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Using multilayer network analysis to explore the temporal dynamics of collective behavior

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Abstract

Social organisms often show collective behaviors such as group foraging or movement. Collective behaviors can emerge from interactions between group members and may depend on the behavior of key individuals. When social interactions change over time, collective behaviors may change because these behaviors emerge from interactions among individuals. Despite the importance of, and growing interest in, the temporal dynamics of social interactions, it is not clear how to quantify changes in interactions over time or measure their stability. Furthermore, the temporal scale at which we should observe changes in social networks to detect biologically meaningful changes is not always apparent. Here we use multilayer network analysis to quantify temporal dynamics of social networks of the social spider *Stegodyphus dumicola* and determine how these dynamics relate to individual and group behaviors. We found that social interactions changed over time at a constant rate. Variation in both network structure and the identity of a keystone individual was not related to the mean or variance of the collective prey attack speed. Individuals that maintained a large and stable number of connections, despite changes in network structure, were the boldest individuals in the group. Therefore, social interactions and boldness are linked across time, but group collective behavior is not influenced by the stability of the social network. Our work demonstrates that dynamic social networks can be modeled in a multilayer framework. This approach may reveal biologically important temporal changes to social structure in other systems.

Key words: collective behavior, dynamic network, multilayer network, multiplex, social stability, *Stegodyphus*

Organisms interact with one another when they cooperate, fight, communicate, mate, move, or forage together. Social interactions can change over time, that is, they are dynamic. These dynamics may emerge from social processes, changes in the external environment, or other processes (Pinter-Wollman et al. 2014). A useful way of studying social interactions is social network analysis (Whitehead 1997; Whitehead and Dufault 1999; Croft et al. 2008). A dynamic network approach can reveal how social interactions change over time and how different factors lead to the formation and dissolution of relationships. Dynamic network analysis can uncover the effect of changes to the network structure on group-level processes such as

the transmission of information and disease (Blonder et al. 2012; Hobson et al. 2013; Pinter-Wollman et al. 2014; Fisher et al. 2017). However, it is not always clear at what temporal scale these changing networks should be sampled and analyzed. Ideally, we would study social networks at the same temporal scale as the biological dynamics we are interested in. Constructing social networks at a longer temporal scale than the biological process would miss the dynamics of the biological process, whereas studying social networks over a shorter timescale than a meaningful change in the biological process would provide information that is invariant or uninformative (Haddadi et al. 2011; Blonder et al. 2012; Farine 2017; Fisher

et al. 2017). We, therefore, need techniques to identify the temporal scale at which biologically meaningful change occurs in social networks, which may provide insights on the mechanisms that underlie the observed changes.

A potential approach to examining the dynamics of social networks is to use a multilayer network approach, in which each layer is a network at a particular time point (Finn et al. 2019). Multilayer networks (Kivelä et al. 2014) have the potential to provide numerous insights in the study of ecology, evolution, and behavior by integrating the full range of social interactions and associations that organisms engage in (Pilosof et al. 2017; Silk et al. 2018; Finn et al. 2019). When representing the dynamics of social interactions as a multilayer network, each layer represents the network at a particular time point and interlayer edges link individuals to themselves in adjacent time points. One can calculate measures such as the Jaccard index (Jaccard 1901) as a measure of the similarity between adjacent time points (see Supplementary Figure S1), but this does not necessarily indicate whether the network is stable over time or if substantial change has occurred. Measuring the multilayer network “reducibility” (De Domenico et al. 2015a) can test whether different layers of a multilayer network represent similar patterns of social interactions, and if they do, whether we can reduce redundancy by aggregating similar networks into a single layer. If social dynamics are stable over time, all layers will contain the same pattern of interactions and therefore will be redundant, justifying the collapse of the network into fewer layers or even into a single layer. If the network is instead highly dynamic, then each layer will contain different patterns of interactions, and so aggregating layers will hide processes that happen at the timescale on which the layers were sampled (see Chan et al. 2013 for an example of different social dynamics at different time points). The reducibility of a network, therefore, indicates the maximum temporal scale at which change occurs and provides a relative measure of the change versus stability of a network over the time frame studied.

Whether the social networks of groups are stable or dynamic can influence the way in which the groups function. Social network structure can influence group dynamics such as collective prey capture (Hunt et al. 2019) and the cohesion of group movement (Bode et al. 2011; Rosenthal et al. 2015). Meanwhile, groups with stable social relationships (e.g., stable dominance hierarchies) are less susceptible to infighting and membership change (Beisner et al. 2015). Without quantitative measures of network stability, it is difficult to assess how changes to interactions relate to other aspects of a group’s phenotype such as efficiency to complete a collective task. The challenges in estimating the relationship between temporal changes in interactions and other group-level outcomes are further compounded by the fact that replication of experimental observations at the level of the group is required, but seldom achieved.

A group’s collective behavior might be determined by a leader, a dominant, or older individual, or an individual with an extreme phenotype (Sih and Watters 2005) often referred to as a “keystone individual” (Modlmeier et al. 2014). For example, elephant groups with older matriarchs are more likely to find seldom used waterholes (Foley et al. 2008), respond differently to unfamiliar individuals, and have higher calving success per female than groups with young matriarchs (McComb et al. 2001). In a dynamic social network, the identity of a keystone individual could change over time. Changes in the identity of the keystone individual might lead to changes in group behavior. Furthermore, if regularly changing the keystone individual disrupts group dynamics, then group behavior may be substantially altered in groups with a changeable keystone individual

compared with groups in which the identity of the keystone is stable.

An individual’s centrality in a network may relate to its influence on the collective behavior of the group. For example, grey reef sharks *Carcharhinus amblyrhynchos* that have shorter mean association durations with others are more likely to act as leaders (Jacoby et al. 2016). In a dynamic social network, the centrality of each individual may change over time and the mean or variation of the centrality value may represent an important social trait that indicates the individual’s influence on the group. Multilayer network analysis allows one to calculate measures of network centrality that integrate information across time points (Silk et al. 2018; Finn et al. 2019). When the layers in a multilayer network represent different kinds of interactions, measures of centrality that account for connections within and between layers can identify different individuals as central compared with “monolayer” measures that only account for a single type of interaction, or measures of centrality based on aggregates of all layers (Finn et al. 2019). The same could be true for temporal networks analyzed in a multilayer framework; measures of centrality that integrate across all layers may highlight different individuals as being highly central, and therefore more influential compared with approaches based on a single network layer.

To examine the impact of network temporal dynamics on individual and collective behaviors we analyzed freely available data on temporal networks in multiple groups of the social spider *Stegodyphus dumicola*. We asked: 1) Is the time scale of change in a social network slower, faster, or equivalent to the time scale on which interactions were measured? 2) Does the stability of the network, and/or the consistency of the identity of a keystone individual in a group, relate to collective behavior? 3) Do different measures of an individual’s network position over time relate to the mean or variability of an individual’s potential influence on collective prey attack speed?

Materials and Methods

We used an existing dataset on social interactions of individually identified social spiders (Pinter-Wollman 2020) associated with Hunt et al. (2019). These data were previously used by Keiser et al. (2017) to examine global network structures (density and modularity) and Hunt et al. (2018, 2019) to determine the relationship between social interactions and both individual and collective behaviors. None of these studies used a multilayer network approach to examine temporal dynamics. In short, the data we used comprised 24 experimental groups of 10–11 adult female *S. dumicola*, whose resting interactions were observed 3 times a week for 6.5 weeks resulting in 19 interaction networks per group. Hunt et al. (2019) defined an interaction as a physical contact between any body parts of 2 spiders while stationary in the retreat web (see also Keiser et al. 2017; Hunt et al. 2018). Interactions were recorded as either present or absent (i.e., the network at each time point was binary). Resting interactions can influence the spread of cuticular bacteria (Keiser et al. 2016) and the speed prey attack (Hunt et al. 2019).

Multilayer network

To construct a multilayer network from the resting interaction data, we connected the 19 interaction networks from the 19 different time points for each of the 24 groups by linking individuals to themselves in adjacent time points. Interlayer edges were therefore present only

between adjacent time points. All networks were symmetrical, that is, both edges $A1 \rightarrow B1$ and $B1 \rightarrow A1$ were present. Inter-layer self-edges were also symmetrical, so both edges $A1 \rightarrow A2$ and $A2 \rightarrow A1$ were present.

Collective behavior

The measure of collective prey attack was the groups' latency to respond to vibrations on their capture web, a commonly used assay for quantifying colony prey attack in social spiders (Hunt et al. 2019; Lichtenstein et al. 2019). Hunt et al. (2019) used a custom-made vibratory device based on an Arduino board (described in Pinter-Wollman et al. 2017b; Hunt et al. 2019; Wright et al. 2019) to vibrate a 1 cm × 1 cm piece of paper to mimic a struggling prey animal (Hedrick and Riechert 1989). The latency until the first spider touched the paper was recorded as the "latency to attack." The trial continued until spiders attacked the paper or until 600 s elapsed. If no spider attacked the paper by 600 s, the latency to attack was set to 600. For more details on procedures, see Hunt et al. (2019). Each group was tested once per week, after every 3 recordings of resting interactions, giving 6 measures of collective predation behavior.

Boldness measures

In *S. dumicola*, the presence of bold individuals (those that resume movement quickly after a simulated predation threat) can increase how quickly colonies collectively attack prey (Keiser and Pruitt 2014), and therefore increase the mass a colony gains (Lichtenstein et al. 2017). Boldness is therefore a predictor of an individual's influence on colony collective behavior. The measure of boldness of individuals is the time in seconds for a spider to move one body length after experiencing a puff of air from an infant nose cleaning bulb (see Riechert and Hedrick 1993; Hunt et al. 2019). Faster times indicate greater boldness. In isolation, boldness is highly repeatable ($r = 0.63$; Keiser et al. 2014) but in a social setting, boldness is dynamic and depends on the boldness of individuals that one recently interacted with (Hunt et al. 2018). Boldness was measured once before groups were set up, and once a week thereafter, after every 3 recordings of resting interactions, giving 7 measures of boldness per individual (unless the individual died during the study, see Supplementary Figure S2, mean number of measures per individual = 6.20, SD = 1.31).

As noted above, these data have been previously analyzed and published (Keiser et al. 2017; Hunt et al. 2018, 2019). There is some overlap in question between the previous and the current study, as Hunt et al. (2018) looked at change in the networks over time but they did not consider the timescale of network stability. Furthermore, Hunt et al. (2019) related the boldness of the keystone individual to its number of connections. However, we related the boldness of all individuals to their number of connections and ask a series of questions about temporal stability that was not explored by Hunt and colleagues. Finally, our approach uses a completely different and novel methodology in the form of multilayer network analysis. Therefore, the current study extends previous work, both in terms of the questions asked and the methodology used.

Data analysis

Q1. Assessing the reducibility of multilayer networks

To determine social structure stability and the time scale over which changes in the group social networks happen (Q1), we assessed the

structural reducibility for each group (De Domenico et al. 2015a) in the R package "muxViz" (De Domenico et al. 2015b). The reducibility analysis gives a measure of the difference in patterns of interactions in the multilayer network with 1) all layers, 2) versions of the network with gradually more and more layers aggregated, and 3) a network where all layers have been aggregated into one (the "fully aggregated network"). Reducibility determines whether aggregating 2 or more layers can be carried out without a loss of variation, or whether layers need to be kept distinct to maximize the amount of variation in a given multilayer network. "Variation" is defined here as the Von Neumann entropy of the network, which is an extension of the Shannon information entropy, from information theory, to measure the mixedness of a network (see Supplementary Materials and De Domenico et al. 2015a for more information).

When considering temporal dynamics, an unchanging social network can be reduced to the aggregate of all layers without obscuring differences among layers, whereas reducing the multilayer network of a highly dynamic group would lead to a loss in the observed variation in the system (a lower Von Neumann entropy). We performed the reducibility analysis for each group and determined the optimum number of layers that needed to be retained for each group to maintain the largest amount of variation, and the rate of loss of variation due to aggregating layers. We predicted that some layers could be aggregated without the substantial loss of variation, but otherwise had no specific predictions. Note that when individuals die (which occurred in all social groups, see Supplementary Figure S2) there will be fewer interactions in the network, necessarily giving a lower Von Neumann entropy. Furthermore, smaller networks might be more similar to one another than networks with more individuals, so the likelihood to lose variation when aggregating 2 networks decreases as networks shrink in size.

Q2. Relating the stability of group network structure and the identity of its keystone individual to collective behavior

To determine the impact of social stability on collective behavior (Q2), we calculated a group's stability as the difference in Von Neumann entropy between the full multilayer network (with no aggregation) and the fully aggregated network for each group (hereafter "relative entropy"). Higher values indicate there was more variation among layers over time, and so less stability (more details are given in Supplementary Materials). We view this variation as a latent variable of "social stability," which is present at all times, even if the actual changes in the network are only realized at later time points. We then related relative entropy to the mean attack speed and the coefficient of variation ("CV"; SD/mean) of attack speed of the group. We used a Spearman's rank correlation, as the variables were non-normal and could not satisfactorily be transformed toward normality. We predicted that more stable groups (lower relative entropy) would attack prey more quickly (lower mean latency) and at more consistent speeds (lower CV), resulting in positive correlations between a group's relative entropy and mean and CV of attack speed.

To determine how the stability of the identity of the keystone individual in a group influenced collective behavior (Q2—second part), we first defined the keystone individual in each group in each week as the individual with the highest boldness score in that group (Pinter-Wollman et al. 2017b). If all group members scored a 0 for boldness on a certain week, then no individual was assigned as the keystone for that week ($N = 26$ out of 168, 15.5%). We then

counted how often each individual was defined as a keystone for a given group across the 6 weeks. Our measure of the stability of the keystone's identity is the highest of these counts for each group. For example, if one individual had the highest boldness in 2 weeks, and 4 different individuals had the highest boldness in the other weeks, the group would be assigned a score of 2. If a group had a different keystone individual each week, it was assigned a score of 1. Scores ranged from 1 to 3 because no individual maintained a keystone position for more than 3 weeks. We compared the mean and the CV of prey attack speed among groups with keystone stabilities of 1, 2, or 3 with a Kruskal–Wallis test, because the distributions of the response variables were non-normal and could not be satisfactorily transformed toward normality. Pinter-Wollman et al. (2017a) found that replacing the keystone individual in groups of *S. duminicola* does not reduce prey attack speed, and so we predicted that groups with more stable keystone individuals would not necessarily have faster mean attack speeds or less variable attack speeds.

Q3. Relationship between an individual's network position and its influence on group behavior

Our final analysis aimed to measure the relationship between an individual's potential influence on the network (boldness) and different measures of social connectivity (Q3). As a measure of network centrality analogous to overall connectedness in monolayer networks, we calculated the mean of each individual's degree (number of unique connections) for each time point it was alive. We then calculated the CV for each individual of these degree scores as a measure of the variability of their network centrality. To determine the integrated centrality of an individual, accounting for their position in all layers simultaneously, we calculated the eigenvector versatility (EV) for each individual in muxViz. This measure of centrality accounts for both an individual's direct connections and its indirect connections, and considers connections across all layers, giving a measure of how well-connected an individual is across all layers (see De Domenico et al. 2015b for further details). For our measures of influence on group behavior, we calculated both an individual's mean boldness and the CV of its boldness across the 7 measures of boldness. Because being the “boldest” individual in a group depends on the boldness of others (Hunt 2018), we used a relative ranking for both boldness and centrality scores when examining the concept of social influence rather than the absolute values of these traits. To create a ranking for each of the individual-level measures (3 network metrics and 2 behaviors), we subtracted the group means for the measure from the individuals' values.

To assess how the different measures of network position are related to each other, we estimated the pairwise correlations between the 3 network position measures (relative mean degree, relative CV of degree, and relative EV). We expected that mean degree and EV would be positively correlated as they both represent general tendencies to be central in a network. We had no prior expectation as to how CV of degree would relate to mean degree or EV. To then relate these individual network measures to individual boldness measures (Q3), we correlated each network measure with each of an individual's relative mean boldness and its relative CV of boldness, giving 6 correlations. For all correlations, we used Spearman's rank correlations. Previous studies on *S. duminicola* have found no correlation between the boldness of individuals and their number of connections (Keiser et al. 2016; Hunt et al. 2019) and so we predicted no association between the mean or the CV of degree and mean boldness. We did however predict that individuals with a higher mean and CV of degree would have a more variable boldness, as

individual boldness scores depend on previous social interaction partners (Hunt et al. 2018), therefore many different social interactions could give more variable boldness scores. As we expected EV and mean degree to be positively correlated, we expected EV to have similar relationships with the mean and CV of boldness as mean degree.

To account for the nonindependence of network data (Croft et al. 2011), we conducted permutations to determine the statistical significance of the observed correlation between individual behaviors and network measures. We permuted node labels, maintaining edges because we were interested in the relationship between the social position of individuals and their attributes. Using these permutations, we obtained distributions of 1,000 correlations between boldness scores and network measures. If the ρ of the observed correlation was greater or smaller than 97.5% of the randomized values, we concluded that the observed correlation was significantly different from 0.

Results

In total, there were 4,605 interactions, 192 ± 23.8 (mean \pm SD) interactions per group and 242 ± 45.6 interactions per time point across all groups, giving an average of 10.1 ± 4.65 per group per time point. Fewer individuals were alive at later time points (Supplementary Figure S2), giving fewer interactions at later time points (Supplementary Figure S3). The rate of interactions per individual did not decline substantially over time (Supplementary Figure S4).

Q1. Reducibility of temporal networks

The reducibility analysis revealed that, in the majority of groups, all layers should be retained because aggregating layers reduces relative entropy. Therefore, observing the interactions of spiders every 2–3 days is a temporal scale that can capture changes in social interactions. All but 2 groups showed a peak in relative entropy at 19 (the maximum) layers and a largely linear decrease as layers were increasingly aggregated together (Figure 1). The linear decline in variation indicates that no one layer is more different from the other layers than any other layer. Two groups (BR10-9 and BR3-5) showed peaks of in relative entropy at a degree of aggregation of 1, that is, 2 layers of the 19 could be aggregated. Figure 2a shows network plots for the 19 time points for 1 of these groups (BR10-9), and Figure 2b shows a dendrogram illustrating the similarity of different network layers for this group. Equivalent plots for the other group showing a redundancy of layers (BR3-5) are shown in Supplementary Materials (Supplementary Figures S8 and S9).

Q2. Effects of the stability of the group and its keystone individual on collective behavior

Groups that had more variable networks (those with a larger difference between the fully aggregated network and the multilayer network with no aggregation) did not have different mean attack speeds compared with less dynamic groups (Figure 3A; Spearman's rank correlation: $\rho = -0.092$, $P = 0.690$), or higher or lower CVs of attack speed (Figure 3B; Spearman's rank correlation: $\rho = -0.107$, $P = 0.653$). Groups that had the same keystone individual for 1, 2, or 3 weeks did not have different mean attack speeds (Supplementary Figure S5a; Kruskal–Wallis test: $H = 0.602$, $df = 2$, $P = 0.740$) or higher or lower CVs of attack speed (Supplementary Figure S5b; Kruskal–Wallis test: $H = 0.289$, $df = 2$, $P = 0.866$).

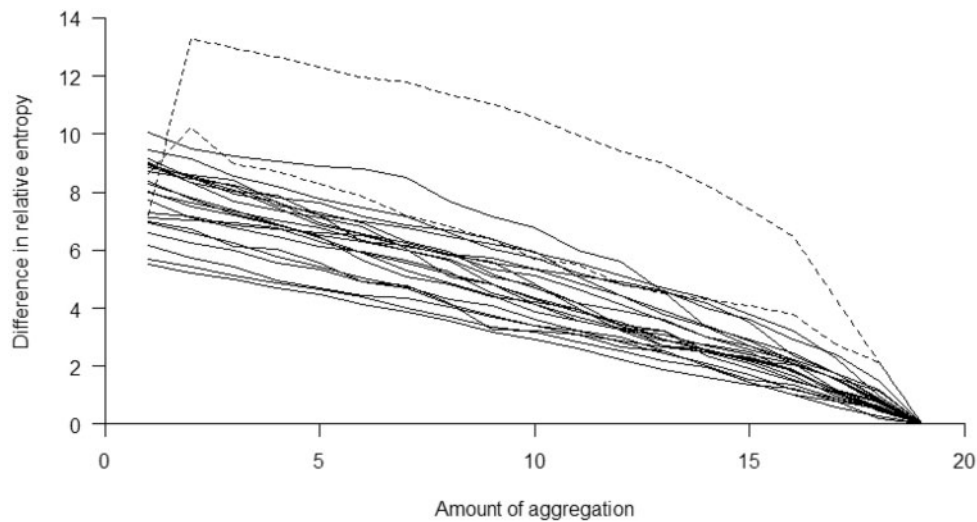


Figure 1. The change in relative entropy in the multilayer network as layers gets aggregated in the reducibility analysis. Each line represents 1 of the 24 groups. Complete multilayer networks are on the left of the plot and completely aggregated networks are on the right. Twenty-two groups showed an approximately linear decline in relative entropy with increasing layer aggregation, suggesting that all networks are approximately equal in their variability. For 2 groups (dashed lines), aggregating 2 layers was supported as it did not lead to reduced relative entropy. These were time points 11 and 13 for group BR3-5, and time points 8 and 13 for group BR10-9.

Note that one group never attacked the stimulus, and another group only attacked it once, giving 23 and 22 records for mean and CV of latency to attack, respectively.

Q3. Individual-level versatility and behavior

The different measures of centrality represented somewhat different aspects of sociality as they were not perfectly correlated. Relative mean degree and relative CV of degree were strongly negatively correlated (Figure 4A; Spearman's rank correlation: $\rho = -0.806$, $P < 0.0001$), whereas relative EV was positively related to relative mean degree (Figure 4B; Spearman's rank correlation: $\rho = 0.439$, $P < 0.0001$) and much less so to relative CV of degree (Figure 4C; Spearman's rank correlation: $\rho = -0.115$, $P = 0.088$) see Supplementary Figure S6 for histograms that contrast the randomized and observed values.

Some measures of centrality related to boldness, but others did not. An individual's relative EV was not related to either its relative mean boldness (Figure 5A; Spearman's rank correlation: $\rho = 0.018$, $P = 0.898$) or the relative variability of its boldness (Figure 5B; Spearman's rank correlation: $\rho = 0.013$, $P = 0.820$). Individuals with relatively more connections had higher relative mean boldness (Figure 5C; Spearman's rank correlation: $\rho = 0.144$, $P = 0.030$), but did not have relatively more variable boldness (Figure 5D; Spearman's rank correlation: $\rho = 0.108$, $P = 0.154$). Individuals with relatively more variable connections had lower relative mean boldness (Figure 5E; Spearman's rank correlation: $\rho = -0.135$, $P = 0.032$), but we did not detect a significant relationship between variability of connections and relative variability of boldness (Figure 5F; Spearman's rank correlation: $\rho = -0.106$, $P = 0.150$). See Supplementary Figure S7 for histograms that contrast the randomized and observed values.

Discussion

We examined how temporal dynamics of social interactions over 40 days, modeled as multilayer networks, relate to both collective

and individual behaviors. First, we found that the temporal scale of change in the network was at most 2–3 days and could occur over shorter timescales (Q1). Second, we found that the amount of change each network underwent over time did not relate to the mean or the variability in collective attack speed (Q2). Furthermore, and congruent with previous work (Pinter-Wollman et al. 2017b), consistency in the identity of the keystone individual did not relate to either mean or variability of prey attack speed. When examining individual level attributes (Q3), we found that bolder individuals, who influence colony collective attack speed, had a higher mean and less variable number of connections. However, an individual's variability in boldness was not related to any of our network measures, and a multilayer measure of network centrality was not related to an individual's mean or variability in boldness. Taking a multilayer approach to temporal network analysis, therefore, uncovered some novel insights, as well as recapturing results obtained in other studies.

We found that the temporal multilayer networks constantly changed at a time scale of 2–3 days. Note that our analysis sets the upper limit for time scale that is worth considering; it is possible that meaningful change is occurring at even shorter time scales. The multilayer networks therefore should not be aggregated into static networks because each time point possesses unique patterns of social interactions. We conclude this because, for 22 of the 24 multilayer networks, we observed a largely linear decline in the relative entropy as we aggregated network layers compared with keeping a multilayer network with each time point distinct (Figure 1). (De Domenico et al. 2015a) found a reducibility pattern similar to the one we observed in a scale-free network that had an increasing percentage of edges (from 5% to 95%) randomly swapped to create new layers. The similarity of our reducibility analysis findings to those from a randomized procedure does not necessarily indicate that spiders are interacting at random, but it does mean that random interactions could explain the patterns we observed. The lack of set patterns of interactions shows that spiders do not possess preferred associates (e.g., Gero et al. 2015). The networks of groups in which some aggregation was supported (Figures 2; Supplementary Figures

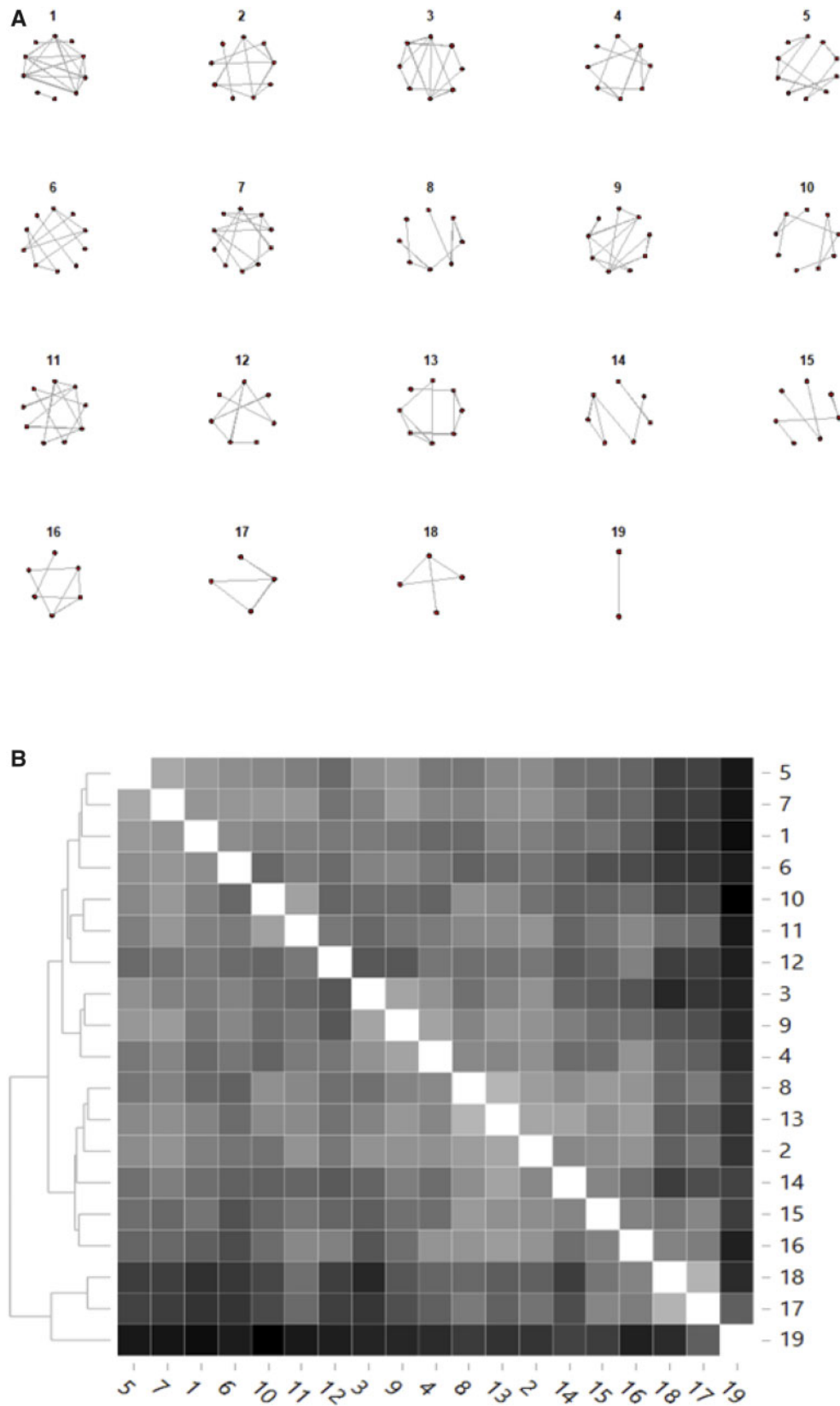


Figure 2. (A) Interaction networks for group BR10-9. Points represent individuals and lines represent social interactions. Time points are plotted left to right, top to bottom, so the 1st row is the 1st–5th time points, the 2nd row are time points 6–10, and so on, with the time point number shown above each network. (B) Similarity among different time points of the group BR10-9. In the correlation matrix, each cell represents the similarity between 2 layers, with darker shades indicating more dissimilar networks. Layers 17–19 are considerably dissimilar to the rest of the network. The dendrogram on the x-axis demonstrates that these later time points are clustered separately compared with the rest of the network.

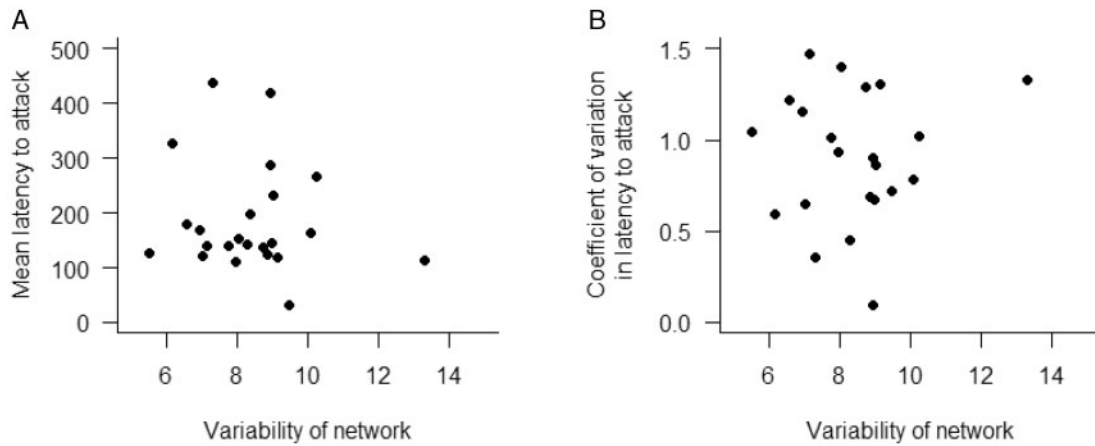


Figure 3. Relationship between network variability (defined as the difference in Von Neumann entropy between the fully aggregated network and the network with all layers maintained) and collective prey attack. (A) Network variability shows no relationship with mean latency to attack prey for all groups. (B) Network variability shows no relationship with variation in latency to attack prey for all groups. Each point is a social group, $N=23$ in (a) and 22 in (B).

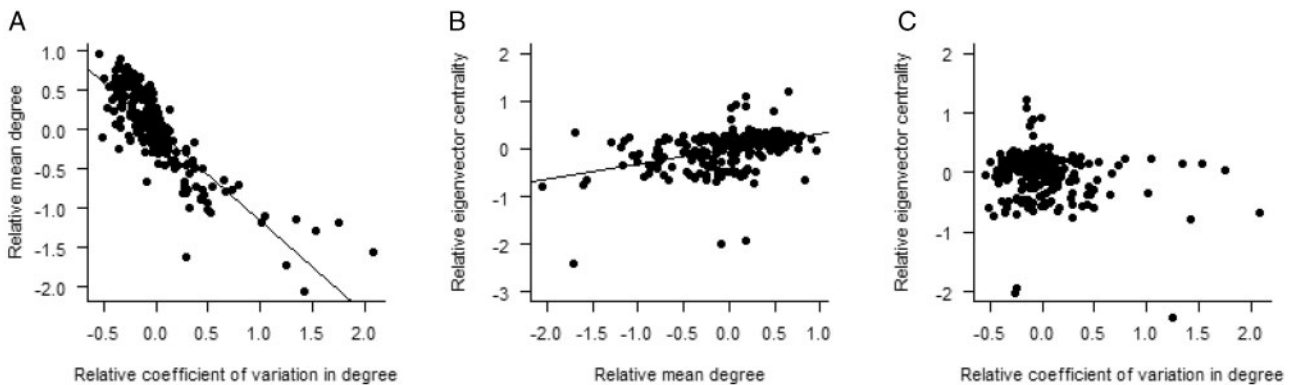


Figure 4. Relationship between measures of centrality. (A) Relative CV of degree and relative mean degree, (B) relative mean degree and relative EV, and (C) relative CV of degree and relative mean degree. Lines of best fit are drawn when there was a statistically significant correlation between the 2 variables. Each point is an individual spider, $N=241$.

S8 and S9) show that there is similarity in network structure among the networks that can be aggregated. We recommend examining the reducibility of multilayer networks to determine if there are redundant layers before aggregating all or some of them. We also note that assessing reducibility on 24 networks each with 19 layers involves testing many times partly aggregated networks against a fully aggregated network, and so there is perhaps the possibility of some false positives. We, therefore, encourage the development of null expectations of network redundancy given various rates of change in social interactions over time.

The highest entropy representation of the networks was in their full multilayer form, that is, without any aggregation. These findings are similar to other studies of multilayer networks of social animals in which the layers represent different social situations rather than different time points (Smith-Aguilar et al. 2019) found that interactions among Geoffroy's spider monkeys *Ateles geoffroyi* in the social situations of aggression, contact, association, embrace, grooming, and proximity were not redundant when represented as different layers in a multilayer network, and so the layers should not be collapsed into a single network. Perhaps as the number of studies of multilayer networks of animal social interactions increases, we will find conditions in which layers can or should be aggregated. For

example, when comparing protein–protein networks of different species, for example, *Mus musculus* and *Candida albicans*; De Domenico et al. (2015) found that some layers could be aggregated, but in other species (e.g., *Caenorhabditis elegans*) aggregation of layers would lead to the loss of relative entropy. In the 2 groups, we identified redundant layers there were 3 or 4 time points (17–19 and 16–19) that were distinct from the rest of the layers (Figures 2; Supplementary Figures S8 and S9). These 2 groups experienced a fundamental change in their network size around these times—the number of individuals was reduced from 9 individuals in Week 5 to 2 or 3 individuals in Week 7. The number of individuals in a network typically influences its structure and changes to group size not surprisingly altered network structure to produce a series of layers that were different from the rest of the layers. The reducibility analysis, therefore, pinpointed observations that are distinct from others. In addition, there was a positive correlation between the number of individuals that died in a group and the group's entropy score (Spearman's rank correlation, $\rho = 0.57$, $S = 982$, $P = 0.003$). The ability of the reducibility analysis to identify such changes suggests that this analysis could be used to identify times when fundamental changes occur in a social group, for example, transitions between states, or tipping points (Flack et al. 2005; Flack et al.

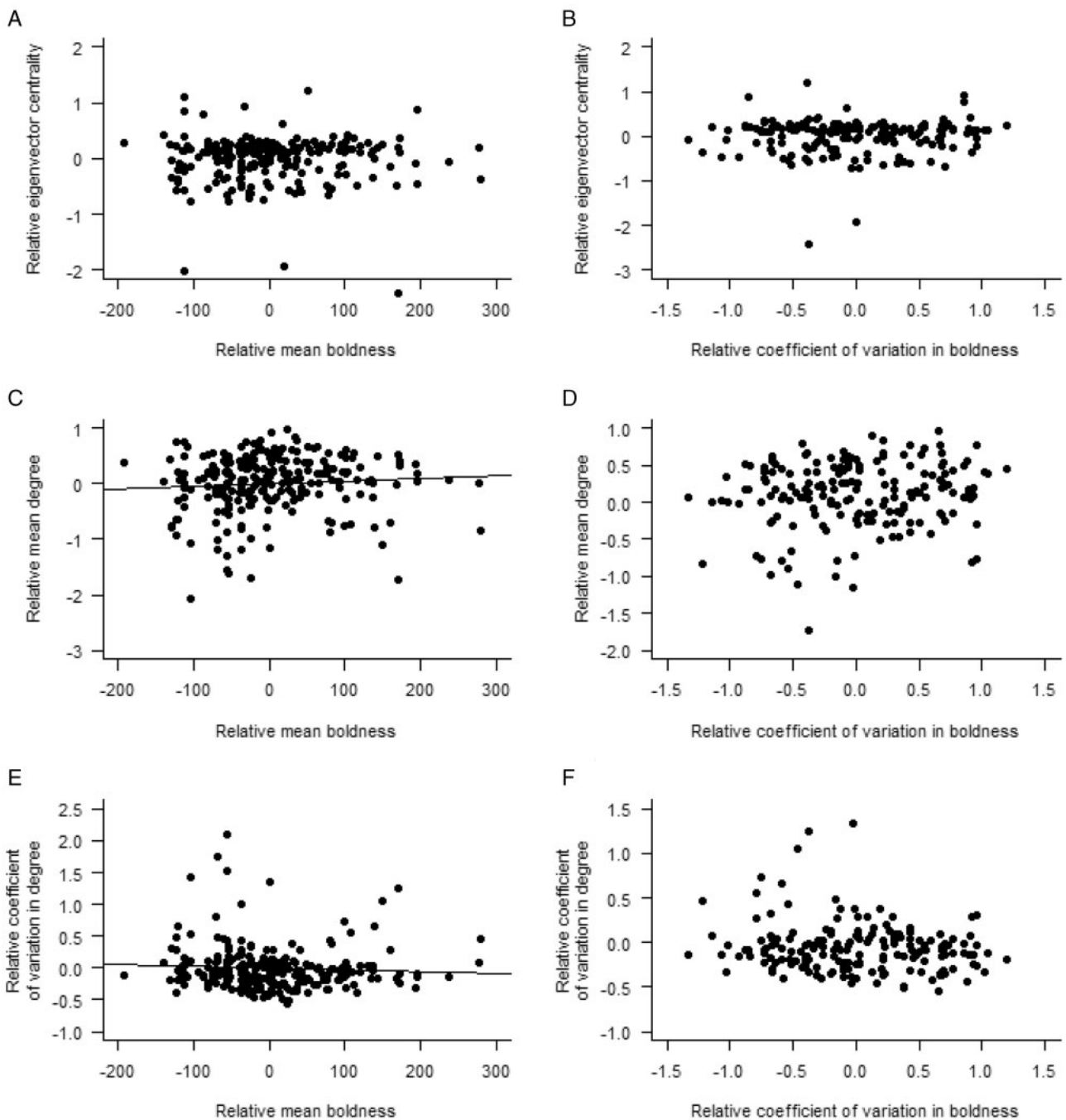


Figure 5. Relationships between relative mean boldness and (A) EV, (C) relative mean degree, and (E) relative CV of degree; and between relative CV of boldness and (B) EV, (D) relative mean degree, and (F) relative CV of degree. Lines of best fit are drawn when there was a statistically significant correlation between the 2 variables. Each point is an individual spider, $N=241$.

2006; for a review see Pruitt et al. 2018). Applying these methods to more time series of social network data, especially some that undergo fundamental changes, will help determine if indeed reducibility analysis is a general way with which to detect gross change in patterns of social interactions.

The stability of the social structure of a group did not relate to either the mean or the variance in prey attack speed. Hunt et al. (2019), who analyzed the same set of observations, found that it was only the social network immediately before the trial that influenced prey capture rather than interactions 2 or 4 days before the

prey capture trial (Hunt et al. 2019). Here we further demonstrate using reducibility analysis that group social networks are constantly changing in *S. dumicola*. This strengthens the conclusion that this species lacks a consistent network structure that determines groups' attack speed, but instead that group attack speed is contingent on the social network properties only immediately prior to a prey capture event. It remains to be determined what processes underlie the changes in interaction patterns over time. Using these data, Hunt et al. rejected the hypothesis that social interactions are influenced by the boldness of interacting individuals. However, other processes,

such as movement patterns and the spatial constraints imposed by the nest structure that influence these movements may determine which individuals interact with one another (Pinter-Wollman 2015a, 2015b; Pinter-Wollman et al. 2017a). The stability of the identity of the keystone individual did not influence prey attack. This result agrees with previous studies showing that experimentally changing the identity of the keystone individual does not affect prey attack speeds (Pinter-Wollman et al. 2017b). In other systems, where other members of a group may not be able to assume the role of a keystone easily (if the keystone possesses a hard-to-obtain phenotype such as unique knowledge; McComb et al. 2001; Brent et al. 2015), stability in the identity of the keystone individual may be much more important.

We found a positive relationship between boldness and number of social associations. This finding is opposite to the relationship between boldness and social interactions in eastern grey kangaroos *Macropus giganteus* (Best et al. 2015) and 3-spined sticklebacks *Gasterosteus aculeatus* (Pike et al. 2008). *Stegodyphus dumicola* tend to assort negatively by boldness, that is, bolder individuals associate with less bold individuals (Keiser et al. 2016). Given that bold individuals are much less common than shy individuals (Pinter-Wollman et al. 2016), this skewed boldness distribution will result in bold individuals having many shy individuals to associate with, giving them a high degree. The association between boldness and variance in degree that we observed likely reflects the same process, because degree is negatively correlated with variance in degree. The positive relationship between boldness and degree may facilitate the influence of bold individuals on colony collective behavior. Note that Keiser et al. (2016) did not find a relationship between boldness and degree in 9 groups of 10–30 *S. dumicola*. However, their groups comprised subadults rather than the adults used in our study, and subadults are more plastic in their social behavior than adults (Hunt et al. 2019). Hunt et al. (2019) did not find a relationship between the boldness of the keystone individual and its degree in the same set of observations analyzed here. However, we used all individuals to test for an association between boldness and degree, whereas Hunt et al. (2019) focused only on the boldest individual in each group. Therefore, the larger sample size we used could have led to our statistically significant but weak relationship, which might suggest only a modest biological importance for this relationship.

We did not detect an association between EV and individuals' boldness scores. This was despite EV being correlated with mean degree, which was itself associated with mean boldness. The lack of a significant relationship suggests that EV captures a different aspect of social behavior compared with mean degree, and perhaps an aspect that does not relate to an individual's influence on the group. Finn et al. (2019) identified several ways in which multilayer network analysis can provide additional insights to monolayer network analysis in animal behavior (see also Pilosof et al. 2017 for ecological networks). However, it should not be surprising that some multilayer network measures do not provide the best representation of some aspects of a system. For example, analyzed the same set of observations we analyze here using stochastic actor-oriented models, a tool for analyzing temporal networks (Fisher et al. 2017), and obtained a separate set of insights that we could not reach using a multilayer network analysis. On the other hand, we estimated measures of whole-network stability that Hunt et al. did not, and related those to measures of group collective action. The range of findings goes to show that social interactions are highly multidimensional and that there is not a single analysis technique that can extract all possible insights from a given set of data. We stress that not every

network analysis needs to be multilayer, but considering a multilayer approach to network analysis, including the analysis of temporal networks, might be beneficial for certain systems and questions.

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Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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