

Ant Scattering: Evaluating Aggregation and Consensus Post Physical Decentralization  
in *Temnothorax rugatulus* ant colonies

by

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## ABSTRACT

Aggregation is a fundamental principle of animal behavior; it is especially significant to highly social species, like ants. Ants typically aggregate their workers and brood in a central nest, potentially due to advantages in colony defense and regulation of the environment. In many ant species, when a colony must abandon its nest, it can effectively reach consensus on a new home. Ants of the genus *Temnothorax* have become a model for this collective decision-making process, and for decentralized cognition more broadly. Previous studies examine emigration by well-aggregated colonies, but can these ants also reach consensus when the colony has been scattered? Such scattering may readily occur in nature if the nest is disturbed by natural or man-made disasters. In this exploratory study, *Temnothorax rugatulus* colonies were randomly scattered in an arena and presented with a binary equal choice of nest sites. Findings concluded that the colonies were able to re-coalesce, however consensus is more difficult than for aggregated colonies and involved an additional primary phase of multiple temporary aggregations eventually yielding to reunification. The maximum percent of colony utilization for these aggregates was reached within the first hour, after which point, consensus tended to rise as aggregation decreased. Small, but frequent, aggregates formed within the first twenty minutes and remained and dissolved to the nest by varying processes. Each colony included a clump containing the queen, with the majority of aggregates containing at least one brood item. These findings provide additional insight to house-hunting experiments in more naturally challenging circumstances, as well as aggregation within *Temnothorax* colonies.

## ACKNOWLEDGMENTS

I could write an entire second manuscript on all of those who have helped me along the way, and for that I am eternally grateful. I want to call specific thanks to my mentor, Dr. Zachary Shaffer, who taught me everything I know about how to be a biologist, conduct research, and most importantly, how to look at all aspects of life with a scientific curiosity and a thirst for knowledge. His guidance has truly shaped me not only as a scientist, but as a person.

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## CHAPTER 1

### INTRODUCTION

Insects are often used as a model for complex systems, namely for their integration of eusocial societies and collective and swarm behavior (Berman, et al, 2007; Brutschy, et al., 2008; Hsieh, et al, 2008; Hunt, 2005; Pratt & Sumpter, 2006). The ability of social insects to solve complex challenges using decentralized cognition has inspired parallel research in multiple fields, such as robotics and sociology (Melhuish, et al., 2005; Parker & Zhang, 2011; Reinhart, 1980; Rodgers, 2008; Soliman, et al., 2021; Werber, 2015). Their ability to solve these problems without the presence of a well-informed leader is dependent upon the group of individuals adhering to the known rules and communication methods by which the colony functions. The use of these behavioral algorithms allows them to form adaptive solutions to maintain homeostasis in changing environments. The question surrounding these complex systems in the majority of these studies, regardless of the field, is 'what are the individual rules by which this process functions?'

The rules which allow *Temnothorax rugatulus* ants to emigrate into new nest sites are generally well understood and used as a model for decentralized cognition. The findings of these emigration experiments typically involve two primary stages. The first stage consists of scouting by approximately 1/3 of the colony, using tandem runs to recruit more workers. The ability to form a consensus and trigger the second stage of mass movement to the new nest site is dependent upon their quorum-sensing ability. Once the scouting ant observes a minimum amount of nest-mates within the nest site, she switches from tandem runs to transports. This commitment and change within the recruitment process, allows for the remaining ants to be brought to the new nest site at a rate nearly three times faster than the beginning scouting process. Through this process, a colony of hundreds of ants is able to form a collective decision without each individual needing to visit each possible site. Instead, this method allows ants to account for their own individual assessment of nest site quality as well as its other nest-mates' assessment. As opposed to a well-informed leader solving this task, the colony must follow a general set of rules to use their collective intelligence for selection of a new nest site. This collective decision is made possible by the competition of efforts as ants follow behavioral rules based on quality-dependent

recruitment and the quorum rule. This process is adaptive and ants are able to slightly alter these rules collectively in response to changes in the environment. For example, in high duress conditions that require a swifter movement to a new nest site, ants are able to increase recruitment effort, and lower the threshold for accepting a new site and sensing a quorum. This allows them to facilitate a quicker, though less accurate, move to a nest site when nature requires (Mallon, et al, 2001; Möglich, 1978; Pratt, 2010; Pratt, et al., 2002; Pratt & Sumpter, 2006; Richardson, et. al., 2007; Sasaki, et al., 2015). These house-hunting emigration experiments are well studied and understood in *Temnothorax* ants. However, all previous house-hunting experiments have kept colonies relatively intact, some even allowing access to the original nest site. This may sometimes vary from the reality of nature where nests are often destroyed by natural disasters or human interference; in these cases, assuming access to an old nest or an intact colony is unlikely in many circumstances.

Presenting ants with more naturally challenging circumstances may provide a change in the behavioral algorithms *Temnothorax rugatulus* ants are known to follow in emigrations. When scattering the colony so that it is decentralized and without access to its original nest site, these additional circumstances may be accounted for. Thus, an additional process in the house hunting experiment is observed in the temporary aggregations forming outside of potential nest sites. Aggregation is a common phenomenon in animal societies with many publications across the animal behavior community. The final aggregations ant colonies are known to form in nest sites are often cited and studied as a leading example of aggregation (Cavil, et al., 1979; Depickère, et al., 2004). However, a lesser studied aspect of aggregation in ants are the temporary aggregates formed prior to the final selection of a nest site. Many potential causes have been theorized for aggregation in general, namely, protection, mating, individual resting-times, resource utilization, and thermoregulation (Allee, 1931; Deneubourg, et al., 2002; Graves & Duvall, 1987; Jermacz, et al, 2017; Khan, et al., 2010; Swartzman, 1991). Collective decisions are thought to be a byproduct of the rules and mechanisms involved within aggregation (Deneubourg, et al., 2002). In addition, aggregations are known to form as a reaction to changes in an organism's physical environment, thus it is logical that aggregates form in these higher duress conditions that involve

a complete lack of normalcy, including connection to the colony (Allele, 1931). This is, in fact, seen when colonies of *Temnothorax rugatulus* are scattered and without access to their original nest site. Almost immediately following scatter, multiple temporary aggregates are seen forming throughout the arena. These aggregates form prior to a quorum and appear to dwindle as consensus is reached.

Our experiment sought to observe consensus formation in scattered colonies of *Temnothorax rugatulus*, while focusing particularly on the potential role and characteristics of temporary aggregations in this process. This aggregation has been previously under-studied and lacks significant publication in *Temnothorax rugatulus* colonies. Accounting for aggregation has implications for broadening understanding of house-hunting processes in eusocial insects and in developing models for fields, such as robotics, that have a more accurate reference to this biologic phenomenon.

In order to conduct this exploratory study, *Temnothorax rugatulus* colonies were scattered in an arena with a binary equal choice of nest sites. The aim of this study was to provide a descriptive overview of this phenomenon to better understand how *Temnothorax* ants use aggregation to recover from physical decentralization, via scattering, and eventually reach a consensus decision on a nest site. Specific focus was placed on the relationship of aggregation with consensus, location of aggregates, and the frequency, composition, and lifespan of these temporary aggregations.



## CHAPTER 2

### METHODS

#### Subjects

Colonies of the ant, *Temnothorax rugatulus*, were collected from rock crevices on December 2021 and February 2022 on Mount Lemmon in Tucson, Arizona at the following coordinates, 32°23'42.0"N 110°41'16.8"W. No permits were required and this species is not protected. The method of retrieval involved aspiration into cylindrical plastic containers and transfer to lab. Once at lab, the ants were maintained within a 11.1 X 11.1 centimeter lidded plastic box containing an artificial nest. This artificial nest was made by sandwiching balsa wood, with a 0.5mm rectangular opening leading to a circular cavity (diameter 3.65cm), in-between two clear glass microscope slides; the thickness of the slides and wood was approximately 1mm and 2.4mm respectively. Maintenance of ants included weekly feedings and watering; ants received an agar diet (Bhatkar & Whitcomb, 1970) and access to water via a test-tube containing water and half of a cotton ball at the tip of the test-tube.

#### Experiment

For this experiment, nine colonies of *Temnothorax rugatulus* ants were transferred separately to a plastic circular arena with a diameter of approximately 21cm. Within the arena two nests of balsa wood and microscope glass slides were housed on the north and south side to provide a binary equal choice of nest sites. These nests were the same thickness detailed above and had a 3.175mm hole on the top glass slide for entrance. The entrance led to a circular cavity in the middle of the balsa wood with a 3.65cm diameter. The ants were transferred into the arena by removing the slides and wood of their original nest and slowly tapping or lightly shaking it over the arena. Any ants that weren't easily transferred were assisted into the arena and scattered using a paintbrush. Care was taken to ensure the ants were roughly equally scattered in the arena in a haphazard manner and not placed in intact groupings. This process was continuously recorded during variable afternoon time frames between February and May (with the exclusion of trial one, which was filmed in September) using a Cannon T2I camera clipped and held

approximately 14 and a half inches above the arena. Recording times varied due to the capabilities of the SD card, however the average length of recording was about 4 hours. A window and supplemental light provided equal light to the entire arena, care was taken to ensure the light was in the same position for all nine trials.

#### Data Collection

The video footage obtained from the trials was manually watched to obtain data. To have a baseline for percentage of consensus, the number of ants in the arena, north nest, and south nest were counted every 15 minutes from the time of complete scatter. The number of clumps were also counted every 15 minutes post complete scatter. Clumps are defined as temporary aggregations not consisting of the primary aggregation within a nest site. In order to be considered a clump, the aggregate must contain at least two items, with at least one item being a living worker ant. Examples of items includes, brood, additional worker ants, debris, or the queen. These clumps must last at least 10 consecutive seconds and items in the clump can be separated by no more than an ant length. As piles of brood could be difficult to count on the footage, the number of brood within the clumps was averaged using the average ant length. One piece of brood was equal to one ant length; the minimum value for a brood piece was one and counts were estimated so that percentages (i.e. half of a brood) did not occur. When a new ant joins the clump and stays for 10 seconds, it must overlap at least five seconds with the other ants in order to be considered an additional part of the clump, and not simply a replacement to an ant that left. When movement and size within the clumps is too great to count the number of ants staying for at least 10 seconds, an approximation is obtained by counting and averaging the number of items at 10 seconds prior to the timestamp, at the timestamp, and 10 seconds post. These clumps were labeled alphanumerically with each clump receiving a unique title, thus the lifespan and changes of each clump can be evaluated. In addition to the 15 minute count, the number of clumps was counted every minute for the first 20 minutes after complete scatter. Each clumps location was labeled using its unique title and tracked on a paper drawing of the arena as

the trial video was manually observed. All other data based on the clumps and ant counts were recorded and maintained in Excel.

## Analysis

Using Excel, results were analyzed. In order to better comprehend the results, the average number of ants in each trial was obtained. This was done by using the counts of ants (workers and queen, brood excluded) in the arena, south nest, and north nest at time of scatter and every 15 minutes following. The total of the ants from the counts were calculated and averaged from each time stamp to obtain the approximate number of ants per trial. This method was used to avoid variability in results due to ants hidden out of frame, escapees, or dead ants. These counts were also used, prior to being averaged, to make a standard line graph detailing the amount of ants at each location, with the x-axis containing the time at scatter and 15 minute intervals post-scatter.

Using the same x-axis, aggregation and consensus were also evaluated. The same 15 minute counts were converted to percentages by dividing the number of ants (worker and queen) in the chosen nest at each given time stamp by the average total number of ants for the trial in order to obtain a percentage of consensus. This percent consensus signifies the ability of the colony to select a new nest site. In split decisions, the colony is considered polydomous (even if only temporarily) and consensus is thought to be formed on both sites; thus, the number of ants in both nest sites is included in the percentage. Using the 15 minute counts for clumps, the number of ants (worker and queen) in a clump at each given time stamp was divided by the average total number of ants to produce a percent aggregation. As defined above, these clumps exclude the aggregation ants are known to form within their nest site and the percent aggregation is a representation of the temporary clumps that are formed within the arena more immediately after scatter. These percentages were then plotted against time on the same graph to provide a comparison.

A more in-depth representation of the clumps was provided by plotting a 3D histogram of the number of clumps and clump size at the time of scatter and then at one minute intervals until

twenty minutes post-scatter. The number of items within the clumps was separated into bins of five, excluding debris or dead ants in the item counts. This method was also repeated using the 15 minute clump data to create an additional 3D histogram showing the progression of clumps throughout the trial.

To better summarize the findings of the 3D histograms, two scatter plots were created. The average number of clumps for each individual trial at 0, 3, 6, 9 minutes post-scatter and every 15 minutes post-scatter was calculated and averaged to yield the average number of clumps for all trials. The same method was used to calculate the average number of items within the clumps throughout all nine trials. This yielded a scatter plot illustrating the average number of clumps and a second scatter plot showing the average number of items within the clumps. The standard deviation of all the averages between trials were calculated and plotted on both graphs.

Every trial received its own individual line graph of the amount of ants in the arena, north and south nest, as well as, a scatter plot of aggregation verses consensus. In addition, every trial produced two histograms showing the frequency of clumps (number of clumps formed) and composition (number of items within the clumps) over time for the first twenty minutes (one minute intervals) and at fifteen minutes intervals throughout. Two scatter plots illustrating the average number of clumps and the average number of items within the clumps were produced to summarize the histograms findings throughout all nine trials

Using the approximate location of every clump recorded, a single image showing the probability of a clump locations could be formed. Using Adobe Illustrator, the location of each individual trial was then transfer into an image containing an arena with two nests to-scale. Colored square dots were used to represent each individual clump. Each trial was assigned a different color for its clumps and the images were overlayed, adjusting opacity of the dots (between 60-80% dependent on color) to increase the visibility of all trials. Thus a single image was formed so that areas with a high probability of aggregation could be seen.

## CHAPTER 3

### RESULTS

#### Reunification

As expected, all nine colonies were able to re-coalesce, shown in Figure One. Three of the nine colonies, illustrated in Figure 1B, 1D, and 1F, became polydomous and occupied both the north and south nest. The other six colonies (66.7%) split equally, with three colonies reunifying in the south and the other three reunifying in the north nest.

#### Temporary Aggregation

All nine colonies (100%) tested experienced an initial stage of temporary aggregation. This consisted of a multitude of clumps developing almost immediately post-scatter. Clumps commonly formed around brood and the queen, with 62.7% (SD 17.2%) of clumps containing at least one brood item and 100% of the trials forming a clump around the queen. Clumps were also commonly observed forming around immobile ants or debris. Initial observations, illustrated in Figure Seven, show that aggregates may exhibit a preference to aggregate alongside walls/corners of the nest and arena, as opposed to the middle of the arena.

The beginning stages of aggregation (within the first hour), especially the first twenty minutes, contained a lot of clumps containing few items. The number of clumps is referred to as the frequency, and the number of items within the clump is referred to as its composition. Thus, the first twenty minutes yielded clumps at a high frequency, that are small in composition. As aggregation developed initial observations of the trials showed that many clumps would merge, or abandon their clump to transport to another existing clump, thus creating clumps with a larger composition at a smaller frequency. The increased frequency and smaller composition during the first twenty minutes was seen in eight out of the nine trials (Figures 3A, 3C-2I). Figure 3B, representing trial two, showed the high frequency of clumps similar to the other eight trials, however, the composition was also high. The high composition during the first twenty minutes may be accounted for by the trials quick transition out of the aggregation stage. Figure Four represents the composition and frequency of the clumps throughout the entire trial. Many of these

figures did not show the trends expected if the small but frequent clumps were merging to form less frequent, high composition clumps prior to the overall decrease in aggregation. Four out of the nine trials, Figures 4B-4C, and 4G-4H, did show this process, with an increased frequency of small composition clumps in the beginning, followed by a low frequency of clumps with a high composition of items, that eventually yields to a low frequency and low composition of clumps as the final clump is transported to the nest. Alternatively, Figure 4I and 4F, trials nine and six respectively, both show the frequency with the maximum number of clumps being reached in the first twenty minutes and decreasing steadily after, however, neither observed a large increase in composition. Similarly, trial five, illustrated by Figure 4E, saw the same high frequency in the beginning of the trial, but its composition never increased. This trial also had a single clump reform at the end of the experiment. Figure 4D, trial four, showed an increase in composition, however, the frequency of the smaller composition clumps did not decrease with these new clumps as expected if these clumps were merging. This is likely indicating that new large clumps are forming in this stage in addition to the existing small clumps; in other words, the small clumps are not simply combining to yield a clump with a large composition. This is less common than individual clumps combining, however, it is still seen at a decent frequency in the video trials and data. This trial also lacked a gradual decrease in frequency of the clumps and went from three clumps (containing 16, two, and three items) at 105 minutes to zero clumps at the next time-stamp, and remained at zero for the remainder of the trial. Trial one, Figure 4A, reached its maximum frequency of clumps at 15 minutes as expected. However, composition failed to increase and frequency failed to decrease. This trial ended with three clumps at the final time-stamp. The fluctuation among histograms likely indicates that though it is likely for small, frequent clumps to combine to form larger, less frequent clumps, other processes are also common. These processes could include ants transporting clumps directly to the nest, colonies favoring smaller aggregates over those with a larger composition, clumps dissipating altogether, and ants migrating in between multiple clumps.

Figures Five and Six summarize the findings of all trials illustrated in Figures Three and Four. In Figure Five, the number of clumps is highest within the first twenty minutes, as seen in

Figure Three across trials, and decreases as time continues. The standard deviation is high within the first twenty minutes, likely due to the variation in colony size among trials. However, it decreases as aggregation decreases throughout all trials. Figure Six, shows the opposite findings for standard deviation. Illustrating the average clump size for all nine trials, the first twenty minutes have low variation and clump size. This is confirmed by Figure Three which shows this relatively unanimously across trials. The variation increases as aggregation rises and falls throughout the trial, indicative of the aforementioned variation in processes post twenty minutes aggregation. In both Figure Five and Six, not all trials ran for the same length of time, thus not all values are indicative of an average of all nine trials. The final time stamp represents only one remaining trial and thus has no standard deviation.

The average number of clumps per colony was 41 (SD 18.83), with a minimum of 17 and a maximum of 70. Six out of the nine trials (66.7%) all reached their maximum percent of colony utilization for aggregation at exactly fifteen minutes post-scatter, seen in Figures 2A-C, 2E, and 2H-I. The other three trials, Figures 2D, 2F, 2G respectively, reached their maximum percent of aggregation by the first hour (two trials 45 minutes post-scatter, and the final at exactly 60 minutes post-scatter). The average maximum percentage of colony utilization for aggregation reached at this time among colonies was 34.8% (SD 10.8%). This is consistent with the expected finding as aggregation is thought to be the first stage of reunification following scatter and decrease with furthering consensus.

#### Aggregation VS Consensus

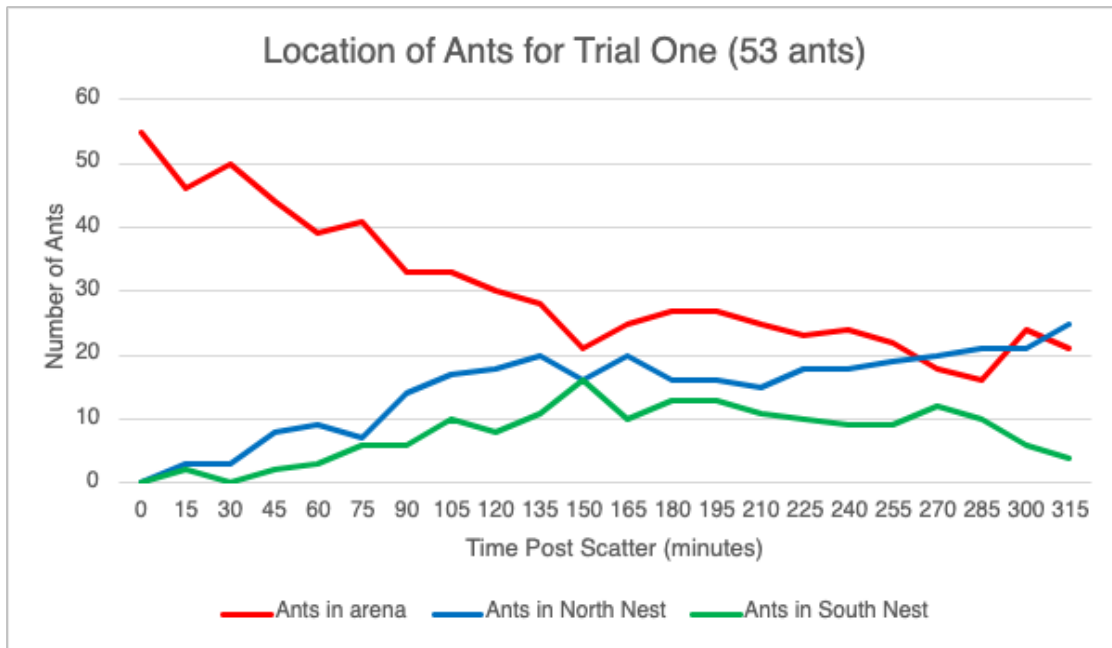
This decrease in aggregation relevant to an increase in consensus is best illustrated by Figure Two. If aggregation is a process forming in the beginning (almost immediately after scatter and before significant transports to the nest), the figures of aggregation verses consensus should show a very brief period of scatter, followed by an almost immediate stage of aggregation. This aggregation should quickly reach its peak as consensus is remaining low, and then steadily decrease as consensus increases. This is best illustrated by Figures 2A-C, 2E-F, and 2I. Figure 2D still observed the general process reaching a maximum of aggregation at 45 and starting to

trend primarily downward following. However, there is more fluctuation seen in peaks and drops between aggregation and consensus than in other trials. Figure 2G reached its maximum consensus at 60 minutes and exhibited a more drawn-out period of aggregation. However, the graph still showed higher percentages of aggregation within the first hour that decrease as an increase of consensus is observed. Figure 2H, though still observing the maximum percent of aggregation at 15 minutes and a decrease following, exhibited lengthen periods of aggregation. However, consensus also remains lower for a much longer period of time and begins increasing more as aggregation decreases later in the trial. Thus, the general process of aggregation forming hastily post-scatter and decreasing as consensus is increasing was observed in the majority of trials.

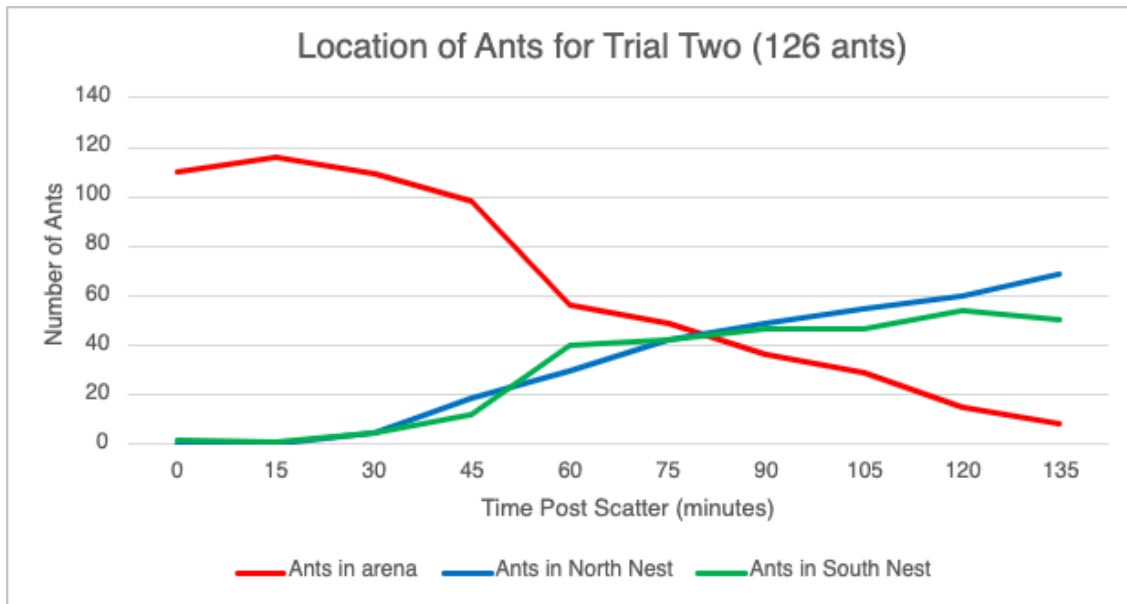


**Figure One.** Location of Ants

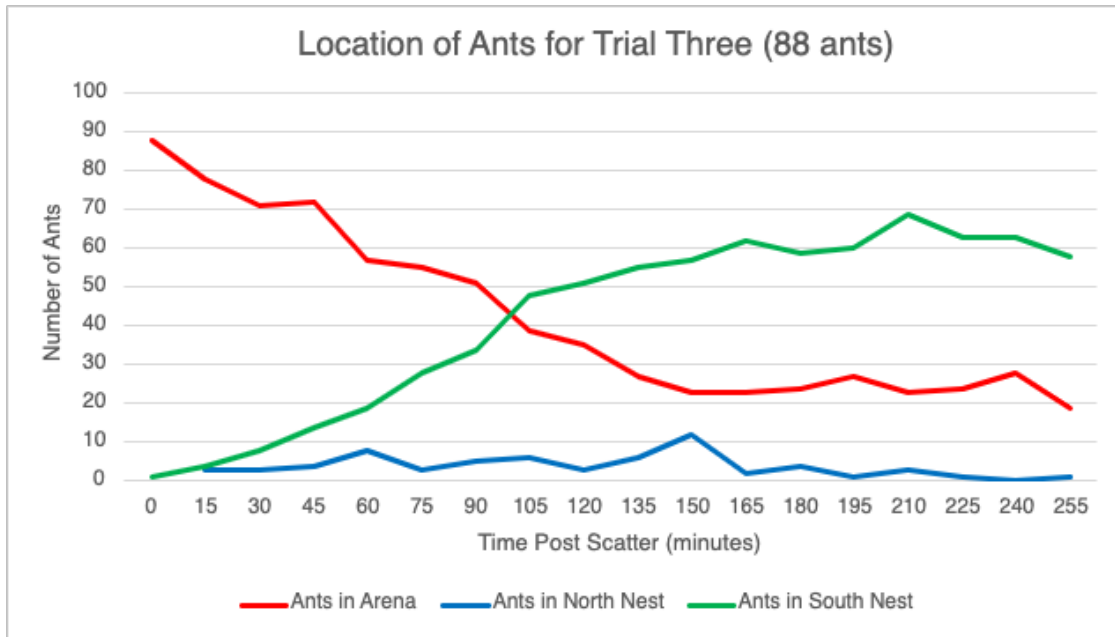
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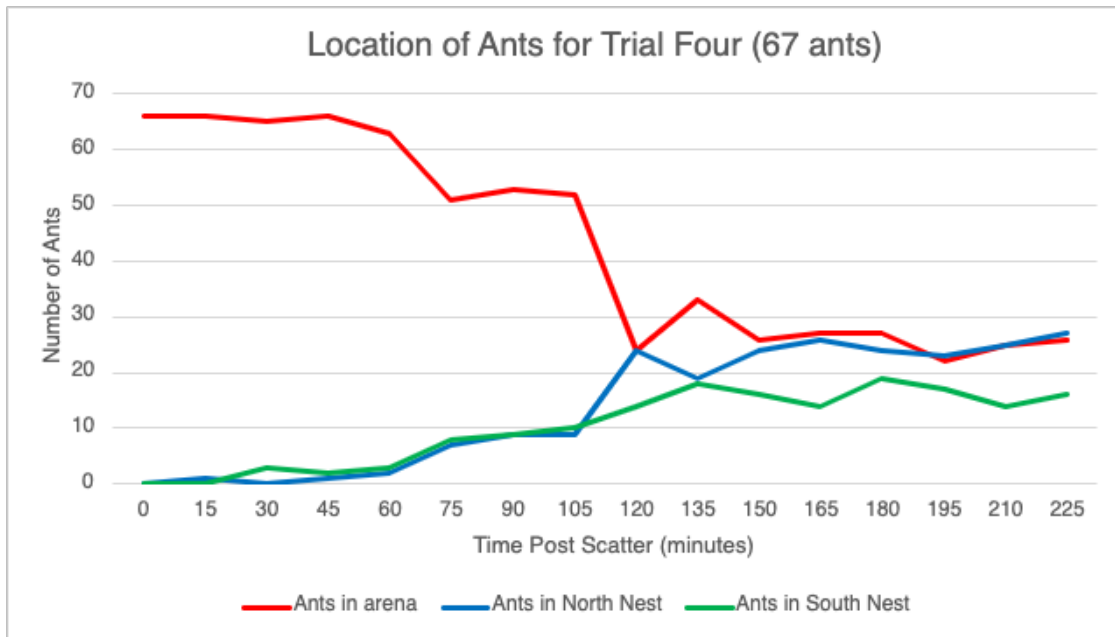
**B.**



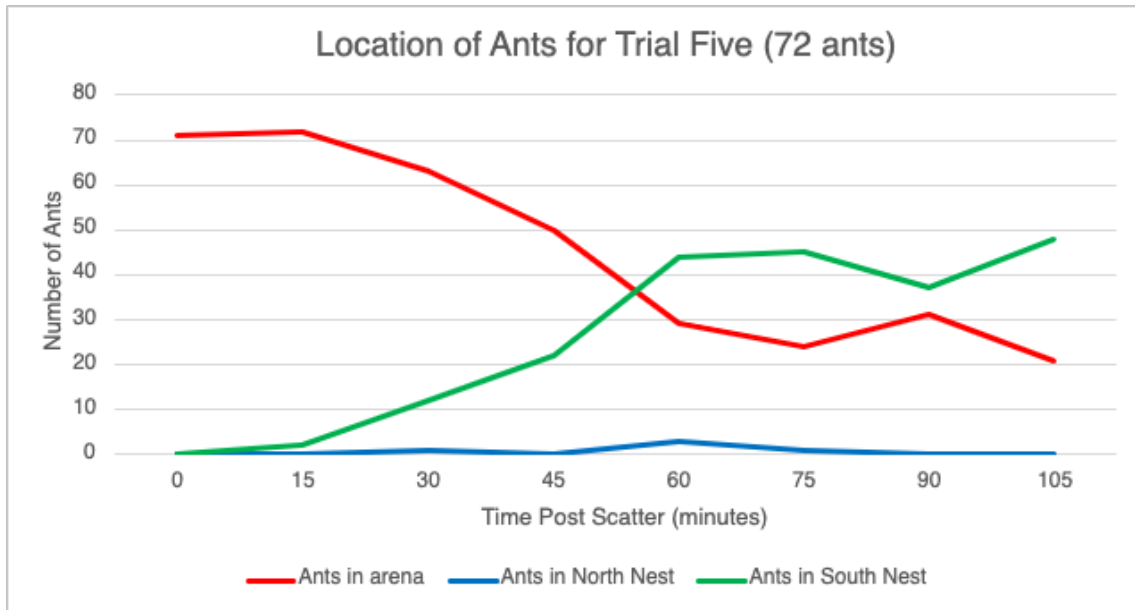
C.



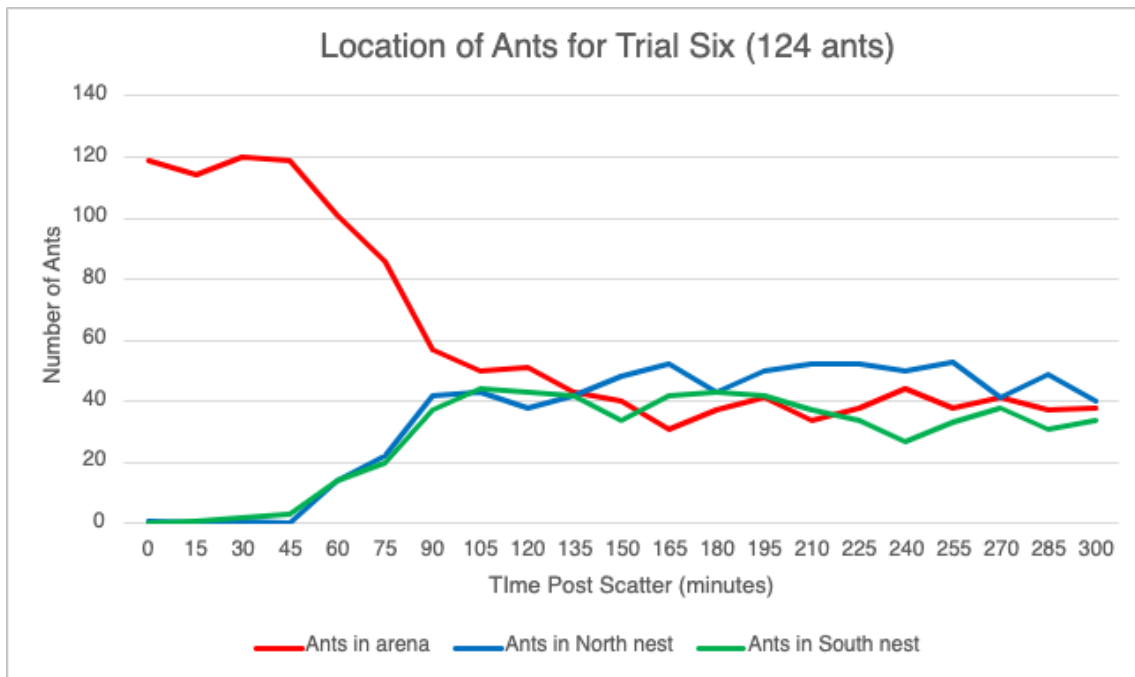
D.



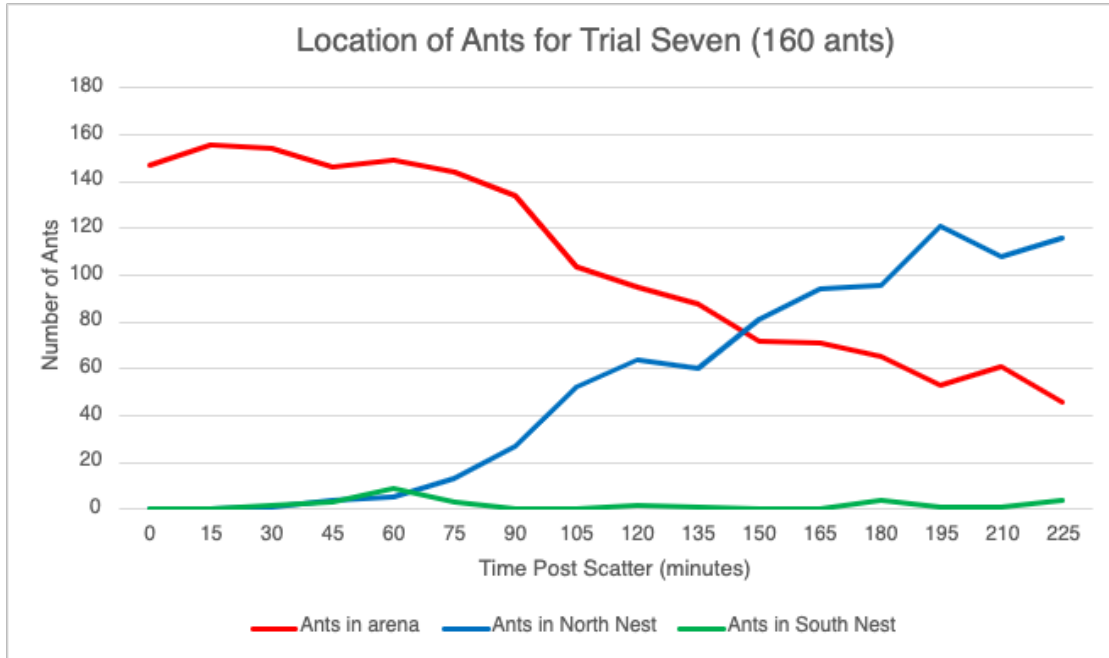
E.



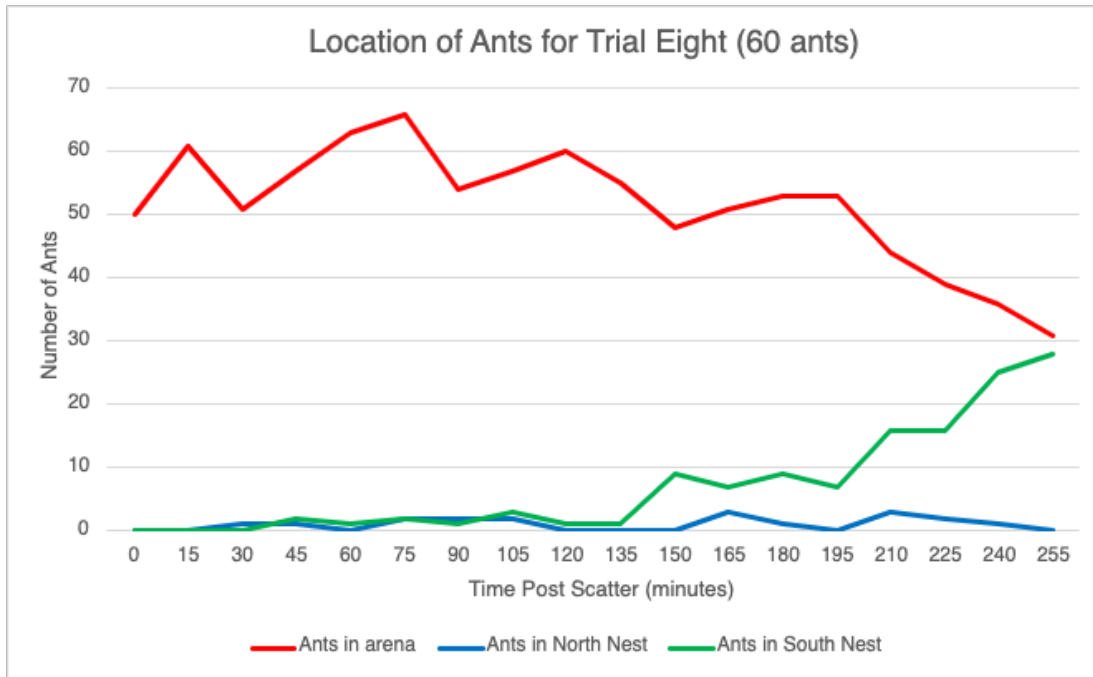
F.



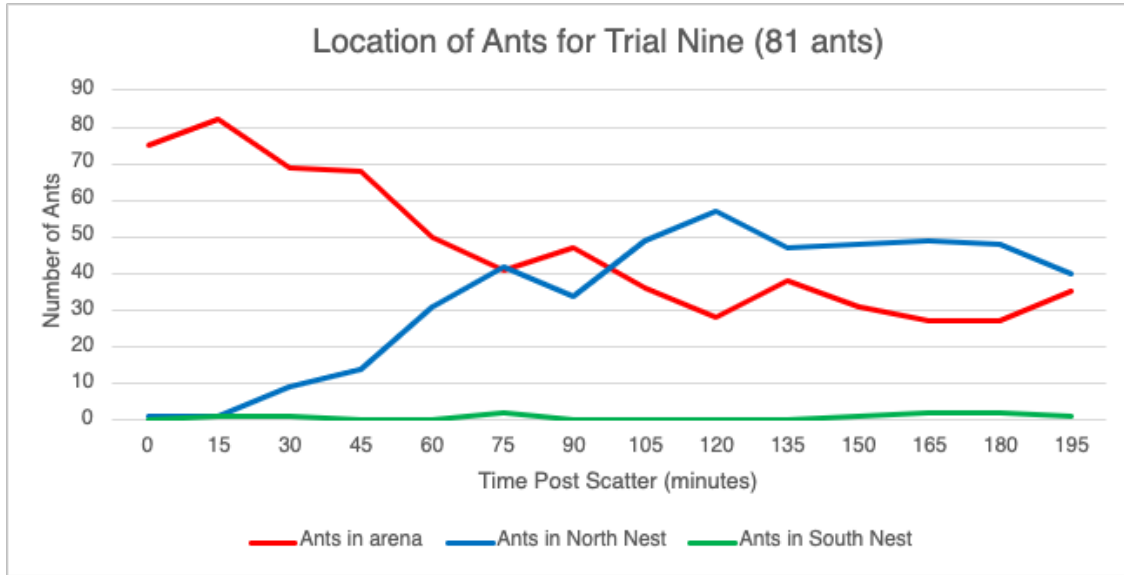
G.



H.



I.

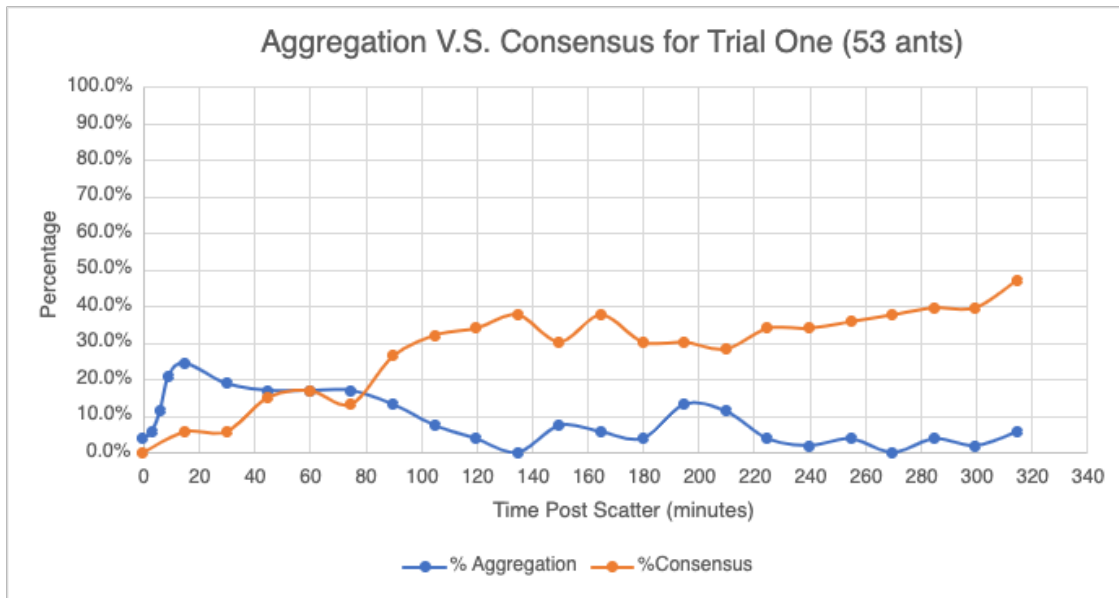


**Figure One.** Location of Ants For all Nine Trials

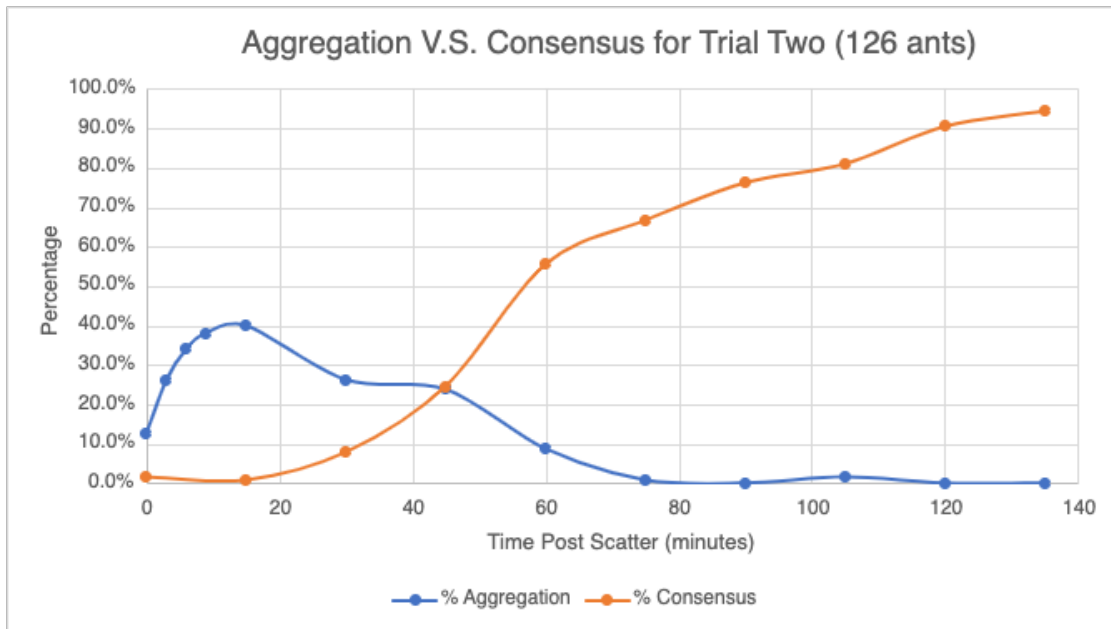
The nine line graphs illustrate the number of ants in the arena, north nest, and south nest at fifteen minute intervals post-scatter, for each respective trial. The average number of ants within the colony for each trial is denoted in the title. Three of the nine colonies became polydomous, with the other six trials forming a consensus on a singular nest site.

**Figure Two.** Aggregation Verses Consensus

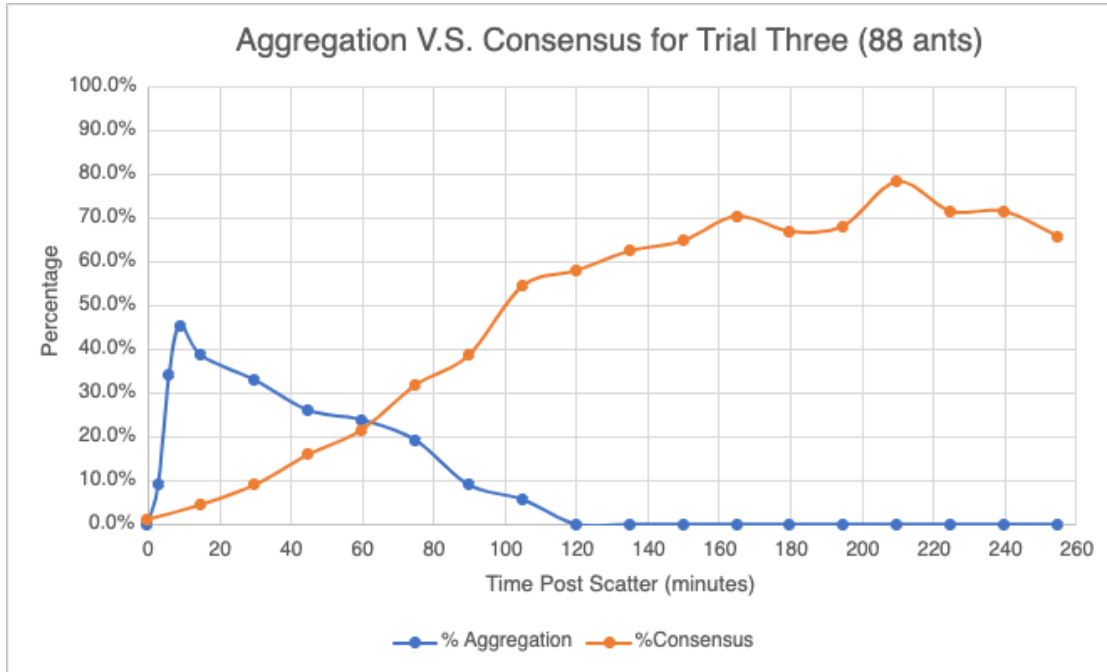
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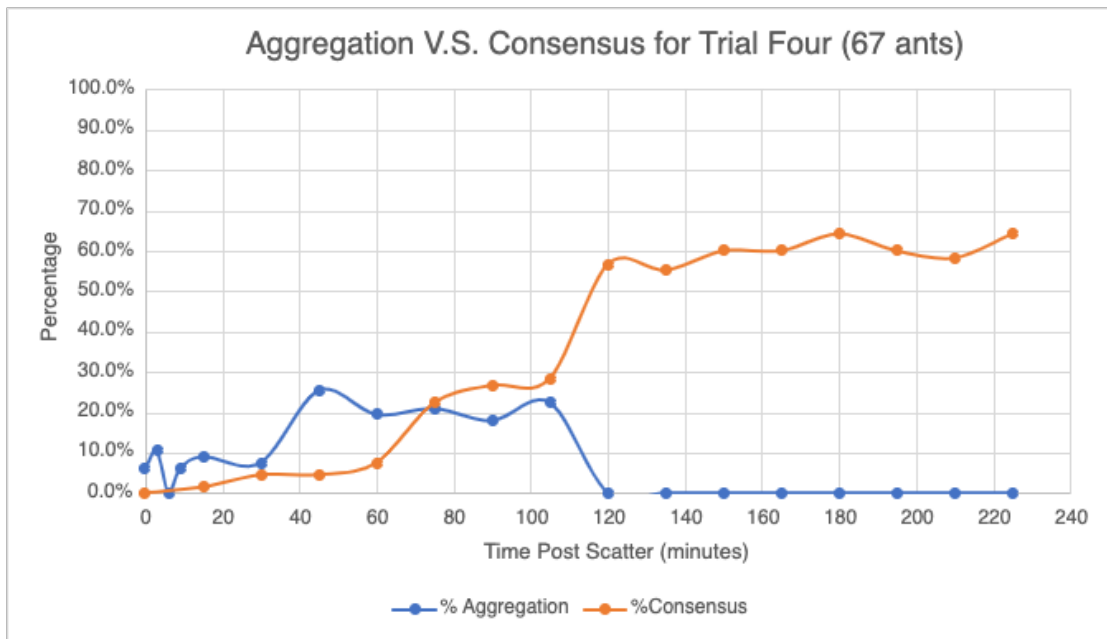
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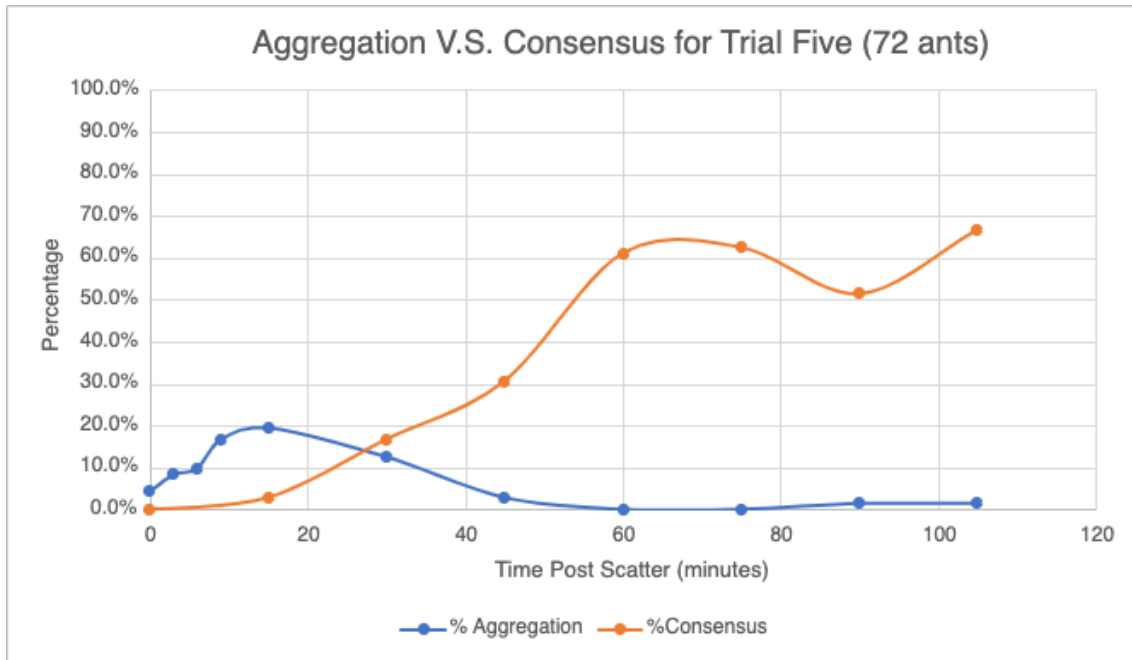
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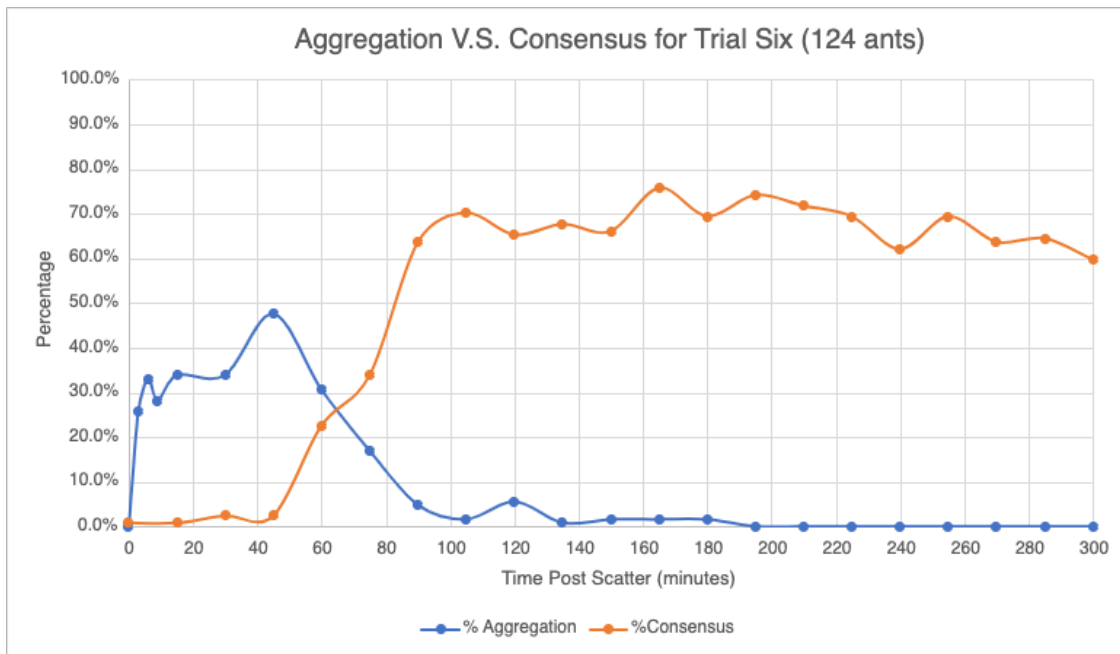
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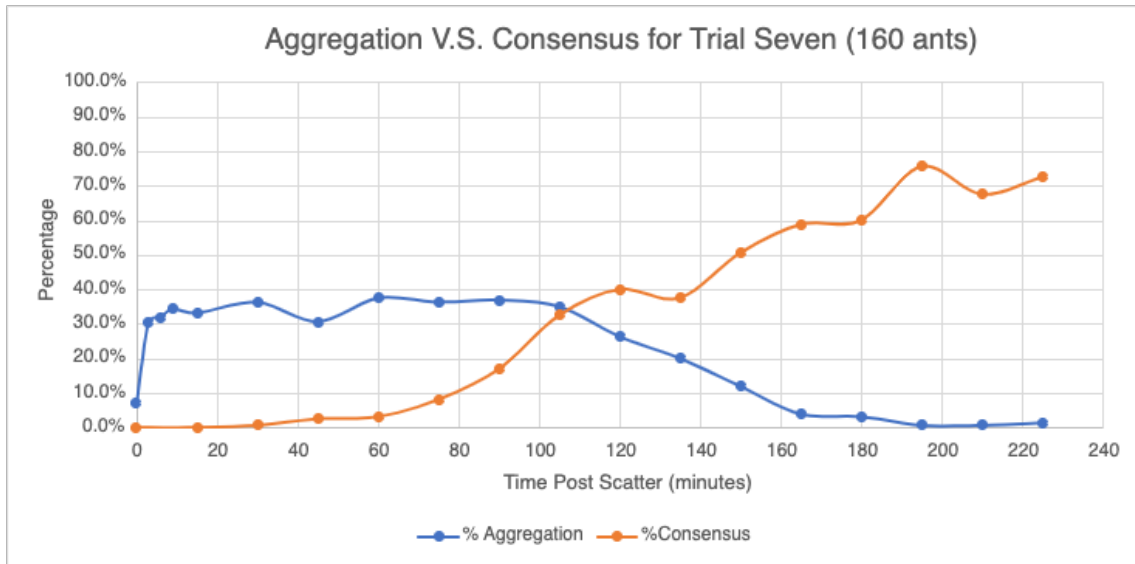


F.

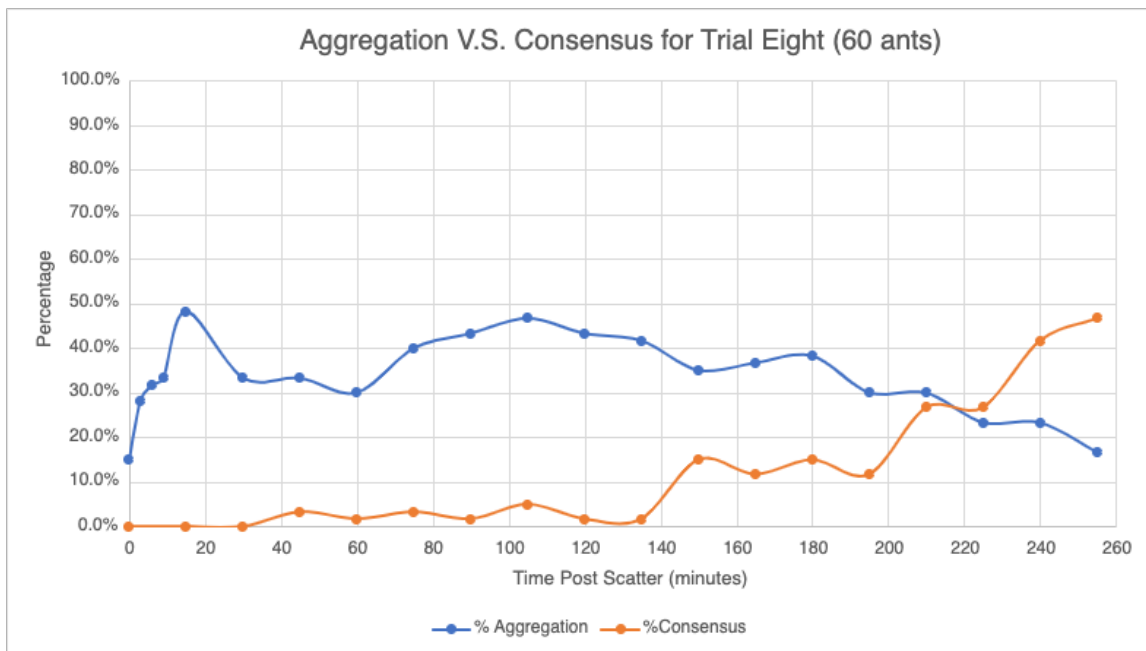




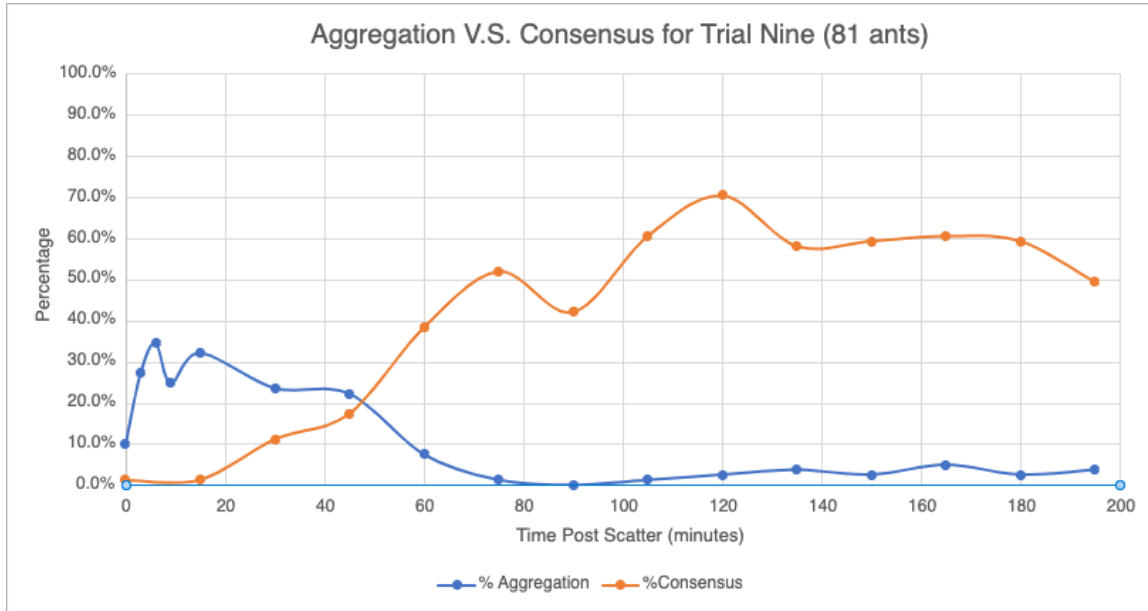
G.



H.



I.



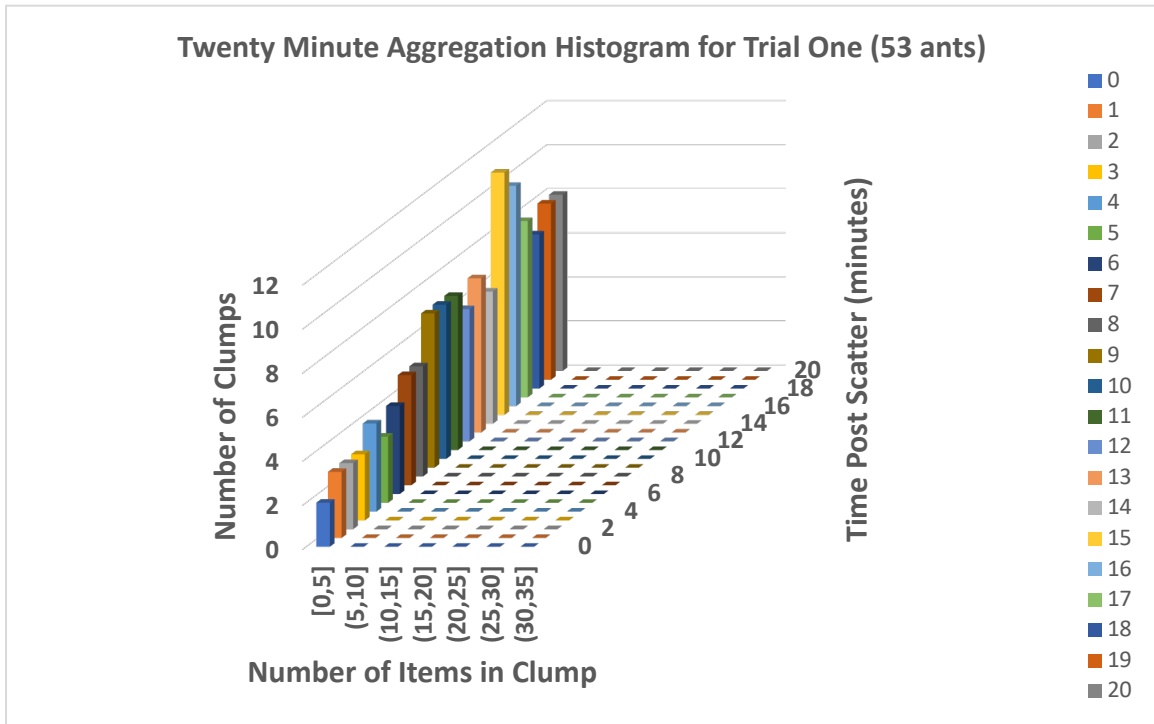
**Figure Two.** Aggregation Verses Consensus

Nine scatter plots illustrate the percent aggregation and percent consensus across time.

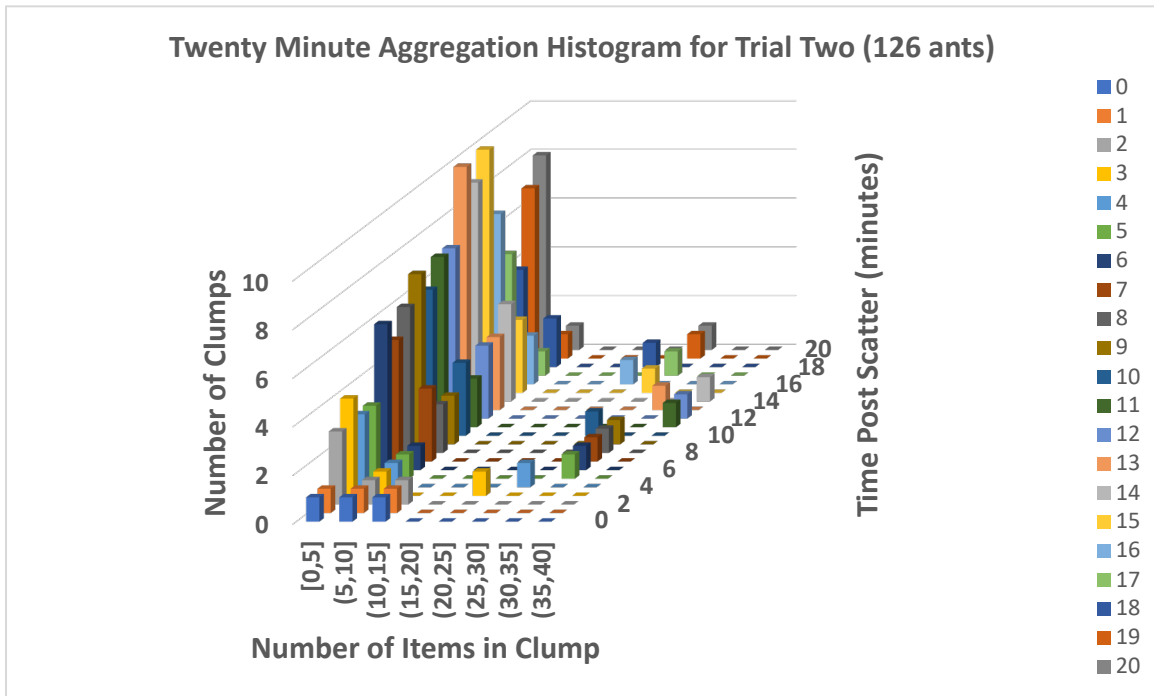
Aggregation reaches its maximum percent of colony utilization within the first hour in all trials, with an average of 35.6%. Six out of the nine trials reach this maximum percent of aggregation within the first fifteen minutes. Following this peak in temporary aggregation, the majority of trials experience a decline in aggregation and an increase in consensus, as ants move from these temporary clumps into the nest site. In cases of polydomy, both nest sites were said to have formed a consensus and were included in the percentage.

**Figure Three.** Twenty Minutes Aggregation Histograms

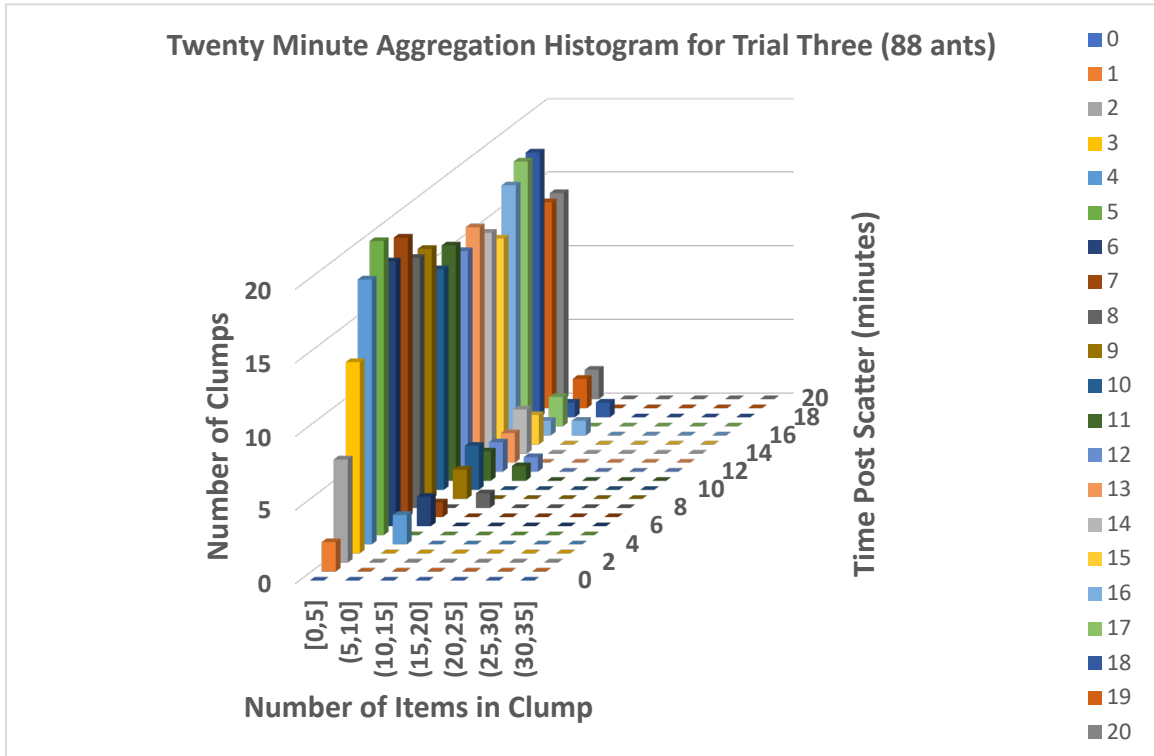
**A.**



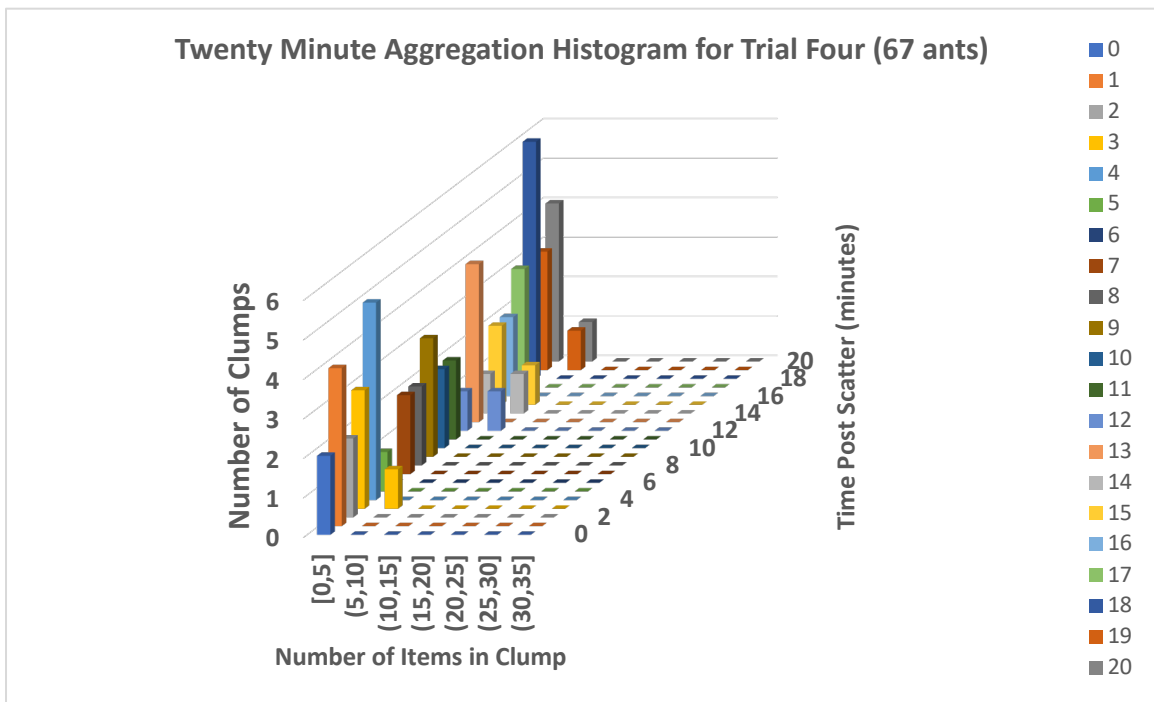
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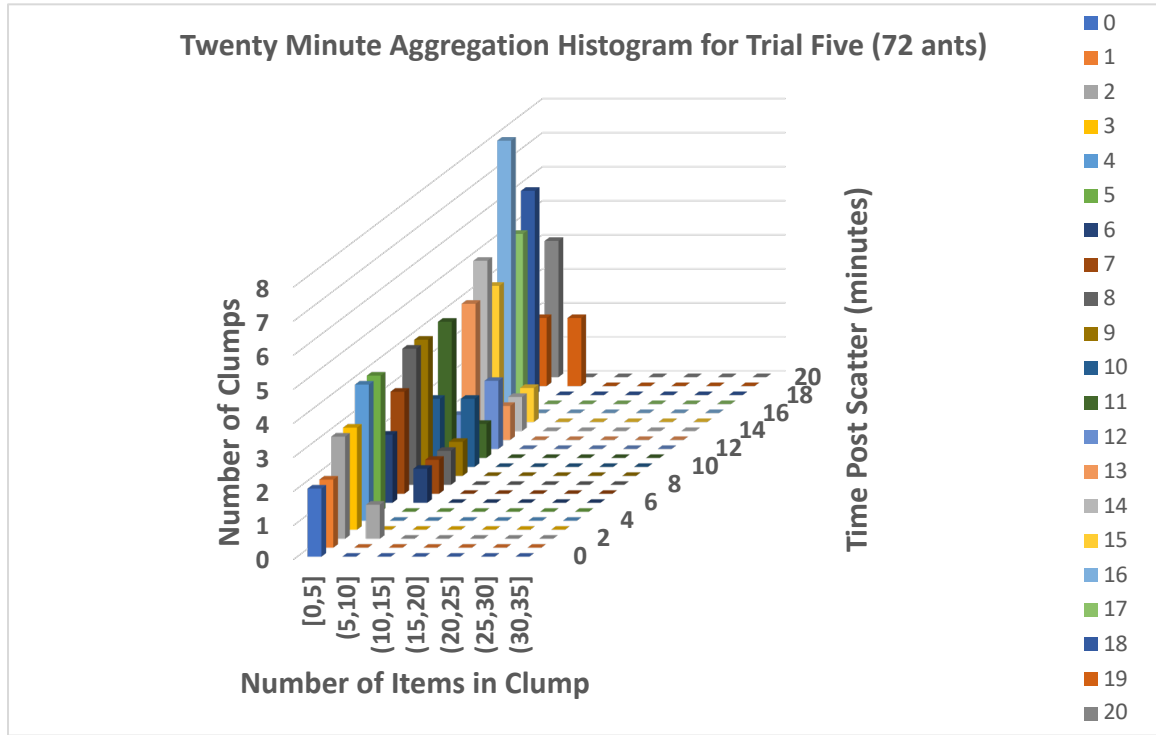
C.



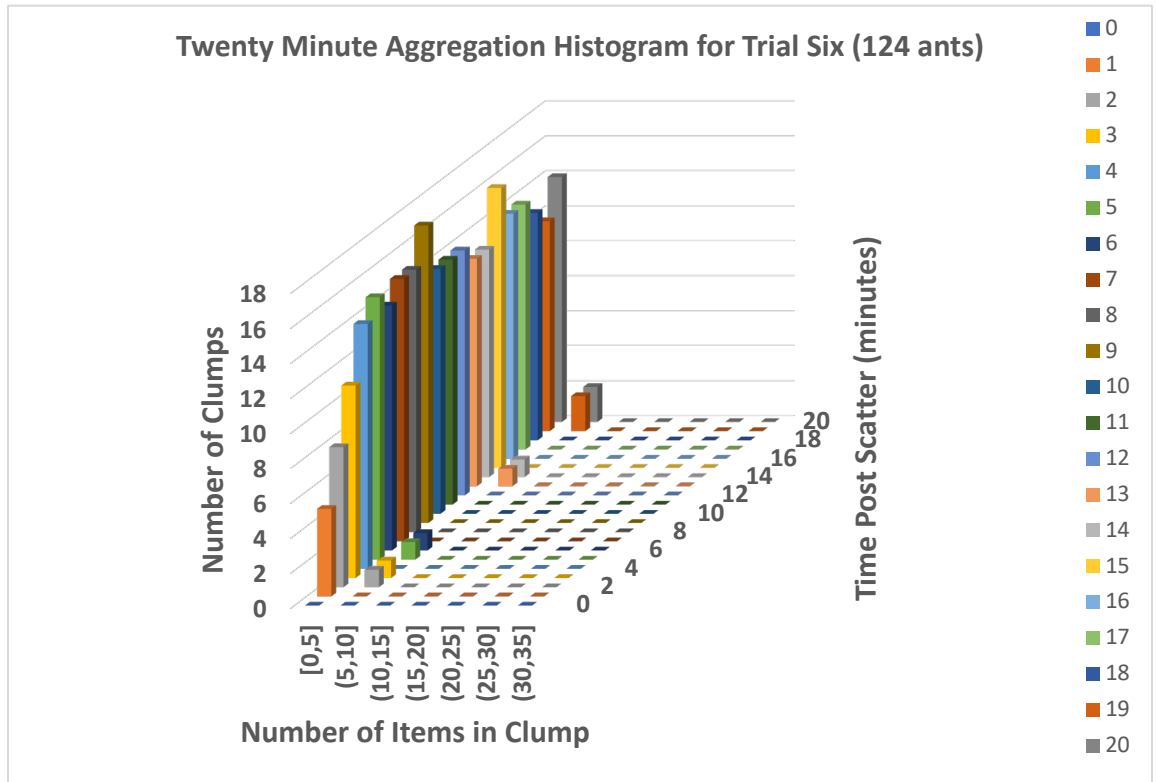
D.



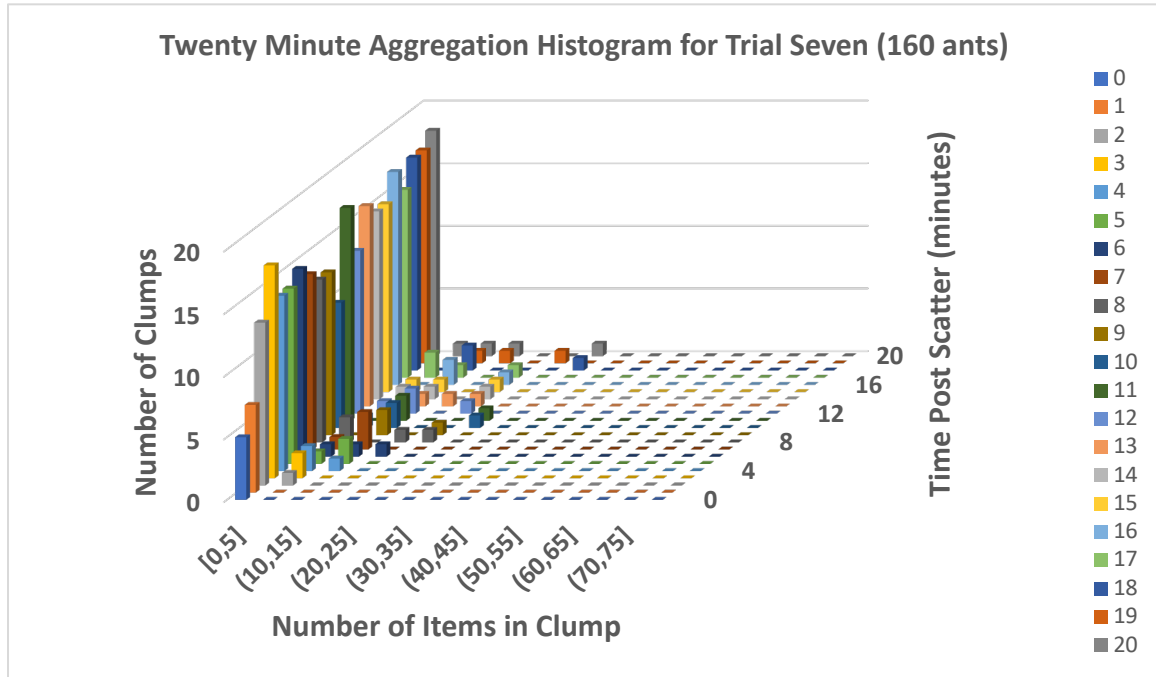
E.



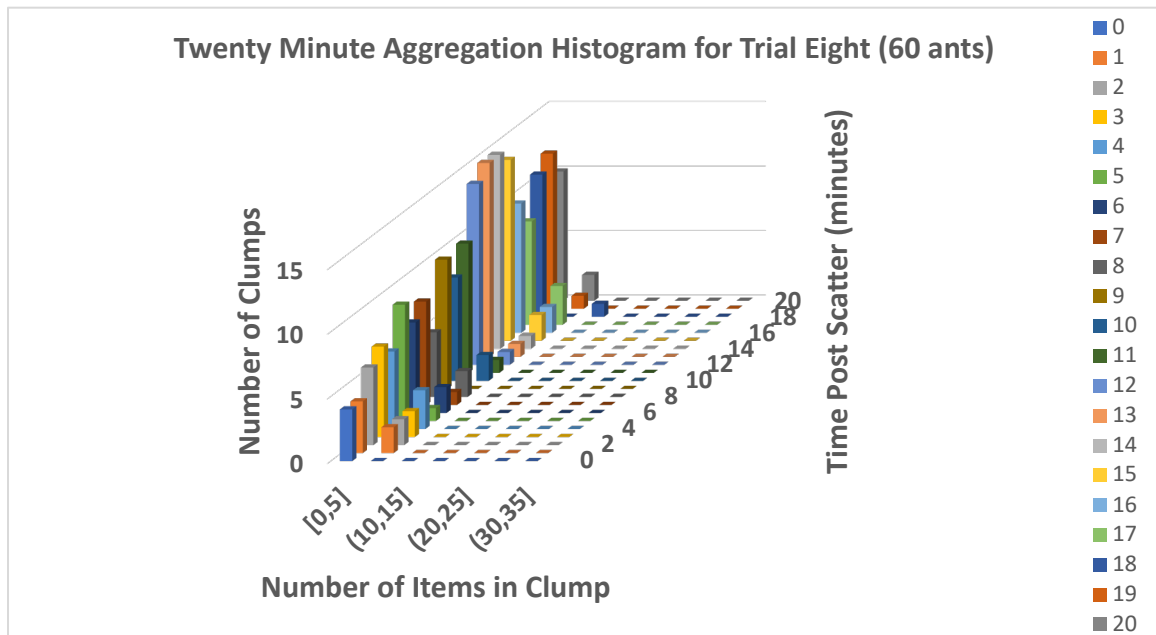
F.



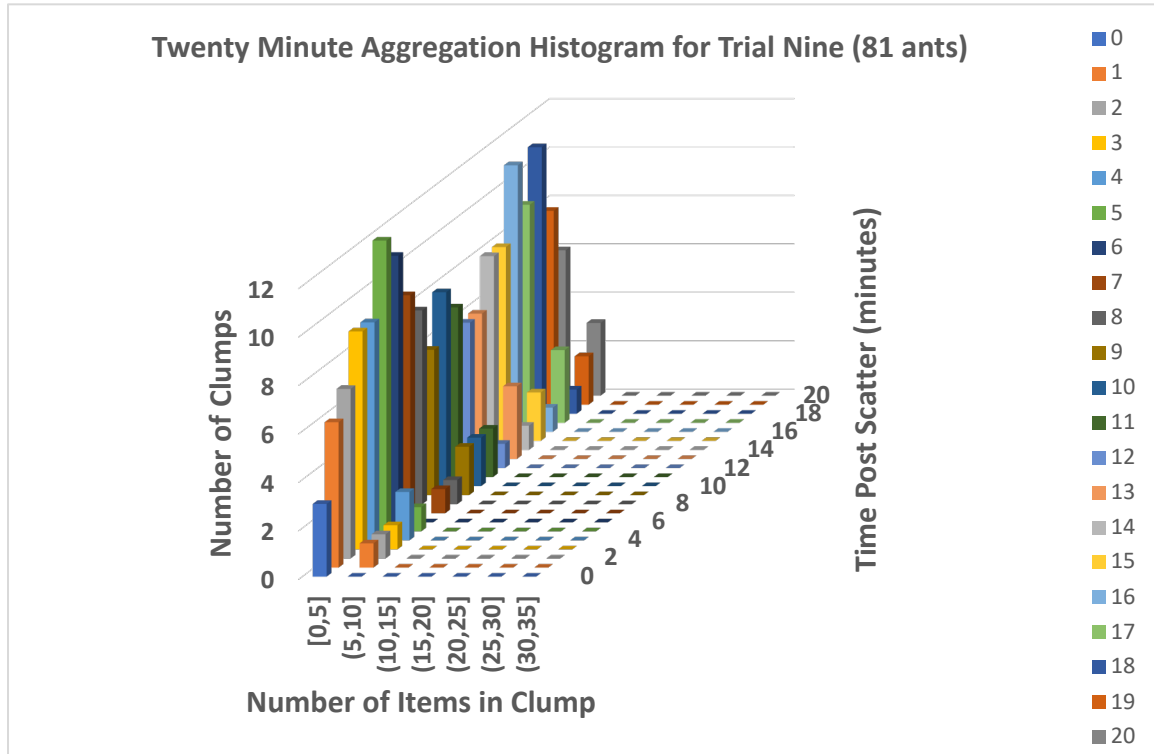
G.



H.



I.

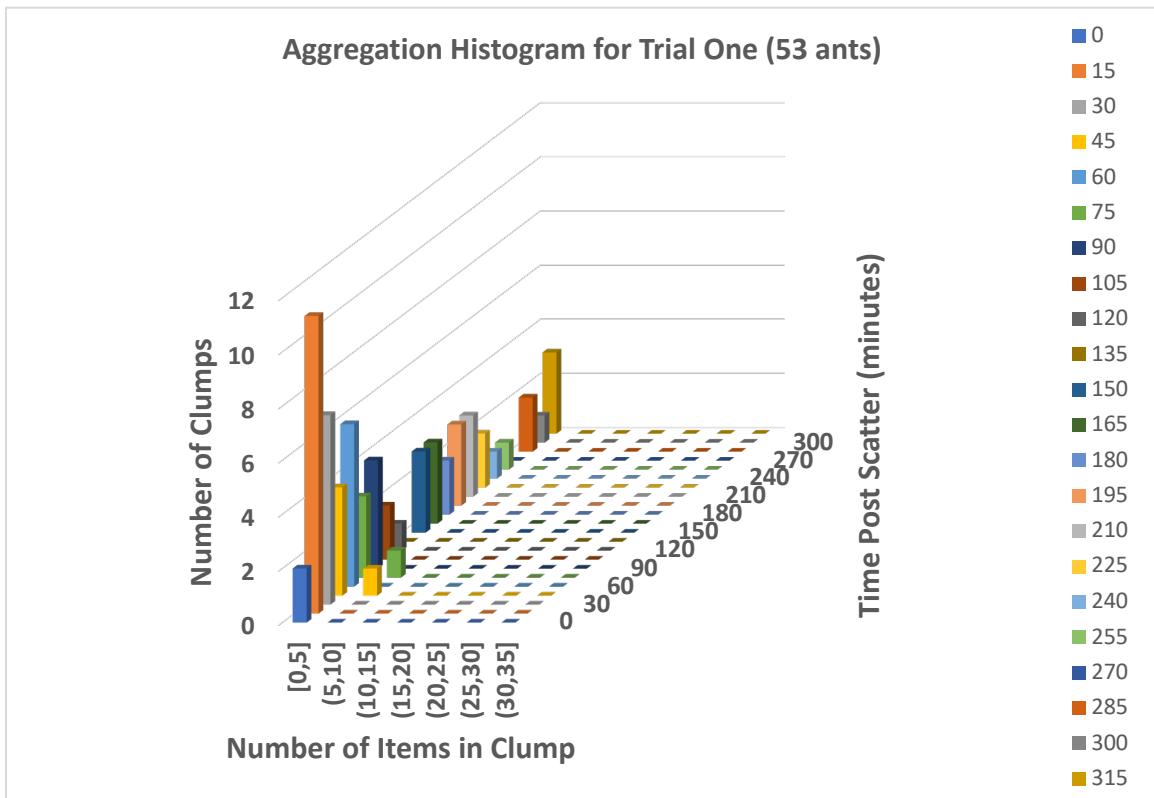


**Figure Three.** Twenty Minute Aggregation Histograms

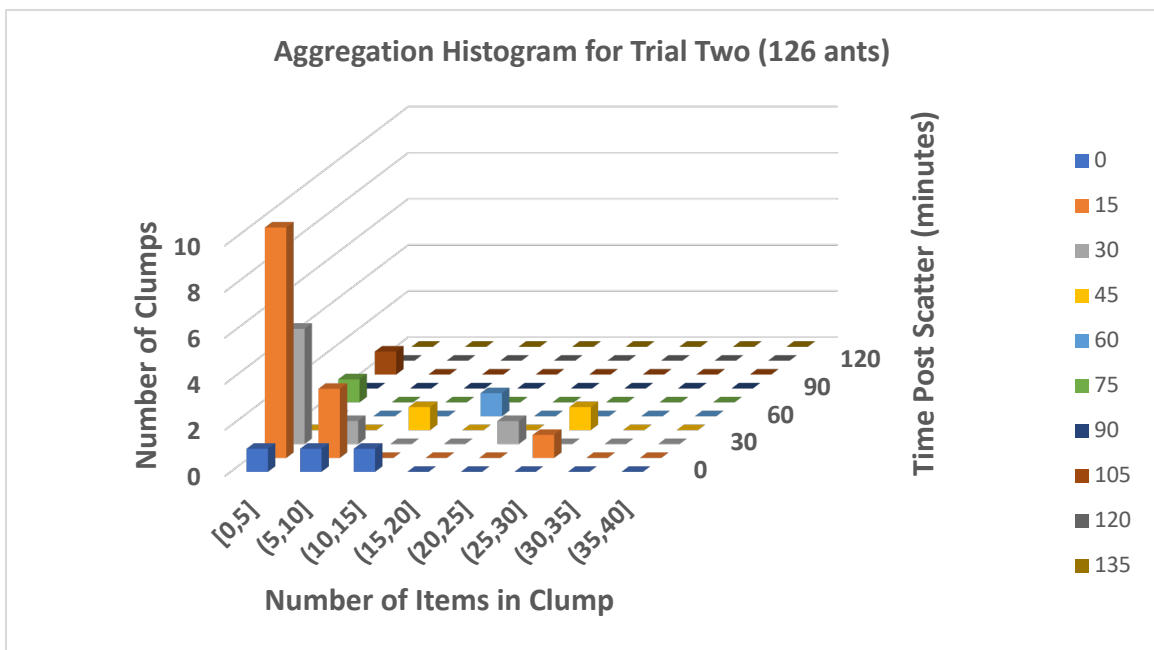
The number of items and number of clumps for the first twenty minutes of all nine trials is illustrated in the 3D histograms. All nine trials show small but frequent clumps forming. A single trial, trial two, had larger composition clumps form in addition to these small, frequent clumps. Trial seven appears to have larger composition clumps forming, however, these clumps are considered small in relation to its colony size and larger clump size throughout the trial.

**Figure Four.** Aggregation Histogram Throughout Whole Trial

**A.**

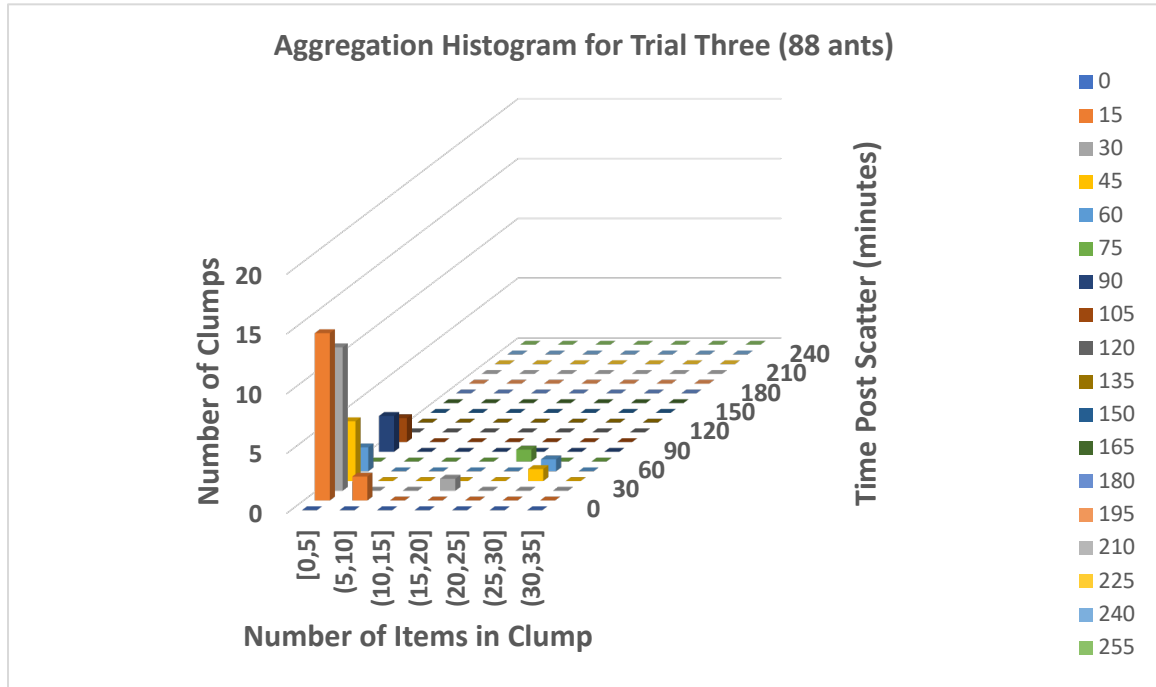


**B.**

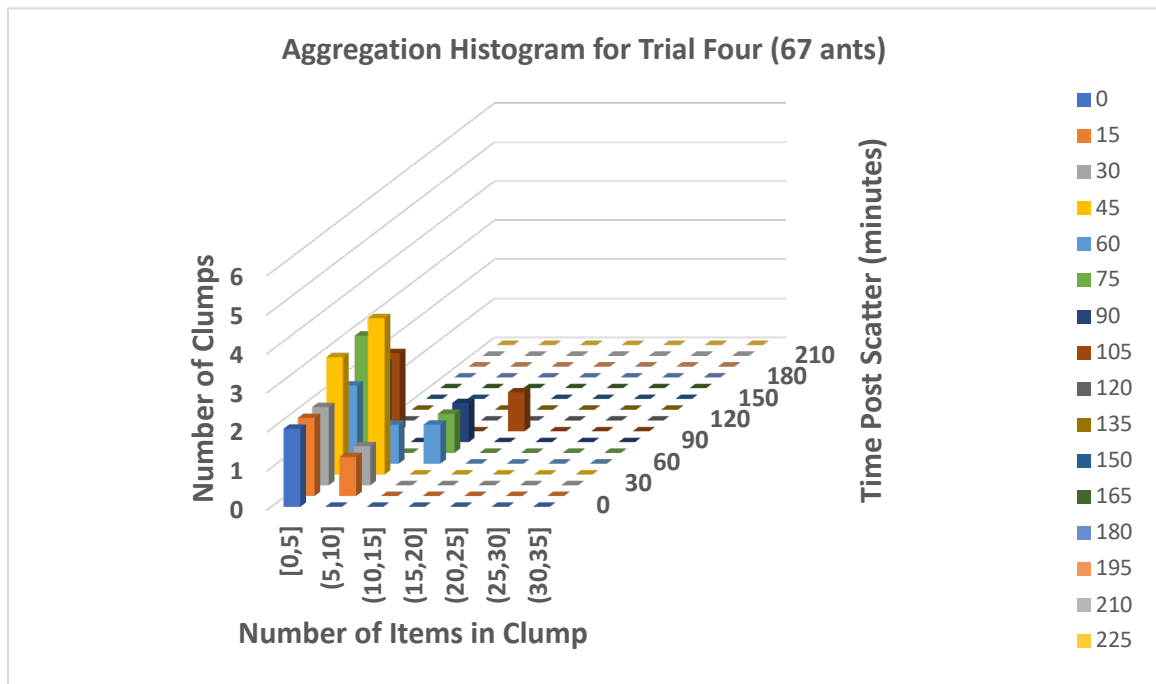




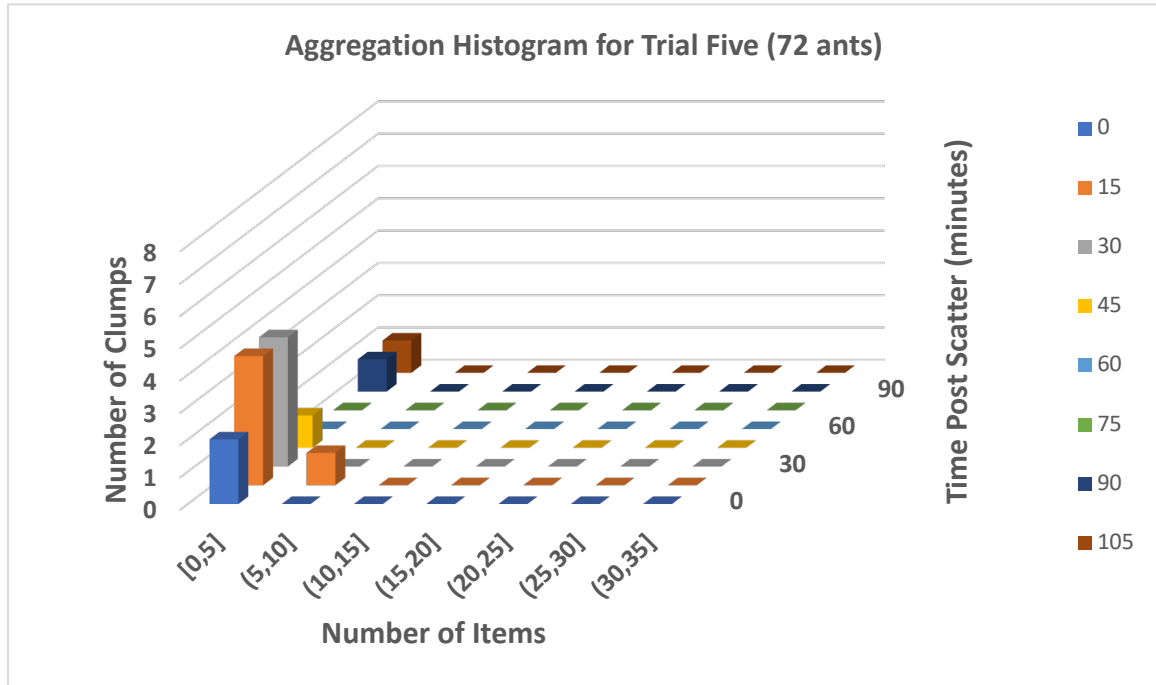
C.



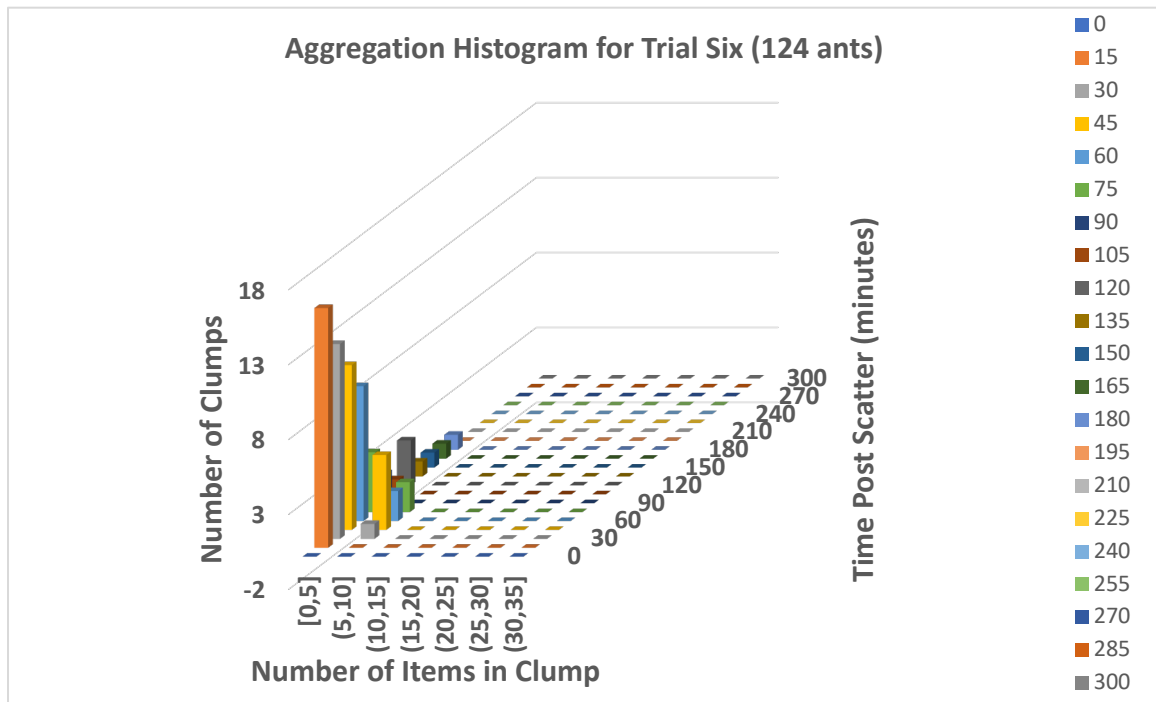
D.



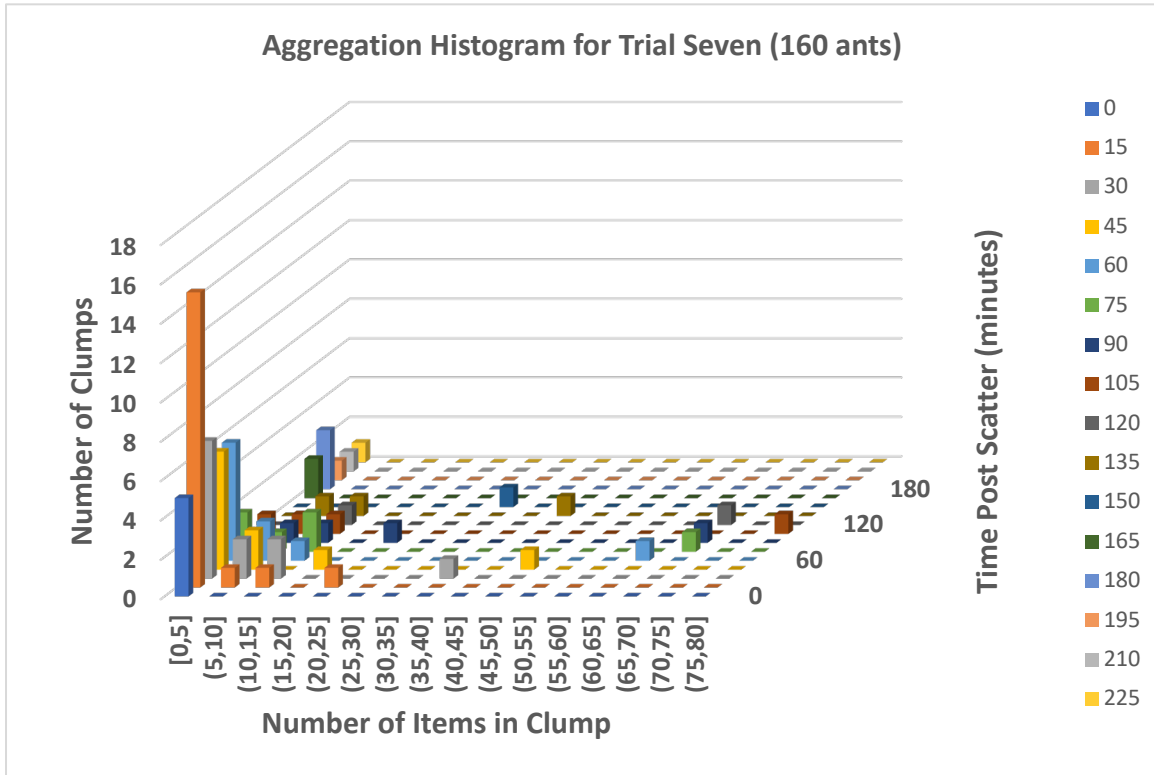
E.



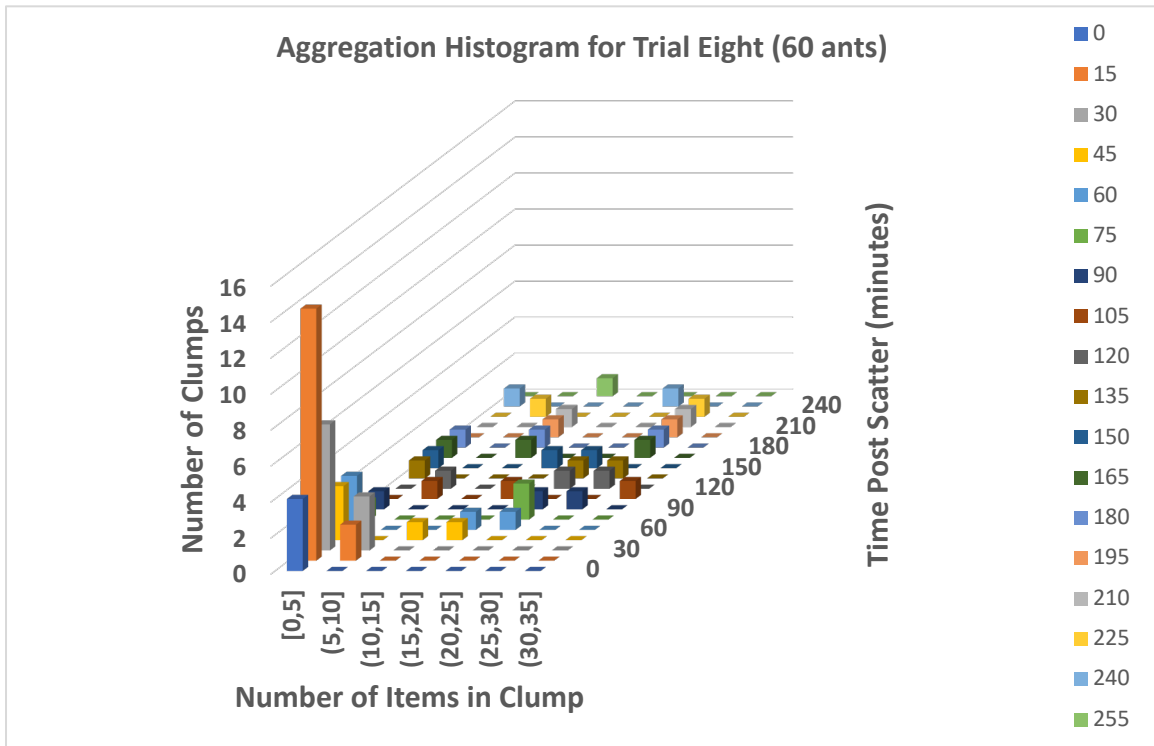
F.



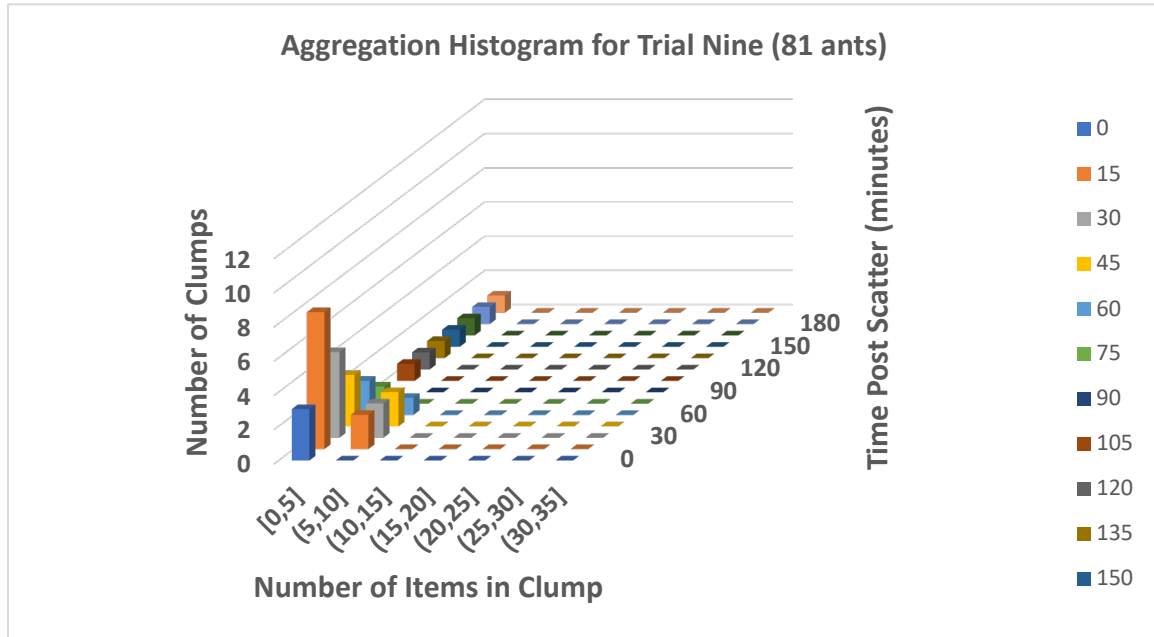
G.



H.

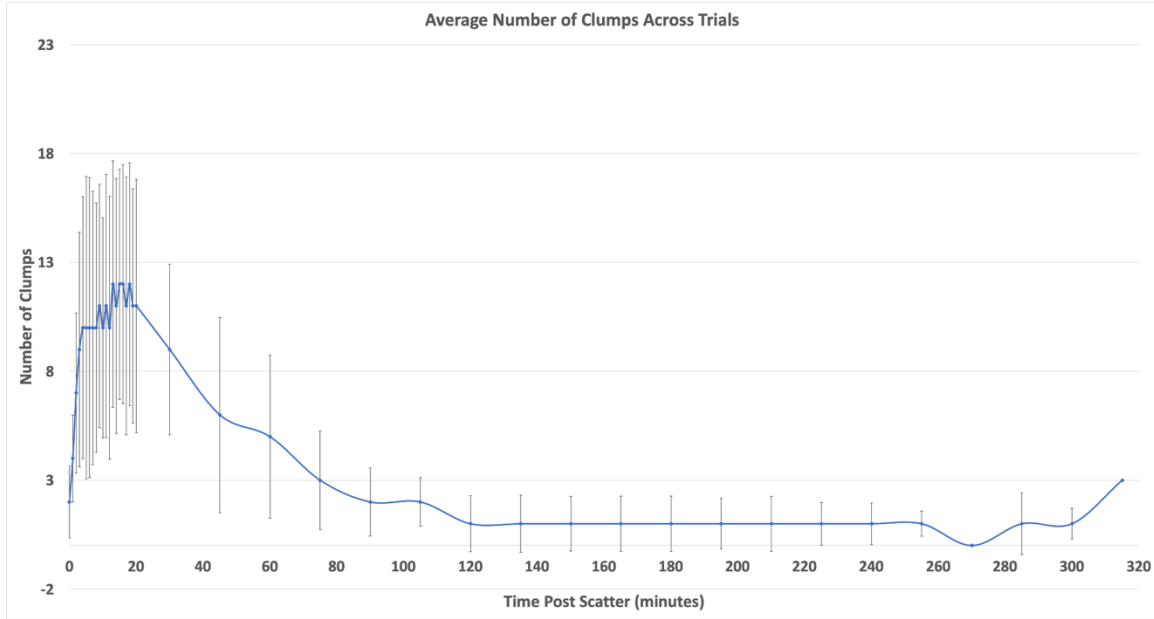


I.



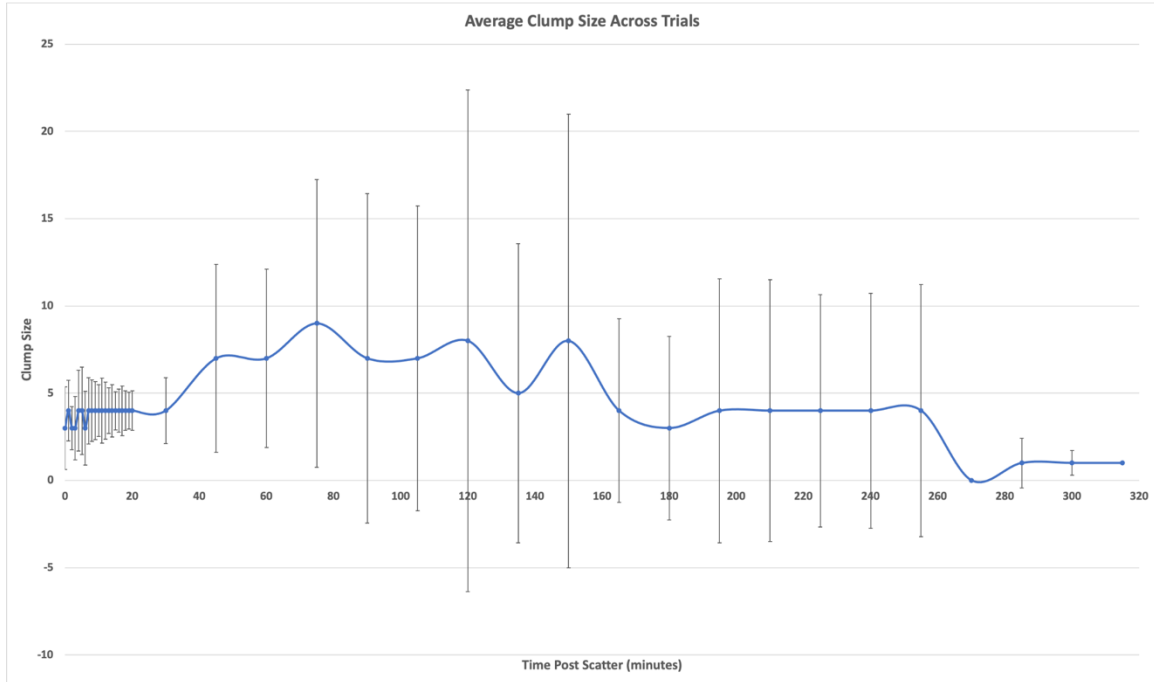
**Figure Four.** Aggregation Histogram Throughout Trial

These histograms show the number of clumps and number of items within the clumps throughout fifteen minute time-stamps for each trial. The number of clumps and items is relatively low at time of scatter. The number of clumps increases during the first fifteen minutes, with the number of items generally remaining low. Following this, composition begins to increase in four out of nine trials, before aggregation decreases entirely. Five of the other trials had varying results, discussed further in the discussion.



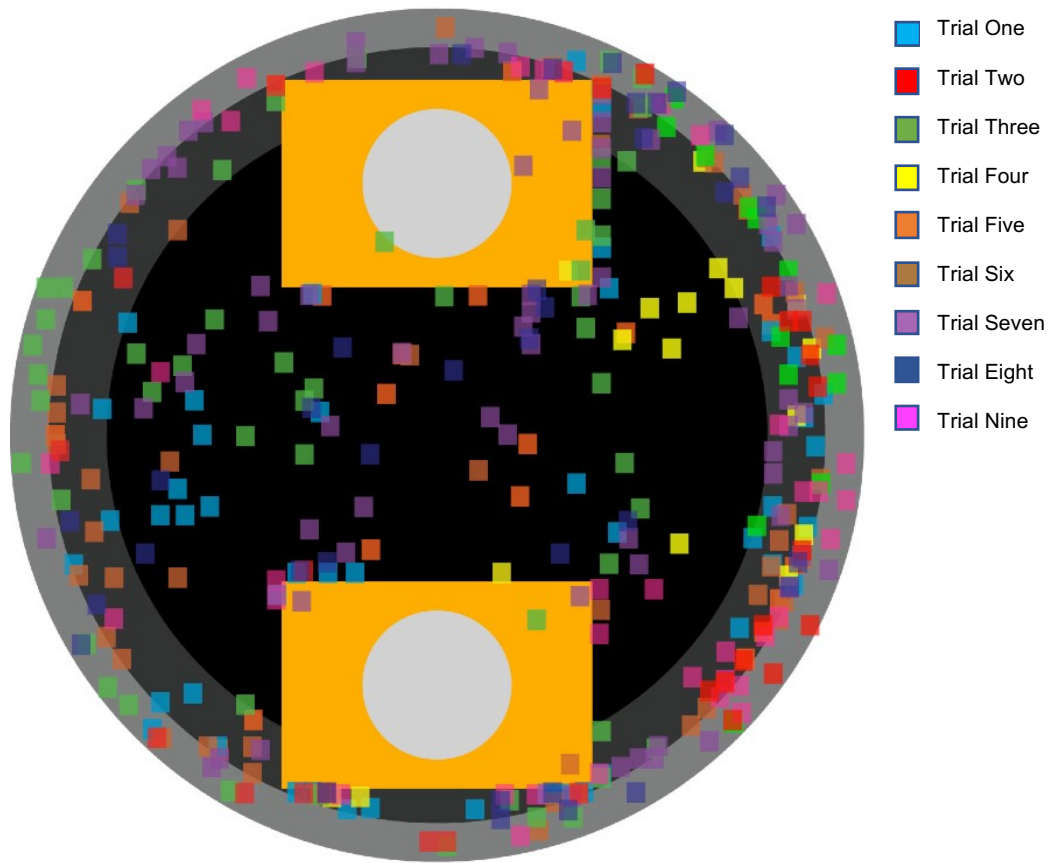
**Figure Five.** Average Number of Clumps Across Trials

This scatter plot combines the average number of clumps across nine trials. The beginning yielded the largest number of clumps, which is supported by the histograms (Figure Three). The largest amount of variation in standard deviation was also seen in the beginning, which is expected due to variations among colony sizes. However, this variation decreases as the number of clumps decreases, as all trials consistently decreased in the number of clumps as time increased. As illustrated in previous figures, not all trials ran for the same length, thus the final time stamp (315 minutes) represents only one singular trial, as opposed to a true average.



**Figure Six.** Average Clump Size Across Trials

This scatter plot illustrates the average clump size for all nine trials throughout the experiment. The clump size is small in the first twenty minutes, as supported by the histograms (Figure Three). The standard deviation at this time shows variation is low as this was seen fairly unanimously across all trials. However, the later stages of clumping, yield much more variation (Figure Four), which is seen by the increase in the standard deviation. Overall, clump size increased post-twenty minutes before decreasing in later stages. Like Figure Five, not all time-stamps are true averages of all nine trials, as each trial ran for a different length.



**Figure Seven.** Location of Clumps

This image shows the approximate location of aggregations for all nine trials within the to-scale circular arena. The image is presented so that the viewer is looking downward into the arena; thus, the outer light gray circle is the walls standing upright and the juncture where the dark gray aligns with the light gray is the wall/corners of the arena. The black circle represents the middle of the arena which had a circular divot distinguishing it in the actual experiment. The nests are represented by the yellow rectangles, with the circular opening of the nest being shown in its middle. There is a total of 369 clumps shown for all nine trials. Initial observations suggest a tendency for clumps to form against the walls of the nests and the arena, denoted by denser overlapping colors.

## CHAPTER 4

### DISCUSSION

Upon randomized physical decentralization, all nine colonies were able to reunify. This result is as expected as such decentralization is a plausible encounter in nature. If a nest becomes destroyed by natural or man-made disasters, ants may naturally scatter away from the threat, and consequently the colony. These disasters could also forcibly scatter the ants without their intention to scatter. In all cases, the colony would require reunification for survival. Along with this need for survival, reunification is expected as previous house-hunting experiments have shown that colonies can readily emigrate and reunify successfully (Doering, 2016; Pratt, 2010; Pratt, et al., 2002; Richardson, et. al., 2007; Sasaki, et al., 2015). When compared with these simple emigration or reunification experiments, all nine colonies experienced the additional phase of aggregation, with an average of 41 clumps forming per colony per trial. The colonies reached their maximum percent of colony utilization for aggregation (average of 34.8) within the first hour, generally the first 15 minutes. The clumps were found to decrease in frequency as consensus rose, though three trials exhibited more fluctuation than expected or lengthened periods of aggregation.

In the first twenty minutes of aggregation, a larger number of clumps were observed containing fewer items (high frequency, small composition). This was consistent for eight out of the nine trials, with one trial containing a higher composition in the beginning stages. Initial observations of this process showed that the beginning stages produce multiple clumps of fewer items (high frequency, small composition) which combine with other clumps to produce fewer, larger aggregates (low frequency, large composition) until all transports to the new nest are concluded. Four histograms (Figures 4B-4C, and 4G-4H) illustrated this process as observed. However, the other five histograms illustrated that while this process of combination likely still played a role, other processes are likely occurring as well. These processes could possibly include ants transporting clumps directly to the nest, colonies favoring smaller aggregates over those with a larger composition, clumps dissipating altogether, and ants migrating in between multiple clumps. This variation in processes is seen in the increase in standard deviation in Figure



Six showing the average clump size across all trials. While the variation and clump size remain low for the first twenty minutes post-scatter, as aggregation rises and falls colonies seem to differ in their approach to form or lack large composition clumps and methods by which to dissolve these clumps to the final nest site. The average number of clumps for all trials was high for the first twenty minutes, after which point it decreased. Figure Five illustrates this, as well as a decrease in standard deviation post 15 minutes, showing that though the difference in colony size likely affected the variation in the number of clumps forming in the beginning, after twenty minutes all colonies are likely to see a decrease in aggregation.

The locations of aggregates appeared to favor the walls of the nest and arena, potentially for additional protection/stability. Debris was also seen being transported to aggregations, and many clumps seemed to form around locations of debris. This could conceivably be due to the added protection and increase in shade/darkness, as *Temnothorax* colonies are known to prefer a lack of light and to narrow entrances of their nest with debris (Franks, 2003; Franks, et al., 2006; Mitrus, 2019). More research is needed to confirm these findings as the location of debris was not accounted for in Figure Seven and the location of clumps are approximate observations. The majority of clumps, 62.7%, contained at least one brood item. Eight out of nine trials contained brood in over 50% of their clumps. The one trial with brood in 28.3% of its clumps, lacked large amounts of brood to form clumps around. All of the trials, 100%, contained a clump around the queen, possibly exhibiting a protective function of aggregation (Allele, 1931; Deneubourg, et al., 2002). We know *Temnothorax* colonies, especially in comparison with other ants, are more likely to favor protection of queen in emigrations. The fitness costs of losing the queen and brood are likely much higher in *Temnothorax rugataulus* ants than in other ants who can simply reproduce and replace mated workers and thus brood (Doering, 2016; Doering et al., 2016; Franks, et al., 2000; Kaur, et al., 2012). This could potentially explain the involvement of queens and brood in the majority of aggregates.

Of all the nine colonies that reunified, three colonies split relatively equally between the two nest sites, becoming polydomous, illustrated in Figures 2B, 2D, and 2E. If allowed more time these colonies are likely to reunify into a singular nest site. This polydomy is likely a fitness trade-

off for speed verses accuracy. The scattering of the colony produces high duress and it is reasonable that colonies may prefer a speedy retreat to any nest over their current predicament, even if it requires a secondary reunification later (Doering, 2016; Franks, et. al., 2013; Franks, et. al., 2003; Pratt, 2010; Pratt & Sumpter, 2006). However, polydomy is seen in some *Temnothorax* colonies, either seasonally or due to overcrowding (Cao, 2013; Debout, 2007; Doering, 2016; Patridge, et al., 1997; Staut, 1985). The first explanation is more likely than these circumstances, as colony size did not seem to directly correlate with a colony's decision to split and the season is unlikely to play a role in this laboratory setting.

Care was taken to appropriately scatter ants from one another, however it is possible that some ants remained close together or that more ants were closer to a particular nest site and this affected the development of clumps or consensus on a nest site. The benefit of manual counting allowed for observation of the time stamp, both at this time, and at least 10 seconds pre and post. This method is likely to provide a more accurate count as opposed to computer models counting a photographed screenshot, as it is difficult to tell whether ants are simply walking over, transporting/tandem running, or truly part of a clump. Similarly, it is difficult to establish which ants are within the nest for consensus counts, verses simply walking on top of the glass slide. These benefits of manual counting were significant, however, it is always possible that human error affected the counts. Care was taken to mitigate this risk and each trial was counted through twice. As trials were manually counted, locations for the aggregates are approximate. The same care detailed above was taken and a size accurate image of the arena was developed to help increase the accuracy of the location of clumps. Results initially suggest a lack of clumps in the middle of the arena and favored aggregation against walls, though locations may differ from reality in the terms of millimeters, this is unlikely to significantly alter any findings.

This observational study existed to provide a basis for the characteristics observed in the understudied phenomenon of aggregation post physical decentralization in *Temnothorax rugatulus* ants. These results are a significant finding in increasing the knowledge of all steps in house-hunting experiments and providing a more accurate biologic reference of aggregation in fields, like robotics, that are dependent on ant models. Additional studies are needed to solidify

these findings and establish an understanding of the division of labor found within these aggregates. This study found many “lazy ants” around which aggregates tended to form whose resting-time could possibly play a fundamental role in clump formation (Charbonneau, 2017; Deneubourg, et al., 2002). Additionally, transports were seen much earlier than in typical emigrations. This is consistent with the previously understood trade-off between speed and accuracy in high duress situations (Doering, 2016; Franks, et. al., 2013; Franks, et. al., 2003; Pratt, 2010). Overall, further studies focusing on the role of transports and tandem runs in the formation and resolution of clumps is necessary to begin to fully comprehend the process. However, this study is limited to establishing the basic characteristics of aggregations and more studies specific to the division of labor and transport methods are needed to confirm findings.

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