



Networks never rest: An investigation of network evolution in three species of animals

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ABSTRACT

Despite considerable advancement in the study of network evolution, three basic limitations are common to the data collected: (1) examining a small number of networks, (2) not observing networks from scratch, (3) not collecting time-stamped, continuous records of all interactions among all members of groups. Here, we avoid these limitations by observing all aggressive interactions leading to network formation from the moment of introduction among all members of 45 groups of four individuals each in three species of animals: chickens, cichlid fish, and mice. We apply several recently developed methods for the visualization and analysis of network evolution to these unique datasets. We discover, first, that network evolution is a remarkably dynamic process across all three species: networks do not evolve to specific structures and then remain in those configurations. Instead, we find dynamic stability in which many groups continually return to a general class of structures. Second, we find considerable similarity across species in the pathways that the groups take through different possible network configurations as they evolve. Third, we show that transitive component triads are more stable than intransitive ones. Fourth, we track the evolution of individual ranks within groups and discover that many individuals do not have stable positions. Finally, we discuss fundamental questions that our findings raise for the study of networks in both animals and humans.

1. Introduction

Most of the early work in social networks examines cross-sectional or static network structures. However, networks are inherently dynamic, and researchers have increasingly recognized that cross-sectional analyses provide only limited views of the actual social processes that generate the forms and operation of these structures. In response to this recognition, a number of researchers have investigated the evolution of networks in both small and large groups, and they have created accompanying methods to explain the development of network structures. Despite these recent substantive and methodological advancements, three limitations still remain in the way that most network data sets are collected.

The first limitation is that most studies have examined only one or a very small number of networks. Without investigating a considerable number of networks of one type, it is difficult to know whether the dynamics observed are unique or more generalizable to other networks.

Second, many networks have not been observed from scratch, that is, from the initial introduction of group members and when the networks first begin to form. If groups are not observed from their beginnings, researchers are limited to truncated records of network evolution, and they cannot understand the initial phases of network development. Third, many studies of network evolution have not collected time-stamped, continuous records of network interaction among all the members of groups. For example, many organizations provide only aggregated, yearly snapshots of network interactions among their members. In these cases, researchers cannot see the timing of interactions within the periods for which the data are aggregated and can only report coarse patterns of network evolution (e.g., Barabási et al., 2002; Garlaschelli and Loffredo, 2005; Gu et al., 2019; Rosenkopf and Padula, 2008). In other cases, particularly in small groups of humans and animals, researchers have not had the technical means to record all the interactions among all the members of a group at the same time. In response, they have had to use focal individual sampling, selecting

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single individuals in succession, and only record the selected individual's network interactions with other individuals (e.g., Daniel et al., 2019; Schafer et al., 2010). Whatever the cause, the lack of complete, time-stamped records of interaction for all group members prohibits researchers from detecting the accurate evolution of ties in whole networks or in their component parts.

In this paper, we avoid these limitations by presenting a study of network evolution based upon aggressive interactions in three species of animals: chickens, cichlid fish, and mice. In precluding the first limitation, we observed a total of 45 groups of four individuals each establishing networks: 14 in chickens, 17 in cichlid fish, and 14 in mice. In response to the second limitation, we recorded interactions in the groups from the moment of introduction for a period of two days in the chickens and fish and three days in the mice. All the individuals in each group were previously unknown to each, or if they had been in the same group earlier, they had been separated for a period sufficient for them to forget one another (Chase, 1982).

In circumventing the third limitation, we recorded *all* instances of aggressive interactions occurring among *all* the members of a group using specified sets of behaviors most appropriate for each species (see the Methods for more detail). This method resulted in the recording of hundreds of interactions in the chicken and mice groups and over 10,000 in some of the fish groups. Each interaction was time stamped giving us continuous records in time order of the interactions in each group (see the Methods for more details). As far as we are aware, these are the longest, time stamped, continuous records of network evolution in small, face-to-face groups observed from introduction in either humans or animals (but some studies have collected quite long, time stamped records of network interaction in large human groups using electronic means, e.g., Kossinets and Watts, 2006; Leskovec et al., 2008; Viswanath et al., 2009).

Our unique data sets allow new insights into the ways in which networks evolve. For example, we can assess the details of group network evolution and the dynamics of interaction that propel that evolution. We can identify the ways in which groups follow similar or different pathways as they evolve through the state space of possible network configurations. We can chart the level of stability of network structures in the groups and whether those structures reach stable configurations or continually change over time. Our data sets also allow us to look at the dynamics of interaction in the component triads, pairs, and individuals that make up the groups. We can determine the stability of transitive and intransitive triads and the interaction processes that convert transitive triads into intransitive ones as well as the converse. And we can evaluate the stability, or instability, of the structural positions – the ranks – of individuals in their groups.

In discovering these insights, we employ and extend several recently developed methods for the visualization and analysis of network evolution (Chase, 2006; Coelho et al., 2019; Doreian, 2006; Lindquist and Chase, 2009). These methods indicate the extent and kind of dynamic processes in network formation at the group level, in component triads, in pairs within triads, and in the ranks of individuals.

The preview of our discoveries, as our title implies, is that network evolution is a very dynamic phenomenon at all levels: the group, triads, pairs, and individual positions.

1.1. Research background

Virtually all the early studies of network evolution examined small groups. Some examples are the development of networks in college students by Newcomb (1961); in school children by Coleman (1961), Hallinan (1974, 1979), Sørensen and Hallinan (1976), and Leinhardt (1973); in monks by Sampson (1969); and in groups of chickens by Chase (1982). Most of these studies investigated only one or a small number of networks and were not able to record data from the introduction of group members. However, Newcomb (1961) recorded relationships in a group of young men from the start of a college year, and

Chase (1982) observed groups of chickens from introduction.

More recently, researchers have investigated the evolution of networks in both large and small groups. Some examples using larger networks include investigations of social networking sites (Backstrom et al., 2006; Leskovec et al., 2008; Kwak and Kim, 2017; Viswanath et al., 2009); scientific collaboration (Backstrom et al., 2006; Barabási et al., 2002); international trade relationships (Garlaschelli and Loffredo, 2005); venture capitalists (Gu et al., 2019); students, faculty, and staff at a large university (Kossinets and Watts, 2006); firms in the mobile communications industry (Rosenkopf and Padula, 2008); and scientific conference participants (Zhao et al., 2011). Examples of recent investigations of network evolution in smaller groups include studies of preschool groups (Schafer et al., 2010; Daniel et al., 2019) and international migrants (Lubbers et al., 2010; Ryan and D'Angelo, 2018).

Like earlier studies, many of these more recent studies investigated only one or a small number of networks (although not examining network evolution, some studies have collected data on large numbers of networks, e.g., Osgood et al., 2013; Kim et al., 2015). This is understandable given the difficulty of collecting network data, and because in some cases, such as the evolution of networks on major social media platforms, there is only one or a very small number of networks to study.

Most of these studies also did not observe groups from scratch, but there are some exceptions such as Kossinets and Watts (2006) and Schafer et al. (2010) that investigated networks from the beginnings of university or school years. Not observing groups from their beginnings is also understandable since the formation of new groups, especially large ones, that will establish networks is relatively rare. And rarer still is the access of network researchers to these groups. One way around this limitation is to establish groups in experimental settings (see, e.g., Newcomb, 1961; Chase, 1982), but this is largely limited to groups with smaller numbers of individuals.

Many of these studies did not have access to time-stamped, continuous records of network interaction among all the members of groups. For example, Barabási et al. (2002), Garlaschelli and Loffredo (2005), Gu et al. (2019), Rosenkopf and Padula (2008) collected information from organizations that only provided aggregated data of interactions among group members on a yearly basis. This meant that they were forced to infer processes of evolution from longitudinal, yearly snapshots of the networks. Other studies (e.g., Daniel et al., 2019; Schafer et al., 2010) relied on focal individual sampling to collect their data and thus had limited views of network evolution in their groups taken as wholes.

Along with their descriptions of network evolution in both large and small groups, researchers have developed a variety of methodological tools to account for the mechanisms that might explain the development of network structures. For example, see Sørensen and Hallinan (1976), Wasserman and Iacobucci (1988), Doreian and Stockman (1997), Barabási and Albert (1999), Robins and Pattison (2001), Barabási et al. (2002), Burk et al. (2007), Leskovec et al. (2008), Snijders (2011), Ghoshal et al. (2013), Richards and Wormald (2014), Chase and Lindquist (2016), Niezink et al. (2019). Researchers have used these tools to analyze network evolution in data that have the weaknesses we have described, but many approaches could just as easily be applied to data that do not have them. In the Discussion, we consider the application of these tools to the data we present here.

The study of network evolution has greatly advanced in the last 20 years from its beginnings in the last century. Despite this advance, there are major limitations in the kind of data that are currently used to investigate the evolution of networks. We suggest that overcoming these limitations will help us gain a deeper and more accurate understanding of how networks form and change. The goal of our work here is to give an example of how that can be achieved when these limitations of data are eliminated.

2. Methods

2.1. Choice of animals and interactions recorded

Chickens, cichlid fish, and mice represent three different taxa in the animal kingdom. The evolutionary line leading to cichlid fish split from that for chickens and mice about 350 million years ago, and the one for mice and chickens separated about 300 million years previously. Consequently, their social systems have evolved separately. This allows us to evaluate our results across three independent data sets.

Our study tracks the evolution of networks based upon aggressive interactions rather than upon “dominance relationships”. Dominance relationships are usually defined by aggregating series of aggressive interactions and thus obscure the detailed dynamics of network evolution which we are investigating here. See Section 3.4, “Dynamics of individual ranks”, below, for more information on the differences between networks based upon aggressive interactions and dominance relationships.

2.2. Animal methods

We provide brief descriptions of the methods we used for observing the three species of animal groups here. More detailed information is provided in Appendix A.

We observed 14 groups of four white Leghorn hens for six hours each day for two consecutive days. The hens were separated by partitions when they were not being observed. We recorded all instances of aggressive behaviors involving physical contact among the hens using a personal computer. We monitored 17 groups of four female cichlid fish of the species *Mylandia lombardoi* for 12 h one day and six hours the next. The fish were separated by partitions when not being observed. We

recorded all instances of the following aggressive behaviors: threat, chase, and nip. We logged the behaviors from video records using a custom-written, voice-recognition program. We used 14 groups of four male mice bred for laboratory work. The mice were placed in an enriched cage system and two video cameras recorded their behavior. Using the video records, we logged the winner and loser in every aggressive interaction occurring during the first 72 h of assembly for each group.

2.3. Network states, network state space, paths through network state space, and state variants

In our analysis of the evolution of network ties, we use and extend the methodology developed by Lindquist and Chase (2009) in their original analysis of the development of networks in chickens (also see Doreian, 2006). Our methodology reveals how groups initiate, maintain, and change their network ties from the moment of introduction until observation ends. Each tie represents an aggressive act directed from one individual toward another. We define a *network state* as each possible configuration of ties among the members of a group. The set of all possible network states is the *network state space*. A *path* is the route that a group takes through network state space. It consists of the successive network states that a group traverses as its network forms and changes. Fig. 1 shows the network state space for the 41 states that are possible for groups of four individuals (not counting state 0 which is the configuration before the individuals are introduced). More generally, this is the state space that is possible for groups of four individuals forming networks with asymmetric ties (and in which only the most recent tie between pairs is counted). For example, consider a group of chickens in which the first several interactions after introduction are: 1 pecks 2, 3 pecks 2, 1 pecks 2, 1 pecks 4, and 4 pecks 1. This group takes

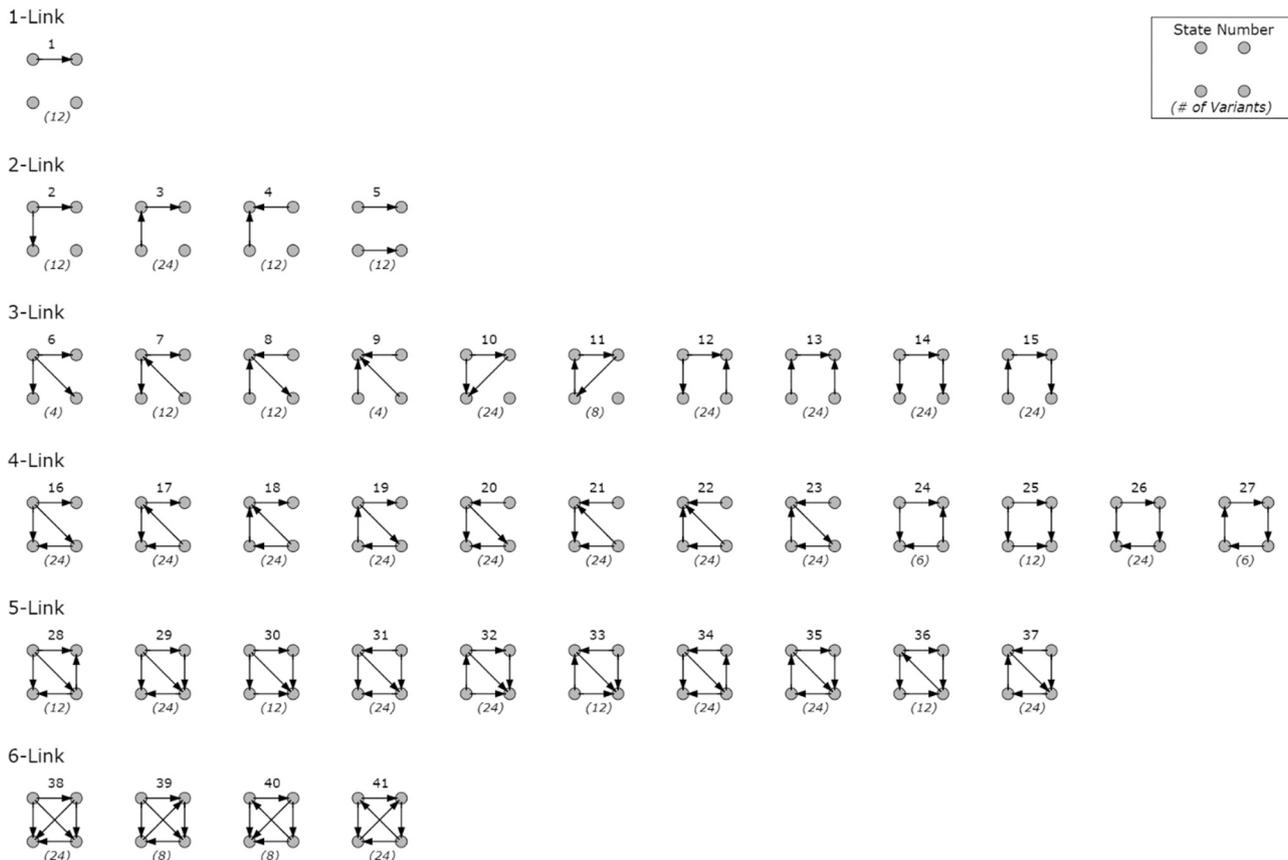


Fig. 1. The network state space for the 41 states that are possible for groups of four individuals (not counting state 0 which is the configuration before the individuals are introduced).

the following path: state 0, state 1 (1 pecks 2), state 4 (3 pecks 2), state 12 (1 pecks 4), and state 13 (4 pecks 1). The third act in the sequence of acts, 1 pecks 2, repeats the previous direction of the tie between 1 and 2 and does not move the group to a new state. In contrast, the last act in the example, 4 pecks 1, does change the direction of the tie between 1 and 4, and consequently does move the group to another state (see Fig. 2).

In tracking a quad through state space, we consider that a tie is formed at the first occurrence of an aggressive act between a pair. If subsequent acts repeat the direction of the first act between a pair, the state of the group does not change. However, as in the example above, a subsequent behavior that does change the direction of attack in a pair – a “pair-flip” – reverses a tie and moves the group into another state. Thus, the state of a group of four individuals, indicates the most recent directions of attack between all the pairs in the group which have interacted.

Each line of Fig. 1 shows the states in the same “link class”, that is, all the states that are possible with the same number of asymmetric ties. Each time a pair in a quad interacts that has not interacted before, the quad moves to a new link class that is 1.0 higher than its previous class. A pair-flip can in some cases move a group from one state to another in the same link class, but not from a state in one link class to one in another link class (see Lindquist and Chase, 2009 for more details).

The 41 states represent only the possible structural configuration of asymmetric ties in groups of four and do not take into account the identity of the individuals. That is, two configurations of ties are the same if they differ only in vertex relabeling. An example using state 38 can make this clear. Consider two groups. In the first, the interaction record shows that the latest attacks are: 1 has attacked 2, 3, and 4; 2 has attacked 3 and 4; and 3 has attacked 4. In the other, 2 has attacked 1, 3, and 4; 1 has attacked 3 and 4; and 3 has attacked 4 (see Fig. 3). Both of these groups are in state 38, but individuals 1 and 2 have swapped places. In the first group, 1 attacks everyone else, and in the second 2 does. We define the “variants” of a state as the set of all the possible vertex relabelings of the state. That is, variants have the same structural configuration of ties but (at least two of) the individuals have different structural positions. (What we call variants are known more formally in graph theory as isomorphism classes.) Thus, in the example, the two groups show different variants of state 38. We use a standard method to label the variants of a state, so that a particular variant of a state has the same configuration of ties in all groups. The number of all possible variants for each state is shown in parentheses under Fig. 1. (All possible variants for each network state are provided in the Supplementary Material.)

The use of states and not distinguishing among the variants of a state reduces the number of network configurations to a more manageable level and allows certain analyses that would not be feasible if the identities of the individuals were preserved. However, in other analyses, where it is possible, we do consider the number of state variants that a group transitions through. That is, we do analyze a group’s movement through versions of a state in which the individuals vary in their positions within the state. Also see this website <https://darius-coelho.github.io/PeckVis/>

for additional analyses using all state variants. Directions for using the website are given in this YouTube video: <https://www.youtube.com/watch?v=2s44L6STf6o&feature=youtu.be>.

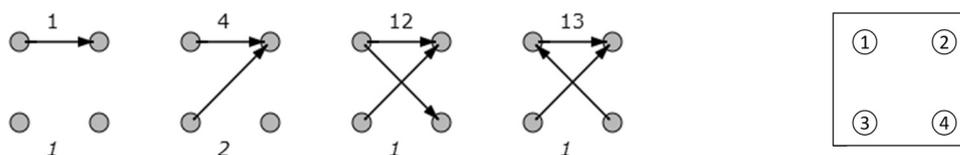


Fig. 2. An example showing the states created for the interaction sequence 1 pecks 2, 3 pecks 2, 1 pecks 2, 1 pecks 4, and 4 pecks 1. The number above each state indicates the state number and the number below each state indicates the number of interactions that the group stays in that state. The box on the right indicates the node positions of the individuals ranked 1,2,3, and 4.



Fig. 3. An example showing two variants - 1 and 7 - of state 38. Here the difference between the two is that the interaction between individuals 1 and 2 are reversed.

[com/watch?v=2s44L6STf6o&feature=youtu.be](https://www.youtube.com/watch?v=2s44L6STf6o&feature=youtu.be).

2.4. Statistical methods

In this paper we are evaluating the stability of network structures and describing the dynamics of network evolution. We use our three independent data sets to explore the level of robustness in our findings. But we are not primarily interested in distinctions among the three species, and consequently, we do not employ statistical tests to examine any possible differences. As much as possible, we present the raw data (e.g., the frequency of total interactions in different network configurations) and descriptive statistics. However, in keeping with our aim of discovering the processes of network evolution, we do employ statistical tests to determine if certain sequences of interaction in component triads and pairs differ from random.

For each species, we performed two randomization tests. The first determined whether the initial structures in the component triads in the groups of a species were more frequently transitive than expected by chance (see Section 3.2 for more details). The initial structure of a triad was determined by its configuration when the last tie in the triad first formed (between the third pair in the triad). In the test, we first generated a set of networks for each species based upon random interactions in four individuals. In the random networks, each interaction was a random attack between two randomly selected individuals (either x attacked y or y attacked x). The size of the set of networks was the same as the number of groups we observed in that species (n = 14 for chickens and mice and n = 17 for fish). We determined the total number of interactions in each random network by approximating the distribution of total interactions for groups in each species and drawing a random number from that theoretical distribution. This process was repeated 10,000 times. We then computed the total number of initially transitive triads out of all triads within the random networks for each species for each of the 10,000 replications. We calculated the p-value for each species by determining how many times out of the 10,000 replications the groups in the random networks had a total number of initially transitive triads greater than or equal to the observed value.

The second randomization test examined whether transitive triads, once formed, were more likely to be converted into new transitive triads than into intransitive triads at a rate higher than expected by chance (see Section 3.2 for more details). (The term “intransitive triad” appears commonly in the animal dominance literature and in some studies of human friendship networks. In graph theory, such triads are referred to as “cyclic”.) We followed a randomization process analogous to the one described above. Using this process, we compared the observed proportions of transitive triads converting to new transitive triads in a

species to the proportions generated in the simulations. We calculated the p-value for each species by determining how many times out of the 10,000 replications the triads from the random networks had a proportion of transitive-to-transitive transitions greater than or equal to the observed value.

We also used Wilcoxon tests to examine the pairs of individuals involved in converting transitive triads to new transitive triads and intransitive triads to transitive ones (see Section 3.2 for more details). For each species, we calculated the proportion of each type of pair-flip that occurred within each quad. We then determined if the proportions for all quads in each species were significantly different from chance by performing a one-sample Wilcoxon test against 0.50 for transitive-to-transitive transitions (where there two potential pair-flips) and 0.33 for intransitive to transitive transitions (where there are three potential pair-flips).

3. Results

3.1. Group-level analysis

3.1.1. Number of interactions per group and visual display of interaction records

We begin our analysis by presenting some basic information about our data sets: numbers of interactions in the groups and visual representations of their interaction records. Fig. 4 provides bar graphs of the total number of interactions recorded per group and median values for the three species. This figure shows that network evolution in all three species is a dynamic process: group members interacted hundreds, and in the case of fish, thousands of times during their observation periods.

Fig. 5 shows visual representations of the complete records of interaction in two selected groups in each species using music notation graphics (Chase, 2006; Lindquist and Chase, 2009; Coelho et al., 2019). For each species, the graphs display the groups with the highest and lowest number of interactions. Music notation graphs illustrate the act-by-act evolution of networks in small groups and provide an indication of the volume and complexity of interaction during the development of networks. These visualizations allow researchers to take advantage of our considerable human abilities of visual pattern recognition and to perceive processes of interaction during network evolution that they might not be able to recognize in simple listings of behavioral acts.

In music notation graphs, horizontal lines represent an individual

animal through time. The lines are arranged from top to bottom according to the David’s scores of the individuals at the end of their group’s observation record. A David’s score calculates the dominance rank of an individual based upon its record of attacking and being attacked by other individuals while taking into account the relative successes of its opponents in attacking and being attacked by other group members (see David, 1987; David, 1988; Gammel et al., 2003 for more details). Arrows indicate aggressive acts from one individual to another. They go from the initiator’s line to the receiver’s, and they are in the color of the initiator (green for the top line, orange for the second, blue for the third, and purple for the fourth). Arrows pointing down represent acts from higher-ranking to lower-ranking individuals, and those pointing up represent acts from lower- to higher-ranking individuals.

Time runs from left to right in the graphs and is measured by interactions rather than clock time. Given various species differences, such as frequency of interaction and the necessarily different sizes and layout of group housing, we determined that using interaction time, rather than clock time, would be best for standardizing comparisons among the species. For example, in the first chicken group, Quad 12, at the beginning of interaction, chicken 1 attacks all the others and chicken 3 occasionally attacks chicken 4. (We refer to the groups of four individuals as quads.) Later in the record chicken 2 attacks 3 and 4. Some examples of music notation graphs using clock time are provided in Chase (2006) and Lindquist and Chase (2009).

We have compressed these music notation graphs, especially for the fish, to show them on one page. (This website <https://darius-coelho.github.io/PeckVis/> allows the music notation graphs to be viewed in less compressed form, and this YouTube video <https://www.youtube.com/watch?v=2s44L6STf6o&feature=youtu.be> explains how to use the website.) But even with the compression, the graphs give an idea of the dynamism and complexity of interaction during network evolution. Certain patterns, such as bursting (Lindquist and Chase, 2009), in which one individual attacks one or more other individuals several times in a row, are also readily apparent. The closed black circles above the graphs indicate changes in the network structure which we analyze immediately below.

3.1.2. How dynamic is network evolution?

Here we investigate the number of structural variations that groups go through from introduction until observation ends. We count all states and variants. For example, a chicken quad evolves through the following

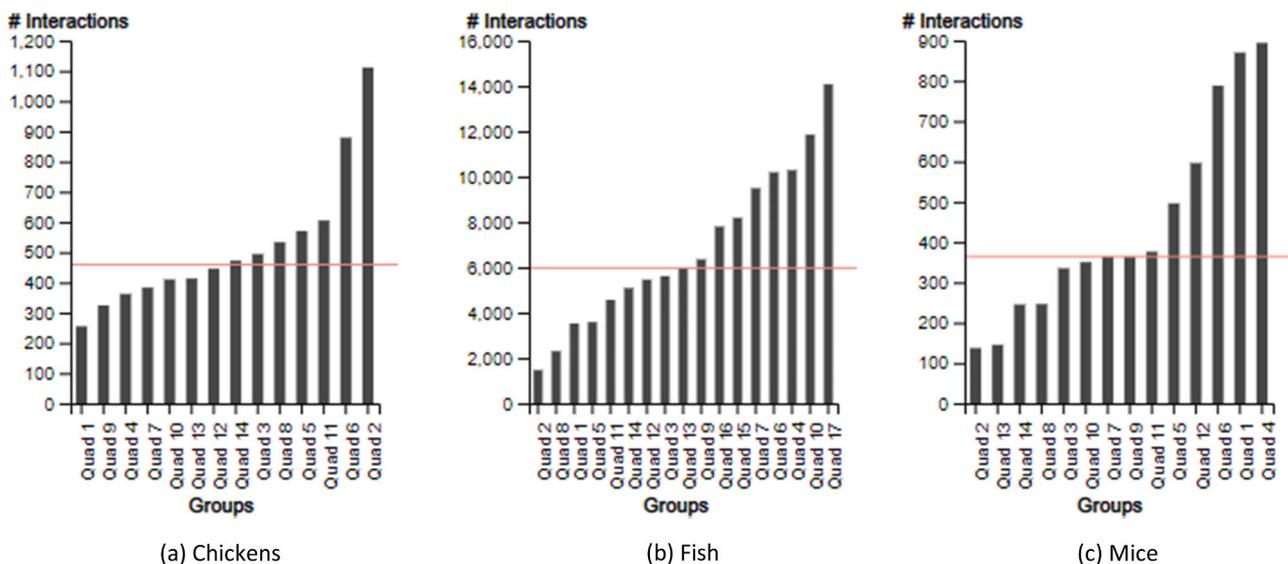


Fig. 4. Bar graphs of the total number of interactions recorded per group and median values (horizontal line) for the three species – chickens, fish, and mice. Note that the number of interactions shown on the y-axis is different in each bar graph.

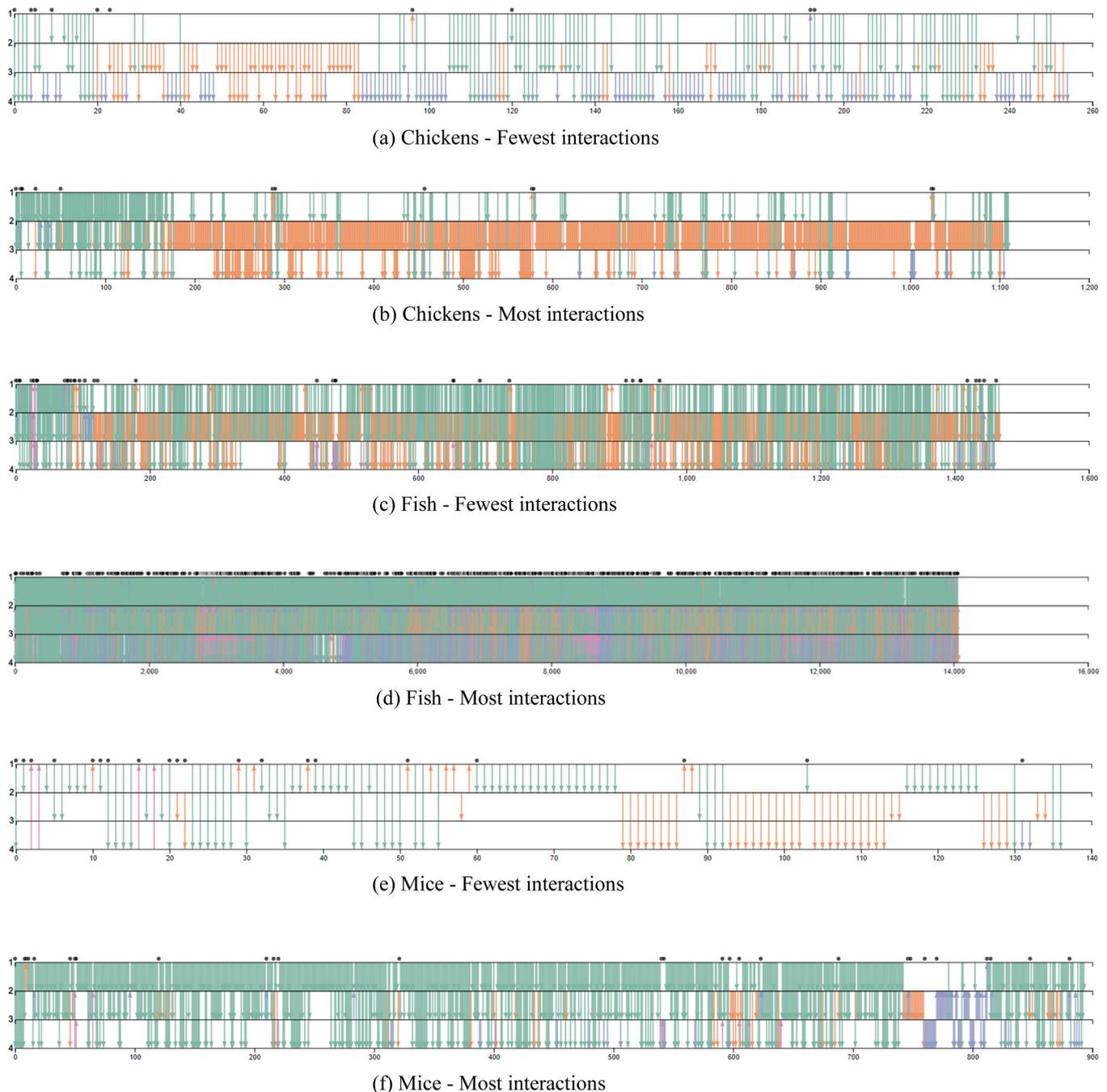


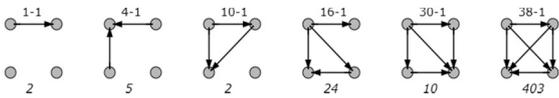
Fig. 5. Music notation graphs for the groups with the fewest and the most interactions in each of the three species - chickens, fish, and mice. The closed black circles above the graphs indicate changes in network structure.

states and variants: state 1, state 2, state 6, state 28, state 38 (variant 1), state 39, state 38 (variant 1), and state 38 (variant 2). This quad progresses through 8 structural variations counting the two times it is in state 38 (variant 1) and the one time it is in state 38 (variant 2).

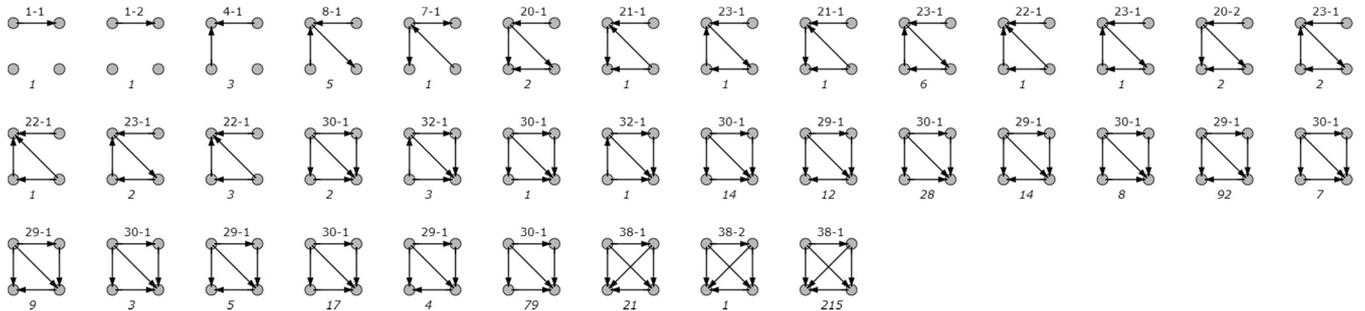
Fig. 6 displays the actual records of network evolution for the chickens and mice quads with the largest and smallest number of structural changes and the fish group with the smallest number of changes. The figure also shows the number of interactions that the groups spent in each structural configuration. Fig. 6 only presents the fish group with the smallest number of changes (40) because displaying the fish group with the largest number of structural transitions (1056) would exceed the space available. However, the records of network evolution for each quad in the three species, including the number of interactions a quad spent in each structural form, are available on

<https://darius-coelho.github.io/PeckVis/>. Fig. 7 provides a bar graph for the number of structural changes in groups for the three species over the course of network evolution. Chickens have considerably fewer structural transformations than fish and mice, and fish also have considerably more transformations than mice.

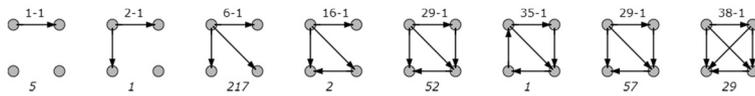
The number of structural changes occurring in the groups can be compared to the minimum number of changes that a group must go through to first reach a 6-link state. That number is 6. This number is achieved when a group moves directly through the successive link classes without ever visiting more than one variant in a link class. For example, a group starts upon introduction with no ties (the 0-link state) moves to some variant of a 1-link state, then directly to some variant of a 2-link state, then again directly to some variant of a 3-link state, etc. In contrast, if a group started in the 0-link state, moved to one variant of a



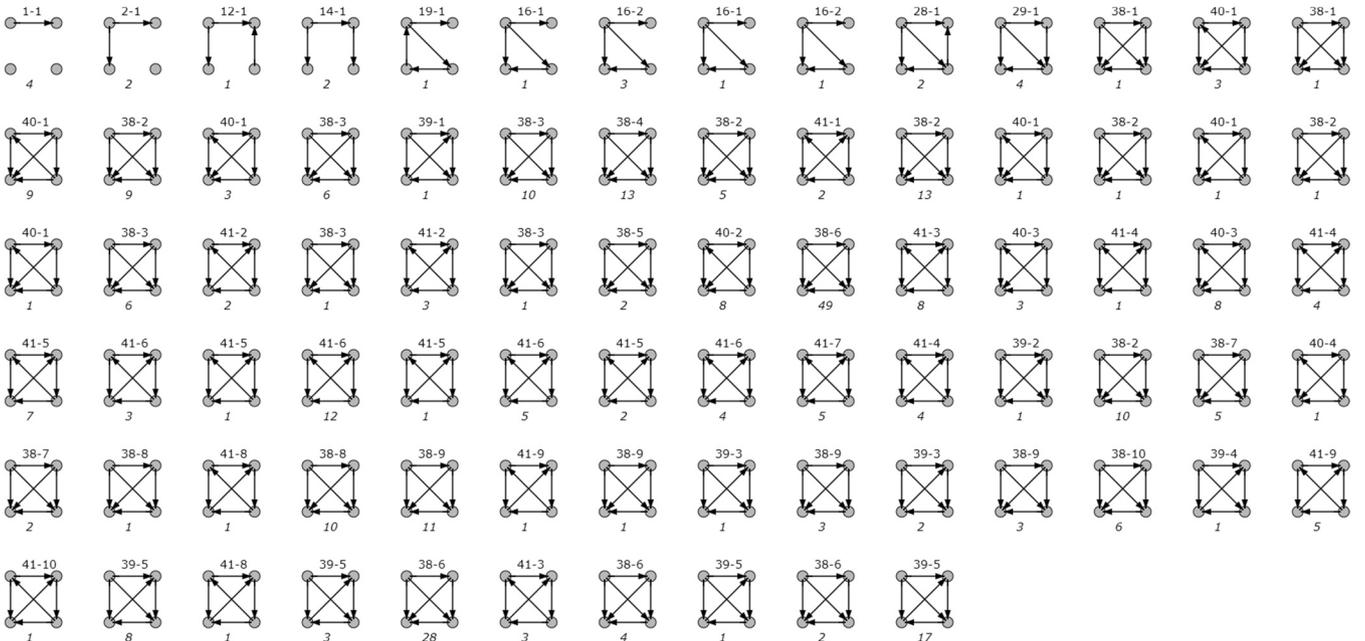
(a) Chickens – Smallest number of changes



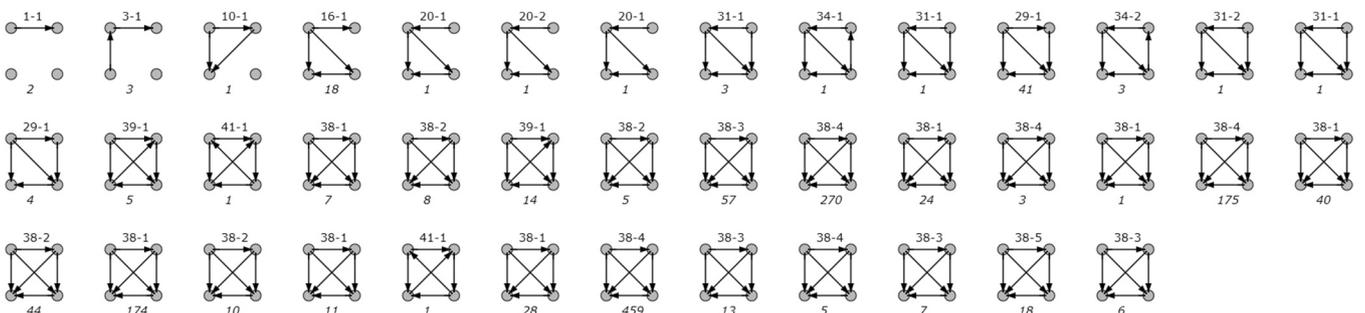
(b) Chickens - Largest number of changes



(c) Mice - Smallest number of changes



(d) Mice - Largest number of changes



(e) Fish - Smallest number of changes

Fig. 6. Network evolution records for the groups with the smallest and largest (except fish) number of structural changes in each species. The variants of states that a group passes through are shown above each network diagram, and the number of interactions that a group remains in a variant are shown below.

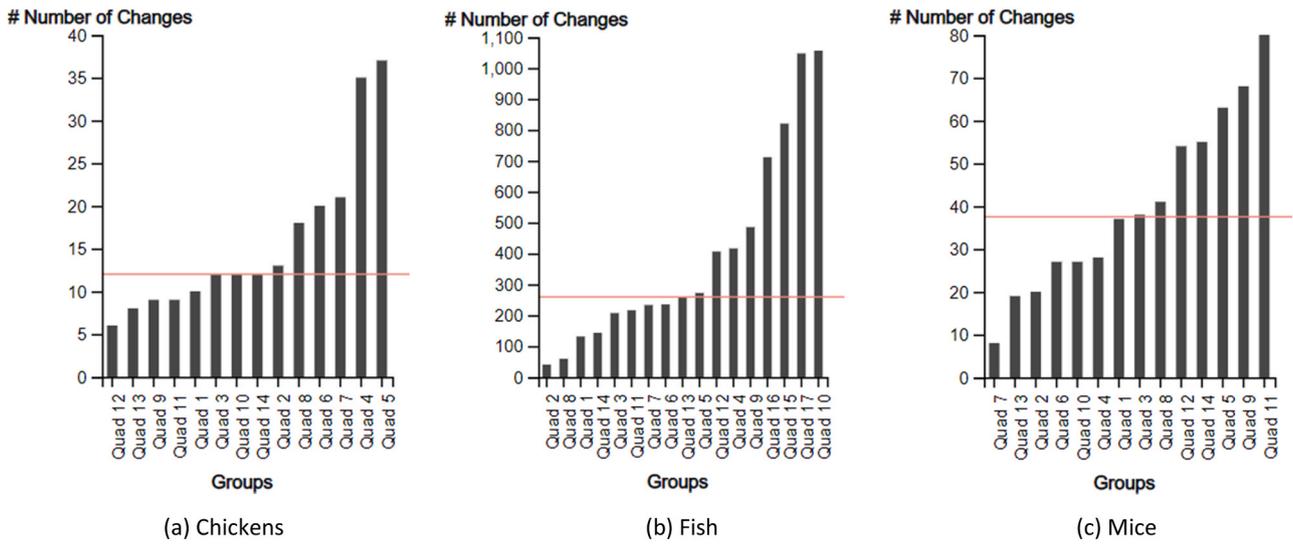


Fig. 7. Bar graphs of the total number of changes in state variants recorded per group. The median values for the three species – chickens, fish, and mice – are represented by the horizontal line. Note that the number of changes shown on the y-axis is different in each bar graph.

Table 1

Heat map for CSF scores of network states for each species. The label “AAO” above a state indicates the presence of an individual that attacks all the others in that state, and the label “INTR” designates a state that contains an intransitive configuration. See the text for more detail.

C.S.F.	1-Link	2-Link				3-Link									
		AAO 				AAO 					INTR 				
Chickens	1.00	0.22	0.15	0.52	0.12	0.64	0.00	0.02	0.00	0.03	0.00	0.12	0.00	0.20	0.00
Fish	1.00	0.67	0.19	0.04	0.10	0.72	0.04	0.00	0.00	0.11	0.03	0.02	0.05	0.02	0.01
Mice	1.00	0.80	0.13	0.00	0.07	0.84	0.08	0.00	0.00	0.00	0.00	0.04	0.02	0.01	0.01
		4-Link													
		AAO 			INTR 				INTR 						
Chickens		0.89	0.01	0.01	0.00	0.01	0.01	0.04	0.04	0.00	0.00	0.00	0.00		
Fish		0.63	0.10	0.01	0.05	0.11	0.03	0.00	0.00	0.04	0.01	0.02	0.00		
Mice		0.81	0.08	0.05	0.04	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00		
		5-Link							6-Link						
		AAO 	AAO 	AAO 				INTR 	INTR 	INTR 	INTR 	AAO 	INTR 	INTR 	INTR
Chickens		0.53	0.30	0.13	0.02	0.01	0.00	0.00	0.00	0.01	0.00	0.98	0.01	0.01	0.00
Fish		0.37	0.38	0.08	0.03	0.02	0.01	0.08	0.03	0.00	0.00	0.90	0.09	0.01	0.00
Mice		0.68	0.21	0.06	0.02	0.01	0.00	0.01	0.01	0.00	0.00	0.87	0.05	0.06	0.02

1-link state, then directly to a variant of a 2-link, next to another variant of a 2-link state, the group would make at least 7 changes over the course of its journey to a 6-link state. Apart from a few chicken quads and one in the mice, most groups – especially in the fish – have far more structural transitions than the minimum number required. More specifically, the chicken groups averaged 2.5 more structural transformations than the minimum 6, the mice groups averaged 6.7 times more, and the fish groups averaged a stunning 66 times more. With just a few exceptions, network evolution in the groups is a highly dynamic and continuing process. Groups do not simply march through state space until they fill in all their ties and then remain in a particular 6-link state for the rest of observation.

3.1.3. CSF and COF analysis

3.1.3.1. Stability of network states. In this section we investigate how long groups stay in different states during network evolution. We ask: Are certain states more “attractive” than others during the development of networks? Are species similar or different in their patterns of visitation to the states? What might explain the differences in visitation patterns to the various states?

We explore these questions using the CSF (Class Stability Factor) index developed by Lindquist and Chase (2009). They considered that the length of time (measured in number of interactions) that groups within a species remained in a particular state was an indication of that state’s stability. More specifically, the CSF score of a network state is the ratio of the number of interactions during which all groups in a species stay in that state to the total number of interactions that all groups remained in all states within the same link class of the state. For example, if the mice quads were in state 28 (one of the possible 5-link states) for 68.3% of all interactions that the quads spent in all the 5-link states combined, the class stability factor (CSF score) for state 28 is 0.68.

An examination of Table 1 indicates high similarity across the three species in the most stable states for each link class. In all three species, the same states were most stable in the 3-, 4-, and 6-link classes – states 6, 15, and 38, respectively. State 28 in the 5-link class was most stable for the chickens and mice, but state 29 was the marginally more stable for the fish (0.37 for state 28 vs. 0.38 for state 29). In the 2-link states, state 2 was highly stable for the fish and mice, but state 4 was for the chickens. Further, in all three species, except in the 5-link class for the fish, one state in each link class was much more stable – had a CSF score of 0.50 or larger – than any other state. (This website <https://darius-coelho.github.io/PeckVis/> gives the CSF analyses by state variants for each group in the three species.)

What factors are associated with high and low CSF scores? Lindquist and Chase (2009) suggested that states that had an individual that dominated all others would be more stable than those that did not. Here we define such groups as including an “AAO”, or an individual that attacks all others. Only states that have at least three links can have an AAO. In the 3- and 4-link classes, only one state in each class has an AAO (6 and 16, respectively), in the 5-link classes there are three (28, 29, and 30), and in the 6-link classes there are two (38 and 39). For all three species, states 6 and 16 were the most stable in the 3- and 4-link classes. Taking their CSF scores together, states 28, 29, and 30 were the most stable for all species in the 5-link classes, and 38 was most stable for all in the 6-link class. Thus, in all three species, states with an AAO were considerably more stable than those without one – except for state 39. As just indicated, state 39 does have an AAO, but it also has an intransitive configuration which, as will be indicated below, is associated with low CSF scores.

Lindquist and Chase (2009) found that CSF scores were low or zero in states that had intransitive configurations. In a state with an intransitive configuration or triad, there is at least one set of three individuals in which a first has attacked a second, the second has attacked a third, and

the third has attacked the first. Table 1 indicates states that have at least one intransitive configuration. These states have either 0.00 or very low CSF scores across the three species. Groups either avoid or spend very little time in states with intransitive triads.

A considerable number of other states besides those with intransitive triads have low CSF scores. It’s hard to say what these states have in common other than that they do not have an AAO. The one exception to this general pattern is for the chickens in 2-link states. However, as noted by Lindquist and Chase (2009) for the chickens, a general tendency across the species is for an AAO (DAO in their terminology) to emerge early in the evolution of networks in the groups.

3.1.3.2. Frequency of occurrence of network states. The frequency of occurrence of network states is different from their stability. The class occurrence frequency (COF) of a state, as defined by Lindquist and Chase (2009), is the fraction of all groups within a species that visited a specific state within a link class of states. For example, 11 out of 17 fish quads visited state 2 within the total of three possible 2-link states for a COF score of 0.65. Because a group can visit more than one state in a link class through a reversal of a previous direction of attack between two individuals, the COF scores for a species for all the states in a link class can sum to more than 1.0.

In general, a majority of the states (95.0%, not counting state 1 since all groups must go through it) were visited by at least one group in the three species during network evolution (Table 2). Consequently, there was much variation among the pathways that individual groups followed in the evolution of their networks. All groups eventually reached state 38, but they did so in many different ways. (This website <https://darius-coelho.github.io/PeckVis/> gives the COF analyses by state variants for each group in the three species.)

However, despite the variation in paths, there is one state in several of the link classes that was visited by half or more of the groups in at least one species. More specifically, the states with the highest COF scores are the same for the 2-, 3-, 4-, and 5-link classes for the mice and fish. But the chickens diverge with their groups most often visiting the same state (16) as the fish and mice only in the 4-link class of states. The mice groups are the most “regimented” in the states they transition with one state in link classes 2 through 5 having a COF score of greater than 0.70.

Although the CSF scores indicate that groups in all three species spent the great majority of their time in state 38 as compared to the other 6-link states, considerable fractions of the groups in the three species at least visited the other possible 6-link states (except for the chickens and state 41) as shown by their COF scores.

The types of configurations in states that had high and low COF scores are less clear than those associated with high and low CSF scores. There was a tendency for large fractions of groups to visit states with an AAO, but there are exceptions in some states for the chickens and fish. Unlike the results for the stability scores, moderate fractions of groups do visit some states with intransitive configurations. And again, unlike the results for the stability scores, some proportions of groups pass through states that do not have an AAO.

3.1.4. Dynamic stability of networks

The CSF analysis showed that the fraction of interactions that groups spent in state 38, compared to the total numbers of interactions in all 6-link states, was very high: 0.98, 0.90, and 0.87, respectively, for chickens, fish, and mice. However, because the CSF analysis did not distinguish among variants of state 38 (see the Supplementary Material for all variants of state 38), a variety of dynamic patterns could have generated these CSF scores. Consider, for example, three different possible patterns of network evolution within a group. One possibility is that the network of ties in the group evolved to state 38, say, variant 1, as its first 6-link state. From that point on, the aggressive interactions in the group repeatedly reenacted the pattern of ties in variant 1 until

Table 2

Heat map of COF scores of network states for each species. The label “AAO” above a state indicates the presence of an individual that has attacked all the others in that state, and the label “INTR” designates a state that contains an intransitive configuration. See the discussion of CSF scores above for more detail.

C.O.F.	1-Link	2-Link					3-Link									
Chickens	1.00	0.36	0.29	0.43	0.14	0.07	0.07	0.07	0.00	0.21	0.00	0.29	0.00	0.50	0.00	
Fish	1.00	0.65	0.29	0.06	0.18	0.41	0.12	0.00	0.00	0.18	0.06	0.06	0.12	0.12	0.06	
Mice	1.00	0.93	0.29	0.00	0.07	0.71	0.29	0.07	0.00	0.00	0.00	0.21	0.07	0.14	0.07	
4-Link																
Chickens	0.64	0.14	0.07	0.00	0.07	0.07	0.21	0.14	0.00	0.00	0.00	0.00				
Fish	0.59	0.23	0.06	0.18	0.18	0.12	0.00	0.00	0.06	0.06	0.12	0.00				
Mice	0.93	0.29	0.14	0.29	0.07	0.07	0.00	0.14	0.00	0.00	0.00	0.00				
5-Link													6-Link			
Chickens	0.29	0.64	0.29	0.14	0.14	0.00	0.07	0.07	0.07	0.07	1.00	0.50	0.29	0.07		
Fish	0.53	0.41	0.23	0.23	0.29	0.06	0.41	0.18	0.06	0.00	1.00	1.00	0.94	1.00		
Mice	0.71	0.50	0.29	0.14	0.14	0.00	0.21	0.14	0.00	0.07	1.00	0.36	0.50	0.29		

observation ended. This would be dynamic stability in that the configuration of ties in variant 1 was continually recreated, but it would be a simple type compared to those we next describe.

In a second and more complex kind of dynamic stability, the network of ties would again evolve to state 38, variant 1. Then as interactions continued, they would reestablish the ties in variant 1, but later, pair-flips would occur, and the group would move to another variant of state 38 or to other 6-link states. These excursions to other state 38 variants or other 6-link states would be brief. After each excursion, the group would return to variant 1 of state 38 and stay there for relatively large numbers of interactions. This group would spend a large fraction of its 6-link interactions in variant 1, but it would do so by returning to that configuration each time it deviated from it.

A third and yet more complex kind of dynamic stability would occur when the network evolved to state 38, variant 1, to begin with, but then moved to a different variant of state 38, say 3, and then to yet another variant, say 5, and so on. The group might also visit other 6-link states, besides variants of state 38, but these visits would be short on average. In this case a general type of network structure, state 38, would be dynamically stable, but the variants of this state and the ranks of the individuals within that general configuration would frequently change.

Tables 3 and 4 give a variety of information about the dynamic stability of variants of state 38 in the networks of the three species. Table 3 provides information about the concentration of interactions for the most visited variant of state 38 in the groups. The column headings indicate ranges in per cents of all interactions in 6-link states that groups spent in their most visited variant of state 38 (not necessarily the same

Table 3

The per cents of groups in each species that spent different per cents of all their interactions in 6-link states in their most visited variant of state 38.

Species	Per cents of all interactions in 6-link states that groups spent in their most visited variant of state 38				
	0–25.0%	25.1–50.0%	50.1–75.0%	75.1–99.9%	100.0%
Chickens	0.0	0.0	7.1	78.6	14.3
Fish	11.8	70.6	17.6	0.0	0.0
Mice	7.1	42.9	21.4	14.3	14.3

Table 4

Dynamics of state 38 variants in the three species.

Species	Avg. # of Variants (with repetition)	Avg. # of Variants (without repetition)	% of Possible Variants	Avg. # of Interactions
Chickens	4.5	2.1	8.9	120.8
Fish	312.1	12.6	52.5	29.7
Mice	19.0	4.9	20.2	18.7

variant in each group). For example, consider the 78.6 entry for the chicken row in the 75.1–99.9% column. This indicates that 78.6% of the chicken groups spent between 75.1 and 99.9 per cent of all their interactions in 6-link states in the one specific variant of state 38 that they visited the most. Likewise, in 7.1% of the chicken quads (row 1, 50.1 –

75.0% column), the most often occupied variant of state 38 was visited between 50.1 and 75.0 per cent of all 6-link interactions.

For Table 3, we operationalize that groups devoting 100% of all their 6-link interactions to one variant of state 38 exhibit pattern one dynamic stability, groups passing between 75.1% and 99.9% of their interactions in their most visited variant of state 38 show pattern two dynamic stability, and groups spending the percentages of time in 6-link interactions indicated by the 0 – 25.0%, 25.1 – 50.0%, and 50.1 – 75.0% columns in Table 3 present pattern three dynamic stability. Table 3 reveals that pattern one dynamic stability was rare. Only 14.3% each of the chicken and mice groups (two groups in each species) followed this type of dynamic stability. A large majority of the chicken quads exhibited pattern two stability, none of the fish quads did, and a small percentage of the mice quads did. Finally, while all the fish quads and a large majority of the mice quads exhibited pattern three stability, only a small percentage of the chicken quads did so.

Table 4 gives some further information about the dynamics of network evolution: the average number of variants of state 38 – with and without repetition – visited per group, the average number of variants visited per group as a percent of the total possible number of variants of state 38, and the average lifetime of state 38 variants. There are 24 (4!) possible variants of state 38. The lifetime of a variant of state 38 is the average number of interactions that quads within a species stay in that variant before transitioning to another variant of state 38 or to another 6-link state.

Inspection of this table reveals that the average chicken group visited a little over two variants of state 38 (without counting repetition of variants), the average mouse group almost five, and the average fish group almost 13. Put differently, the average chicken group explored a little under 10% of the possible number of state 38 variants, the average mice group reached about 20%, and the average fish group traversed over half of all the possible variants. Finally, the average lifetimes of state 38 variants vary from somewhat long to quite short in the various species: 120.8, 29.7, and 18.7 interactions in the chickens, fish, and mice respectively.

3.2. Analysis of dynamic process in the component triads of the quads

We now ask how the dynamics of interaction in component transitive and intransitive triads influence the quad-level findings we have just

presented. We investigate the initial configurations of component triads, how many triads are ever intransitive, and the lifetimes of transitive and intransitive triads. We define a component triad as a subgroup of three individuals within a group of four. A transitive triad is a configuration in which one individual has most recently attacked a second, the second has most recently attacked the third, and the first has most recently attacked the third. In an intransitive triad, the first has most recently attacked the second, the second has most recently attacked the third, and the third has most recently attacked the first (see Fig. 8).

First, almost all component triads in the three species initially formed with transitive configurations. The percentages of triads with initial transitive configurations were 96.4% each in the chickens and mice and 97.1% in the fish. For initial intransitive configurations, the percentages in the species were 3.6% each in the chickens and mice and 2.9% in the fish. These results are highly significantly different from chance in each species (Randomization Tests, all $p = 0.000$).

Second, after their initial configurations, many more component triads in the species became intransitive. In the chickens, 26.8% of the component triads developed intransitive structures at least once in their development, in the mice 46.4% did, and in the fish nearly all or 98.5% did.

Third, while the analysis just presented indicated that large percentages of triads were intransitive at some point in their evolution, our analysis above indicated that states with intransitive configurations had low CSF scores, i.e., groups only visited them briefly. This was true for both networks filling in their ties (3- to 5-link states) as well as for those that had all their ties in place (6-link states). Could this contrast between the low CSF scores and the high rates of occurrence of intransitive triads be explained by high instability in intransitive configurations?

We examine this possibility by comparing the “lifetimes” of transitive and intransitive triads. By lifetime we mean how long in interaction counts a configuration lasts before it changes into a different structural arrangement. A transitive triad can “die” by converting into a different transitive configuration or into an intransitive triad (see Fig. 8). However, an intransitive triad can only die by converting to a transitive triad (see Fig. 8).

In all three species, transitive triads have considerably longer lifetimes than intransitive ones (Table 5). This difference in lifetimes is especially marked in chickens where transitive triads last an average of about 20 times longer than the intransitive ones. In fish and mice,

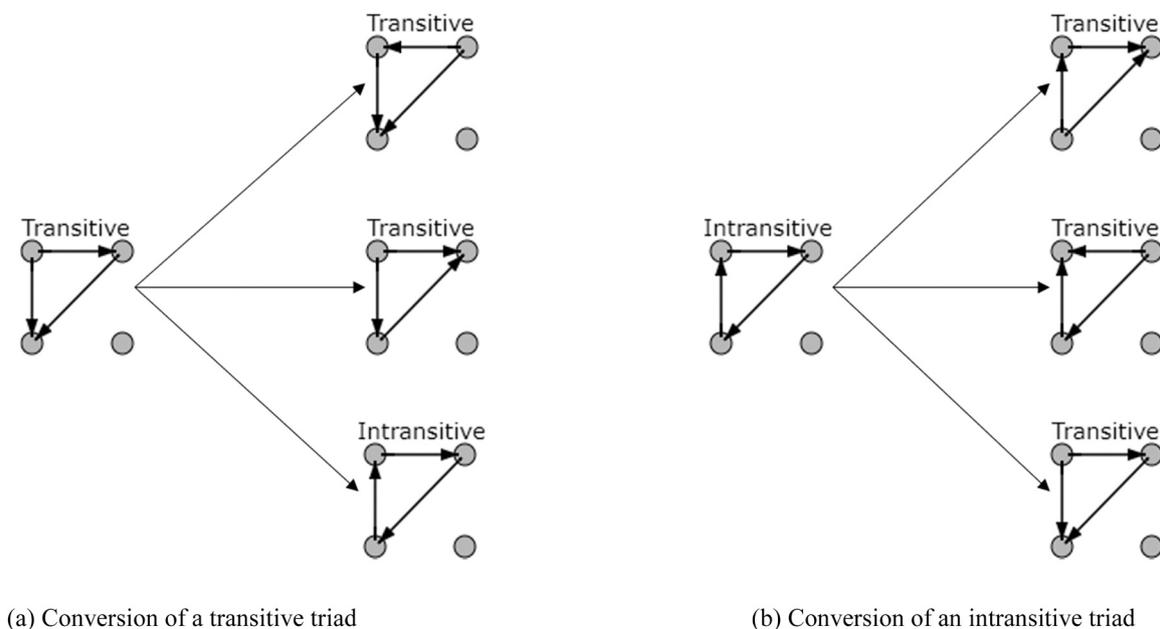


Fig. 8. The possible ways in which transitive and intransitive triads can convert to other configurations.

Table 5

The average lifetimes of transitive and intransitive triads in each species.

Species	Transitive	Intransitive
Chickens	110.2	5.3
Fish	37.5	9.2
Mice	24.6	6.7

transitive triads only survived about 4 and 3.7 times longer, respectively, than intransitive ones.

For the chickens, the differences in lifetimes fits nicely with the CSF and other analyses above. The networks in the chicken quads evolved to mostly avoid states containing intransitive triads and spent all or most of their time in one variant of state 38 once they transitioned to a 6-link state. But for the fish and mice the differences in lifetimes for the two kinds of triads might seem a little perplexing. The networks in the fish and mice also spent large fractions of their time in states without intransitive configurations (from the CSF analysis), although not quite as large as was the case for chickens. Given the still relatively large avoidance of states with intransitive triads (in the CSF analysis), it might seem as if the differences in how long the two kinds of triads lasted in the fish and mice should be more like the case in the chickens. We carried out an additional analysis of the transitions in transitive triads to help resolve this possible confusion.

In this analysis, we investigated how often transitive triads transitioned to either transitive or intransitive structures. If transitive triads often transitioned directly to another transitive configuration, this might explain our seemingly contrasting findings of relatively brief lifetimes of transitive triads, especially in the fish and mice, and high CSF scores in 38 and other states with only transitive component triads in the group network. In this analysis we found that in the chickens 84.4% of transitive triads converted to other transitive configurations while only 15.6% changed to intransitive ones, in the fish the comparable figures were 89.2% and 10.8%, and in the mice 85.3% and 14.7%.

In all three species, very high proportions of transitive triads transition to other transitive configurations rather than to intransitive ones. The proportion of transitions from transitive to transitive versus intransitive was significantly higher than chance in each species (Randomization Tests; all $p = 0.000$).

Table 6

The dynamics in pairs by which transitive triads are converted to other transitive structures and by which intransitive triads are converted to transitive configurations. For transitive triads, the entries are the per cents of all transitive triads in a species that are converted to other transitive triads by the sequence labeling the columns. For the intransitive triads, the figures are the per cents of all intransitive triads that are converted to transitive ones via the sequence labeling the columns. The graphics over the table columns show the pairs involved in the reversals that are responsible for the conversions. Note that the double slash markers (//) on the edges between nodes indicate relationships that have been reversed and cause the triad conversions.

Species	Transitive Triads		Intransitive Triads		
	2 attacks 1	3 attacks 2	1 attacks 3	3 attacks 2	2 attacks 1
Chickens	45.9	54.1	62.5	16.7	20.8
Fish	39.8	60.2	58.1	23.3	18.6
Mice	74.0	26.0	72.4	17.1	10.5

3.3. Analysis of dynamic processes in pairs

In this section we search for patterns of change in the component pairs that might help explain the triad findings. We ask if the relationships in the pairs influence the conversion of one transitive triad to another or of an intransitive triad to a transitive one. Table 6 shows that a transitive triad can transition to another transitive structure by either a flip in the highest-ranking pair (1 and 2) or in the lowest-ranking pair (2 and 3). Does one of these flip types occur more than the other?

Table 6 also indicates that an intransitive triad can revert to a transitive one by a flip in any of the three possible pairs making up the triad. This figure assumes that an original transitive triad (1 attacks 2, 2 attacks 3, and 1 attacks 3) was changed to an intransitive one by 3 flipping against 1 (3 attacks 1). However, which pair of individuals reverses the direction of their tie implies different possibilities for the possible mechanisms underlying the conversion of intransitive triads to transitive ones. First, consider the case in which 1 converts the triad back to transitivity by counterattacking 3. This does not suggest any ability of transitive inference or of a winner or loser effect on the part of the animals (Lindquist and Chase, 2009). Simply, one individual (1) has attacked another (3) in the initial transitive triad, the one attacked (3) counterattacked to form the intransitive triad, and the one counterattacked (1) in turn itself counterattacked. (see, e.g., Bond et al., 2003; Paz-y-Mino et al., 2004; Oyegbile and Marler, 2005; Rutte et al., 2006; Grosenick et al., 2007; Oliveira et al., 2011; Harrison et al., 2018 for discussions of winner effects, loser effects, and transitive inference in animals).

Second, consider the case in which 3 counterattacks 2. The flip between this pair suggests the possibility of a winner effect or transitive inference in the dynamics by which the triad regained a transitive structure. That is, after attacking 1, 3 had a higher probability of attacking another individual (2). Or, 3 was able to infer, in some cognitive form, that if it attacked 1 and 1 attacked 2, then it should be able to attack 2. Third, consider the case in which 2 counterattacks 1. The flip between this pair suggests the possibility of a loser effect or transitive inference in the dynamics of return to transitive configurations. That is, 1 had a higher probability of losing a subsequent encounter with 2 after losing to 3, or 2 inferred that if it had attacked 3 and 3 had attacked 1, then it should be able to attack 1.

Inspection of Table 6 reveals no consistent pattern in the dynamics of reversals in the pairs by which transitive triads are converted to new

transitive triads. In the mice, significantly more conversions than chance are accomplished when the two highest ranking individuals (1 and 2) flip their ties (Wilcoxon test $p < 0.01$). But in the chickens and fish, slightly higher percentages of flips between the two lowest ranking individuals (2 and 3) produce the conversions, although this was not significantly different than chance in either species (Wilcoxon tests, chickens $p = 0.472$, fish $p = 0.071$). However, in all three species, counterattacks by the previously top-ranked member (1) of the triads against currently top-ranked individual (3) are most often associated with conversion of intransitive triads to transitive ones. This type of conversion occurs significantly more than expected by chance across quads in each species (Wilcoxon tests; chickens $p = 0.013$, mice $p = 0.002$, fish $p < 0.001$). This finding suggests that neither transitive inference nor winner or loser effects account for the majority of transformations in intransitive triads.

3.4. Dynamics of individual ranks

Rather than examining networks based upon single aggressive acts, as we have here, most researchers in animal behavior have investigated the properties of what are referred to as “dominance hierarchies”. They view dominance hierarchies as networks of “dominance relationships”. Researchers usually define these relationships operationally by observing aggressive interactions over short periods of time and saying that one individual dominates another if it delivers all or a majority of aggressive acts to the other during that period. A dominance hierarchy is the network composed by all the dominance relationships between the pairs within the group. In line with the common assumption of much of network science, these dominance hierarchies are usually assumed to have static and enduring “linear” structures (e.g., Savin-Williams, 1980; Franz et al., 2015; Holekamp and Strauss, 2016, but see Oliveira and Almada, 1996; Hofmann et al., 1999). In a linear hierarchy, one animal dominates (has dominance relationships) with all the other group members, a second dominates all but the top individual, and so on. In a linear hierarchy, consequently, the individuals can be ranked from top to bottom by the number of other individuals that they dominate. As groups grow larger, more than 10 or so individuals, hierarchies may not be perfectly linear since some pairs may not be observed to interact. In such cases, these hierarchies usually have more transitive component triads, based upon dominance relationships, than expected by chance (Shizuka and McDonald, 2012).

Using this assumption that dominance networks have static and enduring structures, researchers have examined whether the prior attributes of individuals, characteristics such as size, physiological measures, and genetic background, predict later dominance ranks in groups (e.g., Buwalda et al., 2017; Chase et al., 2002; Holekamp and Strauss, 2016; Williamson et al., 2016a; Varholick et al., 2018). Researchers have also investigated how ranks in dominance hierarchies might influence the characteristics that individuals possess after groups have formed. These later characteristics include reproductive success, physiology, and bodily growth (Williamson et al., 2017; Beehner and Bergman, 2017; Snyder-Mackler et al., 2016). However, our results demonstrating that networks based upon aggressive interactions are dynamic, implies that at least some individuals have fluctuating, rather than long-standing ranks within their groups. If this is so, then the correlations that researchers find using networks based upon dominance relationships between the ranks of individuals and either their prior or later attributes may be unreliable in magnitude or simply artifactual.

In this section we investigate the dynamics of individual ranks to evaluate this possibility. We use Elo ratings, a common, well-researched measure of individual ranking within competitive situations (Elo, 1978; Neumann et al., 2011). We employ Elo ratings, rather than the David's scores we used in the music notation graphs, since Elo ratings are more sensitive to short-term changes in individual ranks. In a comparison of ranking methods, Neumann et al. (2011) demonstrate that matrix-based methods, such as David's scores, require longer series of interactions in

making their ratings. They showed that David's scores are less sensitive to rank changes during brief periods of interaction, for example, when individuals are introduced and when pairs of individuals rapidly reverse the direction of their attacks.

We begin this analysis by displaying several possible patterns of individual rank evolution in Fig. 9. Fig. 9a, for example, shows a group in which the ranks of the four individuals emerge early and remain well-differentiated throughout the observation period. This pattern occurred, holding for at least 50% of the interactions, in 7 out of 14 groups of chickens, but never in the fish groups, and only in 1 mouse group. Some groups did show clear differentiation of the four ranks for at least very brief periods of time at the end of the observation periods: 11 out of 14 groups in chickens (counting the 7 groups showing early and lasting differentiation), 4 out of 17 in fish, and 8 out of 14 in mice. The logically possible, but opposite pattern, in which none of the ranks ever clearly differentiated from the others over the course of an observation record was not found, although some groups did come close, like the one displayed in Fig. 9b for a mouse quad. Here the individuals did sporadically achieve distinguished ranks in several brief windows of time.

In nearly 90% of the fish groups, a little over three-quarters of the mice groups, and about a third of the chicken groups, there was little consistent rank differentiation among two or three of the individuals over at least half of the interactions in their respective groups. The two remaining graphs (Fig. 9c and d) illustrate some of the ways in which this happened: the bottom individual developed a clear rank but the top three did not and the top individual achieved a clear rank, but bottom three did not. However, as these latter two figures illustrate, even in groups in which two or three individuals did not show clear distinction in ranks, one individual, either the top or bottom rank, was often delineated.

Overall, the modal pattern in the chickens was for all the ranks to be differentiated (7 out of 14 groups), and in the fish it was for the top rank to be clear and the bottom three not well-distinguished (13 out of 17 groups). The mice groups were spread across several patterns with the most frequent two patterns being the top rank separated and the bottom three not (4 out of 14 groups) and the top and bottom individuals distinguished but the middle two not (3 out of 14 groups).

We show the evolution of individual ranks in all the groups from the three species using small multiples in the [Supplementary Materials](#) (Tufté, 1990). This website shows higher-resolution graphs of rank evolution for each group in the three species: <https://darius-coelho.github.io/PeckVis/>.

4. Discussion

4.1. Main findings

In this study we have described network evolution in three data sets that avoid the limitations in many of the data sets used in previous investigations of network evolution. Specifically, we examined a large number of groups forming networks, observed network interactions from the introduction of group members, and collected time-stamped, continuous records of all network interactions among all group members. In our analyses of the data sets, we employed and extended several recently developed methods for the visualization and analysis of network evolution.

Our findings were robust across all three data sets. Network evolution was a remarkably dynamic process across all structural levels – whole groups, triads, pairs, and individual ranks – in each of the species. The aggressive interaction networks in the groups were not stable and enduring as has often been assumed. The networks did not evolve to specific structures and remain in those structures for as long as we observed the groups (contrast the assumptions, e.g., in Chase et al., 2002; Chase and Lindquist, 2009; Martin, 2009; Chase and Seitz, 2011; Franz et al., 2015; Williamson et al., 2016b). Network evolution was a

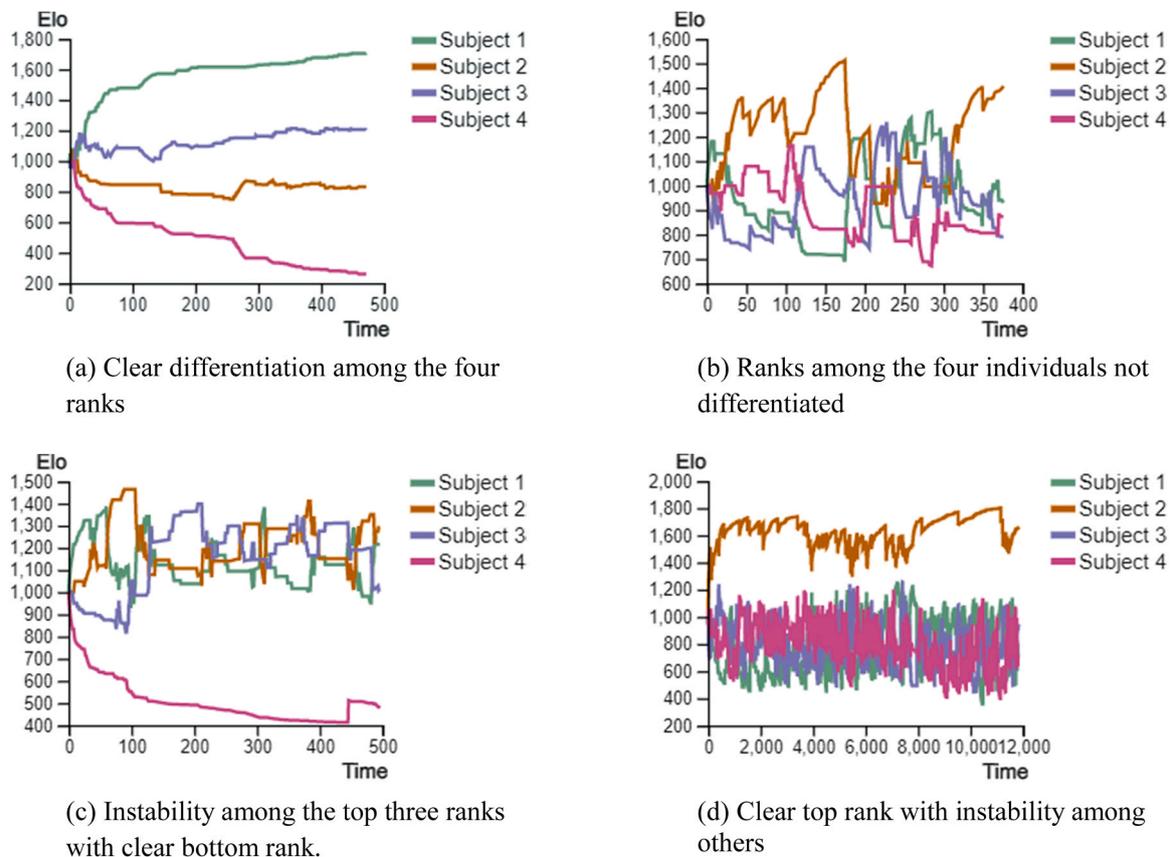


Fig. 9. Several possible patterns of individual rank evolution in groups.

remarkably dynamic process with most groups transitioning through many different configurations of ties during observation. The networks in some fish groups, for example, made over 1000 structural changes.

In formulating the “Freeman-Linton Hypothesis”, [Skvoretz and Faust \(2002\)](#) conjectured and found some evidence for the idea that the structure of ties in groups is more strongly determined by the type of relationship than by the species which compose the groups. The robustness of our findings across the three species suggests a reconsideration of this hypothesis, but for network dynamics rather than static network structures.

Instead of a “fixed-point” stability – a state of unchanging structure – we discovered that the animal networks had, what we termed, dynamic stability. The CSF analyses showed that the groups in the three species spent large proportions of their interactions in state 38 (the complete transitive tournament) among all the 6-link states (0.98, 0.90, and 0.87 of their interactions for the chickens, fish, and mice respectively in state 38). That is, while many of the groups made brief excursions to other 6-link states (those with intransitive triads), they nearly always returned to some variant of state 38. But they did not show loyalty to one particular variant of state 38. Instead, most of the groups moved, often repeatedly, between two or more different variants of state 38.

The CSF and COF investigations provided more detailed information about the transitions of the groups through network state space. The reader should recall that the CSF methods examined what proportions of their interactions groups within a species spent in various states, and the COF methods looked at what proportions of groups with a species visited each state (regardless of how many interactions they spent in those states). The CSF analyses indicated the states that were most “attractive” to a species on its journey of network evolution, and these analyses revealed that there was high similarity in those states across the three species. Many of the most attractive states had an AAO, an individual that had attacked all the others, *but* did not have intransitive triads. The

COF analysis indicated that high proportions of the groups across the species visited the most attractive states in the CSF analysis. However, considerable proportions of the groups also visited almost every possible state in the network state space. Looking at all the groups together, although many of the groups tarried in the same states in their evolutionary journeys, they also at least transitioned through almost all the possible states. In other words, while there was similarity in the states that many groups found “attractive” (in terms of spending high proportions of their interactions), there was also considerable variation in the pathways through state space that individual groups followed in their network evolution.

In investigating the processes within the triads that might underlie the results with the CSF analysis, we discovered that nearly all the component triads in the groups initially formed as transitive configurations. But those initial transitive configurations did not remain in place until the end of observations. Instead, there was also a kind of dynamic stability in the organization of the triads as well as of the quads. Many triads changed configurations over time, but transitive structures usually changed to other transitive structures (see [Chase and Rohwer, 1987](#) for similar findings in large groups of Harris’ sparrows). And if transitive configurations did change to intransitive ones, they usually only abided in those configurations for relatively few interactions before converting back to transitive. Congruent with these findings, we found that the average lifetimes of transitive triads were longer than those of intransitive ones in the three species. There is also evidence that networks of friendship relationships in human groups evolve to have more transitive configurations over time (e.g., [Leinhardt, 1973](#); [Hallinan and Kubitschek, 1990](#); [Krackhardt and Handcock, 2007](#)).

In examining the interactions in the pairs within triads that were responsible for converting transitive configurations to other transitive configurations, we did not find a pattern across the species. Reversals between the second- and third-ranked individuals in converting the

triads were more common in chickens and fish, but those between the top- and second-ranked members were more common in mice. However, there was a uniform pattern in the conversion of intransitive triads back to transitive ones. We found that the most conversions back to transitivity took place when the previously top-ranked individual attacked the previously third-ranked individual, i.e., when the previously top-ranked individual re-reversed its tie with the individual who made the initial reversal to convert the triad to intransitivity.

We found that the ranks of individuals, like the dominance networks themselves, were dynamic within the three species. In many groups, particularly those in the fish and mice, many individuals did not have clear, long-lasting rank positions. In these groups, the ranks of many group members would have varied, depending upon the time at which measurements might have been made. It is important to note that we observed the formation of hierarchies among individuals with no previous experience of each other. It is quite plausible that in long established groups that individual ranks may remain highly stable as has been observed for a number of species (Holekamp and Strauss, 2016).

4.2. Implications

In our studies we only observed three species of animals over the course of two or three days forming one kind of social network. Consequently, we do not know whether our findings will be replicated in humans or in other species forming networks based upon aggressive interactions or in other types of networks in small, face-to-face groups. However, the pervasiveness of the dynamic processes that we observed at every level of network organization raises some fundamental questions for network studies: Are other networks in small groups as dynamic as those we report here? What about networks in large groups? If other networks are similarly dynamic, what does this mean for our descriptions of network organization? The terms that we use in these descriptions? The methods through which we show the dynamics? The models we employ to explain network evolution? How we explain the places of individuals within network organization? Below, we briefly sketch out some points in consideration of these questions.

First, to determine the extent of dynamics in network organization for both humans and animal groups, researchers will have to employ methods for the collection of high-resolution data of the sort we used here: recording time-stamped records of all instances of interactions forming network ties among all group members over relatively long periods of time. Getting these data can demand considerable research time as it did for us in coding video records of interaction. However, new developments in computer vision and other electronic means offer the possibility of making these data easier to collect (see, e.g., Branson, 2014; Peters et al., 2016; Mönck et al., 2018; Nilsson et al., 2020; Wyatt et al., 2011).

Second, if networks of many types are as dynamic as our work here suggests, then many studies are reporting incomplete or misleading representations of network organization. Many studies only consider interactions occurring during brief periods of time, and the resulting network structures they describe may actually be temporary ones. This problem occurs in many studies which assume that networks based upon “dominance relationships” reach static “linear” configurations and then stop evolving (e.g., those such as Chase et al., 2002; Martin, 2009; Chase and Seitz, 2011; Franz et al., 2015). While these depictions may be helpful to some extent, they may not give a full picture of the extent of structural variation over even a brief period in a group’s history. In addition, presenting this view of network organization helps to reinforce the view that networks form stable and enduring structures.

Third, to investigate the dynamics of network evolution in small groups, researchers will need a variety of new visualization and analysis methods. We have presented some methods here, and other researchers have also developed methods for examining network dynamics (e.g., Moody et al., 2005; Bender-deMoll and McFarland, 2006; Chu et al., 2013; Crnovrsanin et al., 2014). We expect that there is much more to be

done in this area.

Fourth, our results suggest that researchers may need to modify and to add to the terms and concepts used in network research. As Moody (2009) points out, although there is considerable research on network dynamics, many of the concepts and terms still used in network research correspond to the conception of networks as having a static organization. Some examples are: “network structure”, “triadic census”, “position within a network”, “network centrality”, and “network configuration”. We have used some of these concepts and terms in this paper because we do not have others that would be more in keeping with the dynamics of network evolution that we have reported. We have suggested some new expressions and ideas in this paper, such as those coming through our CSF and COF analyses and those for the evolution of individual ranks, but there is much more work to be done in this area.

Fifth, our analyses suggest new opportunities for models of network evolution that can account for the continual, dynamical changes of the sort we observed here. We indicated some models of network evolution, mostly in humans, earlier in the “Research Background” section, and some models that apply to dominance relationships and aggressive interaction in animals are Skvoretz et al. (1996), Chase and Lindquist (2016), and Skvoretz and Fararo (2016). A considerable number of these models, particularly those for animals, assume that networks evolve to a stable and enduring structural state. Others are not designed for interactions that repeatedly reinforce the directions of existing ties or that repeatedly alter the directions of existing ties. We propose that models of network evolution that can accommodate the sort of dynamics we have discovered here would be an important contribution to network science.

Sixth, our finding that individuals in the groups we observed often do not have stable ranks suggests possible methodological problems in studies that report correlations between individual attributes and network positions, particularly in dominance studies. The fact that correlations, while perhaps statistically significant, are often of modest sizes, may reflect changing ranks for individuals, particularly for middle-ranking ones.

In conclusion, this study investigates data sets that avoid the three main limitations of other data sets used in examining network evolution. It applies new methods for analyzing network evolution in these data sets, and those methods can be used across species and different types of networks. In the application of these methods, this study discovers several new insights into the dynamical development of network organization. We suggest that collecting and analyzing other network data sets that avoid these limitations will help us make discoveries that can change how we think about network organization.

Data availability statement

The data used in this paper can be made available upon reasonable request.

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Appendix A. Detailed description of animal methods

Chicken methods

We used a total of 21 white Leghorn hens obtained from a commercial supplier. The supplier had given the hens small wing bands with unique identification numbers. During experiments, we used temporary wing badges with large numbers so that we could tell the hens apart. After a short period of group living, the hens were housed individually in $76 \times 51 \times 61$ cm cages between observations. We kept the hens on a 12/12 light/dark cycle with lights on at 0600 h and off at 1800 h. The hens had both water and food ad libitum in their individual cages and when in experimental groups. We observed the hens in groups of four in a separate room in a $152 \times 102 \times 81$ cm cage. Removable partitions kept the chickens apart when data were not being collected. We observed the hens through a small opening in a cloth partition. To prepare for an observation session, we took the hens one at a time from their home cages and placed each in a separate section of the observation cage. This was done about two hours before lights out on the day before observations were to begin. Data collection on the next day began about 0900 h. Under low light, so that the hens would not interact, the observer removed the partitions separating them, switched the light back to normal intensity, and began recording aggressive interactions among the hens. We recorded the interactions live using a personal computer which also noted the time at which each interaction occurred. Each observer recorded interaction in alternate 1.5 h shifts for a total of six hours per day. The observers logged all instances of aggressive behaviors involving physical contact between the hens: peck, jump on, and claw (see Chase, 1982 for more details). After the six hours of recording, the hens were again separated by partitions and observed the next day for six additional hours day following the previous day's procedure. We used a balanced incomplete block design to assemble the groups of hens. This design allowed us to assemble groups so that no individuals met more than once, all individuals were in an equal number of groups, and each hen had at least three days' rest between groups. We carefully monitored the hens for any sign of injury or pain. All experimental procedures were approved by the Stony Brook University Institutional Animal Care and Use Committee.

Fish methods

We used 80 female cichlid fish of the species *Mylandia lombardoi* obtained from a commercial breeder in Florida. This fish is native to East Africa and readily forms dominance hierarchies in the laboratory. We housed the fish in separate 19-liter compartments in 76-liter tanks with constant water temperature 22–23 °C. We kept the fish on a 13/11 light/dark cycle with lights on at 0700 h and off at 2000 h. To form a group of four fish, we weighed the fish, allowing the heaviest individual to be no more than 7% greater in weight than the lightest. The fish had at least two weeks rest between taking part in groups and no pairs of fish ever met more than once. After weighing, we placed each fish in a randomly chosen 19-liter compartment of a 76-liter observation tank in a room separate from the one in which the fish were housed. We put the fish in their compartments at approximately 1700 h and returned the next day at 0700 h to remove the partitions and record the interactions among the fish using high-definition video. After 12 h we replaced the partitions with the fish in their original compartments. We returned the next day at 0700 h and following the first procedure, videoed the fish for an additional 6 h. During observations we monitored the fish at one-hour intervals for any signs of excessive stress or injury.

Trained observers used the video records to record all instances of the following aggressive behaviors: threat (the threatening individual approaches within one body length and the threatened individual swims at least one body length away), chase (the chasing individual approaches another and the approached individual swims at least one body length away with the chasing individual following), and nip (the nipping

fish brings its mouth into contact with the nipped individual). The observers recorded the behaviors using a custom-written, voice-recognition program. The program allowed an observer to say an observation, e.g., "1 chases 2", with the program logging this observation and the time at which it occurred using the time stamp information from the video record. The Stony Brook University Institutional Animal Care and Use Committee approved all experimental procedures.

Mice methods

A total of 56 male outbred Crl:CD1 (ICR) mice aged 7 weeks old were obtained from Charles River Laboratories (Wilmington, MA, USA). All mice were assigned with unique IDs and marked accordingly by dyeing their fur with nontoxic animal markers (Stoelting Co., Wood Dale, IL, USA). We provided standard chow and water ad libitum. Mice were kept under a 12/12 light/dark cycle with white light (light cycle) on at 2400 h and red lights (dark cycle) on at 1200 h and under constant room temperature (22–23 °C) and humidity (30–50%). As it was imperative for this experiment that mice are unfamiliar to each other when introduced to a new social group of four males, we shipped mice in several shipments and noted the shipment groupings. Upon arrival, we housed mice from the same shipment groupings in pairs for seven days in standard sized cages ($27 \times 17 \times 12$ cm) with pine shaving bedding. Then we assigned mice from different shipment groupings into a new social group of four at 8 weeks of age 5–10 min before start of dark light cycle (1200 h) so mice could start socializing in dark. Each quad (group of four) was placed into an enriched cage system of dimensions 48.5 (width) x 35.5 (length) x 14 (height) cm. This enriched cage system consists of two standard rat cages (dimensions of $35.5 \times 20.5 \times 14$ cm) filled with pine shaving bedding and enrichment objects. We installed a GoPro Hero3 camera above each enriched cage system to capture every social interaction during social hierarchy formation for the first 72 h of the group housing period. With the 72-hour video recording data, trained observers scored the winner and loser in every instances of agonistic interactions such as fighting, chasing, lunging, mounting, subordinate posture, and induced-flee behaviors as well as other social behaviors such as allogrooming and sniffing. Mice were monitored each day of the group housing period for any sign of injury or pain. We conducted all procedures with approval from the Columbia University Institutional Animal Care and Use Committee (IACUC protocols: AC-AAAQ4406).

Appendix B. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.socnet.2021.09.002](https://doi.org/10.1016/j.socnet.2021.09.002).

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