficient trophallactic interactions is similar:

4.2. Case II: Speeding up the Random Walk

for higher speed factors, the ants have a higher chance of meeting ants that carry significantly smaller or greater amounts of food than themselves so that they exchange more food per interaction. Furthermore, for a speed factor close to $f_{speed} = 1$, an ant relatively often exchanges food with the same other ant in a row. If two ants that have just interacted with each other both carry food and still have some space left in their stomachs, there is a probability of 50% that an ant that has just received food returns some of it to the ant from which it has received the food if they meet again. Because higher speed factors help to avoid such situations, they make the food dispersion more efficient.

As announced in the previous section, it remains to explain why the Gaussian distributions in figure A.20 move to the left for higher speed factors. Why do higher speed factors lead to less interactions? There are two reasons: both the shorter runtime of the simulation and the increased efficiency of the interactions result in less interactions per ant. Figure A.24 shows that the average number of interactions per time step decreases for higher speed factors. If the smaller total number of interactions were only explained by the shorter runtime, this value would have to be approximately constant. But since it changes, the more efficient interactions play a role in moving the Gaussian distributions to the left, too.

There is one more unexpected observation: for speed factors greater than 15 neither the interaction histograms nor the average runtime of the simulation change significantly. This number is surprisingly low. Why? The food dispersion should be most efficient for an infinite speed factor because then the ants are basically positioned randomly at every time step. But a speed factor of $f_{speed} = 15$ is far from infinity so that the distance that the ants move per time step is small. The mean square displacement of a random walk of N unit steps is N [21]. That is, after a random walk of N steps, an ant is on average a distance of \sqrt{N} [CU] away from its previous position. Due to the walk probability of $p_{walk} = 0.8$, a speed factor of $f_{speed} = 15$ results on average in only 12 random walk steps and $\sqrt{12}$ CU ≈ 3.5 CU of walked distance between two time steps during which an ant does not have to wait (because of the limited size of the grid, this distance is even smaller). Thus, it is surprising that the correlation between two consecutive positions of an ant for speed factors greater than 15 is already low enough to produce the same results as the case of random positioning.

As we have seen, according to the data produced by the simulation, the food dispersion is faster for higher speed factors. Thus, there seem to be some reasons

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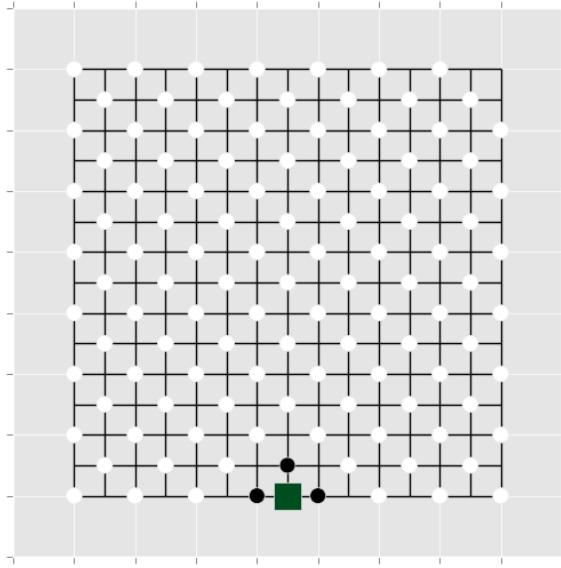


Figure 4.1.: The distribution of ants in case study III. Every circle represents one ant. Only the three black ants at the bottom can pick up food from the square food source. In this scenario, the ants do not move and can only exchange food with their neighbors. For an interaction range of $r_{int} = 1.5$ an ant can exchange food with its four nearest neighbors, and for an interaction range of $r_{int} = 2$ an ant can exchange food with its eight nearest neighbors. (Of course, the ants close to the border of the grid have less neighbors.)

for real ants to walk some distance after a pickup or an interaction before they pick up or exchange food again. Real ants, however, cannot move an infinite distance per time unit so that evolution probably has found a balance between the efficiency of higher speed factors and the limited speed of ants. Unfortunately, this balance can again only be determined with data from nature; the simulation cannot help much in this respect. But there are other uses for the simulation: in the following case study, a completely different mechanism of food dispersion is investigated and compared with the case in this section.

4.3. Case III: The Diffusion Strategy

As shown in table 4.1, in this case study, the simulation is run with almost the same parameter values as in the previous one. But there is one crucial difference: in this case study, the ants do not move because the walk probability is zero. To make up for this fact and still enable the ants to interact with each other, the interaction

4.3. Case III: The Diffusion Strategy

range is greater than zero. Furthermore, the ants are not positioned randomly at the beginning of the simulation, but as shown in figure 4.1. This positioning together with the parameter setting leads to a reversed situation: now not the ants do perform a random walk, but the food does. From the food source, it diffuses through the stationary ant colony. The simulation stops again as soon as the food source is empty.

The purpose of this case study is to test how this diffusion strategy does compared with the movement strategy of the previous case study. *A priori*, the ants might disperse food equally fast by following the diffusion strategy as by moving randomly over the whole grid. In order to obtain enough data to test this scenario, the simulation is again run 100 times for each set of parameter values.

The interaction range r_{int} takes two values in this case study: for $r_{int} = 1.5$ every ant can interact with its four and for $r_{int} = 2$ with its eight nearest neighbors (ants close to the border of the grid, of course, have less neighbors). Greater interaction ranges are not realistic because trophallactic interactions require immediate contact between the ants involved. Actually, any interaction range significantly greater than zero is impossible in nature because trophallactic interactions between ants are realized through mouth-to-mouth contact. A realistic realization of the diffusion strategy in nature would therefore rather be one in which every ant is not completely stationary but still moves in a limited area. The data produced by running the simulation with these parameter values is presented and discussed in the following section.

Results and Discussion

How efficient is the food dispersion using the diffusion strategy? Figure A.25 shows the average runtime of 100 runs of the simulation for the two different interaction ranges. For the smaller interaction range, the simulation runs almost twice as long as in the slowest case of the previous case study, but for the greater interaction range it is not much slower. The reasons for this observation are similar to the ones in the previous case study: for the higher interaction range, the ants have a higher chance of interacting with ants that carry significantly smaller or greater amounts of food than themselves, and they more likely avoid situations in which an ant immediately returns some of the food it has just received. An additional reason is that the ants transfer food over greater distances the higher the interaction range is. Since the

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ants do not move but the food nonetheless has to reach the ants in the corners of the grid, this accelerates the food dispersion.

The figures A.26 and A.28 show the interaction histograms for the two interaction ranges. Both look unusual. Why are there several approximately Gaussian distributions? The figures A.27 and A.29 answer this question. Depending on the position of an ant on the grid, the number of interactions it performs during the simulation varies significantly. The overall variation in the total number of interactions strongly depends on the interaction range. For the smaller interaction range, the limiting effects of the border of the grid play a crucial role: ants with less neighbors also interact significantly less. For the greater interaction range, however, the distribution of the interactions on the grid is more uniform. Ants with less neighbors still interact less, but the difference to the ants with many neighbors is not as great as before.

For both interaction ranges, the ants with the least interactions are those close to the food source. These ants never receive food from other ants because they always pick up food as soon as they have some space in their stomachs. That is why for even greater interaction ranges than the ones in this case study the food source obviously would be empty faster. If more ants can pick up food, it is also dispersed more quickly. That is another reason for not investigating how greater interaction ranges influence the simulation besides the fact that such a situation would not be realistic.

To sum up, for the smaller interaction range the diffusion strategy is far less efficient than the movement strategy of the previous case study. For the somewhat greater interaction range, however, the food dispersion is not much slower, although the ants need far more interactions to disperse all the food. Unfortunately, this finding strongly depends on the not very substantiated choice of the interaction time. Every ant that carries food and has at least one neighbor that has some space in its stomach interacts at every time step (during which both ants involved do not have to wait). Because all ants are always within the interaction range of other ants, thus, many ants interact immediately after they have waited. In the previous case study, however, ants could be outside of the interaction range of any other ant. Changes of the interaction time therefore more strongly affect the diffusion strategy than the movement strategy of case study II. According to this argumentation, comparing the two strategies under fair conditions is only possible given the interaction time of real ants. Again, data from nature are necessary in this respect.

5. Conclusion

As announced in the introduction, the goals of this thesis were to test approaches from network theory for their usefulness and to investigate how the simulation can help to understand the resource dispersion in interaction networks that are similar to the ones of social insects. Has this thesis reached these goals? Yes, with one reservation: we still do not know how the food dispersion in real social insect colonies works in detail. Until now this thesis can therefore only claim to have generated understanding about the theoretical models that were used in this thesis – which cannot be compared with nature yet because experimental data are still pending. But fortunately social insects are promising objects for research. They can be easily tracked and manipulated because of their small size and large number. New tracking techniques and more open attitudes towards the publication of raw data should thus soon allow to compare the simulated social insect colonies with natural ones [3].

Assuming that the data generated by the simulation sufficiently resemble real ones, what did this thesis contribute to the understanding of the resource dispersion in interaction networks?

Case study I showed that the simulation works and results in the dispersion of food from the food source through the ant colony. Since there was enough food to completely fill every ant, however, many of the trophallactic interactions were negligible towards the end of the simulation. This unnecessarily blew up the interaction network so that its visualizations are of limited help; for human eyes they are simply too complex. In compensation, other plots allowed to draw some conclusions regarding the spreading of diseases in the simulated colony.

Case study II found that higher speed factors speed up the food dispersion because of two reasons: both the pickups and the trophallactic interactions between the ants are more efficient. Another intriguing finding of this case study is that the interaction histograms produced by simulation are potentially right-skewed. Although further research is necessary to establish the reasons for this fact, it is promising because there are already findings that this is also the case for real ant colonies.

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Case study III, finally, proved that the diffusion strategy is almost as efficient as the movement strategy of case study II if the ants are allowed to interact with more ants than just their immediate neighbors. For the somewhat greater interaction range, the distribution of the interactions on the grid also is more uniform. Unfortunately, the efficiency of the food dispersion strongly depends on the until now quite arbitrary choice of the interaction time in the simulation so that comparing the two strategies under fair conditions is not possible yet.

There are reasons for hope that the results of this thesis can further contribute to the understanding of interaction networks. Presumably, real interaction networks are not as complex as the ones in this thesis because they do not include the many negligible interactions that occurred in case study I. Applying the visualizations that were presented in this thesis to data from nature might thus still yield reasonable results.

Several measures could improve the visualizations. For example, it is possible to weight the edges of a network not according to how often two nodes interacted but according to how much of a resource they exchanged with each other. When one is interested in resource dispersion, this is probably the more relevant factor than the number of interactions between two nodes that neglects how small or great the exchanged amounts were.

Another possible measure is to use more colors in the visualizations. The different shades of gray in the weighted time-aggregated network in case study I (figure A.12) already made it easier to discern the variation in the number of interactions. Further colors might enhance this effect so that human eyes could draw more useful information from the visualizations.

Finally, incorporating information from the networks into the drawings of the time-aggregated layouts (and maybe even the time-ordered layout) might improve the visualizations, too. The spring layout, in which the distance between two nodes corresponds to the strength of the interaction between the nodes, was not useful for case study I. But this might be different for natural interaction networks in which the interactions do not occur as randomly as in this thesis.

Apart from visualizations, there are also further possibilities to learn something about interaction networks. Network theory has much more to offer than only the approaches used in this thesis. The identification of subgroups of especially strongly connected nodes [1, 17] or the comparison of networks in terms of the motifs that appear in them [9, 19, 20] are only two among many other promising

examples. These approaches could also help to further explore the dynamics of disease spreading in social insect colonies, which probably was an important factor during evolution. Unfortunately, the scope of this thesis did not allow to investigate the disease spreading in detail, even though it would be particularly interesting to compare the movement and the diffusion strategy in this respect.

Finally, analytical approaches could generate understanding about resource dispersion, too. This thesis basically dealt with ant colonies whose members perform a random walk in space and food that again performs a random walk in the ant colony. Since random walks are a well explored concept, it might be worth the effort to cast an analytical eye on the theoretical models that were used in this thesis.

What if the data produced by the simulation do not sufficiently resemble data from nature? An obvious idea in this case is to further explore the parameter space of the simulation. Maybe the parameter combinations in this thesis were just the wrong ones to yield realistic data. Other combinations could well result in data that fit reality more closely.

However, if no part of the parameter space produces reasonable results, an option is to tackle the simplifications that are incorporated in the simulation. Such aspects of the simulation as the absence of variability among the ants, the constant interaction time, or the possibility that an ant immediately returns some of the food it has just received appear highly unrealistic. Bringing these aspects closer to reality could result in more useful data.

Of course, there is unfortunately also the option of complete failure. Maybe the discretization of space and time in this thesis was simply too stark an abstraction from reality to produce sensible results. In this case, other approaches with less coarsely discretized spatial and temporal dimensions might work better. It is certainly feasible to create a simulation that reproduces the phenomena observed in nature – the challenge is just to construct it as simple as possible and as complex as necessary.

To conclude, the theoretical models in this thesis allowed to draw some interesting conclusions. Now it remains to find out whether these conclusions are applicable to real interaction networks and how they can be used to improve the technical and social networks in our world. There is still much to do for future research.

A. Appendix

This appendix contains the figures of the three case studies in chapter 4. The pages 34-43 deal with case study I, the pages 44-47 with case study II, and the pages 48-50 with case study III.

A. Appendix

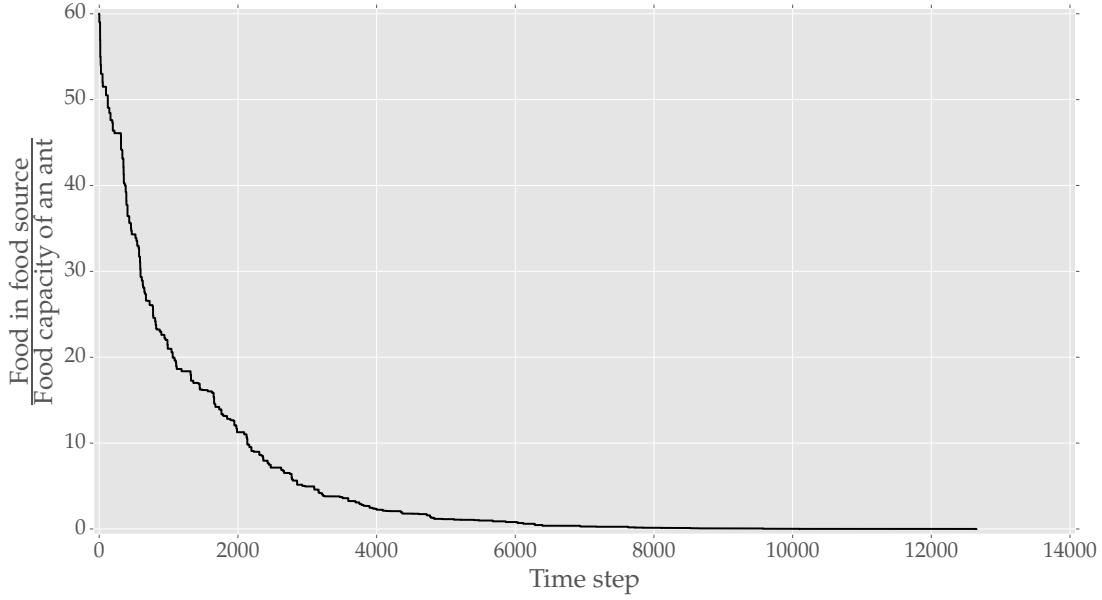


Figure A.1.: **Case Study I.** Plot of the filling level of the food source in multiples of the food capacity of one ant over time. In this scenario, there was enough food to completely fill the 60 ants.

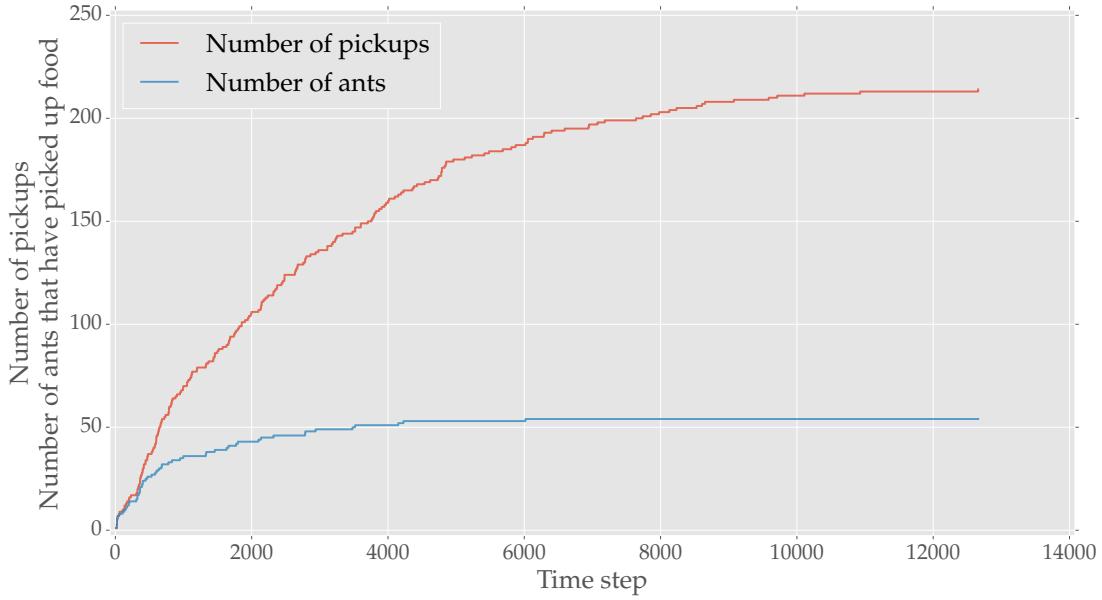


Figure A.2.: **Case Study I.** Plots of the total number of pickups from the food source and the number of ants that have already picked up food over time. The maximum of the blue curve is 54 ants. The difference between the two curves results from the fact that many ants do pick up food several times.

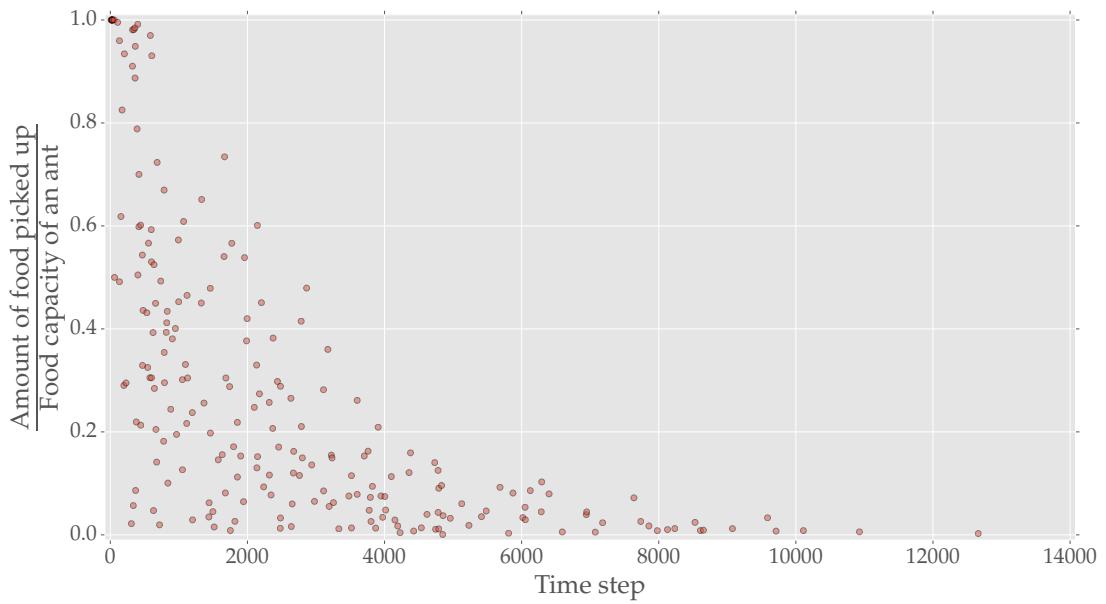


Figure A.3.: **Case Study I.** Plot of the amounts of food that were picked up from the food source in multiples of the food capacity of one ant over time. Every red dot represents one pickup.

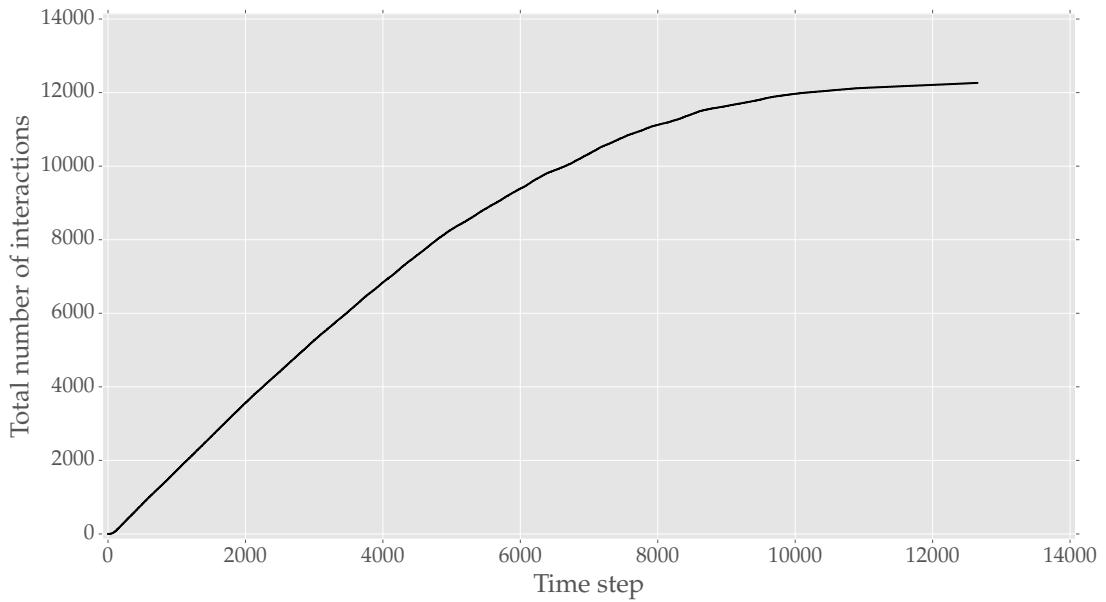


Figure A.4.: **Case Study I.** Plot of the total number of trophallactic interactions over time.

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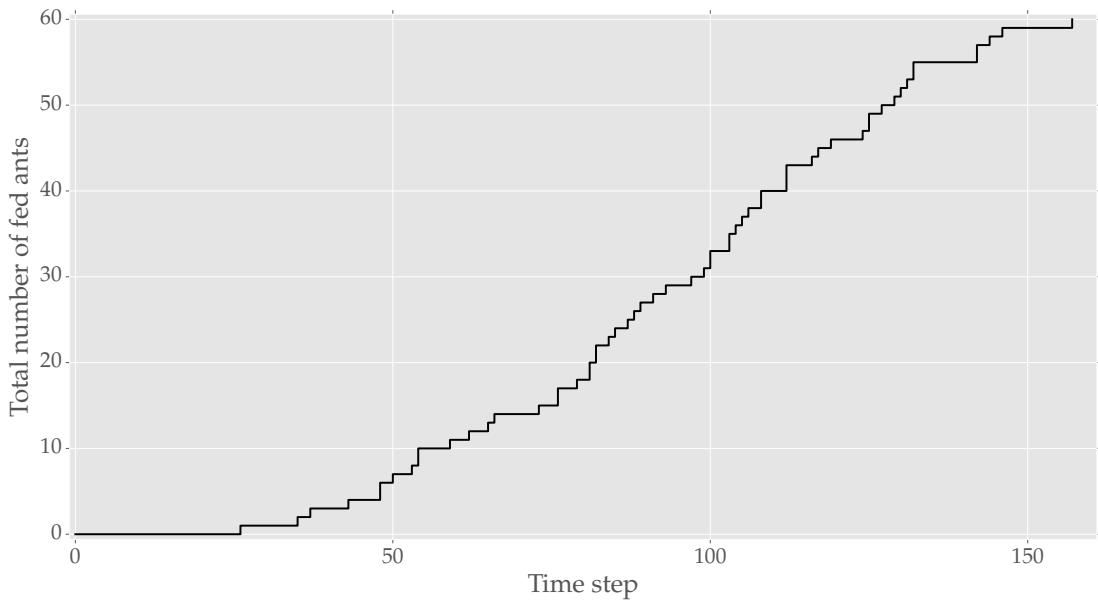


Figure A.5.: **Case Study I.** Plot of the number of ants that have already received food from another ant over time. Pickups from the food source are not included. The plots stops when the maximum of 60 ants is reached.

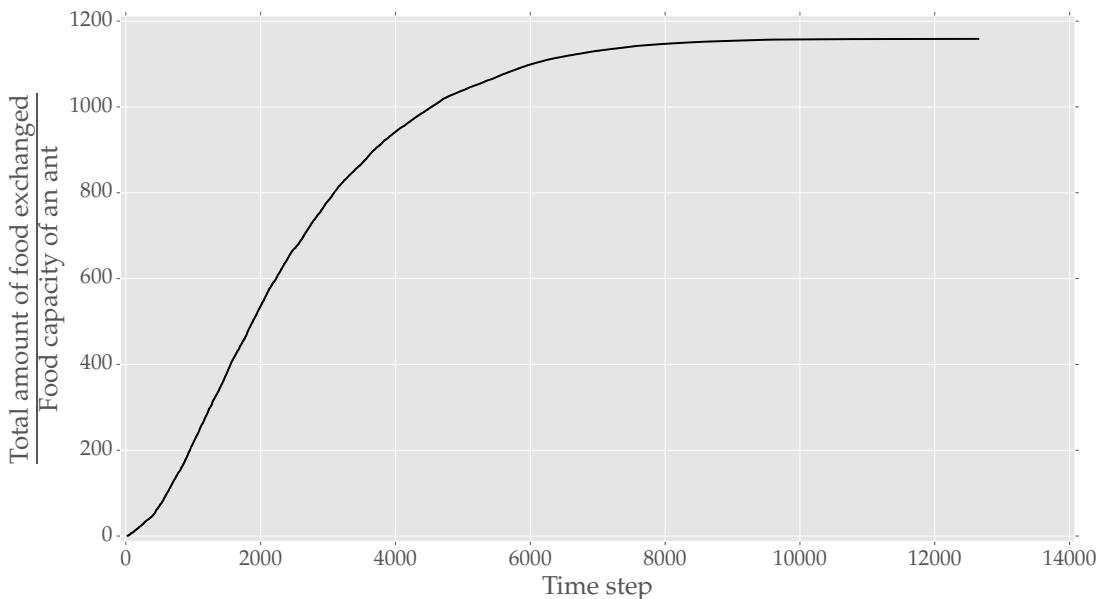


Figure A.6.: **Case Study I.** Plot of the total amount of food exchanged through trophallactic interactions in multiples of the food capacity of one ant over time.

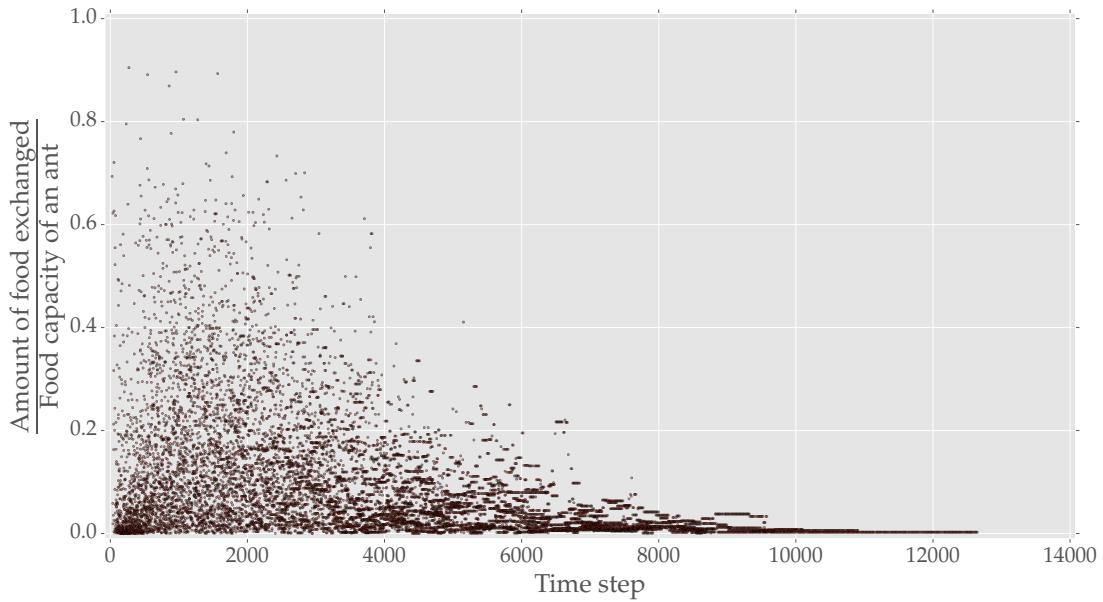


Figure A.7.: Case Study I. Plot of the amounts of food exchanged through trophallactic interactions in multiples of the food capacity of one ant over time. Every red dot represents a trophallactic interaction. The shapes that look like lines in the right part of the figure are actually lines of dots that are very close to each other. They are produced when an ant that is not completely full transfers the small “hole” in its stomach to another ant that is already full, that ant passes the hole to another full ant, and so on. The last 3000 time steps basically only consist of such holes wandering around until they reach the food source.

A. Appendix

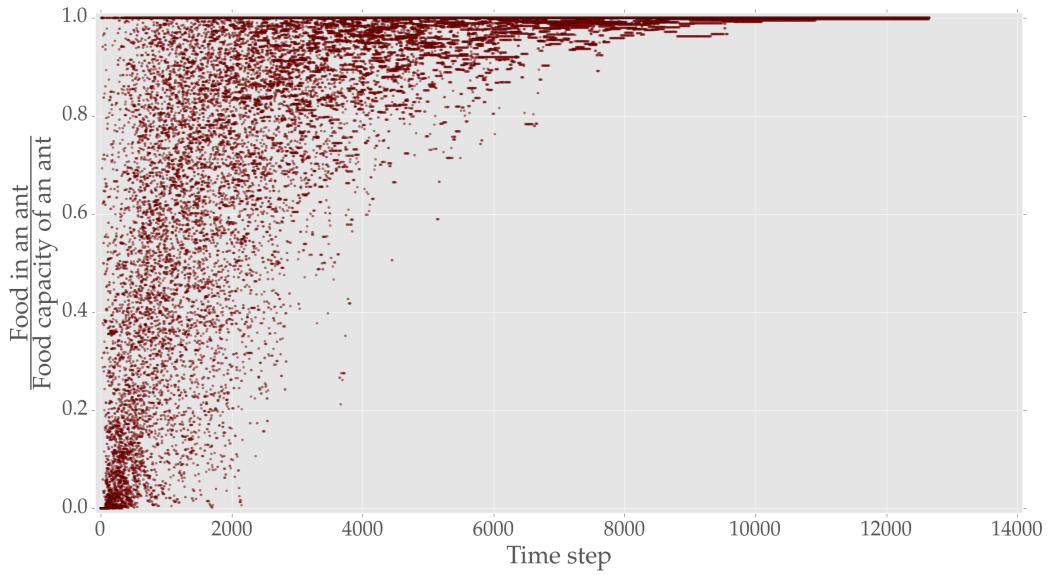


Figure A.8.: **Case Study I.** Plot of the amounts of food in the ants in multiples of the food capacity of one ant over time. For every ant and every point in time, there is one red dot representing the food that the ant carries at that moment. Thus, many of the shapes that look like dots are actually lines of dots that are very close to each other.

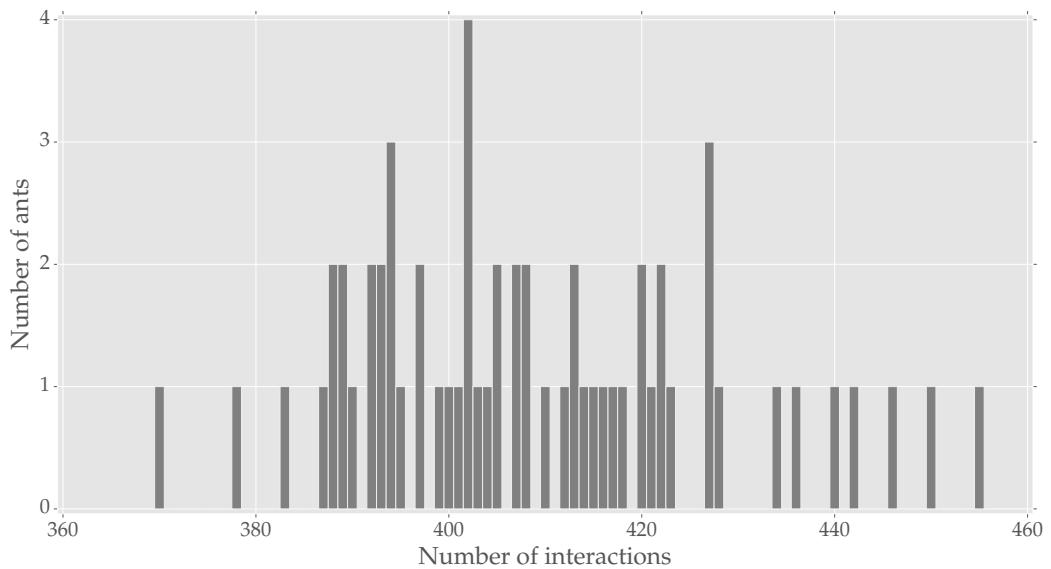


Figure A.9.: **Case Study I.** Visualization of the interaction histogram of the network. Every trophallactic interaction in figure A.4 increases the total number of interactions in this histogram by two because one interaction connects two ants.

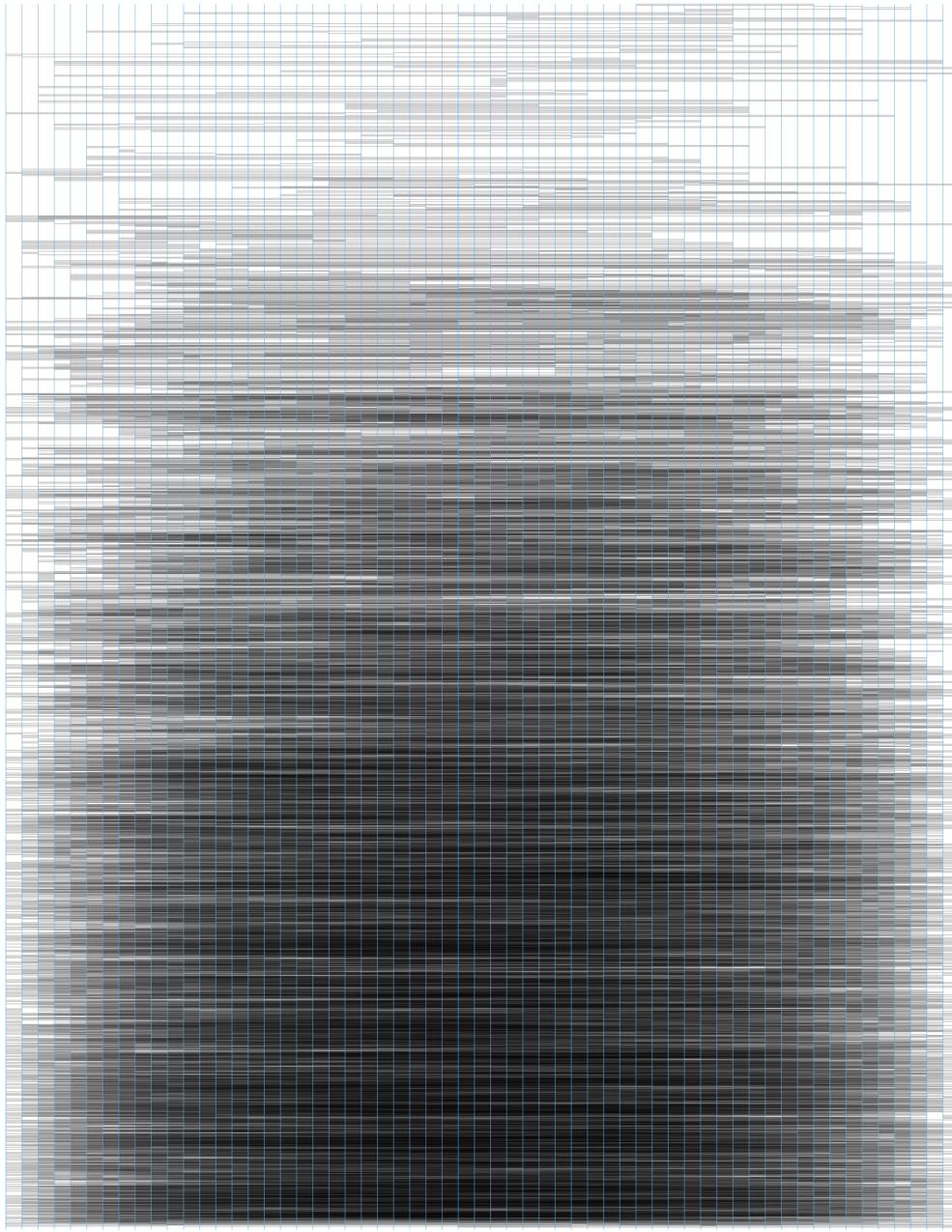


Figure A.10.: **Case Study I.** Visualization of the interaction network using the time-ordered layout. The blue lines represent ants at different points in time, and the black connections represent trophallactic interactions between the ants. The 12646 time steps shown in this figure pass continuously from the bottom to the top. Even though the connections are not drawn as directed connections, one can hardly draw anything from this visualization apart from the facts that there are many interactions and that the number of interactions decreases towards the end of the simulation.

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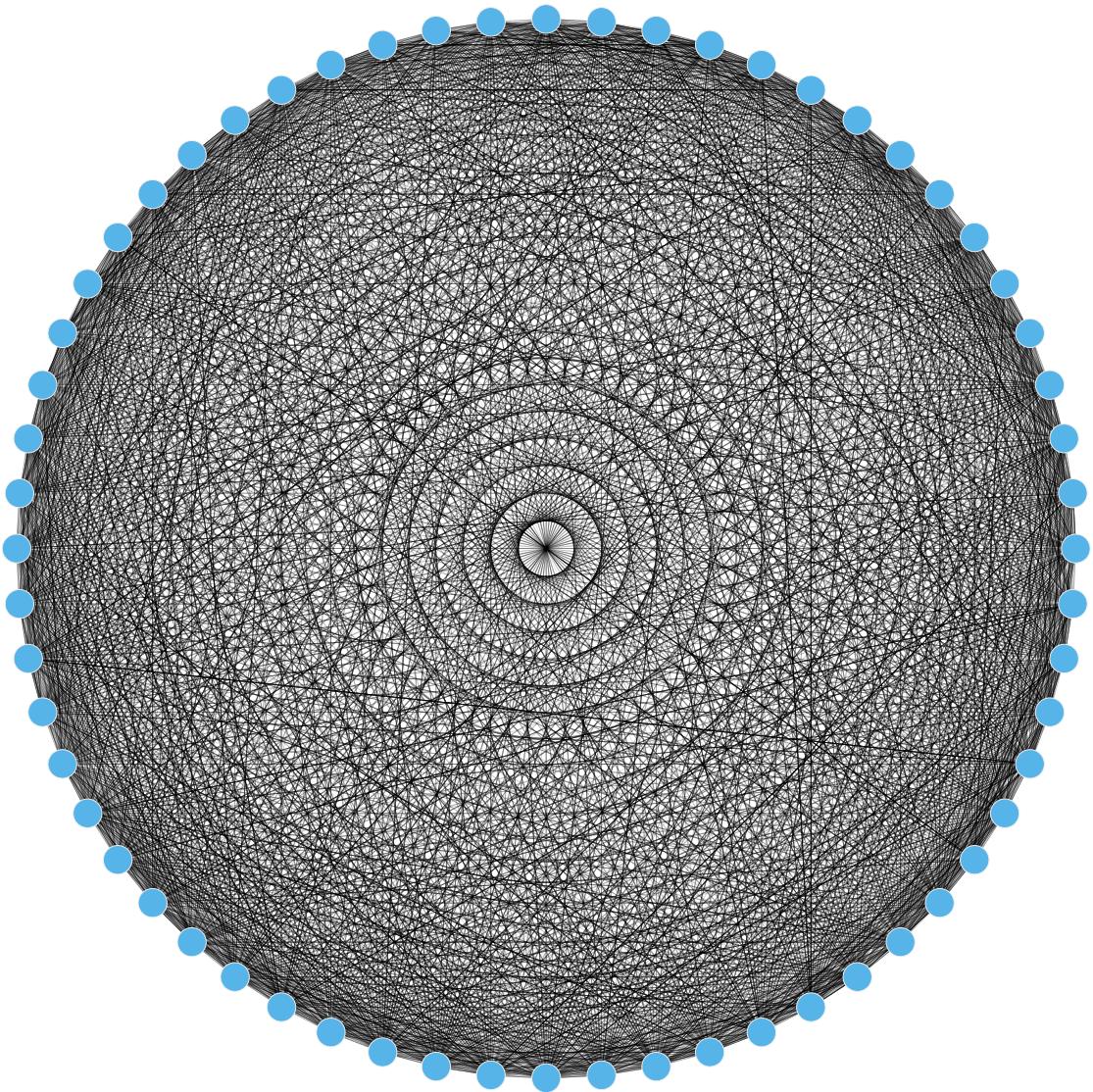


Figure A.11.: **Case Study I.** Visualization of the interaction network using the time-aggregated layout. The blue nodes represent ants, and the black edges represent trophallactic interactions between the ants. Multiple edges between two ants completely overlap each other. Even though the edges are not drawn as directed edges, one can hardly draw anything from this visualization apart from the fact that almost every ant has interacted with almost every other ant.

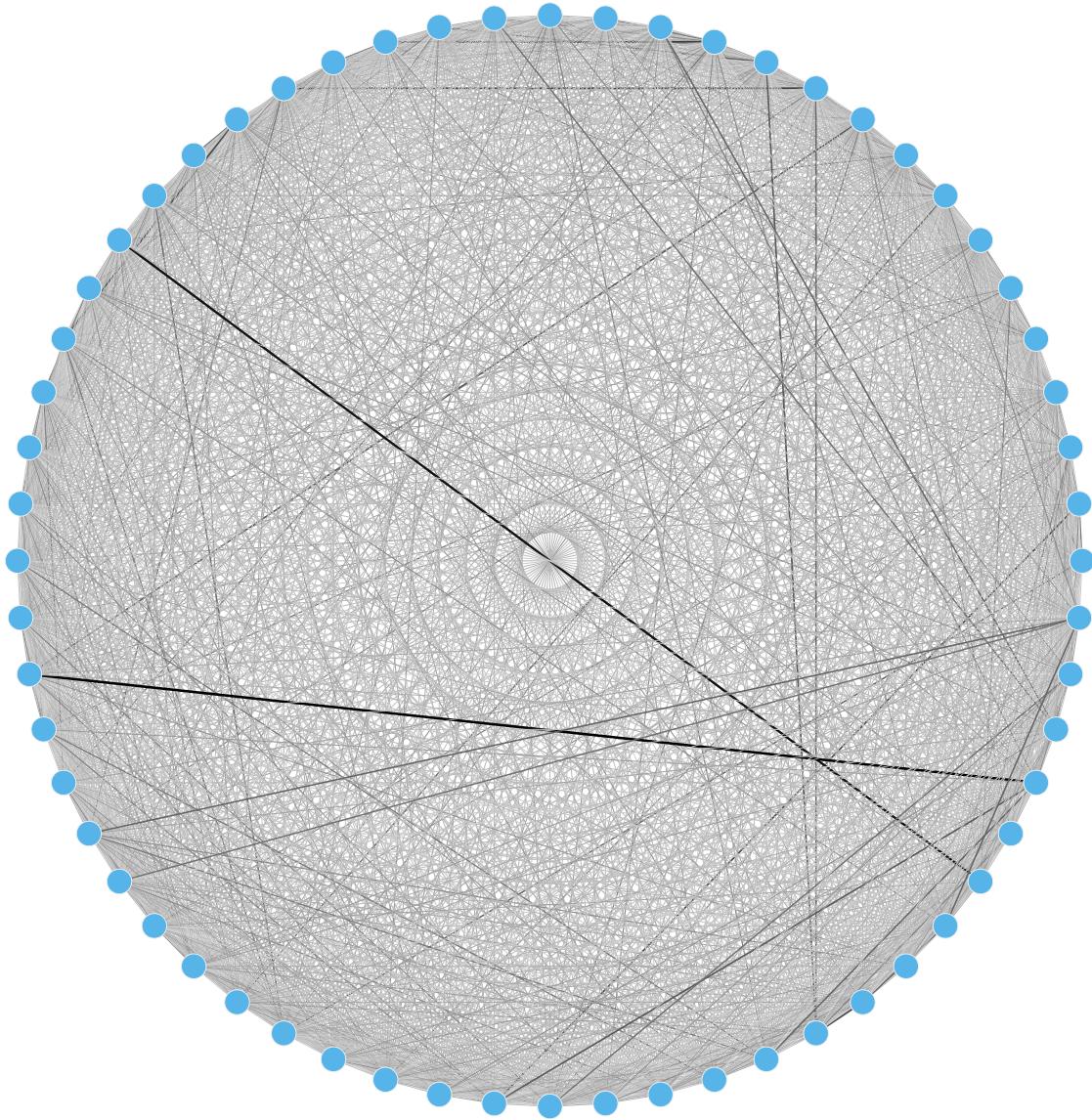


Figure A.12.: **Case Study I.** Visualization of the interaction network using the weighted time-aggregated layout. The blue nodes represent ants, and the black edges represent trophallactic interactions between the ants. The thicker and the darker an edge between two ants is, the more interactions occurred between the two ants. No scale is given because it would be hard to read. Even though the edges are not drawn as directed edges, one can hardly draw anything from this visualization apart from the facts that almost every ant has interacted with almost every other ant and that some ants have interacted more often with each other than other ants.

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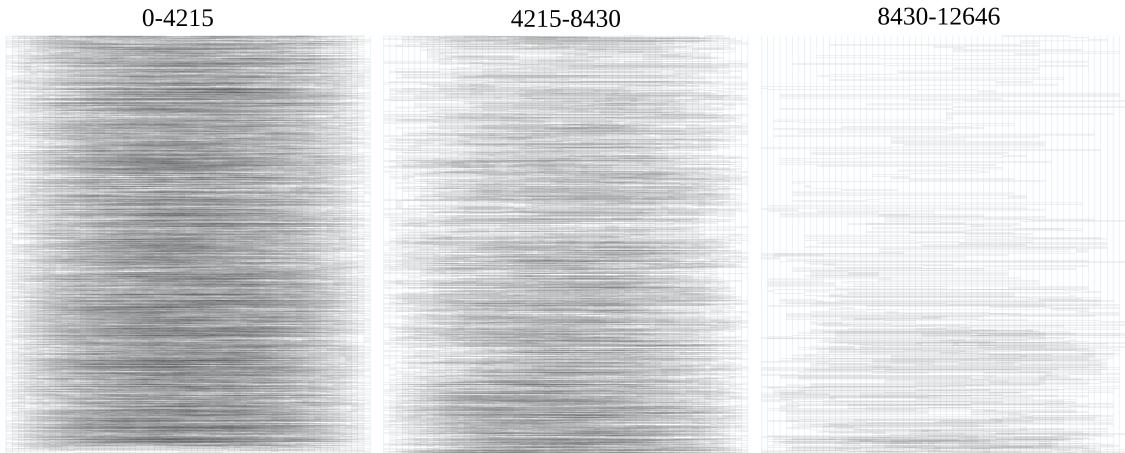


Figure A.13.: **Case Study I.** Visualization of the interaction network using the time-ordered layout (as explained in figure A.10) with different time windows. The numbers give the size of the visualized time windows. In this case, the different time windows only allow to discern more details.

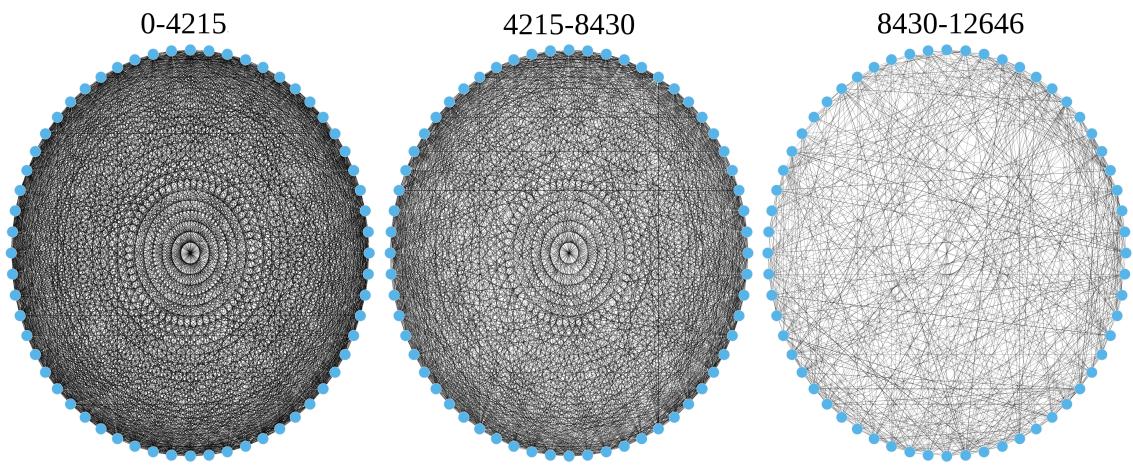


Figure A.14.: **Case Study I.** Visualization of the interaction network using the time-aggregated layout (as explained in figure A.11) with different time windows. The numbers give the size of the visualized time windows. Because of the different time windows, now also the aggregated layout allows to discern that the number of interactions decreases towards the end of the simulation.

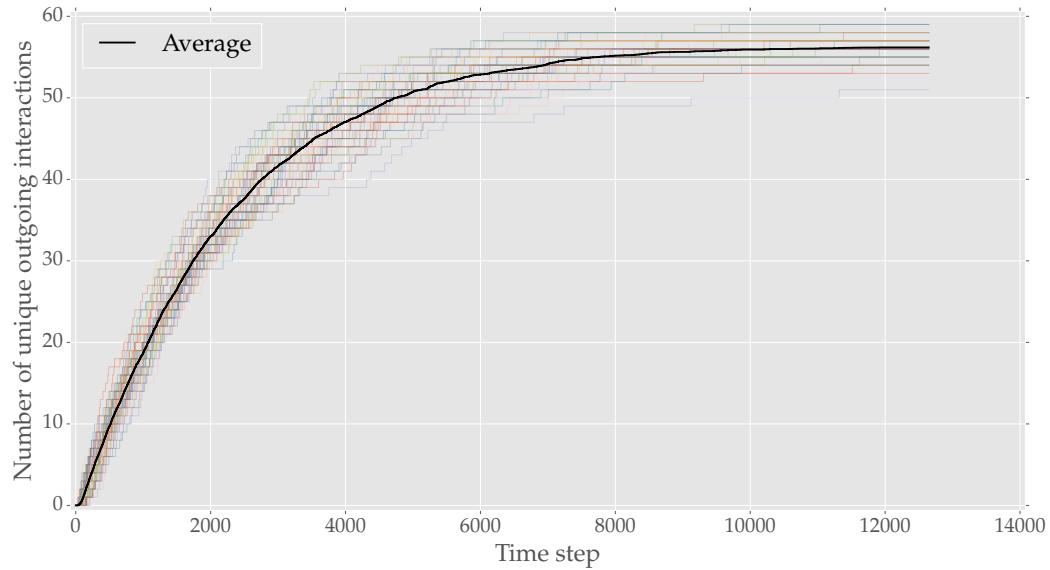


Figure A.15.: **Case Study I.** Plot of the number of unique ants an ant has given food to trough trophallactic interactions over time. Every colored line represents one ant. Ants that an ant has given food to several times are only counted once.

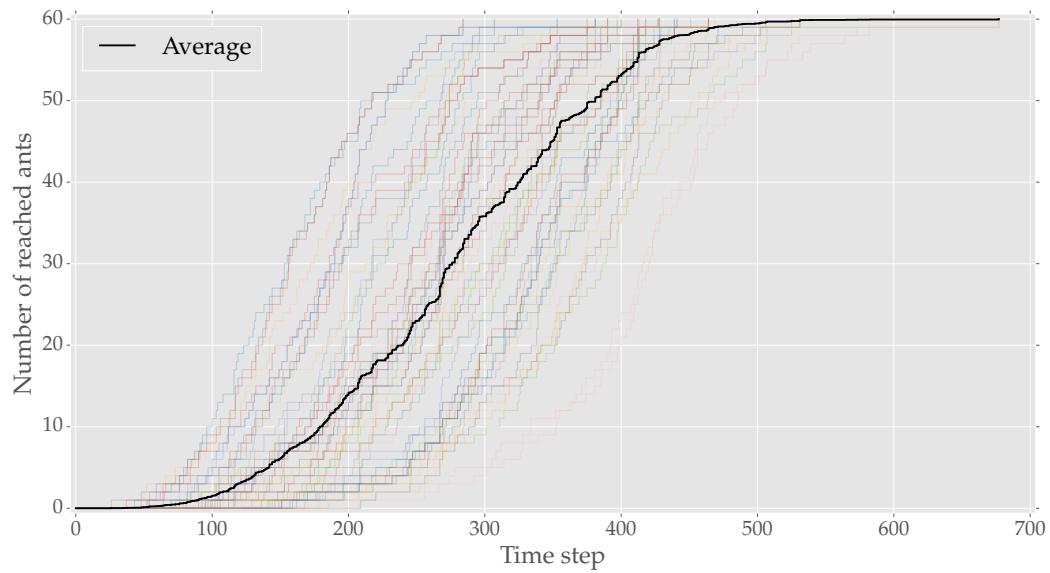


Figure A.16.: **Case Study I.** Plot of the number of ants an ant has reached through trophallactic interactions over time. Every colored line represents one ant. What it means that an ant has reached another ant is explained in section 4.1. The plot stops when the maximum of 60 ants is reached.

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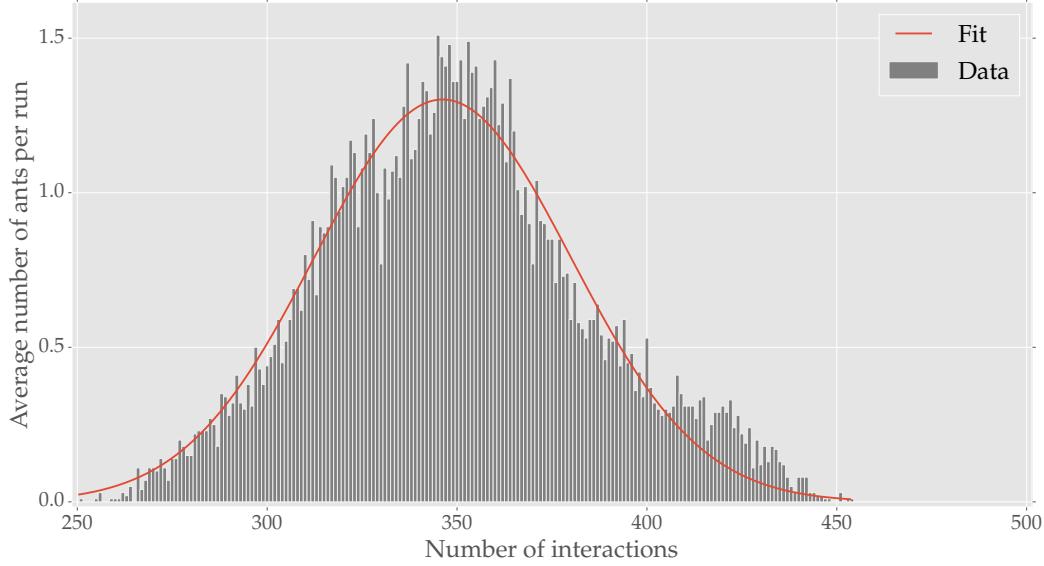


Figure A.17.: **Case Study II.** Interaction histogram for a speed factor of $f_{speed} = 1$ and 100 runs of the simulation. The red curve results from a fit to the Gaussian function $f(x) = A \cdot \exp\left(\frac{x-\mu}{2\sigma^2}\right)$ with height A , mean μ , and standard deviation σ .

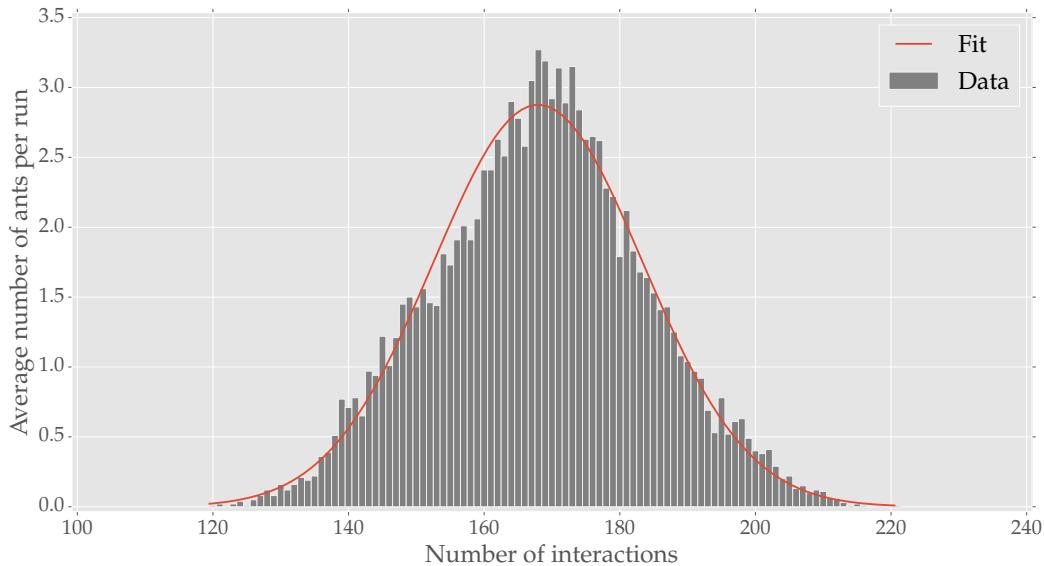


Figure A.18.: **Case Study II.** Interaction histogram for a speed factor of $f_{speed} = 3$ and 100 runs of the simulation. The red curve results from a fit to the Gaussian function $f(x) = A \cdot \exp\left(\frac{x-\mu}{2\sigma^2}\right)$ with height A , mean μ , and standard deviation σ .

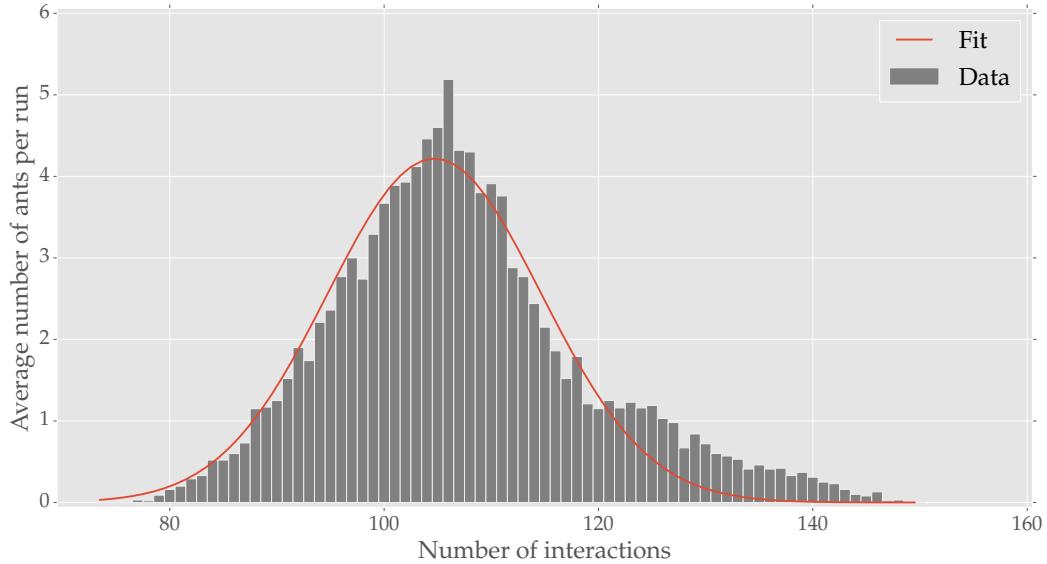


Figure A.19.: **Case Study II.** Interaction histogram for a speed factor of $f_{speed} = 15$ and 100 runs of the simulation. The red curve results from a fit to the Gaussian function $f(x) = A \cdot \exp\left(\frac{x-\mu}{2\sigma^2}\right)$ with height A , mean μ , and standard deviation σ . Because of the high proportion of ants with many interactions, the histogram is somewhat right-skewed.

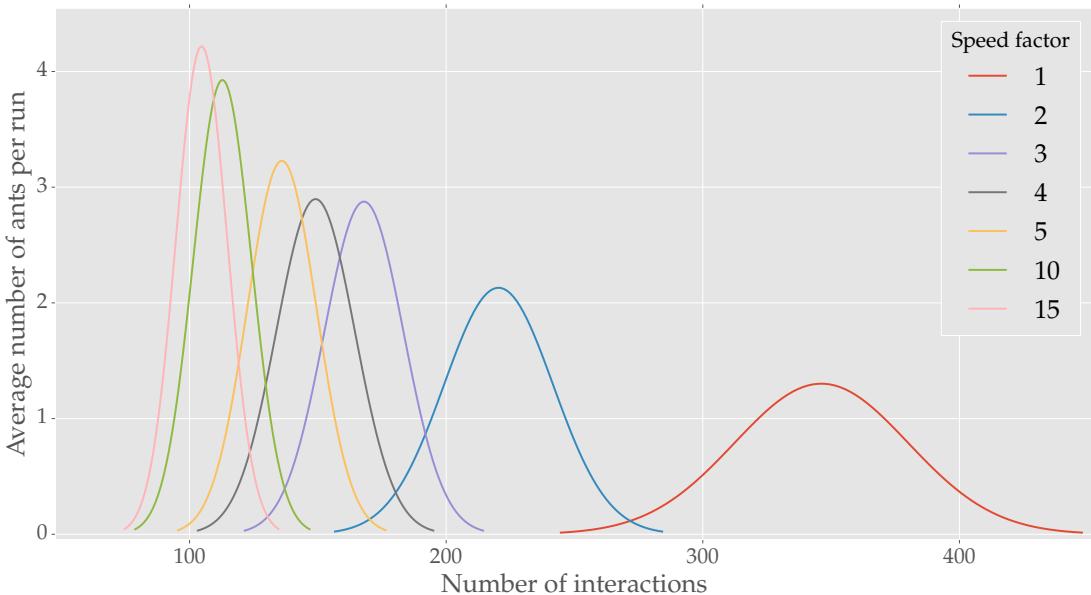


Figure A.20.: **Case Study II.** Plot of the Gaussian distributions fitted to the interaction histograms for different speed factors. For speed factors greater than 15, the distributions virtually look like the pink one in this plot.

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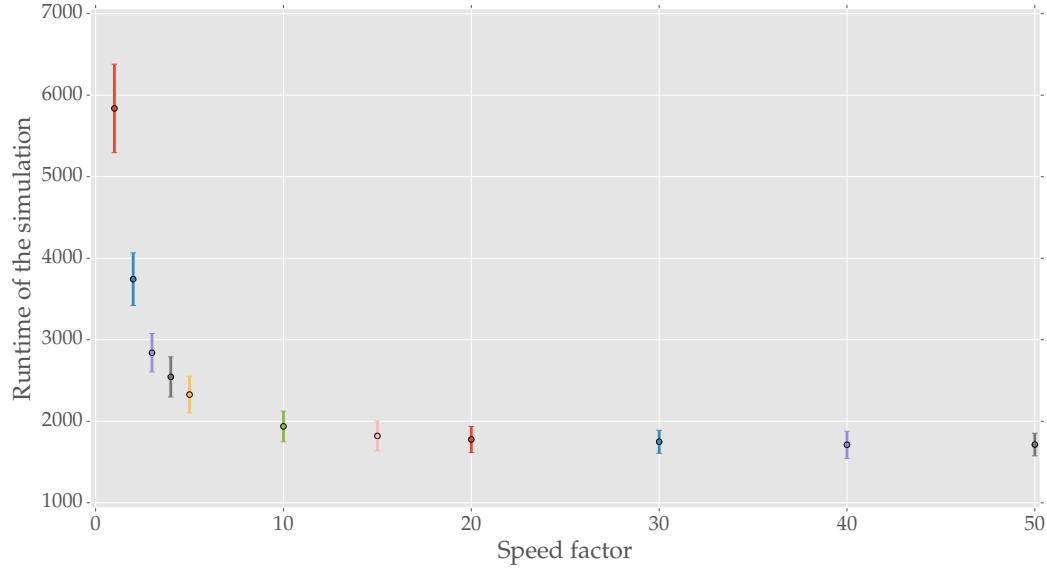


Figure A.21.: **Case Study II.** Plot of the average runtime of 100 runs of the simulation for different speed factors. The error bars give the standard deviation. In this case, the simulation stopped as soon as the food source was empty. There was enough food to completely fill 90% of the ants.

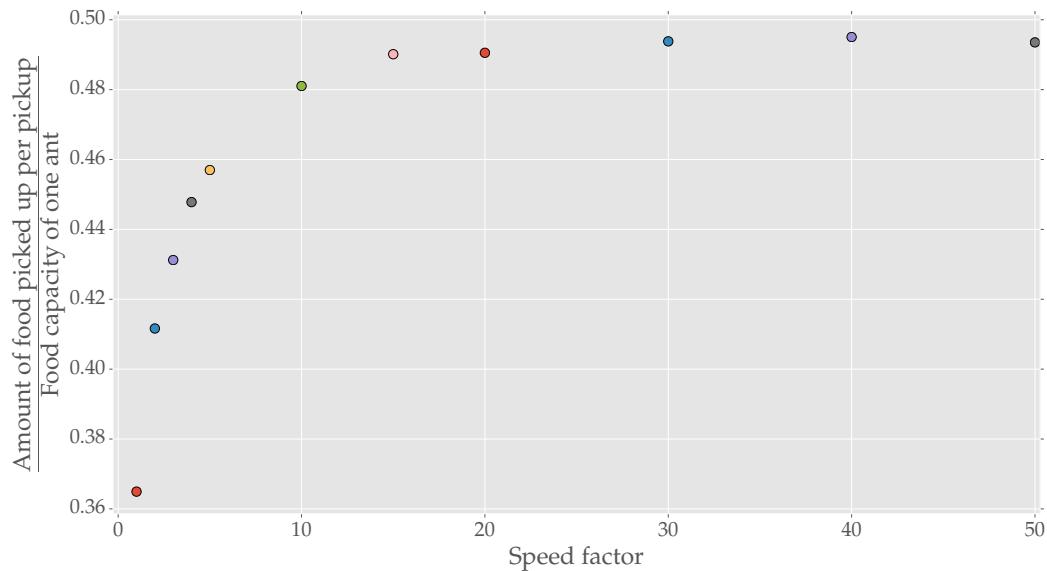


Figure A.22.: **Case Study II.** Plot of the average amount of food picked up from the food source per pickup of 100 runs of the simulation for different speed factors. The standard deviation is not shown in this plot because it is very large.

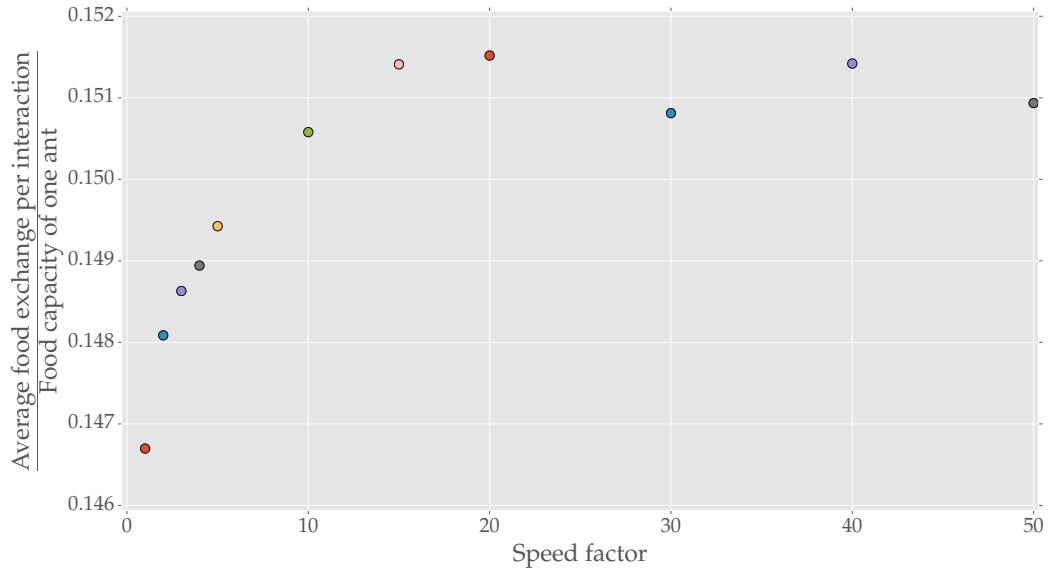


Figure A.23.: **Case Study II.** Plot of the average amount of food exchanged per trophallactic interaction of 100 runs of the simulation for different speed factors. The standard deviation is not shown in this plot because it is very large.

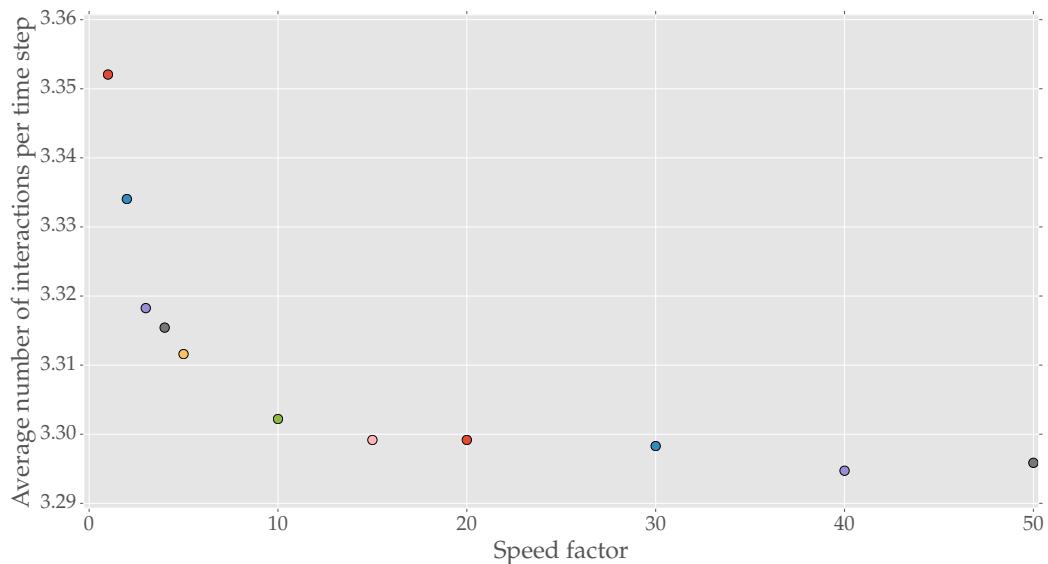


Figure A.24.: **Case Study II.** Plot of the average number of trophallactic interactions per time step of 100 runs of the simulation for different speed factors. The standard deviation is not shown in this plot because it is very large.

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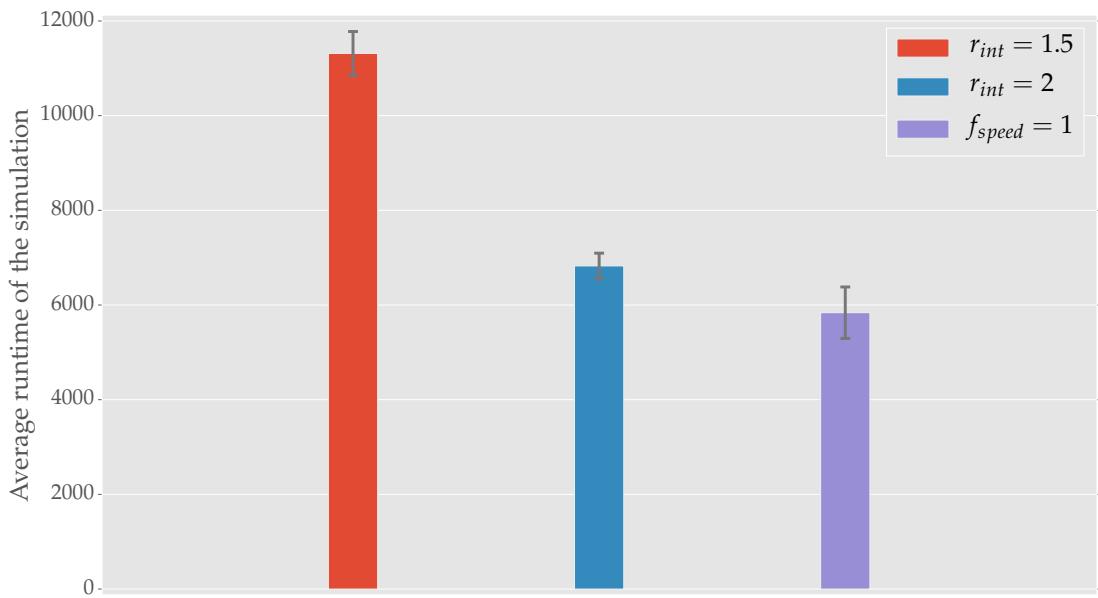


Figure A.25.: **Case Study III.** Bar chart of the average runtime of 100 runs of the simulation for two different interaction ranges r_{int} . The error bars give the standard deviation. The purple bar represents the 100 runs of case study II with a speed factor of $f_{speed} = 1$. In all three cases, the simulation stopped as soon as the food source was empty, and there was enough food to completely fill 90% of the ants.

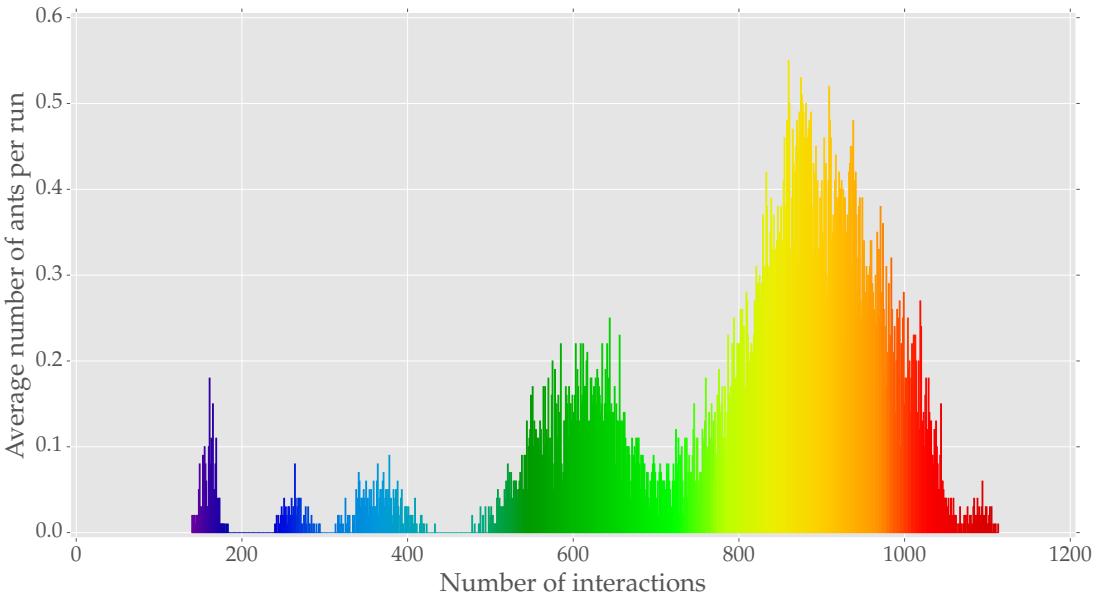


Figure A.26.: **Case Study III.** Interaction histogram for an interaction range of $r_{int} = 1.5$ and 100 runs of the simulation. In this case, the ants do not move and can only interact with their four nearest neighbors (except the ones close to the border of the grid). Figure A.27 shows the average spatial distribution of the interactions.

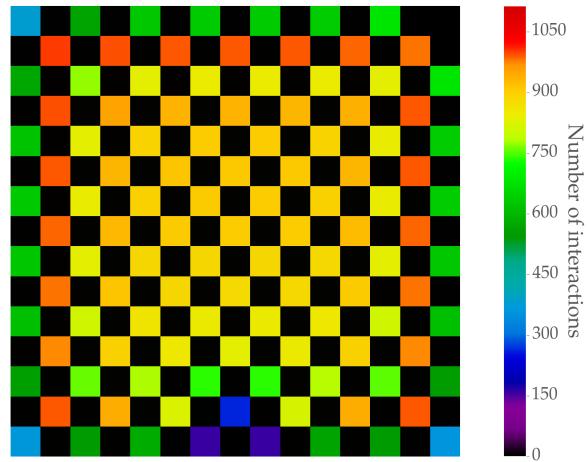


Figure A.27.: **Case Study III.** Visualization of the spatial distribution of the average number of trophallactic interactions of 100 runs of the simulation. Every colored square represents one ant. The food source is between the three blue ants at the bottom. The color coding is the same as in figure A.26.

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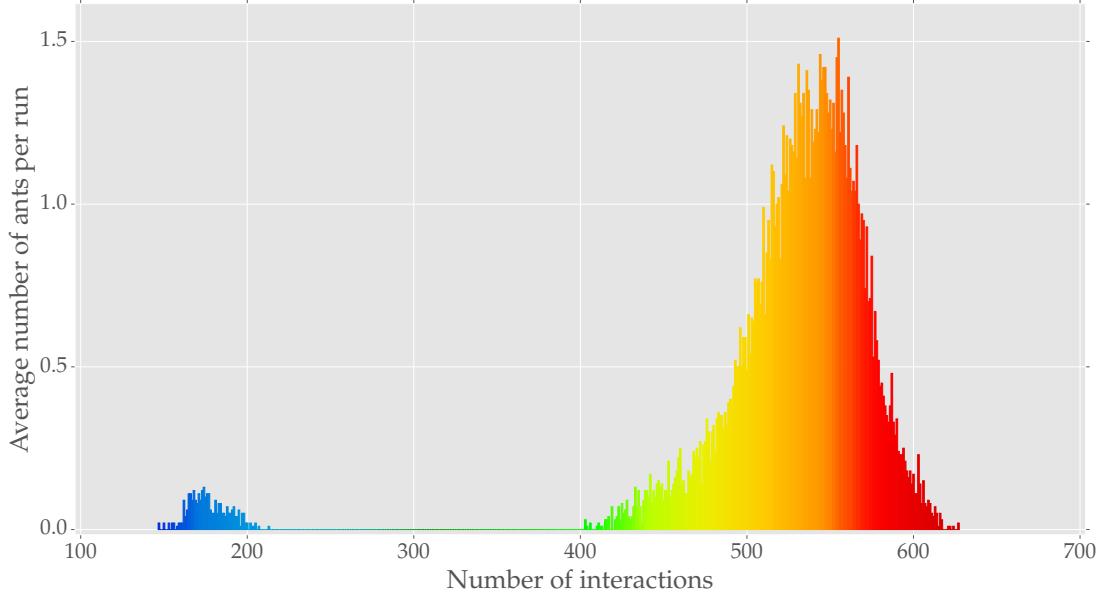


Figure A.28.: **Case Study III.** Interaction histogram for an interaction range of $r_{int} = 2$ and 100 runs of the simulation. In this case, the ants do not move and can only interact with their eight nearest neighbors (except the ones close to the border of the grid). Figure A.29 shows the average spatial distribution of the interactions.

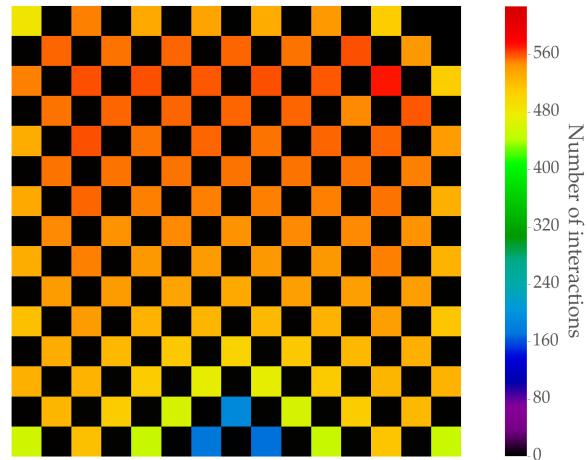


Figure A.29.: **Case Study III.** Visualization of the spatial distribution of the average number of trophallactic interactions of 100 runs of the simulation. Every colored square represents one ant. The food source is between the three blue ants at the bottom. The color coding is the same as in figure A.28.

Acknowledgments

I would like to thank the persons who have contributed to this thesis. I am very grateful to Dr. Eleni Katifori and Prof. Dr. Marc Timme for their advice on the topic of this thesis – also already many thanks in advance for examining and grading the past 50 pages. Furthermore, I am most indebted to Johannes Gräwer. Without his constant advice and his groundwork regarding the simulation, this thesis would not have been possible. To Pascal Weigmann, Martin Spiecker, and Holger Thyen finally, I owe my gratitude for their feedback on different versions of this thesis.

Bibliography

- [1] Tanya Y. Berger-Wolf and Jared Saia. “A framework for analysis of dynamic social networks”. In: *Proceedings of the 12th ACM SIGKDD International Conference on Knowledge Discovery and Data Mining*. ACM Press, 2006, p. 523. DOI: [10.1145/1150402.1150462](https://doi.org/10.1145/1150402.1150462).
- [2] Benjamin Blonder et al. “Temporal dynamics and network analysis”. In: *Methods in Ecology and Evolution* 3.6 (Dec. 2012), pp. 958–972. DOI: [10.1111/j.2041-210X.2012.00236.x](https://doi.org/10.1111/j.2041-210X.2012.00236.x).
- [3] Daniel Charbonneau, Benjamin Blonder, and Anna Dornhaus. “Social Insects: A Model System for Network Dynamics”. In: *Temporal Networks*. Ed. by Petter Holme and Jari Saramäki. Understanding Complex Systems. Springer, 2013, pp. 217–244. DOI: [10.1007/978-3-642-36461-7_11](https://doi.org/10.1007/978-3-642-36461-7_11).
- [4] Jennifer H. Fewell. “Social Insect Networks”. In: *Science* 301.5641 (Sept. 2003), pp. 1867–70. DOI: [10.1126/science.1088945](https://doi.org/10.1126/science.1088945).
- [5] Aric A. Hagberg, Daniel A. Schult, and Pieter J. Swart. “Exploring Network Structure, Dynamics, and Function using NetworkX”. In: *Proceedings of the 7th Python in Science Conference*. 2008, pp. 11–15. URL: <http://math.lanl.gov/~hagberg/Papers/hagberg-2008-exploring.pdf>.
- [6] Heiko Hamann and Heinz Worn. “A Space- and Time-Continuous Model of Self-Organizing Robot Swarms for Design Support”. In: *First International Conference on Self-Adaptive and Self-Organizing Systems*. Ieee, July 2007. DOI: [10.1109/SASO.2007.3](https://doi.org/10.1109/SASO.2007.3).
- [7] Petter Holme and Jari Saramäki. “Temporal Networks”. In: *Physics Reports* 519.3 (Oct. 2012), pp. 97–125. DOI: [10.1016/j.physrep.2012.03.001](https://doi.org/10.1016/j.physrep.2012.03.001).
- [8] John D. Hunter. “Matplotlib: A 2D Graphics Environment”. In: *Computing in Science & Engineering* 9.3 (2007), pp. 90–95. DOI: [10.1109/MCSE.2007.55](https://doi.org/10.1109/MCSE.2007.55).

Bibliography

- [9] Lauri Kovanen et al. “Temporal motifs in time-dependent networks”. In: *Journal of Statistical Mechanics: Theory and Experiment* 2011.11 (Nov. 2011), P11005. DOI: [10.1088/1742-5468/2011/11/P11005](https://doi.org/10.1088/1742-5468/2011/11/P11005).
- [10] Chris Melhuish and Masao Kubo. “Collective Energy Distribution: Maintaining the Energy Balance in Distributed Autonomous Robots using Trophallaxis”. In: *Distributed Autonomous Robotic System 6*. Springer Japan, 2007, pp. 275–284. DOI: [10.1007/978-4-431-35873-2_27](https://doi.org/10.1007/978-4-431-35873-2_27).
- [11] Danielle P. Mersch, Alessandro Crespi, and Laurent Keller. “Tracking individuals shows spatial fidelity is a key regulator of ant social organization.” In: *Science* 340.6136 (May 2013), pp. 1090–3. DOI: [10.1126/science.1234316](https://doi.org/10.1126/science.1234316).
- [12] Mark E. J. Newman. “The structure and function of complex networks”. In: *SIAM Review* 45.2 (2003), pp. 167–256. DOI: [10.1137/S003614450342480](https://doi.org/10.1137/S003614450342480).
- [13] Trung Dung Ngo and Henrik Schioler. “Randomized Robot Trophallaxis”. In: *Recent Advances in Multi-Robot Systems*. Ed. by Aleksandar Lazinica. InTech, May 2008. DOI: [10.5772/63](https://doi.org/10.5772/63).
- [14] Travis E. Oliphant. “Python for Scientific Computing”. In: *Computing in Science & Engineering* 9.3 (2007), pp. 10–20. DOI: [10.1109/MCSE.2007.58](https://doi.org/10.1109/MCSE.2007.58).
- [15] Noa Pinter-Wollman et al. “The effect of individual variation on the structure and function of interaction networks in harvester ants.” In: *Journal of the Royal Society Interface* 8.64 (Nov. 2011), pp. 1562–73. DOI: [10.1098/rsif.2011.0059](https://doi.org/10.1098/rsif.2011.0059).
- [16] T. Schmickl and K. Crailsheim. “Trophallaxis among swarm-robots: A biologically inspired strategy for swarm robotics”. In: *The First IEEE/RAS-EMBS International Conference on Biomedical Robotics and Biomechatronics*. Ieee, 2006, pp. 377–382. DOI: [10.1109/BIOROB.2006.1639116](https://doi.org/10.1109/BIOROB.2006.1639116).
- [17] C. Tantipathananandh, T. Berger-Wolf, and D. Kempe. “A framework for community identification in dynamic social networks”. In: *Proceedings of the 13th ACM SIGKDD International Conference on Knowledge Discovery and Data Mining*. ACM Press, 2007, p. 717. DOI: [10.1145/1281192.1281269](https://doi.org/10.1145/1281192.1281269).
- [18] Stéfan van der Walt, S. Chris Colbert, and Gaël Varoquaux. “The NumPy Array: A Structure for Efficient Numerical Computation”. In: *Computing in Science & Engineering* 13.2 (2011), pp. 22–30. DOI: [10.1109/MCSE.2011.37](https://doi.org/10.1109/MCSE.2011.37).

Bibliography

- [19] Pei Wang, Jinhu Lü, and Xinghuo Yu. “Identification of Important Nodes in Directed Biological Networks: A Network Motif Approach.” In: *PloS ONE* 9.8 (Jan. 2014), e106132. DOI: [10.1371/journal.pone.0106132](https://doi.org/10.1371/journal.pone.0106132).
- [20] James S. Waters and Jennifer H. Fewell. “Information Processing in Social Insect Networks.” In: *PloS ONE* 7.7 (Jan. 2012), e40337. DOI: [10.1371/journal.pone.0040337](https://doi.org/10.1371/journal.pone.0040337).
- [21] Eric W. Weisstein. *Mean Square Displacement*. URL: <http://mathworld.wolfram.com/MeanSquareDisplacement.html> (visited on 06/22/2015).
- [22] Tom Wenseleers. “The Superorganism Revisited”. In: *BioScience* 59.8 (Sept. 2009), pp. 702–705. DOI: [10.1525/bio.2009.59.8.12](https://doi.org/10.1525/bio.2009.59.8.12).

Erklärung nach §13(8) der Prüfungsordnung für den Bachelor-Studiengang Physik und den Master-Studiengang Physik an der Universität Göttingen:

Hiermit erkläre ich, dass ich diese Abschlussarbeit selbstständig verfasst habe, keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe und alle Stellen, die wörtlich oder sinngemäß aus veröffentlichten Schriften entnommen wurden, als solche kenntlich gemacht habe.

Darüberhinaus erkläre ich, dass diese Abschlussarbeit nicht, auch nicht auszugsweise, im Rahmen einer nichtbestandenen Prüfung an dieser oder einer anderen Hochschule eingereicht wurde.

Göttingen, den 6. Juli 2015

(Fabian Steuer)