# Design and analysis of trophallaxis network in honey bees*

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**Abstract.** Trophallaxis is the process of transferring fluids via mouth-to-mouth interactions among nestmates within the honey bee societies. This creates a network of interactions linking almost every member of the colony. In this work, we designed a temporal network to investigate how these interactions evolve over time and comparing the network statistics measures such as mean degree, clustering coefficient, diameter, etc. across discrete time windows. The results of our analysis suggest that honey bee food exchange interaction network show very similar properties to the *small world* networks with shrinking diameters and power law degree distribution, leading to a few dominant hubs with very high degree. We also used *SI* model to create cascades of food flow and measure their size relative to the size of the network. We found that cascades initiated by highly central bees can cover up to 96% of the food spread among the network.

**Keywords:** trophallaxis · temporal networks · honey bees.

## 1 Introduction

Cooperation and division of labor are the hallmarks of eusocial insect societies such as those of bees, wasps, ants and termites. Despite the apparent simplicity of their individual members and the absence of central control, insect societies as a whole exhibit a surprising degree of complexity and can perform complicated tasks such as foraging, food dissemination, brood and nest care that would be impossible for a single individual [5]. Trophallaxis, the direct transfer of liquid food among nest mates, is considered one of the most central features of eusociality in insects. In particular, these trophallactic interactions in honey bees serve not only as a feeding mechanism but also as a medium for information exchange and mediating the uniform scent within the whole colony[2].

Network science has provided a wealth of insights about how interaction patterns impact coordination, information exchange, and disease transmission in animal societies [3]. In this work, we use the idea of temporal networks to model the connection between individuals linked by the trophallaxis event. Temporal networks seem to be a suitable model for our system since they account for the fact that this network grows as time passes and the edges are not continuously

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active and can appear/disappear in time. We use the simple *SI* model to demonstrate the dynamics of food flow within the honey bee colony and find central cascades of food spread in the network. We also look at individual interactions as they appear and how this emergent network evolves over discrete time windows. We believe that beyond its importance for understanding distributed processes in a biological context, it can provide intuition for engineering applications, such as information or electrical power sharing in swarms of search and rescue robots [4].

All of our analysis is done on the data from a recent experimental study on trophallaxis interactions in honey bees *(Apis mellifera)* in [1]. The motivation for this work is to shed some light on the dynamics of food flow and looking at how the honey bee food exchange interaction network evolves over time. More specifically, the questions that we are asking are:

- Can we find central individuals in the network that are initiators of the most central cascades of food flow in the network?
- How long do the connections between individuals last on average?
- How is the structure of the network changing over time?
- How stable are the local neighborhood around each individual honey bee?

The dataset we are looking at, contains the data from monitoring five honeybee colonies for over 8 to 11 day each[1]. Barcoded honeybees were imaged once per second by a computer-controlled high-resolution camera under infrared light. A trophallaxis detector was used to capture every food exchange encounter that occurred between two individual honey bees along with the data about the begin and end time of those events. For simplicity, we only used the data from the first trial in this analysis. Fig. 1, shows the frequency of the trophallaxis encounters at each day in the first trial.

## 2 Network Design

Using this data of all the food exchange encounters in the first trial, we constructed a weighted (because transfer duration is positively correlated to transfer amount), undirected network. Each honeybee observed participating in an interaction corresponds to a node our network. Edges exist between bees at the time they exchange food and they last for the total duration of interaction between them which is reflected in the weights. Since the same pair can exchange food multiple times within a course of one trial, we keep a list of weights containing the duration of every food transfer event for each edge. In order to keep the order of the interactions, we also save the starting time for each interaction.

Therefore, this network can be described as a graph $G$ defined in Eq.(1). Note

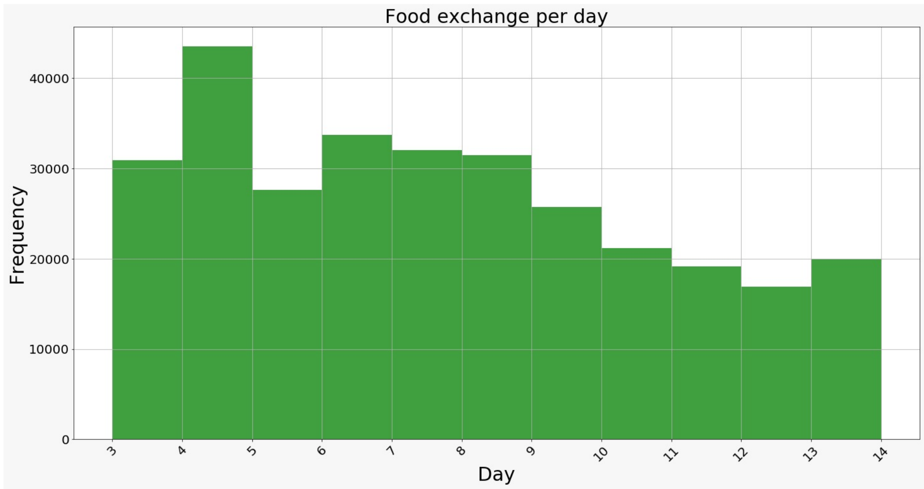


**Fig. 1.** Frequency of the food exchange events per day during the first trial. The numbers on the horizontal axis show the date of the experiment during July 3rd-14th, 2013.

that, $id_1$ and $id_2$ identify the pair of bees that exchanged food, and $t_s$ denotes the starting time and $\delta t$ shows the interaction duration. It has been previously shown that the duration of the food exchange is directly proportional to the amount of food being exchanged [6] so for the rest of this report we will use the $\delta t$ to measure both the quantity and duration of the food transfer.

$$G = (id_1, id_2, t_s, \delta t) \tag{1}$$

## 3 Static Network Analysis

Putting together all of our data from trail 1 and looking at the snapshot of the network at the end of the first trial we got a relatively large sized graph with 1164 nodes and 200723 edges which corresponds to the number of recorded trophallaxis events over a course of 8 days in trial 1. This graph has a mean degree of around 345. The degree histogram of the distribution of degrees is shown in Fig. 2. Not much can be deferred from the degree distribution histogram other than most edges have degree values that are close to the mean degree and there are only few nodes with very high or very low degree values, suggesting bursty interactions as discussed in [1]. This can probably indicate that there are no substantial differences between worker bees in a colony as they are mostly equally active over the course of a few days in a single trial. we suspect that the bees with very small degree may be the individuals who died in a first few hours or days of the trial and were removed from the rest of the dataset.

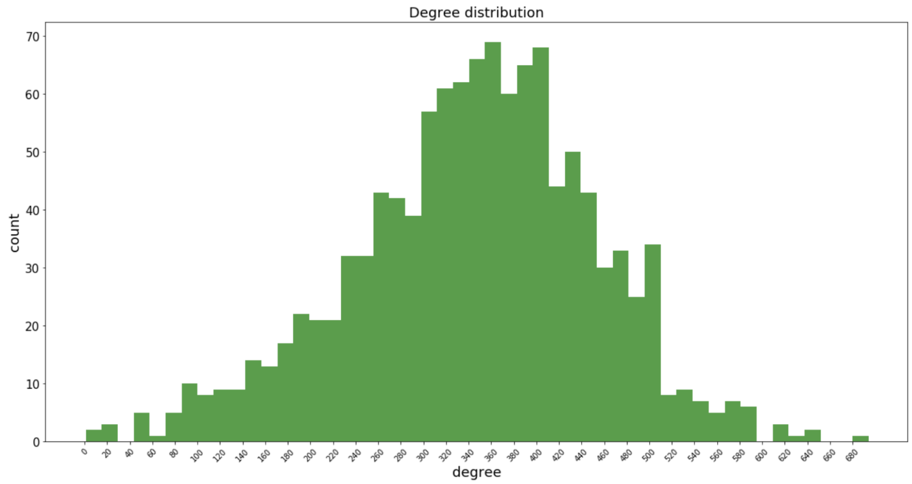


**Fig. 2.** Histogram of the distribution of degrees for the first trial.

### 3.1 Centrality measures

Considering the data for the first trial, we calculated the degree centrality for individuals to identify the most central bees in our network. Table 1 shows the IDs of ten most central nodes in the network. This gives us a good estimate of how influential individuals can be. Higher values of degree centrality means that the corresponding bees are more likely to be involved in a food exchange over the course of the one trial.

In the next step, we decided to narrow down our window of observation to a single day and see if we can get more meaningful results from the centrality values. Fig. 3 shows the values for different measures of centrality calculated

**Table 1.** Nodes with highest degree centrality in all the data from trial 1.

| Node ID | Degree centrality |
|---|---|
| 347 | 0.471195184866724 |
| 332 | 0.470335339638865 |
| 246 | 0.453138435081685 |
| 258 | 0.434221840068787 |
| 262 | 0.425623387790197 |
| 267 | 0.404127257093723 |
| 201 | 0.402407566638005 |
| 335 | 0.398108340498710 |
| 288 | 0.397248495270851 |
| 422 | 0.397248495270851 |

over on the first day of the trial. In particular, eigenvector centrality which is a measure of the influence of a node in a network, is important to consider since it depends both on the number of neighbors of each node and the quality of its connections. It is also interesting to note that a few nodes with higher degree centrality show up on the higher ranks of eigenvector and betweenness centrality. This means that we can probably count on these measures to identify the most influential bees on a single day. However, looking only at the centrality values did not give us much information about the level of impact of these individuals within the network. That is why we decided to investigate the influence of the central bees by looking at the size of the cascades of food flow that they can initiate.

| Node ID | Eigenvector centrality |
|---|---|
| 1543 | 0.05618453430802222 |
| 1671 | 0.05164176520413892 |
| 1667 | 0.05144925765525813 |
| 959 | 0.050313277801118855 |
| 880 | 0.0495667425137899 |
| 918 | 0.049318720359761224 |
| 1484 | 0.04902690738055804 |
| 1764 | 0.04762525909631127 |
| 1484 | 0.04751409496694564 |

| Node ID | Degree centrality |
|---|---|
| 1642 | 0.15676141257536608 |
| 1667 | 0.1429801894918174 |
| 1999 | 0.13522825150732126 |
| 705 | 0.1343669250645995 |
| 262 | 0.1335055986218777 |
| 1543 | 0.12747631352282515 |
| 1671 | 0.12489233419465978 |
| 475 | 0.1223083548664944 |
| 283 | 0.11714039621016366 |

| Node ID | Betweenness centrality |
|---|---|
| 1642 | 0.007389821896953813 |
| 1667 | 0.005829364036614243 |
| 705 | 0.005051178844151836 |
| 1999 | 0.004776908493432097 |
| 1129 | 0.004151343331142971 |
| 1543 | 0.0039876819858099405 |
| 283 | 0.0037146821868888715 |
| 475 | 0.0037105430792010352 |
| 945 | 0.0036257315564805093 |

**Fig. 3.** Centrality measures calculated for the first day of trial1. The number in red highlights an instance of an individual that shows up at high ranks of all centrality measure.

### 3.2 Food Flow Cascades

To figure out the impact of these central bees on the overall food exchange happening in the network we use a simple *SI* model in which donor bees are analogous to infected nodes and the food receiving bees are analogous to susceptible nodes in the network. We assume only one infected(donor) bee is initiating each cascade. Other bee's status can change from susceptible to infected as soon as they engage in one food exchange encounter. The newly infected bees can then spread the food within their own neighbors using the same mechanism. We measure the size of the cascades initiated by a few of the central bees that we identified in the previous section. Table 2 shows the results of the contribution of each cascade to the overall food transfer throughout the whole network on a single day. As is clear from the high percentage of food transferred, we can safely conclude that central bees can initiate very large cascades of food flow which can eventually cover a major portion of the entire food transfer in the network.

**Table 2.** Contribution of each central cascade to the overall food exchange during one day.

| Node ID | Percentage of food transferred |
|---|---|
| 1543 | 95.56% |
| 1667 | 96.4% |
| 1671 | 96.4% |
| 1484 | 96.6% |
| 959 | 96.5% |
| 880 | 96.5% |
| 918 | 96.5% |

## 4 Dynamic Network Analysis

As stated earlier, we designed our interaction network as a temporal network where edges can appear/disappear in time. In this section we are looking at the evolution of the network and how the edges form over time. This would give us a more clear idea of the dynamics of the food exchange and how this collective and efficient food distribution emerge as a result of individual interactions. We will explain our approach to answer each of the questions mentioned earlier, in this section.

**How long do the edges last?** To get an idea of how frequent are the changes happening in our network, we asked the question of how long do the connections last? It is interesting to note that the answer to this question can also provide insights about the average amount of food that is being exchanged in the network (since transfer duration is proportional to transfer amount). To answer this, we basically measured the durations by calculating the $Pr(\langle k \rangle)$ for each mean degree $\langle k \rangle$ value. The *ccdf* for that is shown in Fig. 4. We can see that the shape of the complementary cumulative distribution function is clearly a power law. For the most part, we can say that the longer the edges last, the lower the probability of them being formed within the network but there are also very few nodes with a very high degree on the tail. We can probably conclude that most bees prefer shorter interactions in which they only transfer small amounts of food. The average time that edges last is 40.124 seconds.

Different colors in that plot is related to our attempt to reduce the less influential edges with very small amounts of food transfer and focus more on the more effective edges which carry higher weights. So, we basically set a threshold value which is our tolerance limit for food transfer at each interaction. We discarded anything less than that threshold value from the weight list of that interaction. The blue line in the graph where the threshold is zero shows the probabilities for all the the data, without any edge elimination. For the values of threshold equal to 3 or 6, we discarded the edges with weights less than 3 or 6 respectively. As we start making changes to the graph and discarding the edges with lower weights the probability of having edges will typically increase but the overall shape of the distribution stays almost the same.

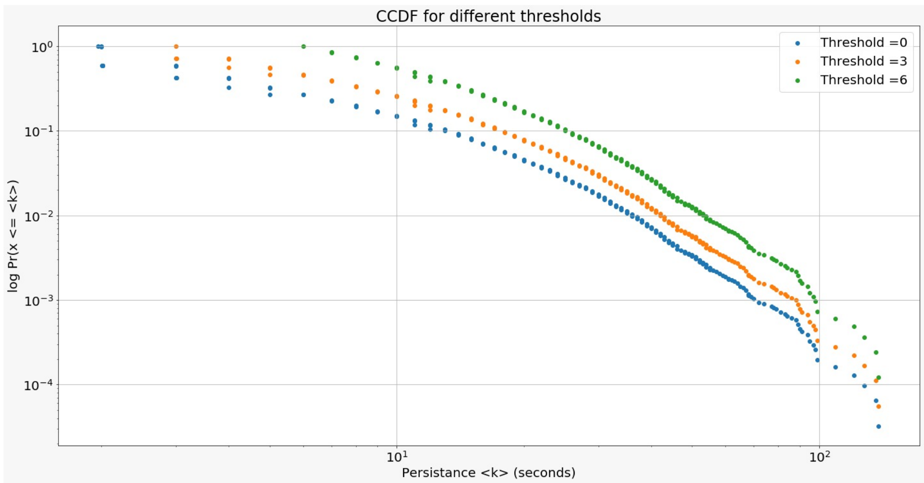


**Fig. 4.** complementary cumulative distribution function calculated for the fist day of trial1.

**How does the structure of the network vary over time?** To answer this question, we assume discrete time windows and calculated the mean degree of the network for each time window, over a single day and plotted the results in 5 which shows how the mean degree of the network changes as we vary the aggregation time. The three different time windows that we used are 15-minutes, 30-minutes and 60-minutes. Overall, we see very small fluctuations in the mean degree over a course of a day (note the very small range of values in the vertical axis). This can be confirmed by looking at how mean degree changes over every hour window, which is almost stable. However, the smaller time windows did show more fluctuations (noise) and provide more details about the nature of interactions especially on the 5-minute window. Note that the sampling time in our dataset starts at 5am, everyday and it ends at around 11pm (which is shown as 23 in the horizontal axis in the plot).

We also looked at the change in the mean degree, clusterring coefficient, assortitivity, and the communities for all of the data in trial 1, using only one hour aggregation time window to see how the network statistics evolve over time. The results are shown in Fig. 6(a-d). As was expected, the mean degree and the clustering coefficient are constantly and almost linearly increasing and there is not much difference in the trend of growth between the different days, at least not at the scale of an hour aggregation time. What we didn't expect to see was very small values of clustering coefficients which normally suggest the

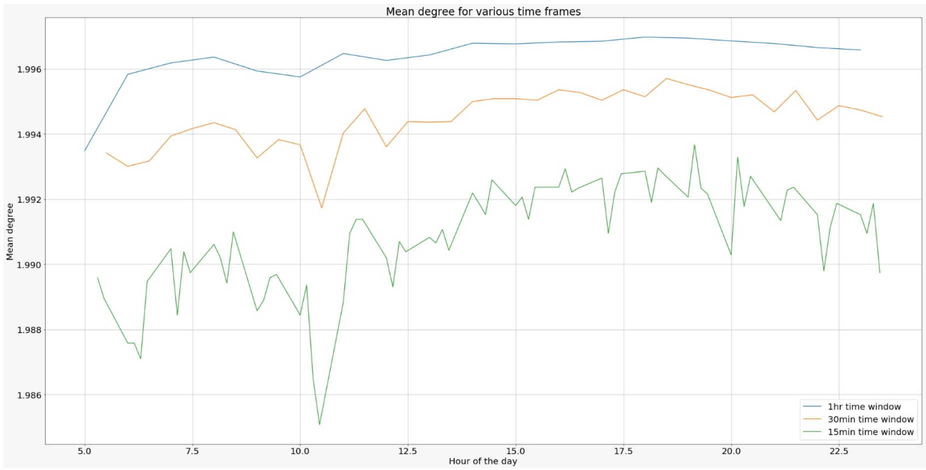


**Fig. 5.** Changes in the mean degree of the network with different aggregation times. Three different time windows are used: 15-minutes, 30-minutes and 60-minutes. The mean degree for each window is shown in different colors.

presence of many isolated or loosely connected nodes in the network. Fig. 6(c) shows the changes in the assortitivity coefficient of the network as we add more edges using the same one-hour aggregation window. Generally, the assortitivity coefficients are very low, starting from a maximum value of 0.12 on the second day which slowly decrease as the network grows suggesting very small correlation between the nodes in the network. However, what is interesting is that as the network evolves, over a course of a day, we can see that all the assortitivity curves will converge to a value close to zero which indicates no correlation between the nodes. In other words, this plot clearly shows that there are almost no preferences for the individual bees to attach to other similar ones which can be due to less variability among the individuals within a honey bee colony. This is very different behavior compare to human's social network where people mostly prefer to connect to the other similar people in their own social group. Fig. 6(d) demonstrates how the number of communities decreases almost drastically as the network evolves and more edges appear in the network. It is again interesting to note that although different numbers of communities are detected in the early hours of each day (starting from 22 to more than 50 distinct communities during the first hours) but the number of communities detected in the network at the end of every day will decrease and converge to about 3 to 5 communities at the end of the day.

Another interesting observation came from plotting the trend of change in the diameter as the network evolves with the same one-hour aggregation window, which is shown in Fig. 7. As it is true for most of the social networks, the diameter of the trophallaxis network also shrinks drastically as the network evolves. It's also worth noting that at some point, the diameter values stay

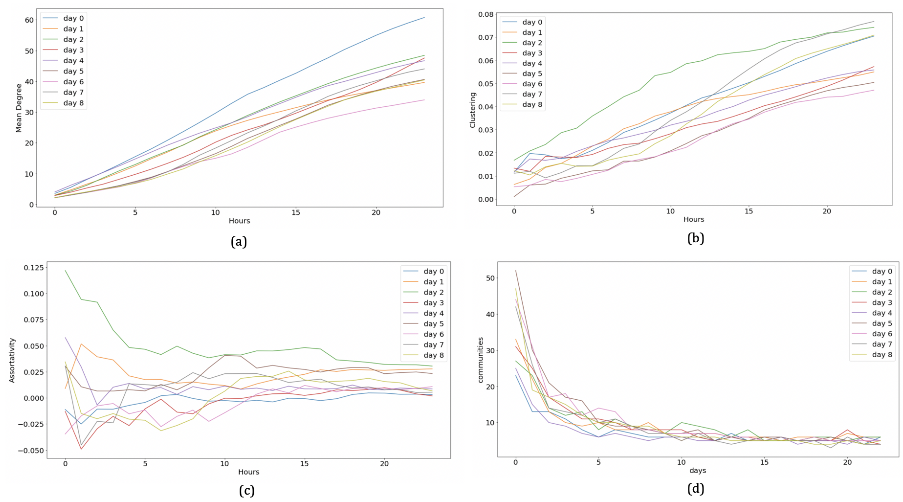


**Fig. 6.** Changes over one-hour aggregation windows for the (a) mean degree, (b) clusterring coefficient, (c) assortitivity, and (d) communities of the network for all the days in trial 1.

constant at a pretty small value for more than 10 hours during the day and finally decreases even more during the last few hours of the day. This trend of change is almost consistent among all the other days of this trial. The change in the diameter values shows that this network can be categorized within the *small world* networks, which mostly end up having very small diameters in the order of $log(n)$, where $n$ is the number of the nodes in the network. If you follow the line plot in Fig. 7, you can see that by the end of the day, the diameter of this network converges to a value of $log(n) = log(1164) = 3.06$.

**How stable are the local neighborhood around each node?** This can be related to a very important question in understanding honey bee behavior which is that, do honey bees have preferences (fidelity zones) for choosing who to share their food with or is it just a result of random interactions? We already know that many other social insects such as ants do have fidelity zones and more central donors in the nest, do not move that much [7], and we are curious to investigate the presence of any similar behavior in honey bees. So, we basically want to know how similar are a random node's neighbors at different points in time? We measure the adjacency correlation for a random node over one hour windows time scale to check how similar are a bee's neighbors at each hour over the course of a single day. We use the adjacency correlation function, described in Eq.(2), to calculate this value for every bee in the network at two consecutive hours time windows during the one single day.

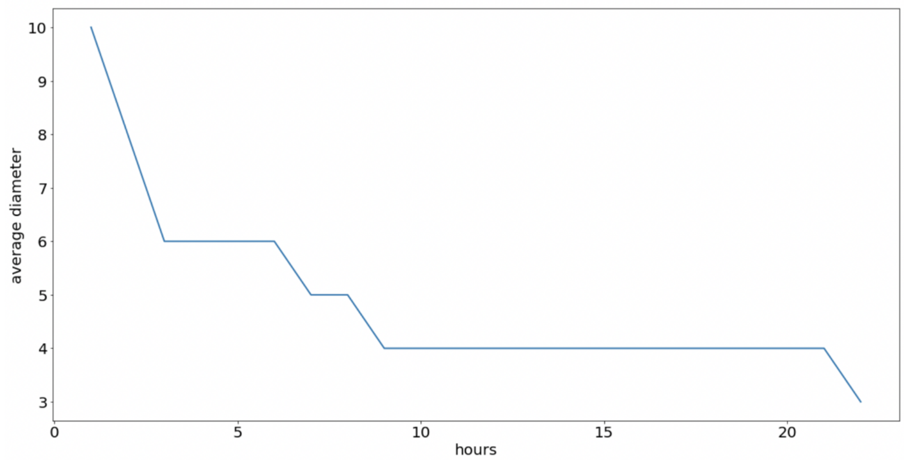


**Fig. 7.** Tracking changes in the diameter of the network for a single day over one-hour aggregation windows.

$$\gamma_j = \frac{\sum_{i \in N(j)} A_{ij}^{(x)} A_{ij}^{(y)}}{\sqrt{\sum_{i \in N(j)^{(x)}} \sum_{i \in N(j)^{(y)}}}} \tag{2}$$

We looked at every consecutive hour within a day and measure the similarities in the neighborhood of all of the bees in the increments of an hour. Table 3 shows the results of those adjacency correlation values that we got for all of the bees during the first day of trial1.

The mean value of the adjacency correlation among all honey bees is $\langle \gamma_j \rangle = 0.24$ which shows there is on average a small overlap in interactions meaning that there is a small similarity between the neighbors of each bee from one window to the next. In other words, every bee is likely to interact with one same neighbor out of four during two consecutive hours. This implies that bees does not show specific interest in exchanging food with the same neighbors set at least not within an hour window aggregation time. Therefore, we can not confidently conclude if bees are just randomly walking around and choosing their exchange partner or they have specific zones of movement. We can confirm these results once we got access to the complete dataset which has the information about the x-y coordinates of the bees at each encounter.

## 5 Conclusion and Future work

We design and briefly analyze a temporal network of food exchange interactions in honey bees. We look at how the food spreads throughout the network by ap-

**Table 3.** Adjacency correlation values for all of the nodes in the network in trial 1 over consecutive one-hours time windows.

| Time window | Adjacency Correlations |
|---|---|
| 5am - 6am | 0.0957 |
| 6am - 7am | 0.2070 |
| 7am - 8am | 0.2783 |
| 8am - 9am | 0.1200 |
| 9am - 10am | 0.1393 |
| 10am - 11am | 0.1503 |
| 11am - 12pm | 0.2105 |
| 12pm - 1pm | 0.0345 |
| 1pm - 2pm | 0.1077 |
| 2pm - 3pm | 0.0818 |
| 3pm - 4pm | 0.3086 |
| 4pm - 5pm | 0.2537 |
| 5pm - 6pm | 0.1693 |
| 6pm - 7pm | 0.2248 |
| 7pm - 8pm | 0.2493 |
| 8pm - 9pm | 0.0569 |
| 9pm - 10pm | 0.0576 |

plying a simple *SI* model and measured the size of the largest cascades of food flow. We find that cascades that are initiated by more central bees can cover up to 96% of the food flow within the network. We also look at how the interactions evolve in time by applying various aggregation time windows and compare the resolution of the changes within different time scales. We find that the social network of honey bees represent some similar properties to *small world* networks such as power-law degree distribution and shrinking diameters.

We couldn't complete our analysis of the temporal network due to time constraints but we are very interested in completing this phase of analyzing the evolution of the network over various aggregation windows and also moving forward to compare the food exchange network with a random temporal generative model such as Forest Fire (FF) and investigate their differences and similarities in more detail. We are also interested in using different methods of measuring the temporal reachability of the network in both the directed and undirected version of the model.

**Data and code:** https://github.com/rc1208/Bees-food-network-analysis

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