
Exploring Prey Capture Networks in Social Spiders

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Network analysis of animal interactions provides a framework to connect individual level behavior to population level characteristics in a biological system. In this project, we constructed and analyzed prey capture networks of group-foraging social spiders, to determine whether social structure plays a dominant role in group-foraging dynamics of social spiders.

Introduction

Social interactions between animals are often non-random, and exhibit complex interaction patterns influenced by various extrinsic and intrinsic factors like resource availability, the individual's social environment, foraging and anti-predatory behavior. Social network analysis provides a toolbox to decipher the causes and consequences of these intricate social interaction patterns, and link inter-individual association patterns to population level structure [6]. For example, Lusseau et al. (2004) [7], analyzed the social network structure in bottleneck dolphins, to identify key individuals crucial for maintaining cohesion between subgroups. Croft et al. (2008) [8], in their study of Trinidadian guppies, used network analysis to show that individuals associate with each other on the basis of their behavioral traits. Recently, Ruch et al. [11] have investigated how network interactions affect the fitness of the individuals in sub-social spiders, by studying the social network structure of group-foraging sub-social spiders.

Sociality among spiders is a rare phenomenon, which makes it extremely interesting to study the origins and consequences of such behavior in social spiders. Social spiders are observed to hunt in groups,

and show long term behavioral consistency in terms of participation in prey capture [1]. Prey capture requires coordination and interaction between the participants, and therefore, relatedness among the participants may have a direct influence on individual-level behavior observed during group-foraging. In this project, we used a network analysis approach to investigate the influence of relatedness on the dynamics of prey capture observed during foraging trials in permanently social spiders *S. sarasinorum*.

Methods¹

S. sarasinorum reside in colonies, and each colony consists of dense web structures called retreats. Spiders remain inside the retreat, and come out primarily during prey capture or to carry out web maintenance [1]. To investigate whether social structure plays a key role during prey capture in group-foraging spiders, we observed how the interactions among individuals observed during prey-capture change, when participants are closely related, moderately related and completely unrelated. To implement this idea, we conducted foraging trials across three different treatments, where each treatment consisted of a collection of spiders that belonged to:

SCSR Same Colony Same Retreat, or

SCDR Same Colony Different Retreat, or

DC Different colonies

¹The experiments and data collection were performed by members of Dr. Hema's group, and the author was solely involved in analysis of the data.

Treatment	F-ID	n_t	n_u	D	TR	M	$\langle N_S \rangle$	$\langle N_D \rangle$	$\langle A_S \rangle$	$\langle R \rangle$	N_C
SCSR	F09	15	6	0.02	0.15	0.28	0.55	2.2	0.0068	0.06	5
SCDR	F14	13	4	0.03	0.16	0.38	0.77	2.7	0.0098	0.07	8
DC	F13	15	1	0.04	0.17	0.23	0.78	3.5	0.0093	0.08	9

Table 1: Network summary for SCSR, SCDR and DC. Columns — n_t : Number of trials, n_u : Number of Unmarked individuals, D : Network Density, TR : Transitivity, M : Modularity, $\langle N_S \rangle$: Average node strength, $\langle N_D \rangle$: Average node degree, $\langle A_S \rangle$: Average association strength, $\langle R \rangle$: Average rank, N_C : Number of communities excluding isolates.

at the beginning of the experiment. We assumed that individuals from the same colony and same retreat would be more related to each other, compared to spiders that belong to a different retreat; whereas spiders from different colonies would be completely unrelated. Thus, according to our assumption, there are two factors that determine ‘relatedness’ among individuals — geographical proximity and gene flow between the target populations. For the experiment, spiders were collected from colonies in and around Kuppam, Andhra Pradesh. To construct an artificial web, frames of dimension $0.91\text{m} \times 0.91\text{m}$ were constructed, and spiders were allowed to build a web covering the entire frame. See Fig. 1 for details. Each frame hosted two groups consisting of 20 spiders each, at the top-left (TL) and top-right (TR) corners of the frame. These groups either belonged to the same retreat (SCSR), different retreats (SCDR) or different colonies (DC). Further, every spider was uniquely color-coded using three colors (the first indicating the side they originally belonged to, at the start of the experiment), for the purposes of identification during foraging trials.

Feeding experiment

The procedure for feeding trials was similar to that followed in [1]. In short, a live bee was placed at the outset of each trial, approximately at the center of the web, and the ID of the spiders that attacked the bee were recorded in the sequence in which they attacked. Further, the side of the frame (TL or TR) they were observed to come from, during an attack, was noted along with their ID. Furthermore, the location of attack on the bee, and the ID of the spiders who came out of their retreats, but did not participate in the attack were documented. Each trial was recorded for the first 15 minutes; however, if the bee was pulled towards a particular side after the trial ended, the location of the bee was noted. Two feeding trials were performed every day (morning and evening) on a single frame, and the spiders were allowed to repair the web overnight.



Figure 1: The experimental setup consists of a frame which hosts a particular treatment. Two dense web structures visible at the two corners of the frame represent retreats on the frame. During a foraging trial, a bee is placed at the center of frame, and spiders from both sides are seen come out from their retreats and attack the bee.

Statistical analyses

Network analyses were performed using Python and the R programming language [10]. Python codes were employed to parse the raw data and generate the association matrix. These matrices were imported into R, and the subsequent analyses were carried out using the *igraph* package [2] in R. All codes used in this study are available on Github (see https://github.com/soham1112/SNA_preycapture.git).

Building the network

To build the interaction network observed during prey capture, we used the sequence of ID of attack-

ers from data collected during the foraging trials. The nodes in the network represent individual spiders, and edges between the nodes represent the interactions between them. In the context of biological networks, the concept of interaction between two individuals is loosely defined, and often based on spatial proximity. In this study, we quantify associations based on behavioral interactions during prey capture, where the strength of the association depends on the frequency of interaction. We define an interaction to be ‘who followed whom’ during attack². However, we do not take into account the time interval between two attacks³. Due to experimental constraints, we restricted our analyses to use the sequence in which the spiders attack the bee, and constructed pair-wise associations from the sequence. The strength of interaction between two individuals A and B , was calculated using the Simple Ratio Index (SRI) [3]:

$$\epsilon_{AB} = \frac{x}{x + y_A + y_B + y_{AB}}, \quad (1)$$

where ϵ_{AB} represents the interaction strength between A and B ; x denotes the frequency of instances where B was seen to immediately follow A during an attack; y_A corresponds to the number of instances where only A appeared during a trial, and not B ; y_B (similar, except B was seen); and y_{AB} is the number of times y_A and y_B were spotted in a particular trial, but not one after another. SRI gives the same answer as a simple count of co-occurrence, scaled between 0 and 1. We converted the color-coding on each spider to a number between 1 and 40. Thus each spider was numbered 1 to 40, the first twenty (1 – 20) belonged to one side of the frame (TL), and the rest (21 – 40) belonged to the other side in the same frame (TR). Therefore, every frame corresponds to a 40×40 association matrix, which represents a weighted-directed network. Shown in Fig. 2, is a graphical analog of the association matrix for SCDR (F13) — a useful representation which allows us to quickly determine qualitative features of the network. For example, one can easily determine how sparse the association matrix is, where do the majority of the interactions come from, and their relative strengths from the representation.

Further, we did not filter individuals or edges before constructing our network. However, we converted our weighted network into an unweighted binary network to carry out certain analyses (node

degree, network density etc.) that are only valid for unweighted networks. Further, we excluded trials with only one attacker, and did not include unmarked individuals in our analyses⁴.

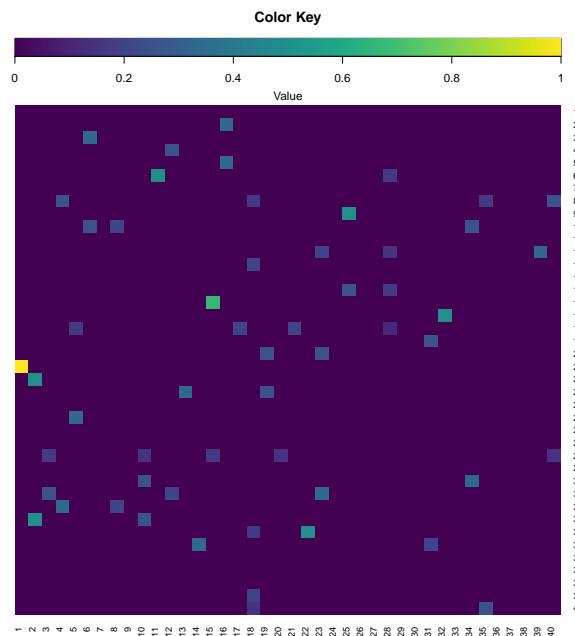


Figure 2: Heatmap of the association matrix for Same Colony Different Retreat (F13). Labels 1–20 and 21–40 represent the two spider colonies from different retreats i.e different sides.

Analyses of node level measures

We computed standard node-level measures like node strength, node degree⁵, betweenness centrality and eigenvector centrality. Further, we checked for behavioral consistency among spiders during prey capture, by noting the number of times a particular individual has been seen to participate in an attack. We also investigated whether spiders who belonged a particular side (TL or TR) in the beginning of the experiment, appeared from the same side during an attack, and enumerated the number of times a spider was seen to switch sides. Furthermore, we assigned a rank to each spider depending on its average position in the sequence of spiders attacking the prey. This can have significant influence on the prey capture network as there is a trade-off involved – early attackers have a higher risk getting injured, but have a higher probability of securing a favorable position

²An attack refers to a spider physically touching the bee.

³A spider who followed its predecessor after 5 minutes, may not be interacting with its predecessor.

⁴This can have a significant impact on the derived network measures, see [3]

⁵After reducing the weighted network to a binary unweighted network

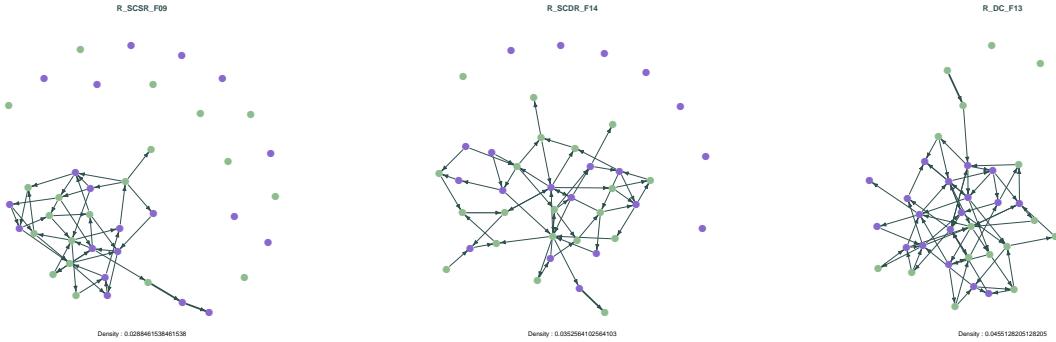


Fig. A: SCSR

Fig. B: SCDR

Fig. C: DC

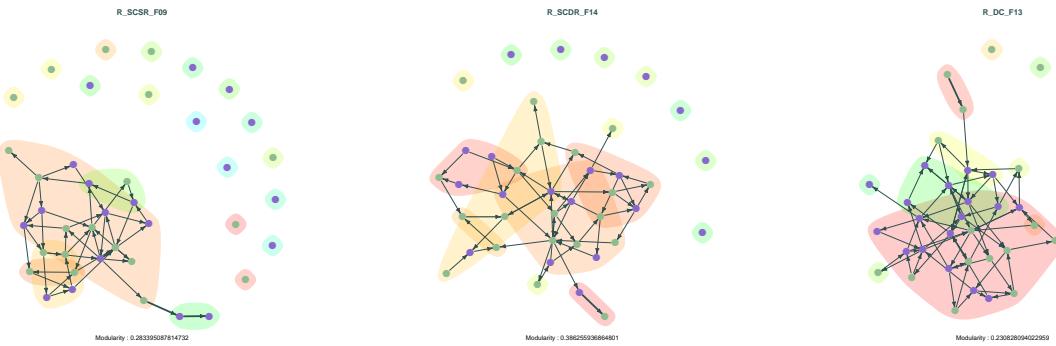


Fig. D: SCSR

Fig. E: SCDR

Fig. F: DC

Figure 3: Network structure represented by Fig. (A, B, C) and community structure shown in Fig. (D, E, F) for SCSR, SCDR and DC. Nodes represent individual spiders, and edges represent the strength and directionality of the interaction i.e the number of times the two individuals were seen to follow each other in a particular order. Nodes representing spiders who belonged to the same side at the beginning of the experiment are of the same color. Further, in community structure visualizations, nodes enclosed by a colored polygon belong to the same community.

while feeding on the bee⁶. We calculated the rank of a spider by averaging over its rank in individual trials. The rank of an attacker in a particular trial was calculated using

$$R_i = 1 - \frac{i}{n}, \quad (2)$$

where i corresponds to the position of the individual in the sequence of attackers, and n corresponds to the total number of participants in the attack. Thus, spiders who attack first, or frequently will have high rank score, compared to a spider who always comes in the end of a trial. We analyzed the correlation between rank of individuals and node-level metrics, specifically betweenness centrality and eigenvector centrality.

Analyses of network level measures

We used the Fruchterman Reingold algorithm [4] implemented as `layout.fruchterman.reingold` in the *igraph* package, for visualizing the network [11]. It is a variant of spring-embedding algorithm, which allows densely connected nodes to be clustered together, and places nodes with few connections at the periphery. To interpret network characteristics, we calculated the network density and clustering coefficient or transitivity for each treatment. We also computed the average degree, node strength, and average association strength.

We assessed the community structure of the prey capture networks and calculated the modularity score for each network. To determine the community structure, we used the `edge.betweenness.community` algorithm present in the *igraph* package for community detection, which is better suited for a weighted-direceted network [1], compared to eigenvector modularity technique commonly used in animal social

⁶There are other factors that can influence this trade-off. For example, the spiders that come first may not inject venom – a rather expensive quantity.

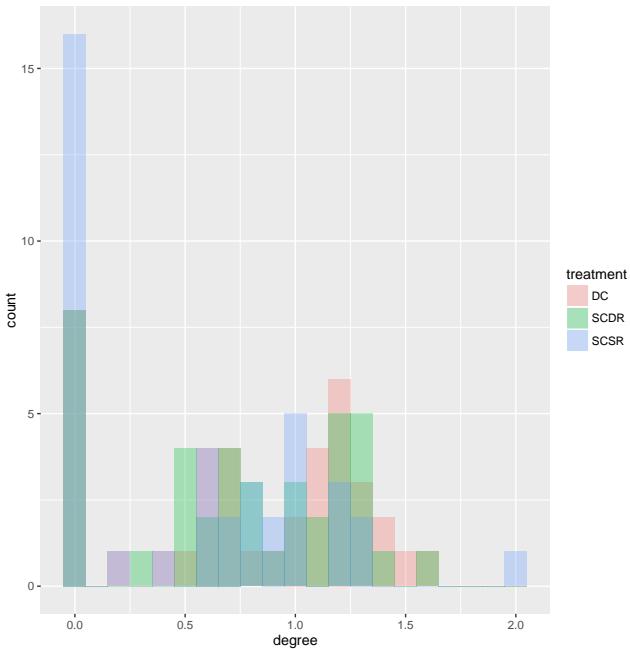


Figure 4: Node degree distribution in SCSR, SCDR and DC.

network analysis. One of the open questions in animal social network analysis is whether enough data has been collected, which can faithfully represent the true network. We looked at the evolution of the network density to get an estimate of the efficacy of the collected data to represent the true network. This is based on the simple assumption that after sufficient trials, the observed network will be a close representation of the true network, and therefore the network density won't change over trials.

Comparison between different treatments

Comparing networks generated by different sets of individuals remains one of the main challenges in animal social network analysis [9], since matrix correlation tests cease to be meaningful in cases which involve different individuals forming separate networks. To compare the different treatments at the network level, we compared the relative frequency of network motifs (triads and dyads) across the three treatments. A dyad consists of a set of two nodes, and the relationship between them can either be mutual or asymmetric, whereas a triad consists of a group of three nodes and there are 16 different ways in which 3 nodes can be connected to each other. For a brief overview of network motifs and their application in biological networks, see [9].

Treatment	% S	S	NS	Unknown	BF
SCSR	40.2	29	37	6	9
SCDR	42.1	32	40	4	15
DC	41.1	37	52	19	16

Table 2: Switch summary – the percentage of spiders seen to attack from a foreign side. Here, % = Percentage switch, S : cases of switch, NS : cases of no switch, BF : instances where the spider is seen to switch back and forth between the sides.

Results

For the purposes of this report, we shortlisted three frames representative of each treatment, which had the highest number of trials and lowest number of unmarked individuals (see Table. 1).

Node level

Node strength distributions (shown in Fig. 4) show that SCSR have lower node strengths compared to DC and SCDR, which, in our context, means that two spiders in SCSR were rarely seen together more than once, and often never. We notice that all treatments show a peak in node strength between 1 and 1.5, which indicates a general trend across all the treatments. Our check for consistency in the attackers revealed that spiders in DC are most consistent in terms of participating in a foraging trial, followed by individuals from SCDR and SCSR.

We observed that in almost 40% of cases (see Table. 2), a spider was seen to come out of a side it originally did not belong to, during an attack, irrespective of the treatment. Further, the number of instances a spider was observed to switch back and forth between sides was found to be the highest in DC. These results show that spiders, irrespective of their initial relatedness, interact with spiders present in their geographical proximity. Hence, in a spider colony, spiders might shift between different retreats, and therefore the population of a retreat may be highly variable. In such case, we will no longer be able to distinguish between the treatments SCDR and SCSR, as spiders from different treatments would mix with each other.

We studied the correlation between rank of a spider in an attack to its eigenvector centrality score. The eigenvector centrality scores represents the potential importance of a node in the network, whereas a high rank score either represents spiders who were among the first to attack the prey, or a spider who has come out often during the trials, but not at the outset. The

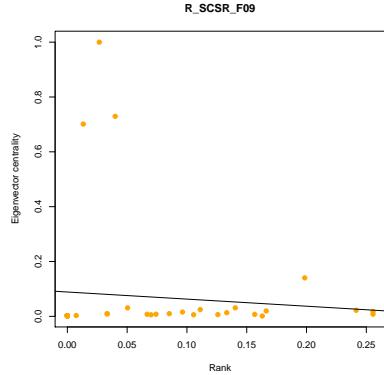


Fig. A: SCSR

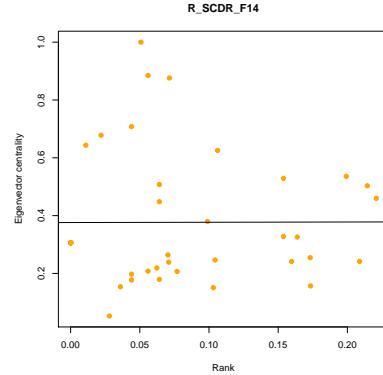


Fig. B: SCDR

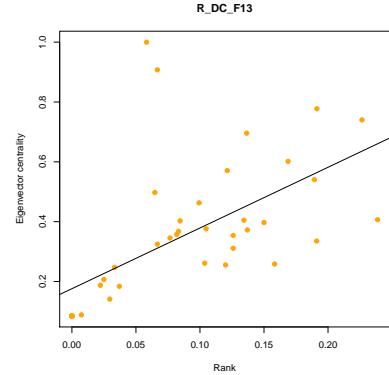


Fig. C: DC

Figure 5: Correlation between rank of attack and eigenvector centrality

results shown in Fig. 5 clearly indicate a difference between the three treatments – we observed negative, zero and positive correlation between eigenvector centrality scores and rank, in SCSR, SCDR and DC respectively. A positive correlation implies spiders who have high ranks i.e attack first, or attack often are the more important in the prey capture network, and their removal will change the computed network measures to a significant extent.

Network level

We summarize the computed network metrics for the three treatments in Table 1. See [3] for an outline of network level measures, and what they mean in a biological context. We found no significant difference between the network density, transitivity and modularity across the different treatments. SCSR showed the weakest connections in terms of average node strength, while DC had the highest average node strength. The average association strength, which represents how many times two individuals have been seen to follow each other in an attack, show the strongest associations to be present in SCDR and DC, and significantly lower in SCSR. These results indicate that spiders in SCSR have few weak interactions, compared to individuals in DC, who seem to interact more frequently with larger number of individuals. In summary, we can say that spiders in DC have a higher participation in the foraging trials, compared to SCSR, which leads to stronger and more number of connections. The average rank, which can be interpreted as a measure of behavioral consistency, showed that the most consistent attackers are present in DC, followed by SCDR and SCSR, which agrees with our previous analysis.

The prey capture networks for the different treatments i.e SCSR, SCDR and DC, are shown in Fig. 3

(A, B and C). There were significantly higher number of isolated nodes (spiders that haven't appeared in any trial) in SCSR, compared to the other two treatments. This may be due to the large number of unmarked individuals that are present in the SCSR dataset. However, even after accounting for the number of unmarked individuals in every trial, we find the number of isolates to be the highest in SCSR, followed by DC and SCDR. This implies that either select individuals participate in foraging trials in SCSR, or we had insufficient data. A closer look at the isolates reveal that in SCSR, the spiders from both sides are seen to contribute almost equally to the number of isolates, whereas in SCDR and DC, a disproportionately large number of isolates belong to one particular side. Further, we observe that the strongest interactions (represented by the thickest lines seen at the periphery) are asymmetric, meaning that strongest associations are highly directional in nature. Fig. 3 (D, E and F) show the community structure in the different treatments. We see that the individuals belonging to a particular community are rarely from the same side, suggesting spiders do not preferentially follow leaders that belong to the same side. Since spiders which are seen to follow each other most frequently would be the part of the same community, we are led to conclude that initial relatedness may not play a dominant role during prey capture.

The evolution of network density with the number of trials for SCSR and SCDR is shown Fig. 6. We observe that both the curves are almost linearly increasing, which suggests that the collected data may be insufficient to determine the true network. Our argument is based on the fact that if our data closely represents the true network, the network density should not change (in this case, increase) dramati-

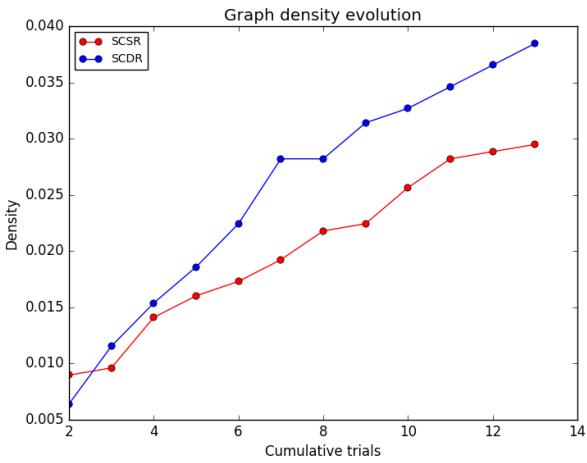


Figure 6: Evolution of network density with the number of trials.

Treatment	Symmetric	Asymmetric	021C
SCSR	0	45	0
SCDR	1	53	29
DC	4	63	114

Table 3: Motif census summary : Symmetric and Asymmetric refer to the dyad census, and 021C refers to the $A \rightarrow B \rightarrow C$ configuration in the triad census.

cally over additional trials, or more concretely, the rate of change of slope of the network density evolution graph should approach zero.

The results of the network motif census are summarized in Table. 3. We found SCSR to have zero mutual connections, whereas the highest number of mutual connections is present in DC. We showcase the numbers of a triad configuration 021C (see [9] for a graphical representation) which showed the maximum variation among the three treatments in Table. 3, column 3. ‘021C’ represents the relational configuration $A \rightarrow B \rightarrow C$. Hence, complete absence of this configuration in SCSR suggests each spider is connected directly to every spider and not through any intermediary. In the context of our experiment, the interpretation reveals that in SCSR, no spider has followed and has been followed by other spiders.

Discussion

We constructed prey capture networks in social spiders based ‘who followed whom’ data collected during foraging trials, and investigated different treatments hosting spider colonies belonging to: same colony, same retreat; same colony, different retreat and different colony. We asked whether there are significant

structural differences in the prey capture networks among the three treatments, and the results from our preliminary analyses are inconclusive, and requires further work.

Our results indicate no appreciable difference between network density and clustering coefficient across the treatments; however, we find that for SCSR, the average node strength is significantly lower than SCDR and DC, suggesting that spiders belonging to the SCSR tend to form weaker and fewer associations, compared to individuals in SCDR and DC. The spiders in DC appeared to be most consistent in terms of participation in an attack. Additionally we found different the correlation between the attack rank of the individual to the eigenvector centrality measure, to vary greatly depending on the treatment. Our observation, that in every frame almost 40% of the individuals are observed to be coming from a side they don’t originally belong to, suggest that spiders are freely moving between the sides, irrespective of the treatment, and hence, from a biological perspective, individuals belonging to the same colony but different retreat may be as related as members of the same retreat. Further, by analyzing the growth of network density over the number of trials, we concluded that more trials are needed to ensure our dataset faithfully represents the true prey capture network.

Future investigations would involve larger number of trials, and inclusion of the comer (spiders who come out during a trial, but do not attack) data, which might shed light on the issue of large number of isolates present in the current networks. The fact that spiders – irrespective of the original side they belonged to – are switching sides freely, necessitates the use of a more robust methodology for constructing associations between individuals, than one being currently used. Furthermore, future analysis can include testing for non-randomness in the observed network, using, for example, the coefficient of variation [5], use of Exponential Random Graph Modeling (ERGM) [9] to analyze the dependence of the observed network structure on the treatment, and an in-depth exploration of triadic motifs and what they might represent in the biological context.

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