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The application of social network analysis to understand acute and chronic post-mixing aggression in commercially reared pigs

Simone Foister

Thesis submitted for the degree of Doctor of Philosophy

University of Edinburgh
Declaration

I declare that this thesis is my own composition and that the research described in it is my own work, except where acknowledged. The work described has not been submitted for any other degree or professional qualification.

Simone Foister
Publications


Conference contributions


Abstract

In commercial systems, pigs are routinely regrouped with unfamiliar conspecifics which leads to physical aggression in order to establish new dominance relationships. Post-mixing aggression lasts approximately 24 hours before steeply declining, although chronic aggression amongst familiar individuals is also observed. These aggressive encounters result in skin injuries commonly referred to as lesions, the number and location of which have been shown to correlate with the type and duration of aggression an individual has engaged in. Correlations between anterior injury rates at 24 hours post-mixing (24hr-PM) and 3 weeks post-mixing (3wk-PM) are inversely related, indicating that reciprocal aggression can only be delayed and not avoided altogether. In order to meaningfully improve animal welfare, a solution that leads to a reduction in aggression at both time points needs to be identified. For this to be achieved, the variation in skin lesions needs to be studied further and better understood. Previous analyses have focussed on interactions only at the dyadic level and failed to explain a large proportion of the variation in lesion scores. As interactions do not occur in isolation but rather as a part of a larger interconnected dynamic, this thesis aims to apply social network analysis to post-mixing aggression in order to examine this behaviour within the wider social context. Social network analysis may reveal group level and indirect behaviours that play an important role in post-mixing aggression that may otherwise be undetectable. In Chapter 2 the relationship between pen level network properties and pen level injury rates were established. This revealed that networks containing large fully connected subgroups (cliques) tend to have fewer injuries 3wk-PM, whereas highly divided networks (betweenness centralisation) have considerably higher lesions. Chapter 3 follows on from Chapter 2 by examining the
effect on lesions for individual pigs when occupying different positions within a social
network. The first part of the chapter focuses on individual position within the network
structures identified in Chapter 2. This chapter also quantifies a variety of commonly
studied individual network positions to examine how these relate to individual lesions,
and compares the model fit to dyadic traits. This chapter presents evidence that
occupying centralised network positions can be beneficial for the central pig, but at the
expense of pen-mates who are at risk of elevated rates of aggression and injury. In
contrast, in pens with large cliques, no significant difference was found in injury rates
between clique members (those who are part of a fully connected sub-group) and non-
members. This chapter concludes that while direct engagement in aggression at 24hr-
PM remains a strong predictor of injury at 3wk-PM, individual injury rates can be
indirectly affected by the behaviours of pen mates that occurred at 24hr-PM.

Chapter 4 builds upon Chapter 2 by quantifying different dominance metrics to
establish whether pen level network properties relate to variations in hierarchical
structure. This chapter revealed that pens with large cliques tend to have well-defined
hierarchies (quantified by linearity and steepness), whereas the hierarchical structure
in highly centralised pens tend to be poorly defined. This indicates that certain network
structures are associated with poor hierarchy formation, which may partially explain
the difficulties certain groups have with achieving and/or maintaining long-term social
stability.

Together the results indicate that SNA can complement conventional analyses of
dyadic interactions to predict and understand the outcomes of aggressive interactions.
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Chapter 1. Literature review
1.1 Prelude

In commercial systems, housing design and commercial pressure often necessitates unfamiliar pigs to be mixed together. Upon mixing pigs must establish their dominance rank within their new social group, and commonly do so by engaging in aggressive behaviour (Meese and Ewbank, 1973). Whilst the most intense aggression is displayed within the first 24 hours, low levels of aggression are commonly observed in familiar groups primarily in the form of dominance ‘maintenance’ and bullying. Post-mixing aggression is a major concern in the pig industry, both in terms of animal welfare and economic costs. Many intervention strategies have been explored (e.g. Gonyou and Parfet, 1988; Guy et al., 2009), but none have been adopted systematically at a commercial level.

Understanding the mechanisms underlying post-mixing aggression has been the focus of many studies. Such research has provided considerable insight into the variability and complexity of this behaviour. Most intriguing of all has been the study into long term social outcomes of the acute phase of post-mixing aggression (Desire et al., 2015; Turner et al., 2017). Uncovering additional behaviours that may be contributing to this variation could prove extremely useful in finding a solution to post-mixing aggression.

Nearly all research on pig behaviour to date has focused on different aspects of the dyadic interaction; however in other species, evidence is mounting that missing social information may be obtainable by extending the phenotype beyond the dyad (Brent, 2015). Social network analysis (SNA) is the primary tool enabling this evidence to be gathered, by providing researchers the ability to analyse social behaviour within the wider social context (Krause et al., 2015). A key advantage of SNA is that it provides a variety of measures of individual sociality that can take account of both the direct
and indirect social connections (Makagon et al., 2012; Wey et al., 2008). By doing so, it allows researchers to describe and investigate the significance of social positions that were previously unrecognised and beyond the reach of traditional dyadic analysis.

The purpose of this thesis is to investigate whether social network analysis can be applied successfully to post-mixing aggression to identify new behavioural traits that may help to explain the observed variation in post-mixing aggressive behaviour at group level and shed light on the mechanistic underpinnings of this behaviour. It is anticipated that new information gained from the social network approach can inform future strategies to strongly reduce post-mixing aggression to both the animals and industry.

Section 1.2 of this literature review provides a detailed breakdown of social network analysis, including individual descriptions of each network measure. Section 1.3 provides a brief introduction to sociality in animal species. It leads on to a comprehensive review of how social network analysis has been applied to both free-living species and captive populations and the evidence that demonstrates the insights SNA has provided in multiple species. Section 1.4 introduces pig behaviour and the issue of post-mixing aggression. This section outlines our current understanding of the behavioural phenotypes that affect long term social stability, and individual social and injurious outcomes. This section concludes by discussing what we can expect by re-examining post-mixing aggression with social network analysis. By drawing on the previous three sections, I discuss how we aim to extend our current understanding of post-mixing aggression in pigs by incorporating information regarding their indirect social connections. This section will also provide the behavioural context of centrality measures that will be extracted from the networks and used to formulate the
hypotheses on which this thesis is based. Together, these sections give the reader a synopsis of current understanding on how behavioural phenotypes drive aggression in social groups of pigs, the terminology needed to understand SNA in the rest of the thesis and a summary of how SNA has previously been applied to understand social interactions in other species.
1.2 Social Network Analysis

1.2.1 Introduction to social network terminology

A network (also referred to as a graph) is comprised of the actors (also referred to as nodes or vertices (V)), and the sets of interactions or edges (E) between them (see Figure 1.1). The number of steps between two nodes is called a path (e.g. the dashed lines represent the path between nodes 2 and 7, which has a path length of 3).

![Figure 1.1. Model network](image)

Edges can be directed or undirected, which is depicted graphically as an arrow from sender to receiver (see Figure 1.2). Direction allows us to incorporate who initiated or received the interaction, which can be valuable information if trying to identify important individuals in terms of information flow, social diffusion, or contagion.

![Figure 1.2. Directed edge](image)
Edges can also be weighted by the frequency, duration, or intensity of the interaction (Figure 1.3). The stronger the weighting, the more that connection contributes to the animal’s centrality rank.

![Figure 1.3. Weighted networks. Network A depicts multiple interactions between certain individuals and in network B these multiple interactions are depicted as thicker edges which are weighted by the frequency of interactions. Network C is a binary network which only depicts whether an interaction occurred or not.](image)

1.2.2 Levels of analysis

A connection between two individuals is the most basic level of social network analysis and is referred to as a dyad. Dyadic analyses focus on pairwise relationships, such as whether the relationship is reciprocal or not, and what types of interactions have occurred. There are a variety of methods in network analysis that analyse the nature of dyadic relationships and is commonly the basic unit of analyses in SNA. Relationships among larger subsets of individuals can also be analysed. Triad refers to the relationships between three individuals, and many social network methods and models focus on patterns within triads. An example of a social network method that focuses on triad patterns is the clustering co-efficient method, which is a widely used measure in the field of SNA and will be discussed in detail later in this section. While we can define the relationship between two or three individuals as a dyad or triad, we
are also able to specify any subset of individuals as a **subgroup**. How a subgroup is identified has been the focus of many social network analysis methodology studies and models. Such examples include fully connected subgroups (e.g. cliques), or clusters within a network where a subset of nodes show a higher degree of connectivity compared to the remainder of the group. However, one of the most powerful features of social network analysis is the ability to model the relationships between all actors in a particular **group**. Wasserman and Faust (1994) defined a ‘group’ in this context as ‘*a finite set of actors who for conceptual, theoretical and empirical reasons are treated as a finite set of individuals on which network measurements are made*’. We can therefore define a **social network** as consisting of a finite set of individuals and the relationships or interactions that occur between them (Wasserman and Faust, 1994).

### 1.2.3 Social network measures

A network is comprised of individuals with separate motives and personalities initiating and receiving social interactions. These interactions create a social structure, which inevitably affects future individual behaviour and the functioning of the group. Depending on the research question, one may choose to study the overall structure of a network, which is referred to as a **global measure**, or to quantify the position of an individual, where a **local** measure is used instead (Wasserman and Faust, 1994).

The following two subsections present the network measures that were utilised in this thesis. In the first subsection, I present four local measures that were used in Chapter 2. In the second subsection, I present the method by which local measures can be applied to provide a global metric. I also provide global measures that describe
subcommunities present within networks. Where applicable, I aim to put these seemingly abstract mathematical concepts into the context of animal behaviour.

Local network measures

Degree centrality: Degree centrality is one of the simplest network measures, based upon the number of connections a node has. For example, individual 5 in Figure 1.4 is connected to 3 individuals, and therefore has a degree of 3. However, it is common to scale centrality to between 0-1 (Wasserman and Faust, 1994).

Networks can be scaled by a theoretical maximum (the maximum possible degree in a network of the same size) or by the highest degree present in the network. In these cases, the node with the highest degree in the network has a degree centrality of 1, and the centrality of every other node will be a fraction of its degree in comparison to the most popular node. However, in this thesis we use the theoretical maximum degree for any one individual which is simply \( n - 1 \) in an undirected graph, and \((n \times 2) - 1\) in a directed graph. This decision was made because the networks studied in this thesis were the same size (15), and therefore normalising by theoretical maximums allowed us to compare centrality and position not only within networks, but also between networks (Wasserman and Faust, 1994).

To apply this to Figure 1.4, the theoretical maximum is 10 (11-1). The highest degree node in the network is node 7, with a degree of 5, and degree centrality of 0.5 (5÷10). In a directed network, this can be adapted to describe the number of received interactions (in-degree), and initiated interactions (out-degree).
Figure 1.4. Node level 'importance' according to different network measures. The node ID is within the node, and the node position/centrality value is next to the node.
The theoretical maximum for in and out degree is the same as the theoretical maximum for an undirected network but only counts the in or out degrees when calculating the centrality (see Figure 1.5).

For example, node 7 has the highest total degree (5), however it is no longer the most central individual in terms of in-degree centrality as only 2 of its connections are incoming. It therefore has the same centrality (2/10=0.2) as all other individuals with 2 in-coming connections (nodes 2, 9, and 10).

![Figure 1.5. In and out degree centrality](image)

**Eigenvector centrality:** Eigenvector centrality considers the number of connections an individual has, but also how well connected an individual’s network partners are. Thus, interacting with a well-connected individual leads to a higher eigenvector centrality than interacting with a poorly connected individual (Makagon et al., 2012; Wey et al., 2008).

The eigenvector centrality $x_i$ of an individual (node) $i$ is defined as the proportional sum of the centralities of the focal node’s neighbours $j$ in group $G$. The focal node can
obtain a high centrality ranking by being connected to many others, by connecting with individuals that are highly central, or a combination of both. This is expressed as

\[ x_i = \lambda^{-1} \sum_{j \in G} A_{ij} x_j, \]

Eq 1.1. Eigenvector centrality

where \( \lambda \) is a constant. In matrix notation this becomes \( \lambda x = Ax \), so that \( x \) is an eigenvector of the adjacency matrix (Newman, 2004).

Therefore, two individuals may have the same degree however the “quality” of their connections are also incorporated into the overall centrality ranking. In Figure 1.4, node 1 and 8 both have 1 connection, however node 8 is connected to an individual with 5 connections whereas the social partner of node 1 only had 2 connections. As a result, node 8 has a higher eigenvector centrality (0.38) than node 1 (0.02).

**Betweenness:** Betweenness describes how central an individual is depending on how often the individual is a part of the shortest path between other nodes in the network (Wasserman and Faust, 1994). Individuals with high betweenness centrality tend to be individuals connecting otherwise unconnected individuals or subgroups (Gilby et al., 2013).

Let \( \sigma(i,j) \) be the number of shortest paths between nodes \( i \) and \( j \) in group \( G \), and \( \sigma(i,j)(w) \) be the number of shortest paths between \( u \) and \( v \) that pass through the node \( w \). Then the betweenness centrality of an individual \( w \) is provided in Eq 1.2.
Betweenness provides the sum of the ratio of the number of paths that pass-through a given vertex divided by the number of paths present in the network. Where \( \frac{\sigma_{(i,j)}(w)}{\sigma_{(i,j)}} = 1 \), then all the shortest paths between individual \( u \) and \( v \) contain individual \( w \), and where it is 0 then none of the shortest paths contain individual \( w \). If the sum of these ratios is \( |V| - 1 \), where \( |V| \) is the number of individuals in any given network, then all shortest paths between two vertices pass through individual \( w \) (Nguyen, 2013).

In Figure 1.4, we can see that nodes 5 and 7 have the highest betweenness in the network and are positioned between two otherwise separated groups.

**Closeness:** Closeness quantifies how ‘close’ an individual is to all other individuals in the network, in the context of how many ‘steps’ there are in each path between the focal individual and all the others (Wasserman and Faust, 1994). Closeness of individual \( i \) in group \( G \) is defined as

\[
C(i) = \frac{1}{\sum_{j \in G} d(i,j)}.
\]

**Eq 1.3. Closeness centrality**

Where the sum of the distances between individuals \( i \) and \( j \) is high, then the closeness is small and vice versa. In Figure 1.4, node 5 has the highest closeness, as it has the lowest number of steps required to reach any other node in the network.
Closeness is also related to the concept of reach which quantifies the degree of separation between two individuals. Reach reflects the degrees of separation or steps between individuals (Milgram, 1967). Individuals with a high reach tend to be connected to many others who are \( k \) degrees of separation away (Brent, 2015).

*Clustering co-efficient:* Clustering co-efficient, as indicated by the name, quantifies the extent to which nodes in the graph tend to cluster together. Clustering co-efficient differs to the previous measures as it is based on triplets (or triangles) in the graph. Clustering co-efficient at the local level quantifies what proportion of an individual’s social partners are also connected, and divides this by the possible number of theoretical connections that could have occurred between the social partners (Watts and Strogatz, 1998). It is therefore a measure of the density of connections in the area of a graph local to a focal individual.

To identify the clustering co-efficient for individual \( i \) with vertex \( v_i \) we define the set of its immediate neighbours \( (N_i) \) as the set of all individuals \( j \) that are directly connected to \( i \), i.e. by edge \( e_{ij} \).

We define \( K_i \) as the number of individuals \( |N_i| \) in the immediate neighbourhood, \( N_i \).

The local clustering coefficient \( C_i \) for individual \( i \) is calculated by the proportion of the links that could possibly exist between all immediate neighbours.

In a directed network, \( e_{ij} \) differs from \( e_{ji} \), but in an undirected network they are identical. In chapter 2, where the local clustering co-efficient is used, we only utilise the undirected form, and so this will be focused on here.
Where an individual has \( k_i \) neighbours, then \( \frac{k_i(k_i-1)}{2} \) edges could exist between all immediate neighbours, and so the local clustering coefficient for an undirected graph can be defined as

\[
C_i = \frac{2|\{e_{jk}: j, k \in N_i\}|}{k_i(k_i - 1)}
\]

*Eq 1.4. Local clustering co-efficient*

In Figure 1.4, node 9-11 have a clustering co-efficient of 1 as all of their connections are also connected. Whereas node 7 has a clustering co-efficient of 0.3 (3÷10), because of the 10 possible connections that could have occurred between the 5 social partners (5*(5-1)/2), only 3 occurred (9—10, 10—11, 11—9). The remaining nodes all have a clustering coefficient of 0, as none of their social partners are also connected to each other to create a triangle.

*Global social network measures*

*Freeman’s centralization:* The global centralization of an entire network is calculated by comparing how central the most central node is to all other nodes in the network (Freeman, 1978). Centralization therefore sums the differences in centrality between the most central node \( (i) \) and all other nodes \( j \), and divides this by the theoretical largest difference that could exist in a network of this size (Freeman, 1978).

Eq 1.5 provides Freeman’s centralization equation applied to the degree centrality \( C_D(G) \) of the network \( G \).

\[
C_D(G) = \sum_{v \in G} \frac{|\text{deg}(i) - \text{deg}(j)|}{N^2 - 3N + 2}
\]

*Eq 1.5. Freeman’s centralization equation*
Where $N$ is the number of nodes in network $G$.

In Figure 1.5, node 7 is the most central individual with a degree centrality of 5. We then sum the difference between all other nodes and node 7 and divide this by the theoretical maximum number of connections that could occur in a network this size $(11 \times (11-1) = 110)$. The sum of all differences between the degree value of node 7 and the remaining nodes is 27, which divided by 110 gives us a network centralization value of 0.245.

Centralization provides us with a scale from 0 to 1, with 0 indicating that all individuals in the network have equal centrality and 1 indicating maximum inequality (see Figure 1.6).

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Figure 1.6. Ring and Star network. A ring network has a centralization value of 0, with all nodes having equal centrality. In contrast the star network is maximally centralized with a centralization value of 1.
Freeman’s centralization equation can be applied to all the *centrality* network measures outlined in section ‘Local social network measures’, to provide a global measure that informs us how unequal the individual nodes are in terms of network centrality.

*Clustering co-efficient:* To calculate the clustering co-efficient of a graph, let $\lambda_G(T)$ be the number of triangles (subgraphs in $G$ that contain 3 edges and 3 individuals, where one node is an individual) in undirected graph $G$. Then let $\tau_G(v)$ be the number of triplets of $v \in G$, with 2 edges and 3 individuals, one of which is vertex $i$, where $v$ is incident to both edges (Watts and Strogatz, 1998). This allows us to define the clustering coefficient as shown in Equation 1.6.

$$C_i = \frac{\lambda_G(v)}{\tau_G(v)}$$

*Equation 1.6. Global clustering co-efficient*

*Cliques:* A clique is a fully connected subgroup of 3 or more individuals (Wasserman and Faust, 1994). Cliques can be quantified in a number of different ways. The number of cliques describes how many cliques exist in the network and the size of the largest clique describes how many individuals are a part of the largest clique. For example, nodes 7,9,10, and 11 form the largest clique in our model network (see Figure 1.4). However, within this clique of 4, there are 4 smaller cliques consisting (7,9,10), (7,10,11), (7,9,11) and (9,10,11). Therefore, the total number of cliques present in our model network is 5, with the largest clique consisting of 4 nodes.
Cliques are often utilised in social network analysis as a method of identifying cohesive subgraphs (i.e. groups of nodes that are either fully connected or densely connected in comparison with the rest of the network, see Everett and Borgatti 2009)).

In this thesis, ‘cohesion’ is used in the context of the structural properties of social networks and does not refer to affiliative or pro-social behaviour.
1.3 Understanding animal sociality with social network analysis

1.3.1 Animal Sociality

Understanding how complex sociality emerged and evolved is a central question in ecology and evolutionary biology (Wilson, 2000). The extent to which an animal species is considered social is commonly reliant on the type and frequency of social interactions individuals display toward one another, the extent to which conspecifics show a degree of cohesion and coordination between each other and the stability of such relationships over time (Krause and Ruxton, 2002). However, as Krause & Ruxton (2002) pointed out, the distinction between group living and solitary species is a somewhat artificial one, as even the most solitary animals will engage in social interactions or join a group at some point in their lives. For example, solitary adult male wild boar will interact with a matrilinear social group during the mating season (Gonyou, 2001; Kurz and Marchinton, 1972).

The many different benefits of group living that aid survival and reproduction in challenging environments has led to multiple potential evolutionary selection pressures on sociality (Le Galliard et al., 2005). For example, living in groups offers access to breeding opportunities that solitary individuals tend not to have, such as greater opportunities to select mating partners and to share the cost of parental duties (Emlen and Oring, 1977). Another advantage is that group living allows certain species to achieve feats that could not have been accomplished alone. For example, the cumulative physical strength group living provides enables group predators (e.g. wolves or lions) to bring down larger prey than a solitary individual could achieve. Co-operating and co-ordinating hunting and foraging also reduces hunting time and improves capture rate. For example, co-ordinated efforts to drive prey into smaller
areas in order to increase prey density (e.g. sperm whale trapping fish in ‘bubble nets’ Leighton et al., 2007) increase the entire group’s hunting success and capture rate. Harris Hawks (*Parabuteo unicinctus*) form hunting groups of approximately 2-6 individuals, and co-ordinate their attacks in a tactic called the ‘seven kills’ strategy, whereby they cooperatively attack from multiple directions and converge on the target prey (Heidari et al., 2019). This approach leads to an increased capture rate and a lower energy cost per unit of time spent hunting (Bednarz, 1988). Group living also offers an advantage in locating resources, as larger groups are able to explore more of the environment and share information in the event of finding a large food source (Pitcher et al., 1982). Group living also enables animals to defend their resources from solitary animals or rival groups from the same or a different species (Port et al., 2011). Reduced energy costs are also observed in movement and migratory behaviours. By allowing animals to ‘take their turn’ leading the group and disrupting air or water resistance, the remaining group is able to travel behind at a reduced resistance and energy expenditure (Duman et al., 2012). Similarly, in cold climates animals can share their body heat by huddling together and thus reduce the cost of keeping warm for all the group members (Scantlebury et al., 2006; Schradin et al., 2006). Group living also offers security and reduced risk of predation. Living in groups provides the ‘many eyes’ effect and reduces the likelihood of a predator going undetected (Krause and Ruxton, 2002). Many species have alarm calls to alert group members to predators (Townsend et al., 2011), and some species have developed advanced calling systems that inform conspecifics about the type of threat they have spotted, which can help their conspecifics know where to look and how to appropriately react (Kiriazis and Slobodchikoff, 2006; Slobodchikoff and Placer, 2006). Often groups will take it in
turn to be on ‘look out’, while the others forage. The frequent rotation of the role of ‘sentinel’ maintains a balanced distribution of foraging activity amongst group members (Brandl and Bellwood, 2015). Early work by Hamilton (1971), noted the individuals on the periphery of the group are at higher risk of predation than individuals in the centre, and that often animals will try to place other individuals between themselves and danger. The strategic efforts to minimise individual risk follow certain rules which can explain the aggregation, spatial arrangement, and phenotypic assortment of social living species.

Yet, sociality is not without cost, and social species face considerable competition for resources, space, and mates, and are at greater risk of the spread of contagious pathogens (Ezenwa et al., 2016; Krause and Ruxton, 2002) than their solitary counterparts. To reduce the cost of conflict that arises from such competition, animals have developed a wide array of social organisation strategies to promote functionality of the group and to pre-emptively manage conflicts (Krause and Ruxton, 2002). One of the defining features of a gregarious social species is the formation of a dominance hierarchy. Dominance relationships are often established by displays of aggression and intimidation (Drews, 1993). The outcome of such aggressive interactions often mould future behaviour, suggesting that animals often remember the outcome of previous interactions (Goubault and Decuignière, 2012). This creates a stable social order that reduces costs associated with repeated conflict over resources (e.g. food and mates) as would otherwise occur (Goubault and Decuignière, 2012; Gurney and Nisbet, 1979). Dominance hierarchies tend to allow a few high ranking individuals a greater share of resources and mates (Ellis, 1995). However, this comes at the cost of stress on themselves and on the low ranking individuals (Sapolsky, 2005). Commonly high
ranking members tend to have superior fitness (defined in genetic theory as reproductive success relative to other individuals in the population (Emlen and Oring, 1977)), which suggests that traits which predispose an individual to high rank have been selected for. Interestingly, low ranking individuals may also have traits that are exposed to evolutionary selection. For example, victimization (receipt of agonistic interactions) was found to be a heritable trait in yellow-bellied marmots (*Marmota flaviventris*) (Lea et al., 2010).

### 1.3.2 Social network analysis

Until recently analysis of social interactions has predominantly focused on dyadic associations, such as determining the participants and the behaviour shown by each. However, such dyadic associations do not occur in isolation, but rather as a part of a wider polyadic (defined in ethology as containing three or more individuals) network of social interactions (Brent, 2015), whereby individuals in a group are connected to others even if a direct interaction between the two has not occurred (Croft et al., 2008; Krause et al., 2007; Sih et al., 2009; Wey et al., 2008).

---

*Figure 1.7 Schematic relationship between individual behaviour and population dynamics (adapted from Krause et al., 2009)*
Social network analysis offers a unique quality not offered from other analytical tools. As the approach always deals with nodes (individual animals) and edges (the interactions between them), this allows researchers to study multiple levels of social organisation without needing to decide which level is of most importance a priori (Krause et al., 2009). By doing so, it allows study of the feedback loop (see Figure 1.7) i.e. how individual behaviour influences the wider population and how in turn the resulting population affects the individual (Camazine et al., 2003; Couzin and Krause, 2003).

**Variability in network structure**

This section will present a comprehensive review of variables that effect social network structures, with emphasis on individual characteristics and demographics. This section will also explore how network structure can affect how an entire group functions, and how network position can affect the success of the individual.

**Seasonality and food availability:** The social interactions between individuals can change due to a variety of factors, particularly when animals must respond to changing environmental pressures. For example, seasonal changes can bring about a wide array of behavioural changes that are reflected in changes in network structures. Some seasonal changes are expected, such as the breeding season, where animals start to search or compete for mates. Likewise, rearing offspring can also lead to behavioural changes, and new mothers may have less contact with peers as more energy and focus is aimed towards their young (Duboscq et al., 2016). Seasonal changes often affect food availability which can lead to different foraging behaviours as animals compete for different food sources in different locations. Such changes to network structure in response to food availability has been noted in orcas, where a greater abundance of
salmon was associated with higher connectivity in the social group compared to lower availability (Foster et al., 2012). However, unseasonal weather changes that lead to reduced food availability can cause severe disruptions to breeding behaviour (Schülke, 2003). For example, Drewe et al., (2009) noted while the network structure in meerkat groups were fairly consistent between years, one time period showed a network that was structurally dissimilar to any other season studied. Drewe et al., (2009) suggested that the unusual patterns compared to the previous year were likely a result of unusually low rainfall which severely affected the availability of food. This led to reduced body condition in the group and lowered mate seeking behaviour in males and reduced the connectivity between groups.

Human interference that affects food availability patterns has also been found to shape population networks. A longitudinal study of two distinct dolphin populations that had overlapping home ranges found that one group specifically foraged near prawn trawlers whereas the other group sought food elsewhere. However, when fishery legislation changed and the number of trawlers significantly decreased, this led to a change in food availability which resulted in the two dolphin groups merging and creating a cohesive network (Ansmann et al., 2012).

**Environmental complexity:** The complexity of physical or topographic structures of the environment (commonly referred to as environmental complexity), can also affect how individuals interact with one another. For example, Drewe et al., (2009) noted that exceptionally high rainfall led to reduced interactions between groups of meerkats. They hypothesised that the high rainfall had led to a growth surge in vegetation which obscured the view of the other neighbouring groups, leading to less interaction between the two. This was also demonstrated by Leu et al., (2016) where
environmental complexity was experimentally altered in groups of wild lizards. By inserting mazes in the habitat of one of the groups, they found evidence that increased environmental complexity lead to increased movement, increased stability in network structure over time, and increased network density (more interactions between individuals occurring). Leu et al., (2016) suggested that the increased movement may have led to more interactions occurring by chance, but also noted that increased complexity may have limited the alternative pathways that the lizards could choose from. This forced individuals to take established pathways which led to more encounters with others who were also forced to travel via the same route.

These examples demonstrate how much of the variability in network structures is an inevitable result of animals overcoming external constraints (e.g. environmental complexity), attempts to reproduce by finding a mate, and adapting to changing food availability (e.g. seasonal changes). These variables can be considered unavoidable external challenges that animals must rise to in order to survive. It also highlights how changes to network structures may not always indicate a weakening of social structure, but rather temporary changes due to seasonal factors. However, as will be discussed later in this section, interpersonal variation (in personality traits for example) can provide an explanation for why animals show considerably different behavioural patterns when facing similar (or the same) challenge.

**Stress:** Stress has been found to significantly affect the physiology and behaviour of captive and wild populations, which can alter individual behaviour and overall network structure (Boogert et al., 2014a). In captive populations, stress from unpredictable feeding schedules has been shown to elicit higher rates of aggression compared to groups on a predictable feeding schedule. In turn, this increased the
degree centralization in the feed restricted groups (Cañon Jones et al., 2010). Social stress due to inadequate enclosures can also trigger changes in behaviour. For example in chimpanzees, space restriction is commonly associated with an increased risk of conflict. Koyama and Aureli (2019) demonstrated that chimpanzees alter their behaviours in order to reduce social tension when the space in their enclosure was experimentally restricted. The chimpanzees showed significantly fewer positive social interactions (lower network density) and a less cohesive grooming network. In wild populations, the stress response from the threat of predation has been shown to modulate the associations that animals make. Hasenjager and Dugatkin (2017) studied guppies where one group was exposed to a conspecific alarm cue (normally released following epidermal damage), while the other served as a control. Guppies exposed to the alarm cue showed an increased tendency to associate with guppies their own size (size assortment), and to spend a greater duration in the company of their preferred associates (greater strength). This change in assortment is likely to minimise risks of being targeted by a predator if the individual would otherwise stand out from the rest of the group.

*Phenotypic distribution:* Changes to phenotypic distribution or variance can also significantly affect the overall group structure. For example changes to sex ratio caused by male migration has been found to effect female centrality (primates Jacoby et al., 2010; sharks Borgeaud et al., 2017). Many species display forms of assortment according to phenotypic variation (Farine et al., 2015). Changes to the phenotypic variation can therefore lead to group-level changes in association patterns.

*Social and demographic variability:* Social and demographic changes can also lead to disruption of social behaviours, and lead to changes at the population level. Changes
to social networks primarily fall into three categories which are; the loss of a member (node removal), addition of a member (node attachment), or changes in social relationships (edge re-wiring) (Shizuka and Johnson, 2020). Figure 1.8 demonstrates the drastic change in network structure (in this case, network fragmentation) that can occur as a result of edge rewiring. A similar effect would have occurred, had one of the nodes involved in that interaction been removed entirely (e.g. Figure 1.8b). In wild populations, this loss of a group member would commonly occur due to death or dispersal. In commercially farmed species, death can also occur, but more commonly removal of individuals is due to management requirements such as sickness, behavioural issues, or weight uniformity. For example, ‘early depopulation’ is a common practice in the pig industry and occurs when a certain proportion of the group members are large enough to go to slaughter and smaller animals are left behind. Node removal (as shown in Figure 1.8b) is disruptive; however, the severity of the disruption is heavily influenced by the position the individual held in the group. The removal of a heavily connected so called ‘key stone’ individual (also commonly called ‘hubs’ or ‘bridges’) (Modlmeier et al., 2014b; Verdolin et al., 2014), or a high ranking animal (Flack et al., 2006) would be considerably more disruptive than the loss of a more peripheral animal (Modlmeier et al., 2014b).
As losing an individual can substantially disrupt a group, having a network structure that minimises the chance of a major disruption is advantageous. Degree distribution in some animal communities show a scale-free power law pattern (Barabási and Albert, 1999) which makes them highly resistant to fragmentation when key individuals are removed (Lusseau, 2003). Studying how groups respond to loss of individuals commonly relies upon computer simulated removal (as in with Lusseau, 2003), or ‘knock out’ experiments where individuals are removed from a group (Flack et al., 2006). While simulated networks are the most widely used, due to the ease with which such models can be carried out with modern technology, they do not include the indirect effects that may occur due to the behavioural modification in response to the loss of a group member. This was demonstrated in colonies of Indian queenless ants (Diacamma indicum) which showed that the level of social disruption that occurred
due to the experimental removal of individuals was less than in the simulated removals (Annagiri et al., 2017). This was likely due to the role of individuals adapting to the new social environment, and their collective efforts to rewire the network to account for the lost group members. Such change at the individual level has been observed in temporal network analysis of great tits during the removal of group members. It showed that individuals who had strong ties to the removed individuals engaged in increased social interactions with new individuals and strengthened their existing connections (Firth et al., 2017), thus showing a behavioural modification in response to the loss.

The role of personality: Consistent differences in individual behavioural tendencies have been defined as ‘animal personalities’ but have also been defined by other researchers as coping styles (Koolhaas et al., 1999), temperament, (Réale et al., 2007), and behavioural syndromes or types (Sih et al., 2004). The term ‘personality’ is used to describe the individual differences that are consistent over time and different contexts (Dingemanse and Wolf, 2010; Réale et al., 2007). Such consistency has been demonstrated in a range of behaviours such as aggressiveness, (Koolhaas et al., 1999), cooperativeness (Bergmüller et al., 2010), responsiveness (Dingemanse et al., 2010), and mating behaviour (Montiglio et al., 2016). These consistent tendencies to behave and socialise in a certain way have a profound effect on both individual and group level social patterns, and there has been a wealth of research to understand how such tendencies evolved and are maintained.

One of the most commonly studied personality trait is boldness. For example Aplin et al., (2013) studied the difference between fast exploring (bold) and slow exploring (shy) great tits, Parus major and found that fast exploring birds tended to have weak
associations with many individuals and socialise between groups, whereas slow exploring birds had well developed connections with a smaller number of individuals. This has also been observed in a number of other studies where bold individuals show higher activity and explore larger spatial areas than shy individuals, leading to a higher degree but lower association strength (Pike and Samanta, 2008; Tanner and Jackson, 2012). Fast explorers also tend to have higher betweenness centrality, due to their inclination to join up with many different foraging groups (Aplin et al., 2013). As a result, fast-exploring birds are likely to play an important role in the spread of information or disease. In contrast, shy birds tend to have lower centrality (Snijders, 2011).

Bold/shy personality types have also been shown to correlate with other behavioural and physiological responses including metabolic speed (Careau et al., 2009), hypothalamic pituitary adrenal axis response (Koolhaas et al., 1999), and contest behaviours (Amy et al., 2010). Furthermore, personality can also incorporate elements of behavioural plasticity and variation in stress reactivity, which enables the maintenance of normal behavioural repertoires in a wide range of challenging environments (Boyce and Ellis, 2005). Furthermore, such traits have been found to be heritable (Schjolden and Winberg, 2007). In many cases, the advantage served by a certain behavioural trait can vary based on changing environmental and social pressures (Dingemanse et al., 2004; Réale and Festa-Bianchet, 2003), which may serve to maintain selection pressure on a range of behavioural types and personalities (Boon et al., 2008).

The combination of personalities in a group is a fundamental concept in game theory (Smith, 1976), and experimental manipulation of personality types in a group suggests
that composition of personalities strongly effects group outcomes. For example, Sih and Watters, (2005) demonstrated that the behaviour of one ‘hyper aggressive’ individual was enough to significantly change social dynamics and the mating success of an entire group.

*Intelligence:* Research between network structures and neocortex size across 78 species of primate has demonstrated a strong link between putative intelligence and network efficiency. Efficiency in a network is defined as providing fast accurate information transmission with the least number of ties between actors, as these are costly to maintain (Pasquaretta et al., 2014). This is likely to be due to highly intelligent species having the ability to adjust their social position in order to get better access to information, which consequently makes the network structure more efficient. Similarly, neocortex size has also been found to be positively correlated with the size of networks (Kudo and Dunbar, 2001). However when controlling for group size, Lehmann and Dunbar, (2009) noted that neocortex size was negatively associated with network density, connectivity and relative clan size, and networks that were more vulnerable to fragmentation in the event of removal of a central individual. Lehmann and Dunbar (2009) suggested that as neocortex size increases, primate groups become more deeply structured.

*Consequences of network structure for group functioning*

*Communication:* Effective communication is essential for coordinating group behaviour (Strandburg-Peshkin et al., 2013) and transmission of novel and/or valuable information (Thornton and McAuliffe, 2006; Van De Waal et al., 2013). Many species (e.g. dolphins Lusseau, 2003, and guppies Croft et al., 2004) have been found to form network structures that show small world characteristics (such as many small
clustered subgroups (modularity) and short average path lengths) which are characteristics associated with efficient communication in humans (Watts and Strogatz, 2011). Simulated and real-life network studies have shown that homogenous networks (where all individuals have a similar network position) are the most effective at transmitting information and for reaching faster group consensus. This was tested by Boogert et al., (2014b) who demonstrated that the spread of a novel foraging technique within a population of birds was best predicted by a homogenous network structure. Therefore, network structures such as that presented in Figure 1.4 with large variation in individual eigenvector, betweenness, clustering coefficient and clique membership would be expected to impede information flow.

**Group network structure and disease spread:** Similarly, differences in disease spread have also been found to be associated with network structure (Shirley and Rushton, 2005). For example, modularity (presence of well-connected subgroups and weakly connected to other subgroups) has been found to be associated with the decrease in disease spread and may be the underlying evolutionary pressure for modulated social structures (Griffin and Nunn, 2012).

**Social cohesion and conflict:** Emerging evidence suggests that certain individuals play a critical role in maintaining the cohesion of the group (Kanngiesser et al., 2011; Manno, 2008; Verdolin et al., 2014). This was demonstrated in a study by Flack et al., (2005a) where pigtailed macaques that been identified as disproportionately responsible for conflict management were removed from the group. The removal of these individuals led to network fragmentation and system destabilisation with a significant increase in aggression and decrease in positive social interactions and reconciliation.
Effect of individual network centrality on individual fitness

Survival and longevity: Animals are constantly in a battle of survival, yet certain stages of life can pose particular challenges and increased risk of mortality. Juveniles and offspring are at particular risk due to their dependence on parental care for food and protection. Infants are smaller in size, have less energy reserves than adults, and are inexperienced at hunting and/or foraging, which puts them at risk of starvation during times of low food availability. Infants are also at much higher risk of predation. However, the likelihood of succumbing to such threats during infancy has been found to be greatly affected by the social network position of the parent. The survival of both juvenile dolphins and wild baboons were found to be positively associated with the eigenvector centrality of their mother (Stanton and Mann, 2012). This means that infant survival is enhanced when the mother is connected to other adults who are themselves well connected in the network. It is also highly likely that offspring of central individuals benefit from their parents’ position not only during infancy, but also for the remainder of their lives. Wooddell et al., (2019), found that offspring born to high centrality parents also tended to go on to be highly central themselves, particularly in affiliative networks, and suggested that early life experiences shape the social competency which affects future social success. Adults can also face increased risk of mortality during severe winters, as food is less available and a high amount of energy is needed for thermoregulation. Network position (in particularly, degree centrality capturing the number of social partners) has been found to be positively associated with survival of cold winters in barbary macaques (Lehmann et al., 2016; McFarland and Majolo, 2013). Likewise, individual centrality has also been found to be positively associated with longevity in rock hyrax (Barocas et al., 2011).
Mating success: Current social connections can influence individual mating success, but interestingly in some cases network position early in life can affect mating success in adulthood. For example, in long tail manakins the mating success of males can be predicted nearly 5 years earlier by their information centrality (a measure of connectivity that accounts for indirect social connections and shortest paths between individuals) when a juvenile (McDonald, 2007).

In adulthood, a number of different network traits have been found to be associated with copulation success. For example, in forked fungus beetles (*Bolitotherus cornutus*) network strength (weighted degree centrality) was positively related with mating success, whereas individual clustering coefficient was found to be negatively related. No relationship was found between the beetles’ betweenness centrality and their mating success. In contrast, a study of social lability (tested by an individual’s betweenness centrality which was higher in birds that moved between social groups) in wild house finches (*Carpodacus mexicanus*) was found to be positively associated with their mating success. The wild house finches demonstrated a degree of assortment based on their ornamental plumage which is an adaptive trait to attract females. The statistical interaction between social lability and ornamental plumage and mating success indicates that males may be deliberately choosing to associate with individuals of similar or lower attractiveness than themselves in order to boost their chances of attracting a mate. Birds with higher betweenness centrality were most likely to move between social groups in order to find the group where they appeared most attractive in comparison to their rivals (Oh and Badyaev, 2010).

Information sharing: Being relatively well connected can also provide the advantage of being one of the first to receive useful information. Aplin et al., (2012)
studied wild songbirds and found that the discovery of and arrival at a new food source could be predicted by a bird’s social associations, suggesting that news about a new food source spread across the group and birds less socially connected were the last to arrive. Similarly, Allen et al. (2013) found evidence that the spread of ‘lobtailing’ behaviour (a variation of bubble-net feeding) could be explained by an association network in humpback whales (*Megaptera novaeangliae*).

**Individual network position and disease spread:** As with being the first to learn of new information, certain individuals can also find themselves more likely than others to be exposed to infectious pathogens. Social grooming networks in particular are associated with the transmission of parasites and pathogens, as it involves extended periods of close proximity and physical contact. This was demonstrated by MacIntosh et al., (2012) who found that female eigenvector centrality in grooming networks was positively associated with parasite load. The ability to include direction in social network analysis can also help differentiate whether receiving or initiating interactions can affect disease spread. Drewe (2010) found that meerkats who groomed others were at a higher risk of infection (out-degree) than individuals who received lots of grooming (in-degree). Roving males who moved between isolated groups (betweenness centrality) were also more likely to subsequently test positive for tuberculosis than non-roving individuals.

Another study looked at the social structure of gidgee skinks (*Egernia stokesii*) who tend to form large aggregations and share shelters in rocky crevices. The study looked at both direct interactions as well as shared crevice networks (where individuals were considered connected if they were in the same crevice within a certain timeframe). Interestingly the study noted that networks constructed from subsequent occupation of
crevices were more predictive of transmission than direct contact networks, as the former were better connected than direct social connection networks that tended to be smaller and more fragmented. The study found that individuals with higher degree centrality tended to have a significantly higher parasite load than non-central individuals (Godfrey et al., 2009).

*The social networks of farmed animals*

I have chosen to discuss the social network of farmed species separate from the above sections (which primarily discuss wild species and populations in zoos), as I believe the two to differ considerably in the methods with which they have been studied and are therefore not necessarily comparable. In this section I aim to outline the main differences that need to be considered when applying SNA to farm animals, and the difficulty in applying or comparing the findings of much of the current SNA literature to commercially reared species.

*Differences between wild/captive and commercial species:* Commercially reared animals are restricted in the behaviours that they can show, which has a considerable impact on how networks will form. For example, in many wild or captive species a defeated animal will retreat and keep distance from the winner in order to reduce any further interactions and confrontations. However, animals in intensive systems do not have the option to leave and may not have the option to keep a distance or hide, due to high stocking density and lack of hiding places. Thus, repeated interactions may result leading to changes in edge density and other centrality metrics. Furthermore, certain network positions and structures are potentially less likely to emerge from individuals in densely populated commercial species. For example,
betweenness tends to be thought of as a ‘broker’, ‘bridge’, or ‘hub’ position and therefore a highly important individual to look for in wild populations in order to understand the flow of information or disease within a group, or between groups. However, high betweenness is constrained in commercial species. Firstly, such distance between ‘sub-groups’ is unlikely to form in a densely populated group in order for ‘bridges’ or ‘brokers’ to emerge. Secondly, in such highly densely populated groups the probability of an additional connection being made by another individual is far greater than between two wild populations that are spatially distant (Büttner et al., 2015a). With that said, if these behaviours do emerge it is also highly likely to reflect a behaviour quite distinct from such behaviours associated with betweenness in wild populations, and so our interpretations need to be mindful of the environment and conditions the animals are in.

Likewise, concepts that may seem applicable to both wild and commercial species such as social disruption or social stability, are usually not comparable. For example, disruption to a social group in the wild usually comes in the form of the death of a group member or natural disaster. Therefore ‘knock out studies’ (e.g. Flack et al, 2005) on wild populations have attempted to understand the effects of removal of one individual and how this can affect the overall group. However, in wild species there are fewer equivalents to what happens during mixing in commercial settings, whereby entirely unfamiliar individuals are suddenly introduced to each other without the ability to move apart and must create a social hierarchy from nothing.

Furthermore, in commercial systems animals are often housed in group sizes far exceeding that which would occur in the wild. For example, domesticated chickens are descendants of red jungle fowl that tend to live in small groups (<10) consisting of a
dominant male and a harem of females in the wild (Johnson, 1963), whereas in commercial colonies group sizes are often in the thousands.

Finally, and perhaps most fundamentally, is the fact that commercial species tend to be housed in abiotic environments with evenly distributed resources, and a deliberately narrowed variation in age, weight, and size, and in some cases sex ratio. We therefore have stripped away much of the variation that has been found to shape social networks in wild species, and as a result, the social network analysis of farmed species provides a unique perspective of variation in network position and structure that is shaped due to the variation and combinations of individual personalities.

*Farm animal networks:* While SNA in farmed species is still in its infancy, research is beginning to uncover considerable variation in network position within and between groups. To date, social network analysis has been applied to dairy cows (Boyland et al, 2015), pigs (Büttner et al., 2015b, 2015a, Liu et al 2018) and farmed salmon (Cañon Jones et al., 2010).

Boyland et al., (2015) examined the social network structure of dairy cows. The study showed that cows show assortment based on behavioural traits, but also based on production metrics such as lactation number, breed, and milk production. The social groups tended to show significant centralization, indicating that a few individuals had disproportionately more social contact than the remainder of the group which may indicate greater risk of social disruption in the event of removal. However, the network structures only showed moderate stability over time, with a maximum of 57% of the structure repeated the following week, and in some cases repeatability was as low as 17%.
Similarly, Büttner et al. (2015b) looked at the social network structure of pigs across three different mixing events. While no ‘consistency’ of network structure could be found in this study, as each mixing event resulted in a new combination of individuals, it did provide indication that network structures from different age groups show significant differences. In particular each mixing event lead to a lower number of contest partners and reduced network density. Most interestingly, Büttner et al., (2015b) noted that networks from all mixing events had consistently higher out-degree centralisation than in-degree centralization, indicating that small numbers of highly aggressive individuals were most influential in determining overall network structure and that the group as a whole did not target a particular victim. A later study looked at how individual network position correlated between the different mixing events and age groups (Büttner et al., 2015a). Interestingly, centrality traits were correlated between those mixing events that occurred closest together in time (i.e. weaner and grower, grower and gilt) but there was no correlation between weaning behaviour and gilt behaviour. Degree and out-degree were moderately correlated between weaning and growing stages (0.23 and 0.33 respectively), and also out-going closeness ($r_s = 0.31$). These traits were also moderately correlated between the growing pig and gilt stage (degree, $r_s = 0.23$, out-degree $r_s = 0.28$, and out-going closeness $r_s = 0.19$). However, betweenness centrality was less well correlated at 0.18. This was only significant between the weaner and grower stages.

Certain traits were highly correlated within mixing events. For example, betweenness was correlated with degree at $r_s = 0.78$ at growing and $r_s = 0.86$ for gilts, but only at $r_s = 0.41$ at weaning. Büttner et al (2015a) hypothesised that this may be because the pigs are inexperienced during the first mixing event (weaning) and do not employ a
clear strategy and the network develops high density as the animals engage in fighting fairly equally throughout the group. Whereas in grower and gilt stages, previous fighting experience may lead to specific opponent choice, which allows for more detail in the network structure to become apparent (i.e. betweenness centrality). This is also the reason Büttner et al (2015a) proposes for the decrease in closeness across mixing events; as the interactions become more strategic the closeness and density of the network decrease.

Büttner et al’s (2015a, 2015b) work suggests that certain individual behaviours may be more consistent than others, particularly out-going behaviours, whereas other behaviours are less likely to be maintained. For example, Büttner et al (2015a) points out that betweenness centrality is highly sensitive to changes in the network, which may be why it is less consistent across stages. It is also likely that the stability of behaviours is highly dictated by the behaviours of others. For example, an aggressive individual may attack considerably more individuals than the remainder of the group (creating a heterogeneous/ highly centralised network). However, if during the next mixing event the individual is grouped with similarly aggressive individuals, it is likely the result will be a homogenous network with all animals occupying a similar position. Thus, even if the behaviour of the central individual has not particularly changed, its relative network position has.

Social network analysis has also been applied to tail biting behaviours in pigs (Li et al., 2018), under the hypothesis that social dynamics that lead to an ‘unbalanced social structure’, may induce tail biting outbreaks and other abnormal behaviours. The hypothesis that early-life experiences can shape future social behaviour was also incorporated in this study by creating three treatments at the nursery stage prior to
being grouped into their study groups. Piglets were either not mixed during the nursery phase (littermates only), mixed with their littermates and with another group (half littermates), or placed into an entirely novel group (no littermates). While this study did not find that individual position in proximity networks related to tail biting, it did identify differences in network structure amongst treatments and subsequent tail biting outbreaks. In particular, pigs from the ‘littermates only’ treatment were most likely to have poorer connectivity (lower network density and strength of connections), compared to groups comprised of non-littermates and half littermates. Li et al., (2018) found that groups comprised only of littermates were more prone to tail damage than non-littermate groups and suggested that the poor social connectivity may increase their susceptibility to abnormal behaviours.
1.4 Pig behaviour

1.4.1 A pig’s life: then and now

The commercial breeds of pigs which are commonly reared for meat today all originate from the wild boar (*Sus scrofa*). Whilst humans have diligently selected for traits relating to growth and meat quality which has led to considerable physiological differences between modern pigs and wild boar, they remain extremely similar in their behaviours and instincts (Graves, 1984; Mauget, 1981; Špinka et al., 2000; Stolba and Wood-Gush, 1989). Unfortunately the recent changes in management methods and housing environments have occurred rapidly in relation to both the evolution of pigs and also domestication (D’Eath and Turner, 2009).

Wild boar live in matriarchal groups, primarily consisting of 4-6 females and their most recent litter (Graves, 1984; Mauget, 1981). Sows have a strong instinct to build a nest and to distance themselves from the group as farrowing approaches. They will remain alone with their piglets for approximately 1 week before they return to their group. As the offspring mature, juvenile females will either stay with the group or create a new group on their own. Young males will leave the family unit and live in small groups of juvenile males (consisting of 3 – 4 individuals) but will become increasingly solitary as they mature (Frädrich, 1974; Mauget, 1981). The dominance hierarchies in wild boar are relatively stable, and social positions are governed primarily by sex. Within all female groups social rank is closely correlated with age, weight, size, and strength. Males over 3 years old dominate all other classes, and within groups of females, the dominant animal is usually the oldest (Mauget, 1981).

Under commercial settings, pigs are not afforded the stability of a long-term social group. Piglets are weaned artificially early, at 4 weeks of age in the majority of
countries, however some countries wean as early as 2 or 3 weeks (Worobec et al., 1999), whereas in the wild, piglets would not be weaned until 10 weeks (Newberry et al., 1985). At weaning they are commonly grouped with other newly weaned litters and must establish a new hierarchy. Weaning is a particular stressful time for piglets, as they need to overcome the distress of premature separation from their mother (Weary et al., 1999), gastrointestinal distress from abrupt change in diet (Campbell et al., 2013), and the stress resulting from identifying their place amongst their new conspecifics (Couret et al., 2009; Merlot and Meunier-Salaün, 2004). The stress associated with the weaning period commonly leads to a significant drop in growth rate, and vulnerability to numerous infectious pathogens that commonly exist in commercial farms (Campbell et al., 2013). In wild litters, piglets are exposed to other litters at around 1 week of age, which gives them the opportunity to learn social skills and dominance relationships earlier than commercially reared piglets.

The piglets will be moved from weaner accommodation, to grower and then finally finisher housing. They are likely to be mixed into new social groups at each transitional period between housing units. Pigs will also experience mixing when they are loaded on to transport lorries and in the lairage pens at abattoirs.

1.4.2 Post-mixing aggression

Engaging in aggressive contests as a means of establishing dominance is a common behaviour in social living species and is widely seen in wild species from the suidae family (Barrette, 1986; Frädrich, 1974). Thus it is unsurprising that each time pigs are grouped with unfamiliar conspecifics (hereafter referred to as mixing), intense aggression occurs while they attempt to establish new dominance relationships (Meese and Ewbank, 1973). However, in a commercial setting, pigs are deprived of the
environmental and social conditions that played a critical role in the evolution of their contest behaviour. As outlined in section 1, boar evolved small stable family units, commonly consisting of no-more than 7 adults. Inclusion of new group members occurs infrequently. In such settings, dominance can be inferred easily by weight, size, and strength of the group members. Unfortunately, in commercial systems grouping animals based on weight similarity is common throughout the growing and fattening stages. This is partially due to data suggesting that it improves average daily gains (Tindsley and Lean, 1984), although evidence for this is not consistent (Francis et al., 1996; O’Quinn et al., 2001). However, at slaughter, uniformity is a requirement from many processors and retailers (Hennessy, 2005), as variation in the carcass shape, size, and composition affect the costs associated with packing and acceptability to consumers (Alfonso et al., 2010; Patience et al., 2004). By purposefully reducing the natural variation that occurs within a group, we compromise pigs’ ability to identify and maintain their social standing within their group. When housed in groups containing larger asymmetry in size, duration of aggression over resources decreases (Andersen et al., 2000; Francis et al., 1996), suggesting that recognising social status is easier for pigs with clearer variation in fighting ability (weight, size, strength).

In addition to the artificial uniformity, the group sizes on commercial farms may be vastly larger (>50) (Turner and Edwards, 2004) than the small family units that pigs would form if left to act on their own instincts (Mauget, 1981). Whilst aggression does not appear to increase in large pens of animals (Turner and Edwards, 2004), either in number of fights or duration of fights, the unnatural group sizes may still create an environment where achieving a stable hierarchy amongst conspecifics is challenging. Turner and Edwards, (2004) suggested that aggression may continue to decrease after
24hr due to exhaustion and habituation to unfamiliar individuals in the group. The stocking density typically used in commercial environments is also incomparable to space availability in free living animals. This impacts individuals’ ability to escape when threatened or clearly signal submission.

Upon mixing with unfamiliar conspecifics, there is an intense period of aggression that reduces drastically 24 hours post-mixing (Meese and Ewbank, 1973). Aggression is also observed amongst individuals in stable groups and is likely to be a method of reinforcing the dominance hierarchy (Newberry and Wood-Gush, 1986). Aggression primarily takes two forms, reciprocal and non-reciprocal.

During reciprocal aggression (hereafter referred to as fighting), typically two individuals will take an aggressive stance by standing either parallel or in front of their opponent and engaging in pushing and thrusting their head against the other (Meese and Ewbank, 1973; Signoret et al., 1975). If neither individual shows submission at this stage, the encounter will escalate to bites targeting the face, ear, and shoulder region (McGlone, 1985a). In the majority of cases, one individual will eventually show submission by turning away and retreating from the fight (Meese and Ewbank, 1973), tilting the head (Jensen, 1982), or releasing olfactory cues (McGlone, 1985b). In non-reciprocal aggression (hereafter referred to as bullying), one individual will attack another without the other animal retaliating (Turner et al., 2009). The victim usually attempts to escape from the aggressor, and as a result usually receives bites to the posterior portion of the body (Meese and Ewbank, 1973; Turner et al., 2006).
Consequences of aggression

Post-mixing aggression has numerous negative consequences for pig welfare and productivity. Injuries can occur during contests. These are commonly skin injuries (hereafter referred to as lesions) (Turner et al., 2006), and lameness from slipping and falling while fighting (Rydhmer et al., 2006). Whilst the physical injuries can be severe, the stress caused by aggression and disruption to their social stability is likely to be the greater welfare concern. Research has demonstrated that pigs that experience mixing show elevated salivary cortisol (Couret et al., 2009; Coutellier et al., 2007; Otten et al., 1997), increased heart rate (Marchant et al., 1995), and suppression of normal immune function (de Groot et al., 2001).

Post-mixing aggression can occur during transportation to slaughter and during lairage and can contribute to a decrease in carcass value (Faucitano, 2001) as a result of necessary trimming and an increase in pale soft meat (D’Eath et al., 2010). Furthermore, even when such gross effects on the carcass are not seen, the stress can negatively affect muscle pH and meat quality.

Management of aggression

Reducing the number of mixing events is unlikely to be widely adopted. Furthermore, farms tend not to be designed to have the same group size at all stages of production. Therefore, to keep a group size small enough for the smallest pens inevitably means that the pens at other stages of production will be under-stocked. This reduces the throughput of the farm, greatly increasing the fixed costs per animal. Furthermore, pigs grow at different rates and it may be necessary to change group membership to minimise the within-group weight variation.
However, the extent to which an animal displays aggression can be influenced by a number of factors. For example, allowing litters to mix with other litters prior to weaning has been shown to reduce future aggression (D’Eath, 2005). In contrast, prenatal exposure to stress can increase offspring reactivity, mixing aggression, and aggression towards their own offspring (Jarvis et al., 2006).

A number of management approaches to reduce post-mixing aggression have been trialled, including; use of synthetic pheromones (Guy et al., 2009; McGlone and Morrow, 1988), and odour masking agents (Barnett et al., 1993), alternate pen shapes and the use of partitioning (Olesen et al., 1996; Waran and Broom, 1992), weight asymmetry within groups (Andersen et al., 2000), providing space to hide from attacks (Francis et al., 1996; McGlone and Curtis, 1985), and manipulating group size and feeder space (Turner et al., 2002). However, these solutions have proven to be either too impractical or costly to be routinely implemented on commercial farms.

Additionally, there have also been attempts to mitigate aggression with the administration of pharmacological treatments, including lithium (McGlone et al., 1980), and amperozide and azaperone (Gonyou and Parfet, 1988). These experiments have been useful in demonstrating that the animals may be experiencing negative emotional states (e.g. anxiety) due to mixing, and that these negative emotions can be managed pharmacologically and reduce the rate of aggressive interactions. However, this effect only lasts as long as the pharmacological treatment continues and therefore only delays aggression and does not offer a viable management solution. From an ethical standpoint, utilising pharmacological treatments to manage negative emotions and behaviours may alleviate suffering in the short term, yet in the long term such an approach only perpetuates the premise that commercially reared animals can be altered
to better withstand management systems that fail to allow animals to show their natural behaviours. In this case, the natural behaviour would include the ability to stay in stable social groups.

**Aggressive behavioural phenotypes**

Counting skin lesions is the primary method researchers use to retrospectively quantify the amount of aggression an individual has engaged in. The location and number of lesions has been shown to correlate with the type and duration of aggression. Turner et al (2006) reported that reciprocal aggression correlated with lesions between $r=0.15$ and 0.25. A later study containing a larger sample size reported the residual correlation between reciprocal aggression and anterior lesions at 24hr-PM to be $r=0.52$ ($p < 0.01$), and $r=0.39$ ($p < 0.05$) with central lesions, and $r=0.29$ ($p < 0.05$) with rear lesions. Delivery of non-reciprocal aggression was correlated with anterior lesions $r=0.29$ ($p < 0.05$), central lesions $r=0.32$ ($p < 0.05$), rear $r=0.23$ ($p < 0.05$) (Turner et al., 2009). However, receipt of non-reciprocal aggression did not significantly correlate with anterior lesions $r=0.13$ (ns), central lesions $r=0.0.8$ (ns), and rear lesions $r=0.08$ (ns).

While aggression and the accumulation of lesions is most apparent during the first 24hrs of mixing, aggression between familiar individuals is well documented (Coutellier et al., 2007; Stookey and Gonyou, 1994), and evidence suggests that engaging in aggression during the initial mixing period reduces aggression later in life (D’Eath, 2005; Turner et al., 2009). The relationship between lesions at mixing (24hr-PM) and three weeks post mixing (3wk-PM) was studied in detail by Desire et al. (2015).
Desire et al (2015) confirmed that traits positively associated with skin lesions at mixing were also negatively associated with lesions in stable groups. More so, this was validated at both the individual and group level. At the group level, traits positively associated with lesions 24hr-PM were negatively associated with lesions 3wk-PM; however, this was mostly observed for the central portion of the body. This study did not find evidence that the proportion of repeated fights, fight intensity or proportion of ambiguous outcomes at mixing affected the group level lesion outcomes in stable groups, however there was a moderate correlation between a high proportion of successful fights (measured by proportion of fights won) and decreased lesions at 3wk-PM. Interestingly, Desire et al., (2015) identified that aggression tended not to be directed towards unaggressive individuals, but rather individuals who were aggressive but unsuccessful. None-the-less, the results show that engagement in aggression, even when unsuccessful, led to a reduction in both individual and pen level lesions.

However, a later study by Turner et al., (2017) demonstrated that a wide range of aggressive behavioural strategies at mixing could lead to the same lesion outcome 3wks post mixing. The study clustered pigs based on 80% behavioural similarity at mixing. The individuals within each cluster were shown to have a wide range in lesion outcomes at both mixing and in stable groups. Within this study, pigs identified as having low lesions at both mixing and in stable groups (LL pigs) were of particular interest, as they may possess a behavioural strategy that enables them to avoid aggression at both time points. However, a wide range of behavioural strategies were associated with the achievement of LL status and it appears impossible to identify and promote a single strategy to successfully reduce aggression across social contexts. The considerable variation in lesion scores has been noted in a number of studies (Erhard
et al., 1997; Turner et al., 2009, 2017), and not only reflects variation in individual aggressive propensity at the time of mixing but also suggests that individuals deploy different fighting strategies which greatly affect the long term outcome.

The role of intelligence, personality, and strategy in aggressive behaviour

Aggressive interactions are assumed to require rapid and accurate information gathering, decision making and memory – and hence good cognitive skills. Lesions are therefore expected to be affected by both physical and cognitive skill. The cognitive determinants of aggressive behaviour are yet to be studied in detail in pigs, but it can be assumed that the ability to make use of information on third party interactions requires a further level of cognitive ability beyond simply that to navigate dyadic interactions (Byrne and Bates, 2007).

Animal intelligence has been widely researched, and a variety of tests have been developed as a way of identifying different aspects of cognitive ability and intelligence. The ability to understand the relevance of third party interactions has been documented in pinyon jays (Gymnorhins cyanoccephalus) (Guillermo Paz-Y-Miño et al., 2004), great tits (Parus major) (Peake et al., 2002), hyenas (Crocuta crocuta) (Engh et al., 2005), and species of fish (Groenick et al., 2007; Oliveira and McGregor, 1998) (for full review see Brent, 2015). Pigs have demonstrated similar intelligence (Kornum and Knudsen, 2011; Marino and Colvin, 2015; Nawroth et al., 2019), in particular the ability to manipulate conspecifics to their advantage in foraging situations (Held et al., 2001). When such behaviours are observed in primates it is commonly referred to as ‘tactical deception’, and such behaviours suggest that pigs may have advanced levels of perspective taking comparable to many primate species, suggesting that they may possess the cognitive capacity to understand the relevance of
third party social interactions (Marino and Colvin, 2015). However, as this has not been directly researched, this ability in pigs remains uncertain. However other cognitive abilities in pigs have been tested using a variety of methods including the use of ‘T-mazes’ to test reversal learning ability (Mendl et al., 1997), eight-arm radial maze tasks to test working memory (Laughlin et al., 1999), spatial hole board discrimination tasks to test spatial working and reference memory (Arts et al., 2009), the Morris water maze as a more rigorous test for spatial working memory and declarative memory (Siegford et al., 2008), and the Y-maze to test social recognition (Kristensen et al., 2001). These studies on the cognitive abilities of pigs (reviewed by Kornum and Knudsen, 2011) demonstrate that they possess the cognitive capacity for a wide range of problem solving tasks and the ability to learn. Other studies have investigated social learning in pigs, which has demonstrated that Kune Kune pigs can learn from others to complete a task in order to receive a reward (Veit et al., 2017). Another method commonly used to test animal intelligence is the ‘mirror test’, which has been widely used on a range of species to determine whether they can identify themselves in the mirror, and whether they can utilise the information presented in the mirror. Dolphins, elephants, chimps, and corvids, who are widely recognised to be intelligent animals, have all been found to pass the mirror test, and as of 2009, so have pigs. Broom et al., (2009) tested whether pigs were able to learn the properties of a mirror from simply having a mirror in their pen for 5 hours. The ability to use a mirror to accurately locate a bowl of pig nuts was then compared between the ‘mirror naive’ pigs and ‘mirror experienced’ pigs. The results showed that from one exposure to a mirror, pigs were able to accurately interpret information from the mirror to locate the food bowl. In contrast, pigs that had never been exposed to a mirror attempted to find
the food behind the mirror. However, one of the mirror-experienced pigs did not learn and instead repeatedly went looking for food in the wrong place. Broom et al., (2009) noted that this individual ‘either could not learn or did not have enough time to learn’. This variation in learning ability has also been noted by a number of other studies and has also been found to be associated with personality. Research has identified that that pigs tend to adopt either a more “active” or “passive” approach when faced with a challenging situation (Benus et al., 1991; Hessing et al., 1993). This trait is commonly tested for in pigs by using the ‘back-test’, where piglets are placed on their backs in a V-shaped apparatus and the number of escape attempts are monitored to determine whether the pig actively tries to escape (high-resisting/HR), or passively accepts its unfortunate situation (low resisting/LR) (Hessing et al., 1993). Much like other personality traits, this trait has been found to be consistent over time and across situations and associated with various physiological, endocrine and immunological responses, and to be determined largely by genetic and environmental factors (Forkman et al., 1995; Hessing et al., 1993, 1994).

Bolhuis et al., (2004) found evidence of cognitive differences between HR and LR pigs, in particular that HR pigs struggle with reversal learning exercises and show a tendency to become stuck in maladaptive behavioural patterns, which may indicate that HR/LR traits represent individual ability to respond to a changing environment. Hessing et al., (1993) also noted that HR pigs tended to engage in more aggressive behaviour than LR piglets; an observation that was later confirmed by Bolhuis et al., (2005) who reported that HR piglets tended to start more fights, started fights earlier and spent a greater proportion of their time engaged in fights but are not more successful. However, these results were not found by D’Eath and Burn, (2002) when
testing the relationship between HR/LR characteristics and latency to attack in resident intruder tests. This may be due to this study using a dyadic test compared to a group level testing approach used in other studies (Bolhuis et al., 2005; Hessing et al., 1993, 1994; Ruis et al., 2001). This may indicate that group level dynamics (or indirect social effects) may exert an influence on aggressive behaviour that is not present in dyadic tests.

Notably, the final dominance rank does not tend to differ between HR and LR pigs, despite LR pigs engaging in considerably lower rates of aggression (Bolhuis et al., 2005). However, Bolhuis et al., (2005) demonstrated that the dominance rank of low resistance pigs was highly correlated with their fighting behaviours, indicating that when LR pigs did engage in aggression they tended to achieve higher social rank. These findings are supported by work done by Melotti et al., (2011) that showed that LR pigs tend to win a higher proportion of fights than HR pigs. Bolhuis et al., (2005) suggested that this indicated that LR pigs were capable of adjusting their aggressive behaviour, whereas HR pigs continue to fight regardless of the outcome. This finding was also reported by Ruis et al., (2002) who found that HR pigs would continue engaging in aggression even once dominance status had been settled. Similarly, Turner et al., (2017) identified a behavioural cluster which they named ‘selectively aggressive’ and was characterised by pigs that were more successful at winning fights than ‘extreme’ and ‘persistent aggressor’ groups which were primarily characterised with longer fight durations and repeated interactions. While these clusters were not strongly associated with lesion outcomes, it does provide a preliminary basis for hypothesising that pigs may deploy different contest strategies that may significantly affect their long term social success.
Aggressiveness as a personality trait has also been found to influence contest escalation. Camerlink et al., (2016) identified additional non-aggressive contest behaviours including mutual investigation, and non-contact displays such as parallel walking which may be a ritualised method of assessment and decision making. Non-aggressive winners (as determined by resident intruder tests) displayed more opponent investigation and showed less aggression towards losers after retreat. Camerlink et al., (2016) noted that certain pigs with lower aggressive personality traits were more likely to resolve aggression without engaging in overt aggression.

1.4.3 Post-mixing aggression re-examined with social network analysis

As outlined in section 3, social network analysis offers a wide variety of ways to quantify an individual’s social position that provides information not offered by conventional dyadic measures. Therefore, it is an exciting prospect to apply such measures to a social species in order to determine whether network position or structure are related to social outcomes.

Applying social network analysis to post-mixing aggression will allow us to expand upon current behavioural phenotypes and potentially identify new traits at both the individual and group level that affect social outcomes. By identifying the variation in overall network structures and how these correspond to group level lesions, we may be able to identify so called ‘key-stone’ figures that may either aid or disrupt the formation of stable hierarchies. As we have the unique opportunity to study replicate networks in a controlled physical environment, this research may also be valuable in furthering our understanding into how personality (in this case, aggressive personalities) can lead to variation in network structure.
Expansion on current behavioural phenotypes

Social network analysis may be able to expand our understanding of certain aggressive traits in a number of different ways. Aggression is commonly quantified by the frequency of aggression, duration of aggression, number of aggressive encounters, or number of individuals fought with. Social network analysis can quantify such behaviours in terms of *degree* (i.e. number of attacks received (in-degree), and initiated attacks (out-degree)). However, SNA has the ability to weight such interactions by either the duration or frequency and provide a value that reflects how central an individual is in relation to the remainder of the group and the nature of the behaviour.

For example, an individual may be central based upon the number of unique fighting partners (e.g. Figure 1.9). However, if we wish to take into consideration the number of repeated fights, and weight interactions accordingly (e.g. Figure 1.9b), this may demonstrate two individuals have similar centrality when additional aspects of the behaviour are included, or another individual is actually more central (e.g. Figure 1.9c).

*Figure 1.9. Example model demonstrating the shift in centrality when behaviours are weighted. A) Model network for an unweighted network. B) Same network weighted by frequency (in this example, the thicker line represents 3 interactions) and C) weighted for duration (in this example the unit is minutes). Node 3 had the highest centrality in terms of number of fighting partners (A), however when repeated fights are included node 4 has*
equal centrality to node 3 (B). When considering duration (C), node 1 actually engaged in disproportionately longer fights than the remainder of the pen and is therefore more central.

In this way, social network analysis makes it easier for us to integrate additional information than standard direct behavioural measures and to examine how this may affect social outcomes. Hypothetically, we could see distinct differences in lesion outcomes based on different weightings. For example, much like HR pigs, those with high degree centrality weighted by frequency may show signs of an inability to accept or recognise the outcome of an interaction and continue to engage in repeated fights. In contrast, a high degree weighted by duration may correspond to lengthy fights with definite outcomes, and thus reduce the need for repeated interactions later on (Desire et al., 2015).

However, SNA’s real benefit is the incorporation of indirect social connections which provide an entirely new perspective on the social interactions and help us differentiate between two seemingly similar individuals.

For example, in Figure 1.10. Model network illustrating effect of indirect social connections on eigenvector centrality.node 3 has the highest eigenvector centrality (1.00). Both nodes 1 and 7 only have one connection, however node 1 has the lowest centrality because it is connected to another poorly connected node (node 2 also only has one connection). Whereas node 7 is directly connected to node 3 who is well connected. Node 7’s eigenvector centrality is 0.35 whereas node 1 is less than half that at 0.14.
In terms of aggression this difference could hypothetically affect the social outcomes in a number of ways. For example, a high eigenvector central pig has fought with other individuals who have also engaged in numerous fights. High eigenvector centrality therefore could reflect a predisposition to fight with other highly aggressive animals or may even reflect alternative aggressive traits. In contrast lower eigenvector individuals tend to engage in fights with less experienced individuals. How this may affect lesion outcomes is yet to be discovered, however it is possible that high eigenvector individuals may inflict or accrue more injuries compared with low eigenvector individuals with the same number of fights if this does indeed reflect a different fighting experience. On the other hand, one could argue that high eigenvector individuals may gain better fighting experience than low eigenvector individuals due to their choice of opponent also having a lot of fighting experience. This could potentially translate as the opportunity to learn and improve self-assessment skills that may be beneficial during future encounters which could reduce long term lesion scores.
Similarly, clustering co-efficient may also reflect a similar tendency for aggressive individuals to fight amongst themselves. However, the difference here would be the tendency for social partners to also be connected to each other as opposed to any other highly connected individual as with eigenvector centrality. This may have implications for the formation of transitive triads and reflect hierarchy formation. As individuals with a high clustering co-efficient tend to form such triads, it may lead to the formation of a stable social position. In turn, this will lead considerably fewer lesions from chronic aggression in the weeks following mixing compared with individuals whose aggressive interactions do not form transitive triads.

In contrast, betweenness centrality indicates an individual who connects otherwise non-connected individuals or groups of individuals (Gilby et al., 2013; Wasserman and Faust, 1994). This measure depends on at least two animals having no direct interaction with one another and failing to form a triad and this may impact on social rank certainty or hierarchy formation.

At the group level, high levels of centralization indicate high inequality in social position. For example, a pen with high eigenvector centralization informs us that there is likely to be a cluster of well-connected pigs engaging in aggression with one another in the presence of poorly connected individuals. On one hand this may reduce lesions, with more aggressive individuals fighting amongst themselves and less aggressive individuals managing to stay out of the way of conflict. On the other hand, it could reflect that a certain proportion of the pen has established dominance relationships, while another proportion contains pigs that are less integrated and may have more ambiguous social positions which could reduce long term social stability.
Chapter 2. Social network properties predict chronic aggression in commercial pig systems

Chapter 2 contains the published manuscript of the following paper:


A note on author contribution: The data collection and experimental design was not carried out by the author. The authors contribution has been to re-examine a pre-existing dataset collected by SRUC staff for a prior research project, and to apply new statistical methodology.
2.1 Prelude

In Chapter 2, we utilise a variety of global network measures (see Chapter 1, section 1.2.3.2) to quantify the variation in network structures across 78 pens with the same resources, and to determine whether such network properties are predictive of pen level lesion scores. Identification of such network properties will provide a valuable starting point in determining which network positions at the individual level may be particularly important for further study. In particular, we anticipate it may reveal individuals that have an especially influential role in shaping the group network structure.

Chapter 2 is an insert from the published manuscript (Foister et al., 2018). Supplementary material referenced in this chapter has either been included in the Chapter 1, or is provided in the Appendix (please see below).

S1.File. Freeman Centralisation Equation (Provided in Chapter 1 Equation 1.5 (pp 14)).

S1.Table. Network properties estimated from the behavioural networks and entered in the stepwise regression (Provided in Appendix A).

S2.Table. Summary of key terms and network properties (Provided in Appendix B).

S3.Table. Descriptive statistics of network properties in fighting, bullying and combined networks (Provided in Appendix C).

S4.Table. Spearman rank correlation of dyadic and network properties (Provided in Appendix D).
2.2 Abstract

Post-mixing aggression in pigs is a harmful and costly behaviour which negatively impacts both animal welfare and farm efficiency. There is vast unexplained variation in the amount of acute and chronic aggression that dyadic behaviours do not fully explain. This study hypothesised that certain pen-level network properties may improve prediction of lesion outcomes due to the incorporation of indirect social interactions that are not captured by dyadic traits. Utilising current SNA theory, we investigate whether pen-level network properties affect the number of aggression-related injuries at 24 hours and 3 weeks post-mixing (24hr-PM and 3wk-PM). Furthermore, we compare the predictive value of network properties to conventional dyadic traits. A total of 78 pens were video recorded for 24hr-PM. Each aggressive interaction that occurred during this time period was used to construct the pen-level networks. The relationships between network properties at 24hr and the pen level injuries at 24hr-PM and 3wk-PM were analysed using mixed models and verified using permutation tests. The results revealed that network properties at 24hr could predict long term aggression (3wk-PM) better than dyadic traits. Specifically, large clique
formation in the first 24hr-PM predicted fewer injuries at 3wk-PM and high betweenness centralisation at 24hrPM predicted increased rates of injury at 3wk-PM. This study demonstrates that network properties present during the first 24hr-PM have predictive value for chronic aggression and have potential to allow identification and intervention for at risk groups.

2.3 Introduction

Post-mixing aggression occurs as a means of establishing a social hierarchy amongst unfamiliar conspecifics [1]. In commercial industry, pigs are frequently regrouped as they are transferred between production stages. Regrouping starts at four weeks when piglets are weaned from the sow and moved to their weaner group (which can be mixed or single sex groups) consisting of multiple different litters. This process is repeated when pigs are moved from their weaner groups to grower and finisher housing. Mixing will occur again once animals are transported to the abattoir and kept in lairage. Whilst aggression during the first 24hr-PM is mostly explained by the need to establish dominance relationships, pigs also display chronic aggression associated with the maintenance of these relationships within stable groups of familiar conspecifics [1] [2].

Pig aggression is highly overt and causes injury in the form of skin lesions (hereby referred to as lesions), the location and number of which correspond to the type and duration of aggressive interactions [3]. Lesions provide a distinctive and quantifiable cost to the interaction, and a reliable outcome measure for hypothesis testing. In addition to physical injury, aggression induced stress is associated with elevated cortisol and heart rate [4,5], and compromised immunocompetence [6]. Aggression
also reduces carcass and meat quality [7,8], as well as stunting growth and reducing feed efficiency [9,10].

A group’s ability to form a lasting dominance hierarchy is necessary for long term group stability, and there is evidence that engagement in aggression soon after mixing can improve productivity and reduce chronic aggression over the growing-finishing period [11]. In contrast, avoidance of aggression during the acute post-mixing phase tends to only delay aggression [12]. This suggests that there is a trade-off situation whereby aggression during the acute phase appears to be necessary in order to reduce chronic aggression, improve welfare, and maintain productivity. However, a large proportion of variation in the severity of aggression at both time points remains unexplained by the animals’ engagement in aggressive behaviours at the dyadic level. Even where cluster analysis identifies pigs that share greater than 80% similarity in dyadic behavioural traits (behaviours that describe the direct interactions that an animal has engaged in), large differences exist between these pigs in their number of chronic injuries. This suggests that a more refined approach to quantify behaviours may be necessary in order to fully understand the variation in injuries [13].

Social network analysis (SNA) has rapidly risen in popularity amongst behavioural scientists [14], as it offers the ability to capture and quantify social behaviours beyond the dyadic framework. A growing body of evidence suggests that an animals’ indirect social connections or ‘friends of friends’ [15] have important fitness consequences, highlighting the need to consider animal behaviour within its wider social context. Although the majority of SNA has been largely descriptive in nature [16,17], there has been a considerable increase in experimental and predictive use of network properties in recent years. Individual network position is an important predictor for survival in
wild Barbary macaques [18] and juvenile male dolphins [19]. Most notably, network position exceeds the predictive value of dyadic traits for offspring survival in baboons [20]. Network level properties have also been found to be predictive of aggressive outbreaks [21], parasitism load, and infectious disease spread among social animals [22]. However, despite having considerable potential for improving welfare [23], application of SNA to farm animal behaviour, especially in a predictive context, is considerably underrepresented in the literature [24–26].

In this study we quantified commonly studied group-level network properties [23,27] in multiple groups of pigs (*Sus scrofa*), with the objective of examining the hypothesis that network properties can be used to predict subsequent levels of injury resulting from aggressive interactions and account for variation that is unexplained by dyadic behaviours. Additionally, we compared the predictive value of network properties to that of conventional dyadic interactions in order to determine whether network properties (in particular, network properties that incorporate indirect social connections) are an important factor for subsequent injury rate. It is anticipated that applying social network analysis to post-mixing aggression in pigs will reveal the mechanisms by which certain groups manage to establish stable social relationships more rapidly and effectively than others.

2.4 Method

2.4.1 Data collection

The study was conducted and the video data collected on a private commercial farm in Ransta, Sweden with permission from the farm owner. The study comprised 1,170 pigs housed in single sex (intact males, castrated males and females), and single breed (705 purebred Yorkshire and 465 crossbred Yorkshire x Landrace). Analyses
conducted with a larger dataset on the same farm have revealed no significant breed effects for aggressivity [28]. The groups were comprised of 15 pigs; 3 from 5 separate litters. The pigs were moved into their new social groups at 8 weeks old, creating 78 pens of 15 pigs. One pig was removed from the study due to injury, and which left one pen containing only 14 animals. There is a positive correlation between live weight and aggression [29,30], and weight asymmetry within a group can significantly affect the type of aggression and duration of fighting that occurs. Therefore, where possible, pigs of similar weight were grouped together (mean 27.6 kg (SD = 5.6)) to limit this effect.

Each group was video recorded for 24hr-PM. Using all-occurrence sampling, the details of aggressive interactions that each individual engaged in was recorded, including time, type of aggressive interaction (see ‘behaviours’), initiator, and receiver, as well as the animals’ pen identity, sex, breed, litter identity, and unique pig identification. Video analysis was conducted by three observers using time-lapse video software to record the duration of each behavioural occurrence to the nearest second. Inter-observer reliability was tested using three 1-hour samples of data and showed a significant degree of inter-observer agreement (mean r =0.83, p < 0.001).

Lesions were counted at three intervals: before being mixed, 24hr-PM (24hr-PM), and 3 weeks later (3wk-PM) once the groups were assumed to be stable. Lesions were recorded in three regions of the body; anterior, central, and posterior, as these regions are associated with different aggressive behaviours. Lesions in the anterior portion of the body are predominantly associated with engaging in reciprocal fighting, and lesions to the posterior portion of the body are predominantly associated with receipt of non-reciprocal aggression (referred to as bullying in this study) [3]. Lesions were
recorded immediately before mixing and were subtracted from those recorded at 24hr to estimate the number of lesions received due to the establishment of new dominance relationships.

**Behaviours**

Pigs display both reciprocated fighting and unreciprocated bullying. Fighting was defined as aggression that lasted at least one second where both pigs engaged in biting, pushing, or head knocking the opponent. Bullying occurred when one pig received or delivered aggression with no observable retaliation occurring [28]. In this paper we define dyadic behavioural traits as behaviours derived from direct interactions (e.g. the amount of time the animals spent fighting; the number of fights that occurred). Dyadic behavioural traits derived from fighting and bullying behaviours are detailed in Table 2.1. These behaviours were selected due to being previously identified as significantly associated with lesions at both 24hr-PM and 3wk-PM [12] and provided a useful benchmark with which to compare the ability of network properties to predict lesions.
### Table 2.1. Description of dyadic traits

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean duration of fighting and bullying.</td>
<td>Mean duration of each fight and bout of bullying that the focal pig was involved in.</td>
</tr>
<tr>
<td>Total fight duration.</td>
<td>Total duration of all fights that the focal pig was involved in.</td>
</tr>
<tr>
<td>Number of fights involved in.</td>
<td>Total number of reciprocal fights the focal pig was involved with, regardless of which pig initiated the attack.</td>
</tr>
<tr>
<td>Proportion injurious fights.</td>
<td>Proportion of time the focal pig spent in reciprocal fights engaged in what was deemed to be injurious fighting. Injurious fighting was defined as acts of aggression where bites were delivered at an approximate rate of 1 per 3s [3].</td>
</tr>
<tr>
<td>Duration of bullying given.</td>
<td>Duration of time spent in bullying in which the focal pig was the initiator.</td>
</tr>
<tr>
<td>Duration of bullying received.</td>
<td>Duration of time spent in bullying in which the focal pig was the recipient of the attack.</td>
</tr>
</tbody>
</table>

#### 2.4.2 Social network analysis

Networks were constructed in R (version 3.2.3) using the R package *igraph* [31]. The unit of analysis was the pen level network, providing 78 independent data points. Degree, eigenvector and betweenness centralisation values were obtained via the `centralization.degree`, `centr_eigen`, and `centralization.betweenness` functions in *igraph*.

Separate networks were constructed for fighting and bullying behaviours in order to determine whether they offered different predictive value. Networks were also
constructed containing all aggressive behaviours (both fighting and bullying), which we refer to as ‘combined’.

Network terminology

In SNA, networks are presented as graphs, comprised of the individuals (referred to as nodes) and the line that connects two nodes (referred to as an edge). A directed edge allows the direction of the interactions (e.g. from the sender towards the receiver) to be incorporated in the network, whereas an undirected edge represents a bidirectional relationship [32]. SNA provides methods of describing networks as a whole (global measures), the substructures within a network, and the individuals’ network position (local measures). Identifying whether an individual holds an important or ‘central’ position within the network (known as individual centrality) is a commonly studied local measure. There are a number of different methods to define what constitutes an important position in a network and thus which individual is considered to be central [33]. For example, individuals that connect otherwise unconnected groups may play an important role in group cohesiveness [34].

Network properties

The primary aim of this study was to identify pen-level network properties that explain the variation in injurious outcomes that is not explained by dyadic traits. Due to the limited information regarding the network properties that form during post-mixing aggression in pigs, the decision was made to include a selection of commonly used network measures in animal behaviour and identify traits that were most closely associated with the number of lesions using a stepwise regression (further details under ‘Statistical analysis’). A full list of network properties analysed in this study can be
found in the supplementary material S1 and descriptions of each trait are detailed in S2. Measures that were relevant to the results section are discussed in detail below.

**Centralisation**

Freeman’s centralisation equation calculates a network level metric from individual centrality scores by summarising the disparity in centrality that exists within a network. A global value for a network (the network property) is obtained by the sum of differences in individual centrality scores between the most central animal and all other animals in the network. This sum is divided by the theoretical largest sum of differences in any network of the same size to give a value between 0 and 1, where 1 is considered a maximally centralised network [35] (further details on centralisation can found be supplementary material S1 File). Figure 2.1 provides an example of a non-centralised network (Figure 2.1a) and a highly centralised network (Figure 2.1b). Freeman’s equation has been successfully used to describe the structures of a number of animal social networks [24,25,36,37]. Here we describe ‘degree’, ‘betweenness’, and ‘eigenvector’ centralisation.
Figure 2.1. Example networks with different centralisation. A) A non-centralised ‘ring’ network. B) A maximally centralised ‘star’ network

Degree centralisation

Degree centrality describes the number of direct connections an animal has. In this paper, we present three forms of degree centralisation: in-degree, out-degree and total degree. In-degree calculates how many incoming interactions an animal has (i.e. how many animals attacked the focal animal), and out-degree calculates the number of outgoing interactions (i.e. how many animals the focal animal attacked) [38]. As a pen-level network property, degree centralisation describes whether certain individuals in the network either give or receive considerably more aggression than the rest of the animals in the network.

Betweenness centralisation

Betweenness centrality measures the number of shortest social paths between every pair of group members in the network that pass through a particular individual. (e.g. node 5 in Figure 2.2 has high betweenness). In behavioural terms, networks that have
high betweenness centralisation tend to contain individuals who connect other individuals that do not directly interact \([39]\). For example, removal of node 5 would result in the network dividing into two separate groups (Figure 2.2).

**Figure 2.2. Model network. Dashed lines represent substructures (cliques).**

*Eigenvector centralisation*

At the individual level, eigenvector centrality reflects the sum of the centralities of an individual’s neighbours. An individual may achieve high centrality due to having many connections (high degree), or by interacting with individuals with a high degree, or a combination of both \([40,41]\). Thus eigenvector centrality extends the scope of degree centrality, by accounting for the quality and not just the quantity of connections an individual has. At a network level, a pen with high levels of eigenvector centralisation would have a small number of well-connected individuals, with the rest of the group being considerably less well connected. In terms of aggressive networks in this study, it would suggest that engagement in aggressive behaviour (both giving and receipt) is unevenly displayed within the group.

*Size of largest clique*

A clique represents a fully connected subgroup of individuals whereby each individual in the clique directly interacted with all others in the clique \([32,34]\). In this paper we
present the size of the largest clique. In Figure 2.2 the nodes 1, 2, 3, and 4 form the largest clique in the network. To calculate the size of the largest clique in each network, we used the igraph function “clique_num”. This function finds the largest clique in each network and returns the number of individuals that belong to this subgroup.

2.4.3 Statistical analysis

All statistical analysis was carried out in SAS v9.4.

Identification of predictive network and dyadic traits using mixed models.

Our statistical approach was designed to test the extent to which network properties accounted for the remaining variation in the pen level lesion scores once the fixed effects of breed, sex, mean body weight of the pen, and experimental batch had been accounted for. Furthermore, as the number of aggressive interactions that occur within a pen is a strong predictor of the number of lesions [12], this too was included as a fixed effect. Our statistical approach consisted of three steps. The first step was to run a mixed model with the lesion scores as the response variate and fixed effects as predictors to obtain residuals reflecting the variance in lesion scores not accounted for by the fixed effects (hereafter referred to as the ‘partial model’). The next step was to run a stepwise regression containing the lesion score residuals from the partial model as the response variate and the network and dyadic traits as the predictors in order to identify traits that best accounted for the remaining variation in lesion score residuals. The final step was to incorporate the identified network or dyadic trait into the partial model (hereafter referred to as the ‘full model’) to provide full model fit statistics. This allowed us to compare the improvement that the network properties and dyadic traits provided in contrast with the partial model.
Partial model

To isolate the variation in lesions not accounted for by fixed effects, the average number of lesions in each body region in the pen (calculated by summing the number of lesions in each pen and dividing by the number of animals in the pen) was entered as the response variable. The pen average was used due to the loss of one animal in a pen, which led to one pen having 14 animals rather than 15. Breed, sex, and mean number of aggressive interactions that occurred in the pen were entered as fixed effects; experimental batch was entered as a random effect, and mean body weight of the pen as a covariate. This was carried out using the SAS mixed procedure. The mixed model provided pen level lesion score residuals reflecting the remaining variance.

Stepwise regression.

Stepwise regressions provide a method of fitting regression models by adding or removing predictor variables by an automatic procedure. Variables are either added or removed based upon the test statistics of the estimated coefficient [42]. This was carried out using the SAS regression procedure with stepwise model selection method.

To identify which network properties provided the best model fit once the fixed effects of the pen had been accounted for, the pen level lesion score residuals were entered as the response variable in a stepwise regression with all network properties (see S1 Table) as the predictors. The stepwise regression identified the network trait(s) that provided the best model fit (based on the test statistics of the estimated coefficient) to account for the remaining variance in pen level lesion score residuals. The stepwise regression was then repeated for a list of dyadic traits (see Table 2.1)
**Full model**

Finally, the network properties and dyadic traits that were identified via the stepwise regression to provide the best model fit were then added to the full model in order to provide full model fit statistics (RMSE, AIC, $R^2$). The full model was the same as the partial model described above, with the addition of the traits that provided the best fit for the remaining variance.

Model assumptions including normality and variance inflation factors were checked and confirmed to be within the acceptable range.

**Permutations**

In social network analysis permutations are routinely used in order to generate replicates to compare to the observed dataset and to account for the non-independence of the data [43]. Conventional statistics have been successfully applied in other network data studies that contained adequate replication and independent data [34,41]. In this study we had 78 observed replicates, that each provided an independent network metric. Thus conventional statistics were appropriate [43] and were the primary statistical methodology utilised in this study. The use of conventional statistics was also prioritised as it allowed us to compare model fit between dyadic traits and network properties more easily than would be achieved using permutation methodology alone.

An additional reason for using permutations in SNA is to evaluate whether the observed network is representative of the real network [41]. In this study we recorded and included all interactions that occurred in the 24h period of interest, which provides a high level of confidence that our networks are representative of the real network for this period of time.
However, we utilise permutation tests in this study in order to confirm the results of the mixed models and the significance of the network properties identified by the stepwise regression.

Keeping all other effects stable, the permuted network properties (betweenness centralisation and largest clique size) were entered into the full model to obtain a coefficient for the network property of interest. This was repeated 5000 times to provide a distribution of coefficients with which the coefficient from the observed network could be compared. A $p$-value was obtained by calculating the number of times the observed network coefficient was greater than the coefficients derived from the permuted networks, divided by the number of permutations. This value was deducted from 1 in the case where the observed network model provided a negative coefficient (indicating that the network property predicted a reduction in lesion scores), in order to provide an accurate $p$-value [44].

Correlation of predictive network and dyadic traits

A Spearman rank correlation of the dyadic and network properties was performed to verify the uniqueness of traits and to avoid errors due to duplication.

2.4.4 Ethical note

This study was carried out in accordance with the recommendation outlined in the European Guidelines for accommodation and care of animals and the UK Government DEFRA animal welfare codes. The work was approved by SRUC’s Animal Ethics Committee (application number ED AE 5/2005).
2.5 Results

2.5.1 Descriptive statistics

A total of 9313 aggressive interactions were recorded during the 24hr period post introduction. Animals that did not engage in aggression were still included in the networks as isolates. Fighting and bullying occurred with approximately equal frequency (mean number of fights per pen = 62.38, SD = 24; mean number of bullying interactions per pen = 57, SD = 26.4).

Despite the standardisation of resource provision and the abiotic environment in this study, considerable variation in network structure existed. As expected, there was also large variation in the amount of group level injury at 24hr-PM and 3wk-PM (see Table 2.2). The maximum size of a fighting or bullying clique was 7 individuals (47% of pen members).

Further information on the characteristics of lesions can be found in Desire et al (2015) [12]. Descriptive statistics for all network properties analysed in this study can be found in supplementary material S3.
Table 2.2. Descriptive statistics for a) network properties and b) pen level skin lesions.

<table>
<thead>
<tr>
<th>Network Trait</th>
<th>Network type</th>
<th>Median</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Degree centralisation</td>
<td>Fight</td>
<td>0.30</td>
<td>0.17</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>Bully</td>
<td>0.33</td>
<td>0.12</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>Fight &amp; Bully</td>
<td>0.35</td>
<td>0.14</td>
<td>0.64</td>
</tr>
<tr>
<td>Betweenness centralisation</td>
<td>Fight</td>
<td>0.15</td>
<td>0.06</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>Bully</td>
<td>0.21</td>
<td>0.08</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>Fight &amp; Bully</td>
<td>0.14</td>
<td>0.01</td>
<td>0.53</td>
</tr>
<tr>
<td>Eigenvector centralisation</td>
<td>Fight</td>
<td>0.51</td>
<td>0.32</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>Bully</td>
<td>0.52</td>
<td>0.29</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>Fight &amp; Bully</td>
<td>0.4</td>
<td>0.16</td>
<td>0.60</td>
</tr>
<tr>
<td>Largest clique size</td>
<td>Fight</td>
<td>4</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Bully</td>
<td>4</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Fight &amp; Bully</td>
<td>5</td>
<td>4</td>
<td>8</td>
</tr>
</tbody>
</table>

a) Descriptive statistics of pen level skin lesions

<table>
<thead>
<tr>
<th>Time (24hr-PM/3wk-PM)</th>
<th>Body region</th>
<th>Median</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>24hr-PM</td>
<td>Anterior</td>
<td>18.33</td>
<td>3.67</td>
<td>45.27</td>
</tr>
<tr>
<td></td>
<td>Central</td>
<td>9.33</td>
<td>1.93</td>
<td>26.13</td>
</tr>
<tr>
<td></td>
<td>Posterior</td>
<td>4.07</td>
<td>-19.13a</td>
<td>11.80</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>31.53</td>
<td>8.43</td>
<td>82.47</td>
</tr>
<tr>
<td>3wk-PM</td>
<td>Anterior</td>
<td>10.27</td>
<td>5.33</td>
<td>15.93</td>
</tr>
<tr>
<td></td>
<td>Central</td>
<td>10.07</td>
<td>4.67</td>
<td>18.67</td>
</tr>
<tr>
<td></td>
<td>Posterior</td>
<td>4.40</td>
<td>0.80</td>
<td>7.87</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>24.73</td>
<td>11.13</td>
<td>42.13</td>
</tr>
</tbody>
</table>

a Negative lesion values resulted from some animals having lower lesions in certain body regions after mixing than before.
2.5.2 Fixed effects on number of lesions

There was a significant breed effect for skin lesions in all body regions at 3wk-PM (anterior: $F_{1,59} = 8.13, p = 0.006$; central: $F_{1,59} = 8.81, p = 0.004$; posterior: $F_{1,59} = 5.93, p = 0.018$; total: $F_{1,59} = 9.74, p = 0.003$) with pure Yorkshire having significantly higher lesions at 3wk-PM than Yorkshire Landrace crossbreeds. There was also a significant experimental batch effect on lesions at 24hr-PM (anterior: $F_{13, 58} = 2.22, p = 0.002$; central: $F_{13, 59} = 2.14, p = 0.024$; posterior: $F_{13, 54} = 2.68, p = 0.006$; total: $F_{13, 58} = 3.07, p = 0.002$) and 3wk-PM (anterior: $F_{13, 59} = 3.79, p<0.001$; central: $F_{13, 59} = 2.16, p = 0.023$; posterior: $F_{13, 59} = 5.17, p<0.001$; total: $F_{13, 59} = 3.39, p<0.001$). The number of fights per pen was not found to have a significant effect at either time point.

2.5.3 Predictive value of SNA and dyadic traits on number of lesions

No network trait for posterior or total lesions at 24hr-PM significantly improved upon the partial model. At 24hr-PM fighting eigenvector centralisation (see Figure 2.3) was significantly negatively associated with lesions in the anterior region of the body ($F_{1, 58} = 11.24, p = 0.001$).
Figure 2.3. Example of a pig fighting network with high eigenvector centralization

Individual with the highest eigenvector centrality is highlighted in red.

Pens showing high eigenvector centralisation tended to display highly localised aggression, with few aggressive individuals that engaged in many fights and also fought amongst themselves but with low connectivity amongst the remaining animals. Pens with high combined degree centralisation (see Figure 2.4) had significantly more lesions in the central ($F_{1, 58} = 4.52, p = 0.038$) area of the body. Both eigenvector and combined degree centralisation improved upon the partial model (RMSE, AIC, and $R^2$) (see Table 2.3).
Figure 2.4. Example of a pig fighting network with high combined degree centralisation. An individual engaging in disproportionately more aggression (high degree) than the remaining pen mates is highlighted in red. Thicker edges represent frequency of interactions.

At 24hr-PM, dyadic traits offered a better model fit for lesions than network properties in all body regions, apart from the central-region where no dyadic trait was found to improve upon the partial model.

Anterior lesions were positively associated with the average duration of fighting and bullying ($F_{1,58} = 14.45, p<0.001$), whereas posterior lesions were negatively associated with the proportion of fights that occurred in the pen that were classified as highly injurious ($F_{1,58} = 5.38, p = 0.024$). Total body lesions were positively associated with the average duration of all fighting and bullying behaviour ($F_{1,58} = 5.97, p = 0.018$).

In stable groups (3wk-PM), no dyadic traits offered any significant improvements upon the partial model in predicting lesions. The size of the largest fighting clique (see Figure 2.5) was found to provide the best single network trait model, revealing a strong negative association with lesions in three out of the four body regions at 3wk-PM.
(anterior: $F_{1,58} = 5.02, \ p = 0.029$, central: $F_{1,58} = 10.77, \ p = 0.002$, total: $F_{1,58} = 7.47, \ p = 0.008$). This indicates that pens that contained larger cliques during the 24hr period after introduction had lower rates of aggression related injuries at 3wk-PM.

Figure 2.5. Example of a pig fighting network with a high number of aggressive interactions with a six animal clique. B) Example of a network with a lower number of aggressive interactions with a six animal clique. Cliques are highlighted in red for emphasis. Regardless of the difference in the number of interactions in each network, the presence of a clique is a strong predictor of the injuries the pen will have at a later date (3wk-PM).

Fighting betweenness centralisation (see Figure 2.6) had a positive association with posterior lesions 3wk-PM, indicating that pens that contained disjointed sub-groups connected by only a small number of animals when the group was formed, experience more lesions at the later time point. Fighting betweenness provided the best model for posterior lesions 3wk-PM ($F_{1,58} = 4.74, \ p<0.034$).
Figure 2.6. Example of a pig fighting network with high betweenness centralisation. Highly central individuals highlighted in red for emphasis.

2.5.4 Correlation between network and dyadic traits

The correlation coefficients between network properties and dyadic traits ranged from $r_s$-0.46–0.54 (a complete correlation matrix is available in supplementary material S4).

The only model where a network property and a dyadic trait were both found to be significant predictors was for anterior lesions at 24hr-PM (see Table 2.3). The significant predictors, eigenvector centralisation and average duration of fighting, were inversely associated, although this relationship was not significant ($r_s = -0.21, p = 0.07$).

For lesions at 3wk-PM, the network properties fighting clique size and betweenness centralisation were found to be significant predictors of lesions, and were significantly inversely related ($r_s = -0.35, p<0.01$).

2.5.5 Permutations

The permutations support the findings of the GLMM, and demonstrate that the network properties identified by the stepwise regression account for a significant
proportion of the remaining variation present in pen level lesion scores (see Figure 2.7).
Table 2.3. Model fit statistics.

<table>
<thead>
<tr>
<th>Lesion location</th>
<th>Trait</th>
<th>Estimate (SE)</th>
<th>RMSE</th>
<th>R2</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SNA</td>
<td>Dyadic</td>
<td>Partial SNA</td>
<td>Dyadic</td>
</tr>
<tr>
<td>24hr-PM</td>
<td>Fighting eigenvector</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Average fight duration</td>
<td>-33.87 (10.10)</td>
<td>12.97 (3.41)</td>
<td>5.49</td>
<td>5.03</td>
</tr>
<tr>
<td>Central</td>
<td>Combined degree centrality</td>
<td>4.84 (2.27)</td>
<td>-</td>
<td>4.23</td>
<td>4.07</td>
</tr>
<tr>
<td>Posterior</td>
<td>Injurious fighting</td>
<td>-</td>
<td>-23.65 (10.19)</td>
<td>2.27</td>
<td>2.16</td>
</tr>
<tr>
<td>Total</td>
<td>Average fight duration</td>
<td>15.90 (6.51)</td>
<td>9.85</td>
<td>9.38</td>
<td>0.44</td>
</tr>
<tr>
<td>3wk-PM</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Anterior</td>
<td>Size of largest fighting clique</td>
<td>-0.67 (0.30)</td>
<td>-</td>
<td>1.59</td>
<td>1.52</td>
</tr>
<tr>
<td>Central</td>
<td>Size of largest fighting clique</td>
<td>-1.18 (0.36)</td>
<td>-</td>
<td>2.00</td>
<td>1.84</td>
</tr>
<tr>
<td>Posterior</td>
<td>Fighting betweenness</td>
<td>3.89 (1.79)</td>
<td>-</td>
<td>1.00</td>
<td>0.96</td>
</tr>
<tr>
<td>Total</td>
<td>Size of largest fighting clique</td>
<td>-2.08 (0.76)</td>
<td>-</td>
<td>4.41</td>
<td>3.89</td>
</tr>
</tbody>
</table>

Network properties and dyadic traits that were found to significantly improve model fit (p<0.05) are presented under ‘SNA’ and ‘Dyadic’. Model fit for fixed effects only are presented under ‘Partial’. In all trait models the number of aggressive interactions per pen was included. Blank cells indicate that no dyadic or network trait was found to significantly improve upon the partial model fit. Asterisks under estimate (SE) indicate level of significance. $p<0.05$  $p<0.01$  $p<0.001$
Figure 2.7. Coefficient frequency distributions from lesion models containing permuted network properties and the coefficient from the observed network models. The red line represents the coefficient from the observed network properties. The observed value is considered to be significant if fewer than 2.5% of permuted values are greater than the observed value, or 97.5% of the permuted values are greater than the observed.
2.6 Discussion

Network analysis is fast becoming a common approach to investigate the relationships between individual behaviour and population level functioning [16,17,21,23]. In this study we quantified the social network properties of multiple groups of pigs, with the objective of investigating whether group-level network properties can be used to predict subsequent amounts of pen levels injury at two time points resulting from aggressive interactions, and provide novel insights not captured by dyadic interactions.

Whilst network properties did not offer a model fit improvement compared to dyadic traits for predicting the injury caused by initial aggression associated with the establishment of dominance relationships (24hr-PM), network properties (betweenness centralisation and clique size) did provide predictive value of long term injury (3wk-PM), while dyadic traits did not.

Prior research has suggested that low levels of aggression upon introduction can lead to uncertain dominance relationships and chronic aggression [12]. However, our findings suggest that rather than the number of fights, it is the number of animals that are part of a fully connected subgroup (clique) that is a more important determinant of low chronic aggression. By controlling for the number of aggressive interactions per pen we were able to distinguish between the effect of number of fights and the different network properties that result from these aggressive interactions (see Figure 2.5). Our findings suggest that fights that form large cliques at 24hr-PM are more effective at decreasing chronic aggression than the same number of fights that do not form large cliques. As all animals in a clique have fought each other, clique members may form better established
dominance relationships than non-clique members. This would explain the low level of aggression at 3wk-PM. Furthermore, as clique sizes did not exceed 47% of pen members, this suggests that a central group with established dominance relationships is sufficient to significantly reduce lesions at a pen level, without all group members needing to be involved directly.

Additionally, cliques suggest that in certain pens aggressive animals fight amongst themselves, whereas less aggressive animals are able to avoid engaging entirely. While it is expected that animals that do not engage in aggression at 24hr-PM may engage at a later date [12], the fact that a large clique size significantly reduced lesions to the anterior region suggests that the remainder of the pen did not engaging in fighting at 3wk-PM. However, analysing the individual lesion scores would be required in order to verify this.

Pens exhibiting high betweenness centralisation at 24hr-PM were at greater risk of high levels of posterior lesions at 3wk-PM than pens with lower centralisation. Posterior lesions are predominantly associated with receipt of bullying behaviour, as a fleeing animal turns away and the attacking animal inflicts injuries to the posterior portion of the body [12]. Therefore, it is interesting that a fighting network property (that excluded all bullying behaviour) provided a strong model fit for lesions associated with receipt of bullying 3wk-PM. Once dominance relationships have been established, the maintenance of these relationships is usually achieved by the delivery of bullying to subordinate animals. It is possible that pens presenting high betweenness centralisation contain highly aggressive individuals that engage in excessive bouts of bullying to maintain their position and cause elevated levels of posterior injuries to the remaining pen mates. Alternatively, the division
present in pens with high betweenness centralisation indicates that there is a lack of direct contact between certain groups of animals. If insufficient interaction occurs in order to develop lasting dominance relationships throughout the pen, continued aggression may persist due to uncertain social positions within the group. Whilst network analysis has revealed network properties that predict chronic aggression and injury rates in newly mixed pigs, it has not quantified the costs and benefits to the individuals that have central roles in such networks. It is possible that the majority of the pen displays a form of aggression ‘avoidance’ [13] and are the ones responsible for the poor connectivity between groups, and the high betweenness individuals act as the connectors that improve the cohesiveness of a group that would otherwise be even more poorly connected [34]. Likewise, pens with a large clique may represent a highly aggressive subsection of a pen, and non-clique members are simply representative of animals able to avoid both acute and chronic aggression. Temporal analysis examining the process of network formation could help to understand how these central individuals assume this position. Comparing the injuries of central individuals at 24hr-PM and 3wk-PM to their pen-members may also reveal the long and short terms costs and benefits of occupying a position of high centrality.

The results have revealed that fighting and bullying networks significantly differ in their contribution to chronic aggression. This raises the question of whether the remaining variance in lesions could be further explained by the inclusion of other social behaviours aside from aggression. For example, in rhesus macaque groups individuals that were responsible for the maintenance of social network stability in aggression networks were
also key players in grooming behaviour networks [45], suggesting a variety of social behaviours relate to conflict management. Pigs have a complex range of negative and pro-social interactions and behaviours, which could play a role in resolution of conflict [46]. Future research should consider the inclusion of additional social behaviour, as this may provide a more complete understanding of an animal’s social standing and could improve the predictive value of network properties.

2.7 Conclusion

Our findings provide further support that network properties have the potential to outperform dyadic traits in predicting long term social outcomes [20]. Our results suggest that division in newly mixed groups of pigs is likely to lead to prolonged chronic aggression and elevated injury rates, whereas pens with large cliques (~47% of the pen members) are likely to have significantly fewer injuries in stable groups. We suggest that these network properties indicate that divided networks represent poorly established dominance relationships at a pen level, and large cliques indicate that a sufficient proportion of the group has established their social position and thus reduces the need for prolonged aggression.
2.7.1 Supporting information

S1 File. Freeman centralisation. (DOCX)

S1 Table. Network properties estimated from the behavioural networks and entered in the stepwise regression. Separate networks were created using fighting only and bullying only and these behaviours combined. Directed versions of degree and closeness were applied to bullying networks only. (DOCX)

S2 Table. Summary of key terms and network properties. (DOCX)

S3 Table. Descriptive statistics of network properties in fighting, bullying and combined networks. (DOCX)

S4 Table. Spearman rank correlation of dyadic and network properties. (DOCX)

Acknowledgments

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2.7.2 Author Contributions

Conceptualization: Simone Foister, Andrea Doeschl-Wilson, Rainer Roehe, Simon Turner.

Formal analysis: Simone Foister.

Funding acquisition: Laura Boyle, Simon Turner.

Methodology: Simone Foister, Andrea Doeschl-Wilson, Rainer Roehe.

Project administration: Simon Turner.

Supervision: Andrea Doeschl-Wilson, Rainer Roehe, Laura Boyle, Simon Turner.
Visualization: Simone Foister.

Writing – original draft: Simone Foister.

Writing – review & editing: Andrea Doeschl-Wilson, Rainer Roehe, Gareth Arnott, Laura Boyle, Simon Turner.

2.7.3 References


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2.8 Chapter summation

Chapter 2 successfully identified two key group-level structures that appear to have implication for long term lesion outcomes at the pen-level. We identified that pens that develop large fully connected subgroups (cliques) tend to have considerably lower lesions than pens which develop smaller cliques. Furthermore, we identified that pens with high betweenness centralization are vulnerable to elevated lesion outcomes in stable groups. The reason for this is unclear, however we hypothesise that these different structures may reflect differences in hierarchy formation and investigate this further in Chapter 4.

Both structures highlight key individuals that appear to have had the most impact on the network, namely those who are members of the largest clique, and those who have high betweenness centralization. However, from these results alone we are unable to determine whether these individuals have different lesion outcomes in comparison to the remainder of the group.

Chapter 3 will investigate the effect of such network positions at the individual level in order to answer this.
Chapter 3. Piggy in the middle: The cost-benefit trade-off of a central network position in post-mixing aggression
3.1 Introduction

In current management systems, pigs are frequently regrouped with unfamiliar conspecifics when they are transferred between production stages. The most pronounced displays of pig aggression occur during the first 24 hours post-mixing with unfamiliar conspecifics, yet chronic aggression is also observed in stable groups. A balance between these two types of aggression appears to be necessary for long term social stability (Desire et al., 2015; Turner et al., 2017). Post-mixing aggression compromises welfare and production due to stress and injuries (skin lesions). To date, aggressive interactions have been studied between dyads of pigs existing in a larger social group but the variation in lesion counts is not fully explained by dyadic aggressive behaviours alone (Desire et al., 2015; Turner et al., 2017). This limits understanding of how to manipulate the social or physical environment to reduce injuries from aggression.

Social network analysis (SNA) allows us to study animals as part of their social structure and take into consideration their position within the network (Wey et al., 2008). At the individual level, social network position has been found to influence fitness, with central individuals achieving improved mating success (Oh and Badyaev, 2010), infant survival (Lehmann et al., 2016; Stanton and Mann, 2012), and dominance (Gilby et al., 2013). Individual network centrality has also been shown to outperform dyadic traits in terms of predicting survival (Cheney et al., 2016), further supporting the claim to adaptive value of network position. However, there is also evidence that there are costs associated with central positions, such as increased exposure to pathogens (MacIntosh et al., 2012; Rimbach et al., 2015). SNA is relatively novel in farm animal behaviour (Boyland et al.,
2015; Büttner et al., 2015b; Li et al., 2018), yet already its potential for improving welfare has been recognised (Koene and Ipema, 2014; Makagon et al., 2012).

Chapter 2 (Foister et al., 2018) revealed that pens with networks that had high inequality in betweenness centrality at mixing had significantly more lesions at three weeks post-mixing than pens with low inequality at the group level. Betweenness centrality calculates the extent to which an individual lies on the shortest path between two other individuals (Wasserman and Faust, 1994). In behavioural terms, it reveals an individual that connects two otherwise unconnected individuals (Gilby et al., 2013). In contrast, pens that form fully connected subgroups (cliques) tend to have less long term aggression than pens that engage in the same number of fights but do not form cliques. Whilst the results in Chapter 2 (Foister et al, 2018) revealed that high betweenness centralisation was detrimental to the pen and large cliques appeared to be beneficial, it is not clear what effect occupying the central position had on the individual, and on the remaining pen mates at either time point.

Therefore, the first aim of this study was to build upon our prior research (Chapter 2, Foister et al, 2018) to determine the consequences of cohesive and divided network structures and the relative network position of individuals on their lesions. We quantify how pen-level network structure exerts influence on long term lesion counts (3wks-PM) at an individual level and the cost benefit trade-off associated with occupying a central position in an aggressive network. The second aim was to establish whether commonly used centrality traits could provide an improvement in prediction of individual lesion counts compared to dyadic traits and reveal new information regarding the nature of post-mixing aggression in pigs.
3.2 Method

3.2.1 Data collection and dyadic traits

The data used in this study is the same sample as used in Chapter 2 (Foister et al. 2018). Here we provide a brief overview of the data collection process. For full details please refer to the method section in Chapter 2.

Data was collected on a commercial farm in Ransta, Sweden, between October 2005 and January 2007 and included total of 1,170 pigs. The animals were housed in single sex groups (intact males, castrated males, and females), and per breed (705 pure-bred Yorkshire and 465 Yorkshire-Landrace). The animals were grouped in pens of 15 comprised of 3 piglets from 5 different litters. Animals were grouped by similar weight to reduce within pen variation (average live weight = 27.6 kg SD 5.6). Each animal was marked with a numeric ID on their back using livestock marker. This was done to reduce weight asymmetry which can affect the type and duration of aggression that occurs and adhered to commercial practice (Olesen et al., 1996; Pitts et al., 2000). Fresh skin lesions in the anterior, central and rear body regions were counted prior to mixing, 24 hours post-mixing (24hrs-PM), and at three weeks post-mixing (3wks-PM) using the method of Turner et al. (2006). Pens were video recorded for 24hours post-mixing, and data were gathered from the video footage. For each aggressive interaction the animal ID, direction and duration of the interaction, and type of aggressive behaviour was recorded. Aggression that lasted at least one second where both pigs engaged in biting, pushing, or head knocking the opponent was required to be defined as a fight. If one pig received or
delivered aggression and no observable retaliation occurred, the interaction was defined as bullying (Turner et al, 2009).

A full list of the dyadic behaviours are presented in Table 2.1 in Chapter 2.

3.2.2 Network concepts and traits

In section 1.2 of the literature review, I introduced the concept of network centrality as an umbrella term for a variety of different network measures that quantify how ‘central’ an individual is within its network. The centrality of an individual is calculated in relation to the other individuals in the network. If many individuals occupy similar positions in a network, by default this position is less central, as it is shared by others. Centralisation (Freeman, 1978) is an entire network measure that calculates the inequality in centrality that is present in a network (see Eq 1.5). The greater the degree on individual inequality in centrality, the higher the centralisation of the network (depicted in Figure 1.6).

3.2.3 Concepts and traits related to Aim 1: Effect of network traits on individual pig lesions

Betweenness centrality

In Chapter 2 (Foister et al., 2018) we found that high betweenness centralisation at the pen level (depicted in Figure 3.1) during mixing lead to significantly more pen level lesions at three weeks post-mixing than in less centralised pens. Here we determine whether individuals’ lesion counts are also affected by their betweenness centrality.
Figure 3.1. Post-mixing aggression network with high betweenness centralisation (Foister et al, 2018). Animals within the dashed line have high betweenness centrality, and the animals outside the dashed line have low betweenness centrality.

Whilst betweenness centrality is a continuous trait that assigns each animal an individual betweenness centrality value, for the purpose of this study it was recorded as a categorical trait of ‘high’ or ‘low’ betweenness (further methodological details provided in Statistics below). Betweenness centrality tends to have a highly positively skewed distribution, as often only 1 or 2 individuals in each group will have high betweenness centrality and the majority of animals will have very low or zero betweenness centrality. Therefore, categorising betweenness centrality as either ‘high’ or ‘low’ did not interfere with the accuracy or interpretation of this trait. The equation for calculating betweenness centrality is presented in Eq 1.2.
Clique membership

A clique is a fully connected subgroup of animals (see outlined animals in Figure 3.2). In Chapter 2 (Foister et al, 2018) we used the size of the largest clique (number of animals belonging to the pen’s largest clique) as an entire network measure, and found that pens containing large cliques had on average lower levels of injury at 3wks-PM, compared to pens with the same number of fights that did not form cohesive large cliques. In order to apply this to individuals we categorised individuals as either ‘clique members’ or ‘non-clique members’. We aim to determine whether differences in lesions at the individual level are affected by the pen’s clique size and by the individual’s clique membership status.

Figure 3.2. Post-mixing aggression network with a six animal clique (Foister et al, 2018).

Animals within the dashed line are ‘clique members’ and animals outside the line are ‘non-clique members.'
3.2.4 Concepts and traits related to Aim 2: Quantify improvement in prediction of lesions with SNA

In Chapter 1, I introduced the concept of weighted edges (see Figure 1.3). To recap, weighting edges allows us to incorporate additional information about the interaction that occurred, such as the frequency or duration. Including this information is a valuable way to consider how ‘central’ an individual is, in terms of different behaviours (i.e., does the animal engage in disproportionately longer fights or in more repeated fights than the remainder of the pen). This shift in centrality that can occur from including different behaviours is graphically depicted in Figure 1.9.

Here, we quantified the ability of several commonly used network traits (including weighted eigenvector centrality) (see Table 3.1) to predict skin lesions and compared their predictive power to that of dyadic traits (Table 2.1). Below we discuss eigenvector centrality in detail as it was the trait most relevant to our results section. Full details regarding all network traits outlined in Table 2.2 can be found in the section 1.2.3 of Chapter 1.

Eigenvector centrality

Eigenvector centrality considers the number of connections an individual has, but also how well connected an individual’s network partners are. Thus, interacting with a well-connected individual leads to a higher eigenvector centrality than interacting with a poorly connected individual (see Figure 3.3).

In a weighted network, edges can include information regarding the interaction (e.g. frequency or duration). Eigenvector centrality can incorporate this information when
calculating an individual’s centrality. For example, if a node is connected to a neighbour with an edge weighting of two (e.g. to reflect two interactions that occurred), then the neighbours’ connection now contributes twice as much to the focal nodes eigenvector centrality.

The equation for calculating eigenvector centrality is presented in Eq 1.1 in Chapter 1.

*Figure 3.3. Comparison of binary and weighted eigenvector centrality. Figure 3.3a depicts our starting matrix. Figure 3.3a-d depict different connections node 2 can make (depicted by dashed lines), and below we discuss the difference in eigenvector centrality that each node will receive in response to these different connections. In Figure 3.3a, node 2 is unconnected and has an eigenvector centrality of zero. In Figure 3.3 (a to c) node 3 is the best-connected node and has an eigenvector centrality of 1. In comparison, node 1 is fairly poorly connected and has an eigenvector centrality of 0.46. If node 2 connects to node 1 (Figure 3.3.b), it receives an eigenvector centrality of 0.25, but by connecting directly to the better-connected node 3 (Figure 3.3.c); it receives a higher centrality of 0.42. In the weighted network (Figure 3.3.d), the connection between node 1 and 2 is weighted by 3 (representing 3 interactions). Node 1 now has the highest centrality (1), closely followed by node 2 (0.93). Node 3 now has a centrality of 0.43. These values are normalized by the theoretical maximum eigenvalue for the number of nodes in the network.*
Table 3.1. Definition of centrality traits analysed as part of Aim 2

<table>
<thead>
<tr>
<th>Centrality trait</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Degree</td>
<td>Total number of connections an animal has</td>
</tr>
<tr>
<td>In-degree</td>
<td>Number of received interactions (attacks received)</td>
</tr>
<tr>
<td>Out-degree</td>
<td>Number of attacks initiated towards others</td>
</tr>
<tr>
<td>Eigenvector</td>
<td>Takes into consideration number of connections, but also the number of social partners the connections have.</td>
</tr>
<tr>
<td>Eigenvector weighted by duration</td>
<td>As above, but the duration of each interaction is also incorporated into the individual final centrality value</td>
</tr>
<tr>
<td>Closeness</td>
<td>Number of steps for an animal to reach all others in the network</td>
</tr>
</tbody>
</table>

As in Chapter 2, we include dyadic traits (Table 2.1) to provide a comparison with the predictive value of the network traits.

3.2.5 Statistics

Lesions

Individual lesion counts had a skewed distribution and were transformed using a natural log transformation. Negative lesion counts due to higher lesions pre-mixing than post-mixing were converted to zero. Note that the lesions modelled in chapter 2 were pen level
totals and did not show the same skewed distribution as individual level lesions, therefore did not require transformation.

**Partial model**

A partial model (herafter denoted ‘null model’) was constructed as the basis for both Aims 1 and 2. Null models did not contain dyadic or network traits. Individual lesion counts were entered as the response variable using the *lmer* mixed effects model in R (version 3.5.3, package *lme4*), with breed, sex, and body weight entered as fixed effects, and pen, litter, and experimental batch entered as random effects. Also, the total number of aggressive interactions that each animal received and directed towards others was entered as a covariate in the models. (see Equation 3.1).

We confirmed that a pen effect was still present with the inclusion of pen level network properties, and that the model was not confounded.

**Statistical models for Aim 1**

Betweenness centrality and clique membership were analysed in separate models.

*Betweenness:* In order to assess the effect of pen betweenness centralization and an individual’s betweenness centrality on its lesions, both measures were included as additional covariates in the null models.

Next, to investigate whether animals benefited or were disadvantaged in terms of lesion scores due to their position within the network, the individual network positions were divided into categorical variables. Individual centrality measures were categorised into quartiles, where individuals within the top quartiles were categorised as high betweenness
and the remaining 75% were categorised as low betweenness. The mean betweenness centrality of the top quartile was 0.13 (with a maximum of 0.4), and the low betweenness category was 0.01.

Pen level centralization was entered as a continuous variable.

The statistical model is shown in Equation 3.1:

\[ y_{ij} = FE + Rand + B_j + b_i + B_j \times b_i + e_i \]

*Equation 3.1. Statistical model for betweenness*

Where \( y_{ij} \) denotes the lesion of individual \( i \) in pen \( j \), \( FE \) and \( Rand \) denote the fixed and random effects, respectively, fitted in the null model as outlined above, and \( B_j \) denotes the continuous betweenness centralisation of pen \( j \), and \( b_i \) the categorical betweenness of individual \( i \), and \( e_i \) is the residual.

**Clique size and membership:** Individuals belonging to the largest clique in their pen were categorised as ‘clique members’, and the remaining animals as ‘non-clique members’. The size of the largest clique together with the individual’s clique membership were then entered as additional fixed effects in the null model. Size of the pens largest clique was entered as a continuous variable.

The interaction was added to determine whether clique membership was affected by the size of the pens largest clique.

The statistical model is shown in Equation 3.2:

\[ y_{ij} = FE + Rand + C_j + c_i + C_j \times c_i + e_i \]
Equation 3.2. Statistical model for clique membership

Where $y_{ij}$ denotes the lesion of individual $i$ in pen $j$, $FE$ and $Rand$ denote the fixed and random effects, respectively, fitted in the null model as outlined above, and $C_j$ denotes the categorical size of the largest clique of pen $j$, and $c_i$ the categorical clique membership of individual $i$, and $e_i$ is the residual.

Statistical models for Aim 2

To identify traits that provided the best model fit (determined by lowest AIC) for individual lesion counts, we used a stepwise regression (stepAIC from the R package MASS). The residuals from the null models were entered as the response variable, and the list of centrality traits (see Table 3.1) were entered as the predictor.

The stepwise regression was repeated on the list of dyadic traits (Table 2.1), in order to compare model fit of dyadic and network traits.

Normality of residuals were checked for all models, and variance inflation factors (vif function in the R package ‘car’) was inspected to assess collinearity between predictors and deemed to be within acceptable limits.
3.3 Results

3.3.1 Lesions

There was a large amount of variation in the number of lesions, indicating that individuals considerably differed in the amount of aggression they engaged in. Variation in lesion counts was higher at 24hr-PM than at 3wk-PM (see Table 3.2).
Table 3.2. Characteristics of skin lesion data for individual animals included in the statistical analysis (SK = skewness; K = kurtosis).

<table>
<thead>
<tr>
<th></th>
<th>Original Scale</th>
<th></th>
<th>Log transformed scale</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>min - max</td>
<td>Mean</td>
<td>K</td>
<td>SK</td>
</tr>
<tr>
<td>24hr</td>
<td>Anterior</td>
<td>0 to 87</td>
<td>20.94 (16.74)</td>
<td>1.38</td>
</tr>
<tr>
<td></td>
<td>Central</td>
<td>0 to 58</td>
<td>13.17 (10.16)</td>
<td>1.26</td>
</tr>
<tr>
<td></td>
<td>Rear</td>
<td>0 to 33</td>
<td>7.13 (5.57)</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>0 to 125</td>
<td>35.57 (27.15)</td>
<td>0.94</td>
</tr>
<tr>
<td>3wk</td>
<td>Anterior</td>
<td>0 to 36</td>
<td>12.31 (5.33)</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>Central</td>
<td>0 to 37</td>
<td>12.3 (5.86)</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td>Rear</td>
<td>0 to 23</td>
<td>6.49 (3.47)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>0 to 74</td>
<td>27.07 (12.61)</td>
<td>0.63</td>
</tr>
</tbody>
</table>
3.3.2 **Aim 1: Effect of network traits on individual lesions**

As this study make use of the same raw interaction data as used by Desire et al., (2015), the systematic effects are the same. The systematic effects are reported here for the purpose of making this thesis self-contained. For full results on the characteristics of the lesions for this dataset, see Desire et al., (2015).

**Partial model.**

There was no systematic effect of sex \((F_{2,65} = 0.02, p = 0.9)\) on total lesions at 24hr-PM or 3wk-PM, so sex was dropped from the model. Weight had a significant positive effect on 24hr-PM lesions \((F_{1,678} = 4.07, p = 0.04)\), but not 3wk-PM lesions \((F_{1,702} = 15.9, p = 0.26)\).

There was a significant breed effect with pure Yorkshires having higher total lesions in stable groups \((F_{1,97} = 5.29, p = 0.02)\), but no effect was found for total mixing lesions \((F_{1,97} = 3.88, p = 0.54)\).

**Betweenness centrality**

At 24hrs-PM, the centralization score of the pen did not exert a significant effect on the number of individual lesions in all body regions on the animals in the pen (total: \(F_{1, 98} = 2.51, p = 0.12\)).

High individual betweenness centrality was found to be significantly positively associated with anterior lesions only \((F_{1, 1114} = 7.65, p < 0.01, \text{estimated 6.3 more lesions with standard deviation of 2.3})\). However, the opposite effect was noted within the interaction. The higher the centralisation of the pen, there was a tendency for the most central individuals to have lower anterior lesions \((F_{1, 1099} = 2.77, p = 0.09, \text{estimated 20.5 fewer lesions with a standard deviation of 12.3})\) compared to the rest of their pen mates (see
Figure 3.4), however this was only significant at a 90% confidence interval for anterior lesions. This trend was also observed for mid lesions (betweenness: $F_{1,1096} = 4.8$, $p = 0.02$, estimated 3.1 more lesions with standard deviation of 1.4, interaction: $F_{1,1084} = 3.66$, $p = 0.05$, estimated 14.7 fewer lesions with a standard deviation of 7.7), rear lesions (betweenness: $F_{1,1098} = 4.3$, $p = 0.04$, estimated 1.5 more lesions with standard deviation of 0.7, interaction: $F_{1,1088} = 5.89$, $p = 0.01$ estimated 9.9 fewer lesions with a standard deviation of 4.1), and total (betweenness: $F_{1,1094} = 8.8$, $p < 0.01$, estimated 10.8 more lesions with standard deviation of 3.6, interaction: $F_{1,1082} = 4.69$, $p = 0.03$, estimated 41.3 fewer lesions with a standard deviation of 19.7).

At 3wks-PM, individuals belonging to a pen with high betweenness centralisation resulted in more lesions than belonging to less centralised pens (total lesions $F_{1,88} = 2.69$, $p = 0.01$, estimated 18.5 more lesions with a standard error of 7.08).

In centralised pens there was a non-significant tendency for central individuals to still have lower anterior ($F_{1,1119} = 3.19$, $p = 0.07$, estimated 7.9 fewer lesions with a standard deviation of 4.3), central: ($F_{1,976} = 3.21$, $p = 0.06$, estimated 8.5 fewer lesions with a standard deviation of 4.6), and total ($F_{1,976} = 0.5$, $p = 0.06$, estimated 18.8 fewer lesions with a standard deviation of 9.1) lesions, but not rear ($F_{1,976} = 0.5$, $p = 0.46$, estimated 1.7 fewer lesions with a standard deviation of 2.8), than the remaining pen mates indicating that both central and non-central pen members suffered similar rates of injury.
Clique membership

At 24hrs-PM, the size of the pen’s largest clique was not found to significantly affect the number of lesions for all animals in the pen. However, animals that belonged to their pen’s largest clique had significantly more anterior \((F_{1, 1123} = 61.8, \ p < 0.001,\ \text{estimated} \ 13.77\ \text{more lesions with a standard deviation of } 4.7)\), central \((F_{1, 1103} = 14.7, \ p < 0.00,\ \text{estimated} \ 7.1\ \text{more lesions with a standard deviation of } 3)\) and total \((F_{1, 1104} = 39.3, \ p < 0.001,\ \text{estimated} \ 20.04\ \text{more lesions with a standard deviation of } 7.6)\) lesions than non-clique members. However, this was not true for rear \((F_{1, 1104} = 3.7, \ p = 0.10)\) lesions. The interaction showed no significant effect at the 95% confidence interval.

At 3wks-PM, animals in pens that contained larger cliques at 24h post-mixing showed significantly fewer lesions than those in pens with smaller cliques in the central body region \((F_{1, 1133} = 4.0, \ p < 0.05,\ \text{estimated} \ 7.09\ \text{fewer lesions with a standard deviation of } 3.7)\) and in total \((F_{1, 73} = 6.1, \ p < 0.05,\ \text{estimated} \ 1.12\ \text{fewer lesions with a standard deviation of } 0.83)\). Clique members had significantly fewer central lesions \((F_{1, 1133} =3.9, \ p < 0.05,\ \text{estimated} \ 0.78\ \text{fewer lesions with a standard deviation of } 0.39)\), however there was no effect on anterior \((F_{1, 1134} =0.8, \ p = 0.37)\), rear \((F_{1, 1153} = 1.4, \ p = 0.24)\), or total \((F_{1, 1126} = 1.8, \ p = 0.17)\) lesions.
Figure 3.4. Lesions at 24hrs-PM and 3wks-PM. Visual representation of the contrast in individual lesions gained at 24hrs-PM and 3wks as a result of network position when number of interactions is accounted for. Red represents higher lesions and green represents fewer lesions. 
A) The results show that at 24hrs-PM individuals with high betweenness have on average fewer lesions (in green) than the rest of their pen mates. B) At 3wks-PM high betweenness in a pen increased individual lesions (in red), but no significant difference was found between high and low betweenness individuals (all individuals are in red). C) At 24hrs-PM members of the largest clique had on average more lesions than non-clique members (in red). D) At 3wks-PM the presence of a large clique was associated with fewer lesions at an individual level. A non-significant difference in lesions between clique and non-clique members demonstrates that all pen members benefit from fewer lesions as a result of the pen containing a large clique (all individuals are in green).
3.3.3  **Aim 2: Quantify improvement in prediction of lesions with SNA**

Table 3.3 presents the model fit statistics for models including the network and dyadic traits that best predicted individual lesion counts via a stepwise regression. From the list of network traits, eigenvector centrality was consistently identified as providing the best model fit compared to other network traits. At 24hrs-PM unweighted fighting eigenvector centrality was found to be strongly positively associated with lesions, and at 3wks-PM eigenvector centrality weighted by duration was negatively associated with lesion counts. This means that pigs that chose opponents who themselves fought with many pen mates received a high number of lesions immediately following mixing but fewer lesions 3 weeks later, especially if fights were prolonged.

Comparison between the network and dyadic trait models showed that at 24hrs-PM network traits (eigenvector centrality) provided a moderately better model fit for central and rear lesions whereas for anterior lesions the total duration of all dyadic aggressive interactions provided a better model fit. However dyadic and network models provided equal model fit for total lesions at 24hrs-PM.

At 3wks-PM, dyadic traits provided a marginally better fit for lesions than network traits for central, rear and total lesions. Both models provided a similar model fit for anterior lesions.

Overall, the predictive value of network and dyadic traits appear to be similar. However, Spearman correlations between network and dyadic traits (shown Table 3.3) are in some cases low despite the traits predicting lesions with similar power. For example, the proportion of dyadic fights and weighted eigenvector centrality provided an equal model
fit for anterior lesions at 3wk-PM but have a low correlation of 0.34, suggesting that they explain different aspects if lesion prevalence at an individual level.

When both traits were entered in the model for total mixing, both traits maintained direction of effect and significance (total mixing: eigenvector centrality, $F_{1, 1153} = 7.8, p < 0.001$, estimated effect of 30 more lesions with a standard error of 10.8; total duration of reciprocal and non-reciprocal aggression, $F_{1, 1147} = 65.2, p < 0.001$, estimated effect of 7 more lesions with a standard error of 0.8; and the addition of the eigenvector centrality to the model significantly improved model fit according to the loglikelihood ratio tested by chi-square ($X^2(1) = 7.8, p < 0.01$). The same was found when both traits were added to the stable lesions model (eigenvector centrality, $F_{1, 1151} = 18.8, p < 0.001$, estimated effect of 8.4 fewer lesions with a standard error of 1.9; total duration of non-reciprocal delivered aggression, $F_{1, 1146} = 6.7, p < 0.001$, estimated effect of 0.7 fewer lesions with a standard error of 0.3; and the addition of the eigenvector centrality to the model significantly improved model fit according to the loglikelihood ratio tested by chi-square ($X^2(1) = 18.6, p<0.001$).


Table 3.3. Spearman rank correlation of significant network and dyadic traits. n=1169

<table>
<thead>
<tr>
<th>Weighted fighting eigenvector -</th>
<th>Fighting eigenvector</th>
<th>Total duration of all aggressive interactions</th>
<th>Duration of received bullying</th>
<th>Proportion of fights won -</th>
<th>Duration of giving bullying</th>
<th>Duration of fighting received</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weighted fighting eigenvector</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fighting eigenvector</td>
<td>0.73***</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total duration of all aggressive interactions</td>
<td>0.74***</td>
<td>0.78***</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duration of received bullying</td>
<td>0.11***</td>
<td>0.16***</td>
<td>0.36***</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proportion of fights won</td>
<td>0.34***</td>
<td>0.38***</td>
<td>0.39***</td>
<td>-0.09**</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>Duration of giving bullying</td>
<td>0.47***</td>
<td>0.59***</td>
<td>0.57***</td>
<td>0.14***</td>
<td>0.31***</td>
<td>1.00</td>
</tr>
<tr>
<td>Duration of fighting received</td>
<td>0.66***</td>
<td>0.69***</td>
<td>0.87***</td>
<td>0.39***</td>
<td>0.22***</td>
<td>0.39***</td>
</tr>
</tbody>
</table>

*** p<0.001
** p<0.01
* p<0.05
Table 3.4. Model fit statistics for dyadic and social network analysis traits. +/- indicate direction of effect. Asterisk indicates best model for explaining prevalence of individual lesions (based on AIC, as well as $R^2$ and root mean square error - RMSE). Absence of an asterisk indicates models provided equal model fit.

<table>
<thead>
<tr>
<th>Time period</th>
<th>Lesion location</th>
<th>Model 1 (M1)</th>
<th>Model 2 (M2)</th>
<th>RMSE (Null)</th>
<th>RMSE M1</th>
<th>RMSE M2</th>
<th>$R^2$ Null</th>
<th>$R^2$ M1</th>
<th>$R^2$ M2</th>
</tr>
</thead>
<tbody>
<tr>
<td>24 hours</td>
<td>Anterior</td>
<td>Total duration of all aggressive interactions + *</td>
<td>Fighting eigenvector +</td>
<td>0.92</td>
<td>0.72</td>
<td>0.74</td>
<td>0.26</td>
<td>0.54</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>Central</td>
<td>Total duration of all aggressive interactions +</td>
<td>Fighting eigenvector + *</td>
<td>0.96</td>
<td>0.88</td>
<td>0.86</td>
<td>0.24</td>
<td>0.35</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>Rear</td>
<td>Duration of received bullying +</td>
<td>Fighting eigenvector + *</td>
<td>0.79</td>
<td>0.77</td>
<td>0.73</td>
<td>0.40</td>
<td>0.43</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>Total duration of all aggressive interactions +</td>
<td>Fighting eigenvector +</td>
<td>1.07</td>
<td>0.89</td>
<td>0.89</td>
<td>0.26</td>
<td>0.49</td>
<td>0.49</td>
</tr>
<tr>
<td>3 weeks</td>
<td>Anterior</td>
<td>Proportion of fights won -</td>
<td>Weighted fighting eigenvector - *</td>
<td>0.45</td>
<td>0.43</td>
<td>0.42</td>
<td>0.28</td>
<td>0.36</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>Central</td>
<td>Duration of given bullying - *</td>
<td>Weighted fighting eigenvector -</td>
<td>0.47</td>
<td>0.44</td>
<td>0.45</td>
<td>0.33</td>
<td>0.40</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>Rear</td>
<td>Duration of fighting received + *</td>
<td>Weighted fighting eigenvector -</td>
<td>0.57</td>
<td>0.56</td>
<td>0.56</td>
<td>0.31</td>
<td>0.34</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>Duration of given bullying - *</td>
<td>Weighted fighting eigenvector -</td>
<td>0.44</td>
<td>0.41</td>
<td>0.42</td>
<td>0.35</td>
<td>0.43</td>
<td>0.41</td>
</tr>
</tbody>
</table>
3.4 Discussion

Post-mixing aggression in pigs is a pressing welfare issue that has been shown to cause the participants stress and injury. Whilst pen level network structure was found to predict lesions at a pen level, the effect of overall network structure and the position of pigs within that on the level of injury received by individual pigs were unexplored. We sought to examine whether a network structure that reduced the total number of injuries in the pen benefitted some individuals more than others dependent upon their position in the network. Previous research has identified that aggressive interactions during the first 24hrs-PM are necessary in order to establish dominance relationships and reduce chronic aggression (Desire et al, 2015). However, identification of a behavioural phenotype that strikes a balance between short and long-term aggression is essential to improving pig welfare. Hence, we tracked how network traits created immediately after mixing affected injuries in the immediate post-mixing period and longer-term social context.

Clique membership and betweenness centrality were found to have contrasting effects on the individuals occupying these central positions.

While pen level betweenness centralisation was not associated with an increase in individual lesions at mixing, the interaction showed that the greater the pen level centralisation, the lower the lesions in the most central individuals during mixing. However, this temporarily advantageous combination of network structure and position for a few high betweenness individuals was significantly associated with on-going aggression and injury, shown by the significant increase in lesions for all individuals in the pen at 3wk-PM. Importantly, the lack of a significant difference in
lesions between high and low centrality individuals at 3wk-PM indicates the majority of the pen was engaging in the continued aggression.

In contrast, while membership of the largest clique offered a short-term cost to members in terms of higher lesions at the individual level, there was no increase in individual lesions for the pen as whole regardless of the size of the largest clique in the pen. Groups with larger cliques benefited in the long term, with all animals experiencing fewer injuries at 3wk post-mixing, with no difference being detected between clique and non-clique members.

What stands out from these findings is that the behaviour of one or a few individuals can significantly affect the long-term injury rates of all the animals in the pen, regardless of whether they interact directly. Whilst in this study the final dominance status of high betweenness individuals was not used to quantify social outcome, it is noteworthy that betweenness has previously been found to be advantageous in terms of dominance (e.g. in male chimpanzees, Gilby et al., 2013). Similarly, in long tailed manakins (McDonald, 2007), establishing high betweenness in a social contact network at a young age was the strongest predictor of later ascension in social rank. Although the final dominance rank of the high betweenness animals was unknown in our study, the low lesion counts of high betweenness individuals may reflect higher dominance status at 24hrs-PM. Further research on final dominance ranks of high betweenness individuals may shed light on potential causation or incentives for occupying this position that thus affect the network structure.

On a similar note, how and why large cliques form is currently unknown. One likely possibility is that this is not an intentional behaviour, but rather a result of a favourable
combination of aggressive personalities (Krause et al., 2010). The low level of injuries in clique members at 3wks-PM indicate that the hierarchy established within a clique remains stable over time, and the results showing that clique membership is not associated with the highest rates of injury at 24hrs-PM may indicate clique members are capable of quickly establishing their hierarchical position with minimal injury in the process. The fact that a maximum of 47% of individuals in a pen belonged to the largest clique suggests that the majority of the pen can theoretically avoid excessive aggression at mixing without risking chronic aggression. This finding fits with previous research that found only ~40% of growing pigs fought each other during post-introduction aggression (Arey and Edwards, 1998), indicating that all animals do not need to fight one another in order to establish a hierarchy. Individuals belonging to pens with large cliques ought to be targets for future research, in order to further our understanding of the nature of clique formation and aggressive personality combinations.

In terms of searching for an optimum balance between short and long term aggression, the stepwise regression of continuous and categorical traits allowed us to verify that whilst clique membership offers a significant decrease in lesions at a group and individual level in the long term, it was not found to be the best predictor of lesions at 24hrs-PM. This is a novel finding, as this is the first trait found to provide the best reduction in lesions at the pen level, and for all within the pen at the individual level, without being associated with a high cost of injury at 24hrs-PM.

The stepwise regression identified eigenvector centrality to be the trait providing the best predictor of individual lesions at both time points. The non-weighted version of eigenvector centrality provided the best measure of skin lesions at 24hrs-PM. This
reveals that at 24hrs-PM, fighting with numerous individuals who have also had numerous fighting partners is associated with the highest level of injury. This may be because opponents that have had many previous opponents may be more experienced fighters, or simply may be more aggressive in nature, resulting in more injurious encounters. In contrast, eigenvector centrality weighted by duration provided the best reduction in lesions at 3wks-PM. Achieving high weighted eigenvector centrality is dependent not only on the number and identity of partners but also on the duration of the interactions with them. High weighted eigenvector centrality leading to fewer lesions at 3wks-PM is likely due to prolonged fights leading to less ambiguous outcomes than shorter fights. In turn, this leads to clearer and longer lasting dominance relationship which reduces the frequency of further aggression. Eigenvector centrality has been found to be an important network position in numerous species for infant survival. Eigenvector centrality in proximity networks predicts infant survival in both macaques (Brent et al., 2013) and juvenile male dolphins (Stanton and Mann, 2012) and in baboon communities, eigenvector centrality in grooming networks predicts offspring survival (Cheney et al., 2016). To the best of our knowledge, this is the first time that eigenvector centrality in aggressive networks has been found to offer predictive value.

Whilst eigenvector centrality did not outperform dyadic traits in predicting lesions counts, the closeness in predictive value is noteworthy, especially at 3wks-PM where network and dyadic traits had low correlation coefficients. This low correlation suggests that network and dyadic traits predict social outcomes using alternative social information. Therefore, there is scope for dyadic traits to predict different parts of variation in lesion scores than network traits, and therefore they may both be used to
complement each other, rather than replicate or replace. This can be explained at a biological level, whereby dyadic traits provide sharp focus on the individuals direct interactions which individuals tend to have more control over. Whereas network position can encapsulate the decisions and social interactions of other animals which the focal animal may not have directly interacted with. Both individual level decisions and the wider social context are likely to shape the social environment and influence the number of lesions an animal will accrue. However, some individuals may exert a greater control over the number of lesions they accrue as a direct result of their own decisions and actions. For example, the decision to fight or not to fight will greatly impact the number of lesions an individual gets, as will the decision to submit or to try to avoid further interactions with an aggressor. Whereas other individuals may be more affected by the social environment they find themselves in, and a greater proportion of their lesions may be attributed to the collective decisions and actions of the wider group that have contributed to either a calm or hostile social environment. It is also possible that this may not necessarily be a fixed trait, but rather a transient shift in causation of aggressive behaviour. Further research, such as temporal analysis, would be beneficial in determining whether there is evidence for this.

It is also notable that whilst several different dyadic traits were required to provide the best model fit at each time point (24hrs-PM and at 3wks-PM), eigenvector centrality was a consistent predictor at both time points.

3.5 Conclusion

The results from this study have confirmed that certain network structures are beneficial at not only the pen level, but also at the individual level. This confirms that the behaviour of a minority of individuals can have long term implications for the
stability of their network, which can indirectly affect the injury rates of all the animals in the group. The optimum development of structural traits (particularly clique membership) appears to achieve a balance between short- and long-term aggression. The promotion of animals that lead to such network structures is likely to be a better target for future research aimed at developing management or breeding interventions than an animal’s unique individual position in its network captured by traits such as eigenvector centrality.
Chapter 4. Do network properties relate to hierarchy formation in newly mixed pigs?
4.1 Introduction

The majority of livestock species experience regrouping with unfamiliar conspecifics and engage in forming new dominance relationships. There is considerable evidence that regrouping aggression causes stress which affects the wellbeing and growth of the animals (Marchant et al., 1995; Mendl et al., 1992). However, of all the livestock species, pigs tend to engage in the most physically damaging regrouping aggression. Their display of aggression is overt, easy to record, and results in skin injuries that provide a quantifiable cost to their engagement in aggression (Turner et al., 2006). Therefore, pigs are an obvious species to study as a model of regrouping aggression in commercially reared livestock.

Wild pigs live in matriarchal groups commonly consisting of approximately four sows and their litters of 5 to 6 piglets. A stable dominance hierarchy exists within groups, facilitated by considerable variation in dominance ability (i.e. maturity, body mass, and physical strength) amongst group members (Mauget, 1981). The dominance structure is maintained through non-aggressive behaviours, including avoidance behaviour of subordinates (Mauget, 1981) and occasionally low intensity aggressive acts such as threats and head knocks (McGlone, 1986). In commercial systems, domestic pigs (Sus scrofa) are frequently mixed with unfamiliar conspecifics of similar competitive ability as they transition through production stages and are moved to new housing. Intense reciprocal aggression (fighting) occurs following mixing and lasts between 24 - 48 hours before subsiding (Arey and Franklin, 1995) as the pigs form new dominance relationships. Aggression amongst familiar animals in stable groups also occurs, yet this is usually moderate and mostly in the form of non-reciprocal aggression (bullying) in order to maintain the established hierarchy (Turner and
Edwards, 2004). However, high levels of reciprocal fighting in familiar groups may indicate that the group has failed to form or maintain stable dominance relationships. During aggressive interactions, skin injuries occur (known as skin lesions), the location and number of which have been verified as reliable indicators of the type and duration of aggression that a pig has engaged in (Turner et al., 2006). There is vast inter and intra-group variation in the amount of aggression and injury that occurs in newly mixed and familiar groups of pigs (Desire et al., 2015), but the reasons for this variation are not yet fully understood. Aggressive dyadic traits, for example the duration of aggression an individual has engaged in irrespective of the identity of its opponents, only partly explain the variation in lesions, and tend to explain the injuries gained in the first 24hr-PM rather than the injury variation in stable groups (Desire et al., 2015; Turner et al., 2017). Recent application of social network analysis to post-mixing aggression that mapped actor to receiver interactions and the identity of the opponents, found that pen level network properties could predict lesions at 24hours, and also in stable groups (three weeks post-mixing) better than dyadic traits (Foister et al, 2018). Network traits differ from dyadic traits in that they can quantify indirect social connections, and interaction patterns at the global (pen) level (Brent, 2015; Wey et al., 2008). A possible reason why network properties may predict long term outcomes better than dyadic traits is that they can capture the process of early hierarchy formation in the group, that are not captured by dyadic traits alone.

An association between dominance rank and individual network position has been observed in a number of animal species (fish Dey et al., 2013; chimpanzees Kanngiesser et al., 2011; meerkats Madden et al., 2011; and mice So et al., 2015). However, the relationship between overall aggression network structure and group
level dominance metrics are less well studied. Exploring this connection will potentially bring us closer to understanding what causes the observed variation in acute and chronic aggression in newly mixed groups of pigs.

Therefore, this study aims to determine whether significant differences in hierarchy formation are detectable between groups characterised by different network properties that are known to be associated with chronic aggression.

We hypothesise that pens with cohesive network properties (large cliques) will present clearer dominance relationships (e.g. higher rates of transitive triads, greater steepness, and higher linearity) than pens with high levels of division (betweenness centralisation).

4.2 Method

4.2.1 Data collection, animals, and housing

The data used in this study is the same sample as used in previous chapters. Below is an overview of the data collection process, animals, and housing. For full details please refer to the method section in Chapter 2.

This study was conducted in a commercial farm in Ransta Sweden, with permission granted by the farm owner. Pigs were penned in 78 groups of 15, comprised of 3 piglets from 5 different litters. One pen contained 14 animals due to the removal of an injured animal from the study. They were moved to these new groups at 8 weeks old. Pigs were penned with animals of similar weights where possible to reduce the variation in body weight within the pen.
Behavioural observations

Video cameras were mounted above the pen and recorded all aggressive interactions that occurred between animals. The information gathered for each interaction included the type of aggressive behaviour displayed, the identification of the attacker and receiver and the winner and loser, and the duration of interaction. Videos were analysed by three trained technicians (inter-observer reliability $r=0.8$). We utilised the definition of fighting and bullying as in Turner et al. (2009) where fighting was defined as aggression that lasted at least one second where both animals engaged in biting, pushing, or head knocking the opponent. The winner was determined by a display of submission, which was defined as the defeated animal ceasing to direct aggression towards the opponent and retreating from the fight. Bullying was defined as when one pig received or delivered aggression with no visible retaliation occurring (Turner et al., 2009). All instances of receipt of bullying were counted as a defeat for the receiver and a win for the attacker.

4.2.2 Social network analysis

Here we provide a brief overview of the network analysis methodology and the relevant network properties used in Chapter 2. The network structures that were found to be significantly associated with long-term aggression in Chapter 2 were based upon undirected and unweighted interactions; therefore the interaction matrices were symmetrical and binary in nature (see Figure 4.2a). Full details regarding data organisation and methodology of the network analysis can be found in Chapter 2.

In Chapter 2 we created separate networks for each type of aggressive behaviour (fighting, bullying, all aggressive interactions) in order to test whether different behaviours formed different network structures that predicted lesions with different
accuracies. We used a stepwise regression with the residual average pen level lesion scores as the response variable to identify network level properties that explained the most variation in lesions in stable groups after accounting for systematic effects such as weight. We found that presence of a large fully connected sub-group known as a clique (see Figure 4.1) was highly predictive that a stable group of pigs would receive fewer lesions. In contrast, pens that contained a highly central individual located between unconnected subgroups (high betweenness centralisation – see Figure 4.1) were found to be at risk of higher levels of injury in stable groups. Both of these traits were unweighted and undirected traits, and did not include win/loss data, therefore determining dominance structures from these traits alone was not possible.

Figure 4.1. Examples of pig networks with different network properties. Left) A fighting network that contains a large fully connected subgroup (clique) Individuals belonging to the clique are depicted in darker colour. Right) A network showing high betweenness centralisation. Individuals with high betweenness centralisation are depicted in darker colour. In both images the size of the thickness of the edge represents the frequency of the interaction and the size of the node represents the weight of the animal.
4.2.3 Dominance analysis

Matrix format

All recorded behaviours where a clear winner or loser was identified were organised into square win-loss frequency sociomatrices by behaviour (‘fighting’ and ‘bullying’), and a third which comprised all aggressive interactions by summing the fighting and bullying frequency sociomatrices. The rows and columns corresponded to animal ID. The number of wins for an animal were entered in the corresponding column for that animal’s ID against the loser’s row. This is in contrast to the interaction matrices described above which recorded whether two individuals interacted or not (see Figure 4.2b). In the case of bullying (no retaliation observed), this was recorded as a win for the attacker and a loss for the receiver.

For some analyses, it was necessary to create binary dominance matrices to create dominance matrices. In these matrices, the columns were re-assigned to ‘dominant’ and the rows as ‘subordinates’. Animals that had the most wins over their opponent were deemed to be ‘dominant’. Tied dyads (equal number of wins either way) received an entry of zero, as there was no clear dominance relationship. Here a 1 for matrix element $x_{ij}$ represented dominance for the animal over the animal $j$. Both the win-loss frequency sociomatrices and the binary dominant-subordinate sociomatrices were asymmetric (see Figure 4.2c).
Figure 4.2 The three matrices above provide an example of the different ways the interactions between the same two individuals were recorded in the analysis. Matrix (a) shows a symmetrical binary interaction matrix used in creating the networks and shows that individual A and B engaged in an interaction (no direction or frequency or winner information included). Matrix (b) is an example of the sociomatrixes used in the dominance analysis. It shows that individual B won 7 aggressive interactions against A, and individual B won 1 interaction against individual A. Matrix (c) shows the binarised version of the sociomatrix, and records only which individual won the most interactions. In this case it was individual B. In the case that both individuals had an equal number of wins against got an entry of zero.

Below we outline basic principles of dominance analysis and then detail the dominance metrics used in this paper.

**Dyadic**

D dominance is initially a dyadic level phenomenon, as dominance is an expression of a relationship between individuals (Capitanio, 1991). As the dyad is the minimum unit to which this concept can be applied, Capitanio (1991) states that this is ought to be the starting level of analysis when embarking on studying dominance behaviour.
We quantified six types of dyads in this analysis using win-loss frequency sociomatrices. The first was the possible number of dyads per group \((n(n-1)/2)\). The second was the number of unknown dyads (hereafter null dyads), where two animals either did not engage in an agonistic interaction or where there was no clear outcome. The third was the number of one-way dyads, where one dyad member won all agonistic interactions against the other (see Figure 4.3.A). The fourth was the number of tied dyads, where both dyad members had the same number of wins and losses (see Figure 4.3.B). The fifth was the number of two-way dyads, which indicates that both dyad members had wins and losses, but the number of wins and losses was not equal (see Figure 4.3.C). The sixth was the number of significantly asymmetric dyads (hereafter referred to as significant dyads). A dyad’s asymmetry was tested for significance by applying a binomial sign test to the number of wins in relation to the number of encounters. For example, a minimum of five agonistic encounters with a unidirectional outcome were required to reach significance \((p < 0.05)\) (Langbein and Puppe, 2004). The importance of significant dyads is still under discussion, however a number of theoretical papers have suggested that dyads ought to be tested for significant asymmetry before concluding that a true dominance relationship exists and including such interactions in further analysis (Boyd and Silk, 1983; Lehner, 1996). However, it may not be necessary for two pigs to engage in multiple fights for a clear dominance relationship to be established. While it might be necessary for certain pigs to be defeated numerous times before they accept their position, other pigs may be quicker to accept their subordinate role and avoid engaging in further conflict. Based on this possibility, the decision was made to include non-significant dyads in the group level analysis.
Figure 4.3. Dyad variations. Arrows point away from the winner and towards the loser of the interaction. A) One way dyad  B) Tied dyad  C) Two way dyad

**Group level dominance analysis**

Based on the dyadic relationships formed within the group, the linearity of the dominance hierarchy can be obtained as a measure of its strength. For a dominance hierarchy to be considered strictly linear, high ranking individuals dominate all individuals of lower rank, every triad must be transitive and at the dyadic level, and all individuals have a dominant and subordinate relationship, except in null dyads.

A transitive triad is considered linear, as the dominance relationships follow a clear order where individual 1 dominates individual 2, 2 dominates individual 3, and 1 also dominates individual 3 (see Figure 4.4). This is in contrast from cyclical triads (where 3 would dominate 1). Cyclical triads indicate dominance relationships that are unresolved and prevent the formation of linear rankings (Shizuka and McDonald, 2012). As a result, the majority of linearity measures are based upon quantifying the occurrence of transitive triads.
Figure 4.4. All eight possible patterns of dominant–subordinate relationships that can exist in a fully connected triad. Triangles depicted on the left are transitive and the two on the right are cyclical. Six of the possible eight combinations (75%) of triangles are transitive (Adapted from Shizuka and McDonald (2012)).

In this study, we used two linearity measures. **De Vries’ improved linearity index** calculates a modified Landau’s $h$ linearity index value (denoted as $h'$) which ranges from 0 (no linearity) to 1 (strictly linear). De Vries’ improved linearity index is calculated by a two stage randomisation process which first corrects for the null dyads, and the second tests for probabilistic significance of the linearity. The first randomisation process inputs random dominance relationships into each of the null dyads present in a sociomatrix and calculates an $h$ value for the sociomatrix. This is repeated 10,000 times and the average $h$ value provides the modified Landau’s $h$ (denoted as $h'$) for the sociomatrix. The second randomisation process randomises all dominance relationships and the $h'$ of the randomised sociomatrix ($h_r$) is compared to the $h$ of the observed sociomatrix ($h_o$') . This is also repeated 10,000 times and the one
tailed P value is derived from the proportion of randomisations where $h_r \geq h_o$. This was calculated using the R package *compete* v0.1 (Curley, 2016).

**Triangle transitivity** differs to De Vries’ improved linearity index in that it quantifies the transitivity of *the existing triad subsets* in the graph and does not rely on imputation of null dyads. The proportion of transitive triangles relative to all triangles in the graph ($P_t$) is provided by dividing the number of transitive triads by the sum of the number of transitive and cyclical triads. In a random graph, ($P_t$) is expected to be 0.75. This can be demonstrated by considering all possible configurations between three individuals A, B and C (see Figure 4.4) which illustrates that six of the possible eight configurations (75%), are transitive. Using the expected value of $P_t = 0.75$, the $P_t$ of the observed network can be scaled to provide the triangle transitivity ($t_{tri}$). The outcome ranges from 0 to 1 of the random expectation ($t_{tri} = 1$ indicates all triads are transitive). Although, if more cyclical triads are present than would be expected in a random network, then $t_{tri}$ can be negative. As a result, triangle transitivity scales from -1 to +1. A random network would be expected to have a value corresponding to 0 (indicating 75% transitivity). A group would be assigned a value of 1 in the event of all triads being transitive, and -1 in the event of all triads being cyclic. Triangle transitivity was calculated using *triad_census* function in the R package *igraph* (Csardi, 2015) and the amended code from Shizuka and McDonald (2012).

Greater differences in dominance ranks is considered to reflect higher stability in the social group (Parent et al., 2012). The **steepness** of a hierarchy measures the absolute differences in dominance between adjacently ranked individuals (de Vries et al., 2006).
Steepleness ranges from 0 to 1, where ‘0’ represent very small differences in dominance, and a steepleness of ‘1’ represents large differences.

To calculate steepleness, pairwise dyadic dominance indices ($D_{ij}$) are generated based on the proportion of wins and losses which is then used to calculate normalized David’s Scores for each individual (de Vries et al., 2006). David’s score is a method of ranking the overall success of an individual at winning contests in relation to the success of its opponents. David’s Scores are corrected for the frequency of interactions within a dyad ($P_{ij}$), and can also be corrected for the variation in the total number of interactions between dyads that occur in a group ($D_{ij}$). The degree of dominance ($P_{ij}$) of individual $i$ over individual $j$ is calculated by the proportion of wins by $i$ relative to the total number of dominance interactions between $i$ and $j$. This is expressed as $P_{ij} = \frac{s_{ij}}{n_{ij}}$. $D_{ij}$ is the degree of dominance of $i$ over $j$ corrected for the probability of equal wins and losses, expressed as $D_{ij} = P_{ij} - (P_{ij} - 0.5) \times \text{Prob}[P_{ij} - 0.5]$, where $\text{Prob}[P_{ij} - 0.5]$ is the deviation of the observed proportion from the expected proportion of equal wins and losses.

The David’s Scores for each member in the group is calculated with the following formula

$$\text{David’s Score} = w + w_2 - l - l_2$$

*Equation 4.1. David's Score*

Where $w$ is the sum of individual $i$’s $D_{ij}$ values where $i$ was dominant, $w_2$ is the sum of $w$ values weighted by the $D_{ij}$ values that individual $i$ interacted with, $l$ is the sum of
$D_{ij}$ values where $i$ was subordinate, and $l_2$ is the sum of $D_{ij}$ values weighted by the $D_{ij}$ values that individual $i$ interacted with.

Greater differences in ranks are considered to reflect higher stability in the social group (Parent et al., 2012). The steepness is the absolute value of the slope of the best-fitted line between the normalized David’s Scores, obtained by Ordinary Least Squares method. A permutation test consisting of 10,000 randomisations of the sociomatrices was used to assess whether the obtained steepness value differs significantly from zero. Steepness was calculated using the R package steepness v0.2.2 (Leiva and Vries, 2015).

The final measure considered was the **directional consistency index (DCI)** of the interactions. DCI calculates the direction of behaviours occurring between each dyad and divides the number of interactions in the most frequent direction by the total number of interactions between the dyad. DCI ranges from 0 to 1, where ‘0’ is equal likelihood that directed behaviours within a dyad occur in both directions and ‘1’ is where all directed behaviours occur in one direction. The DCI was calculated using the R package compete v0.1 (Curley, 2016).

### 4.2.4 Statistical analysis

Network properties and dominance metrics were correlated using Spearman’s rho.

Linear mixed models were constructed to test which dominance metrics were significantly associated with pen level network properties, once the fixed effects of breed, sex, mean body weight in the pen, and experimental batch were accounted for. This involved testing whether a model including dominance metrics improved the prediction of network properties relative to a model containing only fixed effects that
did not contain dominance metrics (hereafter referred to as the null model). The pen level network property was entered as the response variable. Breed and sex were entered as fixed effects; experimental batch was entered as a random effect, and mean body weight in the pen was fitted as a covariate. As variation in the proportions of null dyads in each pen has the potential to affect the dominance metrics, this was accounted for by fitting the percentage of null dyads in each pen as a fixed effect. This ensures that any improvement on the null model by the inclusion of the dominance metric is independent of any effect of null dyads in the group.

The full models were calculated by including dominance metrics in the model. Model assumptions were confirmed by examining the normality of residuals and checking that variance inflation factors were within an acceptable range.

All mixed models were carried out using the \textit{lmer} function from the \textit{lme4} R package (Bates et al., 2018).

The model fit improvement was tested by examining the AIC, and a log-likelihood Chi-square test.

Comparison of David’s Scores between clique members and non-members was carried out using a one-way t-test.

\textbf{4.3 Results}

\textbf{4.3.1 Descriptive statistics}

A total of 9389 aggressive interactions (4899 instances of fighting and 4420 instances of bullying) were recorded during the 24hr period post mixing. Of the 4899 fights, 1418 had no identifiable winner and in 36 instances of bullying either the attacker or
receiver could not be identified. These interactions were removed from further analysis. With these interactions removed the mean number of aggressive interactions with a clear dominance outcome per pen was M= 101.7 SD=36.1.

4.3.2 Dyadic dominance traits

There was a high proportion of null dyads, where the dyads had not interacted, or no clear winner was identified (see Table 4.1). The majority of known dyads were one-way dyads whereas two-way dyads were relatively rare. This indicates that in the majority of dyads one animal consistently won and suffered no losses to the opponent. The number of one-way dyads in the pen was highly correlated with the number of dyads that only interacted once \( r=0.67 \), so the number of one-way dyads that involved multiple attacks was calculated by deducting the number of single interaction dyads from the number of one-way dyads (see Table 4.1). This amended version of one-way dyads shows that while the majority of one-way dyads did only contain one interaction, a high proportion of one-way dyads did include multiple attacks. One-way dyads that included multiple attacks was more common than two-way and tied dyads.

Two-way dyads were slightly more common than tied dyads, indicating that even if both animals won an interaction, the successes were most often not shared equally between the opponents.

The number of significant dyads was very low, with the majority of pens having no dyads that reached the significance threshold (see Table 4.1).

4.3.3 Group level dominance metrics

Landau’s \( h' \) calculated using De Vries’ improved linearity index revealed that the majority of pens had moderate to low linearity. A total of 11 out of the 78 pens had a
significantly higher linear structure compared to the randomised sociomatrices ($p < 0.05$). Most pens had moderately high triangle transitivity ($t_{tri}$), indicating the majority of triads were transitive as opposed to cyclical; however, some pens had negative $t_{tri}$, indicating the presence of more cyclical than transitive triads. In contrast, some pens had a triangle transitivity of 1, indicating the absence of any cyclical triads.

The steepness derived from the David’s Scores of each animal was moderately low (med = 0.11 for all aggression sociomatrices). A total of 39 pens had a significantly higher steepness value than that of the randomised sociomatrices ($p < 0.05$) (see Table 4.1).

At the group level, pens had a high degree of directional consistency (med fighting DCI = 0.82, med bullying DCI = 0.83), with certain pens having a DCI of 1, which is consistent with a high number of one-way dyads (see Table 4.1).
Table 4.1. Descriptive statistics of dyad and group level dominance metrics. Values represent the percentage of dyads in a group.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Behaviour</th>
<th>Min</th>
<th>Median</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dyad analysis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Null %</td>
<td>Fight only</td>
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<td></td>
<td>Bully only</td>
<td>34.29</td>
<td>68.57</td>
<td>78.10</td>
</tr>
<tr>
<td></td>
<td>All aggression</td>
<td>21.90</td>
<td>55.24</td>
<td>72.38</td>
</tr>
<tr>
<td>Tied %</td>
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<td>0.00</td>
<td>1.90</td>
<td>5.71</td>
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<td></td>
<td>Bully only</td>
<td>0.00</td>
<td>1.90</td>
<td>8.57</td>
</tr>
<tr>
<td></td>
<td>All aggression</td>
<td>0.00</td>
<td>3.33</td>
<td>8.57</td>
</tr>
<tr>
<td>One way (all) %</td>
<td>Fight only</td>
<td>7.62</td>
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<td></td>
<td>Bully only</td>
<td>11.43</td>
<td>26.67</td>
<td>54.29</td>
</tr>
<tr>
<td></td>
<td>All aggression</td>
<td>20.95</td>
<td>34.29</td>
<td>54.29</td>
</tr>
<tr>
<td>One-way (multiple attacks only) %</td>
<td>Fight only</td>
<td>0.95</td>
<td>5.71</td>
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</tr>
<tr>
<td></td>
<td>Bully only</td>
<td>0.95</td>
<td>6.67</td>
<td>26.7</td>
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<tr>
<td></td>
<td>All aggression</td>
<td>2.86</td>
<td>12.38</td>
<td>31.43</td>
</tr>
<tr>
<td>Two-way %</td>
<td>Fight only</td>
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<td>0.95</td>
<td>6.67</td>
</tr>
<tr>
<td></td>
<td>Bully only</td>
<td>0.00</td>
<td>1.90</td>
<td>10.48</td>
</tr>
<tr>
<td></td>
<td>All aggression</td>
<td>0.00</td>
<td>5.71</td>
<td>18.10</td>
</tr>
<tr>
<td>Significant dyads %</td>
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<td>0.00</td>
<td>0.00</td>
<td>2.86</td>
</tr>
<tr>
<td></td>
<td>Bully only</td>
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<td>0.00</td>
<td>3.81</td>
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<td></td>
<td>All aggression</td>
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<td>0.00</td>
<td>7.62</td>
</tr>
<tr>
<td><strong>Group analysis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Landau $h'$</td>
<td>Fight only</td>
<td>0.16</td>
<td>0.21</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>Bully only</td>
<td>0.18</td>
<td>0.23</td>
<td>0.38</td>
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<td></td>
<td>All aggression</td>
<td>0.18</td>
<td>0.26</td>
<td>0.49</td>
</tr>
<tr>
<td>DCI</td>
<td>Fight only</td>
<td>0.62</td>
<td>0.83</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>Bully only</td>
<td>0.57</td>
<td>0.82</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>All aggression</td>
<td>0.54</td>
<td>0.74</td>
<td>0.95</td>
</tr>
<tr>
<td>Steepness</td>
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<td>0.05</td>
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</tr>
<tr>
<td></td>
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<td>All aggression</td>
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<td>0.29</td>
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<tr>
<td>Triangle Transitivity</td>
<td>Fight only</td>
<td>-1.25</td>
<td>0.37</td>
<td>1.00</td>
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<td></td>
<td>Bully only</td>
<td>-3.00</td>
<td>0.54</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>All aggression</td>
<td>-0.20</td>
<td>0.40</td>
<td>1.00</td>
</tr>
</tbody>
</table>
4.3.4 Correlation of network properties and dominance metrics

The correlation matrix (see Table 4.2) shows that clique size was moderately positively correlated with all dyadic traits, except for null dyads. The opposite trend can be seen for betweenness centralisation. As expected, pens with large cliques or low betweenness had a greater proportion of dyads that interacted or did so with a clear winner. Interestingly greater directional consistency occurred in pens with high betweenness and those with smaller cliques. However, despite being positively associated with directional consistency, betweenness centralisation was inversely associated with significant dyads, suggesting that despite much of the aggression occurring in a single direction in pens with higher betweenness centralisation, the number of fights often did not exceed the threshold to be detected for significance.

Higher linearity (as indicated by Landau’s $h'$) and steepness tended to occur in pens with larger cliques ($r_s=0.27$). Neither network property showed any correlation with triangle transitivity.

In terms of pen level dominance metrics, all were moderately to highly correlated with each other ($r_s=0.14-0.69$), especially the two linearity measures Landau $h'$ and triangle transitivity ($r_s=0.69$).
Table 4.2. Spearman rank correlation coefficient matrix containing aggression network properties, dyadic and group level dominance metrics

<table>
<thead>
<tr>
<th></th>
<th>Betweenness</th>
<th>Size of largest clique</th>
<th>Null dyads</th>
<th>Tied dyads</th>
<th>One-way dyads</th>
<th>Two-way dyads</th>
<th>Significant dyads</th>
<th>Landau’s $h'$</th>
<th>DCI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Betweenness</td>
<td>1.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Size of largest clique</td>
<td>-0.35**</td>
<td>1.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Null dyads</td>
<td>0.24**</td>
<td>-0.49***</td>
<td>1.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Tied dyads</td>
<td>-0.23*</td>
<td>0.25*</td>
<td>-0.53***</td>
<td>1.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>One-way dyads</td>
<td>-0.17</td>
<td>0.34***</td>
<td>-0.87***</td>
<td>0.29**</td>
<td>1.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Two-way dyads</td>
<td>-0.20*</td>
<td>0.46***</td>
<td>-0.69***</td>
<td>0.29**</td>
<td>0.37***</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Significant</td>
<td>-0.14</td>
<td>0.22*</td>
<td>-0.30**</td>
<td>-0.11</td>
<td>0.32**</td>
<td>0.28**</td>
<td>1.00</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Landau’s $h'$</td>
<td>-0.04</td>
<td>0.27*</td>
<td>-0.47***</td>
<td>-0.12</td>
<td>0.52***</td>
<td>0.40***</td>
<td>0.35***</td>
<td>1.00</td>
<td>-</td>
</tr>
<tr>
<td>DCI</td>
<td>0.18</td>
<td>-0.31**</td>
<td>0.31**</td>
<td>-0.65***</td>
<td>0.08</td>
<td>-0.57***</td>
<td>0.16</td>
<td>0.14</td>
<td>1.00</td>
</tr>
<tr>
<td>Steepness</td>
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<td>0.42***</td>
<td>-0.89***</td>
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<td>0.82***</td>
<td>0.67***</td>
<td>0.42***</td>
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<td>-0.15</td>
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<td>Triangle</td>
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<td>0.02</td>
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<td>-0.18</td>
<td>0.18</td>
<td>0.15</td>
<td>0.09</td>
<td>0.69***</td>
<td>0.14</td>
</tr>
</tbody>
</table>

*** p<0.001      ** p<0.01      * p<0.05
4.3.5 Model fit

The addition of steepness to the null model for largest clique size showed significant improvement to the model fit ($X^2 (1, N = 78) = 14.6, p <0.001$). Steepness showed a significant positive association with the size of the largest clique in the pen (See Table 4.3 and Figure 4.5). However, there was no significant difference in David’s Scores between clique members ($M= 6.91 \ SD=0.62$) and non-clique members ($M=6.92, SD=0.63; t_{1100} = -0.17, p =0.9$).

Table 4.3. Parameter estimates from mixed-effects models explaining variation in clique size.

|                | Estimate | Std. Error | df | t value | Pr(>|t|) |
|----------------|----------|------------|----|---------|----------|
| Intercept      | 3.58     | 0.99       | 76 | 3.60    | <0.0001  |
| Mean Weight    | 0.01     | 0.02       | 76 | 0.32    | 0.75     |
| Male           | 0.08     | 0.16       | 66 | 0.48    | 0.63     |
| Castrate       | 0.20     | 0.28       | 76 | 0.71    | 0.48     |
| Breed          | 0.05     | 0.16       | 76 | 0.28    | 0.78     |
| Null dyads %   | -0.01    | 0.01       | 74 | -0.81   | 0.42     |
| Steepness      | 18.08    | 4.16       | 74 | 4.35    | <0.0001  |

None of the other pen level dominance metrics were found to significantly improve upon the null models for clique size or betweenness centralisation.
Figure 4.5 Regressed David’s Scores for pigs from two pens with different steepness gradients. The solid line and circles are obtained from a pen containing a large fighting clique whereas the dashed line shows the slope from a pen with a small clique.

4.4 Discussion

Variation in chronic aggression in commercial pig systems is an on-going problem, and the aetiology behind this phenomenon is not fully understood. Wild boar groups develop strict linear hierarchies (Mauget, 1981), however such well-formed hierarchies are considered rare in commercial systems (Beilharz and Cox, 1967). While instances of linear hierarchies have been observed in gilts (Rasmussen et al., 1962), piglets (Székely et al., 1983), and growers (Meese and Ewbank, 1973), it has been argued that this is unusual for commercially housed pigs (Beilharz and Cox, 1967), and that structure and stability of hierarchies tend to vary between age groups (Parent et al., 2012), sex (Meese and Ewbank, 1972), and group size (Samarakone and
Gonyou, 2009). Even within such categories, variation in linearity commonly exist (Arey, 1999). While the establishment of dominance hierarchies is a dynamic process, with frequent instances of animals changing their social rank across time (Meese and Ewbank, 1972), there is evidence that the early dominance interactions can considerably affect the likelihood of achieving a stable hierarchy (Chase, 1982), which may affect rates of chronic aggression. This study aimed to further investigate network properties that were found to significantly predict chronic aggression by examining the relationship between these network properties and the dominance structures at the pen level.

At the dyadic level, very few dyads were found to be significantly asymmetrical as tested using the approach recommended by Langbein and Puppe (2004) and a large proportion of dyads were null indicating that animals did not aggressively interact or did so without a clear winner. This is in contrast to Puppe et al. (2008) who found 53.6% of weaned pigs that had been recently mixed developed significantly asymmetric relationships, and found that only 2.6% of dyads were null. Similarly, Puppe et al. (2008) found higher linearity (Landau’s $h'$) with an average value $h' = 0.77$ than in our study. However, our Directional Consistency Index findings were comparable with those reported in Puppe et al., (2008). The contrast between Puppe et al., (2008) and our own results may be due to the difference in data collection methodology, as they observed the animals over a period of 2-3 days and had a wider range of dominance behaviours (such as displacement) that were included in the analysis. Potentially, significant asymmetry would have emerged in our study had additional aggressive behaviours been included over a longer observation period. However, our focus here was on the acute phase of intense and damaging aggression.
associated with early dominance interactions and whether the network structure that
develops from this highly dynamic period is manifested in different strengths of
dominance hierarchy.

We found considerable variation in dominance metrics that demonstrate certain groups
of pigs do form considerably different dominance structures during the first 24h post-
mixing. In particular, the presence of negative triangle transitivity values reveals
certain pens contain more cyclical than transitive triads, which is considered to indicate
poor hierarchy (Shizuka and McDonald, 2012).

However, despite considerable variation in dominance metrics, our hypothesis that
pens with large cliques would have significantly higher rates of linearity, steepness,
and transitivity, was only partially correct. We found steepness to be the only
dominance metric to be significantly associated with a network property. This may be
due to a variety of reasons. One possible reason is that very few pens had established
a significantly linear hierarchy and on average linearity was low. This suggests that
the hierarchy formation may not have been fully established by the end of the
observation period, and thus no meaningful difference could be detected between
groups. Work by Meese & Ewbank (1973) suggests that 90% of the aggressive
interactions/lesions occur in the first day following regrouping of pigs. If the
establishment of dominance relationships in our population was not complete during
this first day it would suggest that a secondary phase of less intense interactions is
necessary to complete the establishment of these relationships, as well as to maintain
them as already appreciated. An alternative possibility is that the high proportion of
null dyads limited the accuracy of the dominance metrics, and thus the values obtained
from many groups may not have been a true reflection of the dominance structures present. Another possibility is that pen with similar weight and similar competitive ability may have contributed to the lack of steepness. As a result, the findings regarding steepness ought to be interpreted with caution.

The positive association between steepness and clique size indicates that in pens with large cliques there are greater differences in absolute dominance. The early presence of considerably higher ranking dominant animal/s may impose a stabilising effect on the group, which leads to lower rates of chronic aggression as previously found in pens with large cliques in Chapter 2 (Foister et al., 2018). There is evidence that the presence of larger dominant animals reduces fighting in newly mixed pigs (Rushen, 1987). While our groups did not contain large weight variations as in Rushen (1987), it is possible that an animal attaining high dominance early on in the mixing process may also confer a similar reduction in aggression. Furthermore, changes in dominance rank are common in growing pigs, however it appears to be most common in intermediate ranking pigs (Meese and Ewbank, 1973, 1972). High steepness at mixing indicates larger differences in absolute dominance, and the presence of clearly high and low ranking animals. In a situation where large differences in dominance exist it is less likely that dominance positions will be challenged and animals will change rank (Meese and Ewbank, 1973, 1972). This is in contrast to pens with low steepness that tend to contain all similar-ranking animals with small differences in absolute dominance and a risk of more frequent challenges to established ranks.

However, the lack of a significant difference in average rank between clique members and non-clique members suggests that clique members are no more dominant or submissive on average. It is possible that the variation in dominance within a clique
is greater than amongst non-clique members even though, on average, the rank of clique members and non-clique members is the same and this greater variation could contribute towards greater steepness in pens with large cliques. Further research on the individual network positions and dominance would be necessary to answer this question. Temporal analysis focusing on how certain animals attain high ranks would also be valuable in further understanding the variation in network properties that relate to chronic aggression.

4.5 Conclusion

In conclusion, a number of different dominance metrics did not relate to network properties associated with chronic aggression. However, pens with large cliques show significantly greater differences in dominance soon after mixing than pens with small cliques. The results suggest that emergence of high ranking animals during the early dynamic phase of intense dominance interactions occurs predominantly in pens with large cliques. These may offer a stabilising effect on the wider group, and as a result reduce the rate of chronic aggression.
Chapter 5. General Discussion
5.1 Introduction

Post-mixing aggression is a common issue within the pig industry that occurs in response to frequent mixing with unfamiliar conspecifics. While a great deal of research has been carried out in order to find ways to manage the severity of this behaviour, no solutions have been found to be both practical and cost-effective at a commercial level. However, a greater understanding of the behaviour itself and the root cause of the variation in aggression at both mixing and in stable groups could be a valuable addition in finding a solution to this problem.

While dyadic traits have offered valuable insight into the relationship between engagement in aggression and injury, there is remaining variation in injurious outcomes that remains unexplained. This thesis proposed that applying social network analysis may further our understanding of pig aggression by expanding the behavioural phenotypes beyond the dyad. In order to capture indirect social connections and wider group patterns, which may capture other factors such as personality and variation in fighting skill as a result of different fighting experience.

In Chapter 2, I identify group level network structures associated with group level lesions, and in Chapter 3, I explore the effect of occupying different positions on individual level lesion scores. These two chapters present novel findings regarding post-mixing aggression and support the claim that social network analysis is a useful tool for obtaining new information about social behaviours. The key findings regarding the relationship between global and local network measures and lesion scores will be discussed in section 5.2.
While a relationship between network traits and lesion scores appeared in Chapters 2 and 3, the reason for this relationship was not clear. We hypothesised in Chapter 2 that certain network structures may be associated with differences in hierarchy development. We aimed to explore this idea in Chapter 4 by utilising a variety of dominance metrics to determine whether there is evidence that these structures differ in hierarchy formation. The key findings from Chapter 4 will be discussed in section 5.3.

In section 5.4, I will discuss the overall implications of the findings, and in section 5.5 I will present the limitations of our study and suggestions for future areas of research.

5.2 Relationship between network properties and lesion scores

Skin lesions are an easily quantifiable method of determining what form of aggression a pig has engaged in (Turner et al., 2006). The relationship between these skin lesions and dyadic behavioural traits have been previously analysed by Desire et al (2015), who presented evidence that aggression at mixing was inversely related to aggression in stable groups. This finding suggests that we should not be aiming to eliminate aggression at either time point, as aggression would be likely to increase at another time point. However, research by Turner et al., (2017) identified that the desirable outcome of low lesions at mixing and in stable groups could be achieved by pigs exhibiting a wide range of aggressive behavioural strategies when the group was first formed even if the pigs won and lost a similar number of encounters. This finding suggests that a variety of social strategies may be beneficial in the right social environment, and that an individual’s long term outcome does not solely rely on its own behaviour, but is also dependent on the group in which the individual finds itself.
In Chapter 2, I extracted a variety of commonly used global network measures and used a general linear model to determine whether there was a relationship between different pen level network structures and pen level lesions. The results indicated that pens with large cliques tended to have fewer lesions in stable groups than pens that do not form large cliques. Having accounted for the number of interactions that occur in the pen, the findings suggest that aggressive interactions that form a clique lead to a greater reduction in lesions than the same number of aggressive interactions that do not form a clique. This a key finding in our study, as it demonstrates that not all fights are equal, and that who an individual choses to fight (and who that individual goes on to fight with) is an important aspect in predicting social outcomes at the level of the whole group. Therefore our findings are in agreement with the fundamental theory of SNA which emphasises the importance of indirect social connections (Brent, 2015).

In contrast, I found that pens with high betweenness centralization were prone to fewer lesions at mixing and higher lesions in stable groups, indicating that a divided network at mixing is associated with long-term social instability.

Large cliques became a network property of interest due to their association with fewer lesions at the pen level in stable groups as found in Chapter 2. However, the effect at the individual level, in particular those who were part of the cliques, was unclear. From a welfare perspective, large clique size would not be considered a beneficial trait if clique members were severely injured as a result of their clique membership.

Chapter 3 investigated two aspects of the individual network positions. The first was a direct continuation of Chapter 2, by categorising individuals as having either high or low betweenness centrality and being either clique members or non-members and
establishing whether there was any difference in lesions between the categories (high betweenness vs low betweenness centrality, and clique membership vs non-membership). I found that there were significant differences at mixing, in particular that clique members tended to have higher lesions than non-clique members in all body regions. However, there was no interaction between the size of the largest clique and clique membership on lesion scores. Individuals with high betweenness centrality also had more lesions than non-central individuals, however the opposite effect was found within the interaction, indicating that in pens with very high betweenness centralization the individual with the high centrality actually had fewer lesions than the remaining group. This trend was observed across all body regions.

The most interesting finding was that at 3wk-PM in the majority of body regions there was no significant difference in lesions between categorical network positions. This indicates that all individuals were better off in a pen with large cliques, regardless of whether or not they participated in the cliques’ formation. Likewise, all individuals suffered higher lesions in a network with high betweenness centralization, regardless of whether they had high or low betweenness centrality.

The second aim of Chapter 3 followed a similar approach to that of Chapter 2, by extracting a wide range of commonly used local network positions and entering them into a stepwise regression to identify which was most strongly associated with individual lesion outcomes. This approach identified eigenvector centrality as a strong predictor of lesions. Like certain traits identified by Desire et al (2015), it was positively correlated with lesions at 24hr-PM, but negatively correlated with lesions in stable groups. As this data set had previously been analysed by Desire et al (2015), I was keen to determine whether eigenvector centrality was highly correlated with the
dyadic measure “total duration of non-reciprocal delivered aggression” that Desire et al (2015) had found to show the same relationship with lesions. Interestingly we found that eigenvector centrality and “total duration of non-reciprocal delivered aggression” were not highly correlated ($r=0.34$), yet provided comparable model fit for lesion scores at both time points. While it is disappointing that the inclusion of indirect connections did not improve upon the model fit and explain remaining variation as per our aim, these results still provide an interesting insight. In particular, these traits had moderate to low correlation yet yielded similar model fit. This suggests that these two traits are capturing two distinct aspects of the social environment that both contribute to lesion scores. When both traits were entered into the model, both maintained their significance and direction of effect, and the addition of eigenvector centrality significantly improved upon the model fit.

Therefore, social network analysis may be a useful addition to dyadic traits rather than an alternative altogether. However, Table 3.4 shows that whereas a range of different dyadic traits were selected by the stepwise regression as the best predictor of lesions at different time points, eigenvector centrality was consistently selected throughout body regions and time periods. The reason for this is unclear. While a few other studies have compared the model fit between network and dyadic traits, to the authors knowledge no other study has found this type of contrast in model selection. However, I suggest that the indirect interactions reflected in an animal’s eigenvector centrality impacts lesions across body regions and time periods. In contrast dyadic traits do not reflect the effect of indirect connections and several separate dyadic traits are required in order to explain lesions in different locations and times.
One limitation of eigenvector centrality is that it conventionally applies to symmetric matrices. Half of the dyadic traits selected by the stepwise regression and presented in Table 4 either refer to “given” or “received” interactions. However, as eigenvector centrality does not incorporate this, we lose the effect of direction. This also raises a question about our decision to remove direction from fighting behaviour in all network measures. We decided prior to network analysis that as engagement of aggression was a mutualistic interaction (both decide to engage in a fight), that these networks should be formatted as undirected matrices, in order to reflect the bi-directionality of this behaviour. In future research, we would include both directed and non-directed measures for fighting. However, this would not have changed the fact that eigenvector centrality does not incorporate direction when quantifying social position and thus this information would still be missing. Furthermore, this would have reduced the number of interactions included in the study, as a large proportion of the fighting interactions an initiator could not be identified, as the decision to engage in a fight appeared to occur simultaneously.

Furthermore, dyadic bullying traits appeared frequently as the best predictor for many of the 3wk-PM lesion scores, yet the stepwise regression did not select any bullying network traits. This suggests that the indirect social connections reflected in fighting eigenvector centrality are a consistent predictor of short and long-term lesion scores and more influential than any of the bullying derived network traits.

What is also noteworthy is that the unweighted eigenvector was the most predictive of 24hrs-PM lesions whereas in stable groups eigenvector weighted according to the duration of fights at mixing provided a better model fit for reduced lesions. This makes sense biologically, as fights that last longer are more likely to lead to a clear dominance
relationship and to be associated with a reduction in lesions in stable groups. Therefore, a high eigenvector centrality that is weighted by duration suggests that an individual has fought with other individuals who have clearly established their social rank and also have less reason to engage in any further aggression. In contrast, individuals with high unweighted eigenvector centrality have likely fought with numerous individuals but not achieved the same degree of certainty regarding rank.

To summarise, Chapters 2 and 3, I identified network properties at both the group level and individual level that strongly relate to short and long term lesion outcomes. In Chapter 2 I identified distinct group level characteristics that explained a significant proportion of the variation in pen level lesions at 3wk-PM and found that dyadic traits did not. This supports the premise that social network analysis is a valuable tool in quantifying the wider social context, which can explain variation not captured by dyadic interactions. In Chapter 3, I identified that individual social network positions perform equally well as dyadic traits in predicting lesion outcomes at both time points but appear to be using different aspects of the social environment to predict these outcomes. However, social network position, ‘eigenvector centrality’, appeared to consistently provide the best model fit, whereas a variety of different dyadic traits were required to provide best model fit for each of the body region and for different time points. This may suggest that eigenvector centrality provides a more complete description of an animal’s social position that cannot be captured by a single dyadic trait.

5.3 Relationship between network properties and dominance structure

In Chapter 4, we aimed to explore whether there were any significant differences in hierarchical structures between pens that had high or low betweenness centralization
and pens with large or small clique sizes. Our interest remained on these two structures as our findings in Chapter 3 had confirmed that excessive injury was not associated with clique membership (but instead eigenvector centrality was most associated with injury).

We quantified the dominance attributes of each pen using a variety of metrics that reflect different aspects of dominance relationships. Drews et al (1993) stated that consistent asymmetry in a dyadic relationship is essential in determining whether a true dominance relationship exists between the two individuals. At the dyadic level, we tested for the number of null dyads (where dyads did not interact), one way dyads, two way dyads, and significant dyads, and correlated these with largest clique size and betweenness centralization. We found that null dyads were significantly positively associated with betweenness centralization, indicating that pens with high centralization also tended to have fewer connections. In contrast, large clique sizes were significantly negatively associated with null dyads, which was an expected outcome as cohesive groups are more likely to emerge in groups with fewer null dyads. Interestingly, betweenness centralization was significantly negatively correlated with tied and two-way dyads, suggesting that fewer ambiguous dominance relationships existed in pens with high betweenness. This is rather surprising as clear dominance relationships tend to reduce chronic aggression, yet high betweenness centralisation was associated with increase lesions 3wk-PM. However, pens with high betweenness were also positively correlated with null dyads, therefore it is likely the absence of established relationships in the pen was the main cause of continued social disruption.

In contrast, clique size was positively correlated with tied dyads, one and two-way dyads, and significant dyads. However, while more dyads in pens with large cliques
reached a significant degree of asymmetry, clique size was significantly negatively associated with directional consistency index (DCI), suggesting that many fights were not consistent in direction. In contrast, betweenness centralization was positively associated with DCI, although not at a 95% confidence interval. This outcome appears contradictory; however, this is explained by the different way in which significant asymmetry and DCI are calculated. A dyad is only considered significantly asymmetrical when enough repeated fights have occurred (see Figure 5.1).

*Figure 5.1. In graph A the vast majority of interactions occur in one direction, however none of the dyads have enough repeated interactions to reach significant asymmetry. Whereas in graph B, one dyad has enough repeated interactions to be considered significantly asymmetrical, but the remainder of the dyads are two-way dyads, and this decreases the groups directional consistency.*

For example, one individual may initiate a fight against several individuals without receiving any initiated aggression. At a pen level this translates as high DCI, because all the attacks went in one direction, yet the lack of repeated interaction means that none of the interactions classify as significantly asymmetrical.
The results indicate that in pens with large cliques’ aggression is better distributed amongst all group members, however a higher proportion of these dyads are two way, tied, or do not meet a significant threshold. This was surprising, as this does not reflect a particularly well formed hierarchy as was expected from a structure associated with low lesions. Despite the low number of significant dyads and the high rate of two way dyads, larger cliques were still positively associated with Landau's $h'$ measure of linearity and steepness which may partially explain improved stability over time. Our interpretation of these results is that while a fully formed hierarchy may not be present by the end of a 24hr period, the pens with larger cliques show the start of a linear/quasilinear hierarchy with distinct ranks emerging, whereas pens that have small cliques or a greater degree of division in the network do not show the same level of progress. Furthermore, we do not know what interactions occur between 24hr-PM and 3 weeks later in stable groups. Ultimately, the first 24hr-PM is an intense start to a dynamic long term process of sustained dominance relationships. Potentially the clique structure facilitates further development of dominance relationships better than behaviours that lead to high betweenness centralization. Furthermore, winner-loser effects occur quite strongly in pigs (Camerlink et al., 2016) and the dynamic mixing period creates a scenario of either repeatedly reinforced winner or loser experiences or a very confusing mix. In this chapter, these winning and losing experiences are interpreted the dominance structures that have formed. However, these dominance structures that emerge at 24hr-PM will be profoundly shaped overtime by the winner-loser experiences and the individual animal’s sensitivity to them. These changes to the dominance structure will ultimately affect the long term social stability of the group and future aggressive behaviour. Additionally, stress has been shown to have a
significantly affect cognitive ability and memory in pigs, and it is likely that certain outcomes may be retained better than others (Laughlin et al., 1999; Laughlin and Mendl, 2004). Consolidation and/or disintegration of certain dominance relationships are therefore likely to follow once the initial stress of the mixing event has passed, which is not reflected in the dominance structures obtained at 24hr-PM.

### 5.4 Implications of findings

Individuals who belonged to a pen that formed a large clique tended to have fewer lesions 3wk-PM, but no individual differences were detected between clique and non-clique members at 3wk-PM. This is in contrast to what was expected considering Desire et al (2015) and Turner et al (2017), who found that individuals who avoid fights at mixing are likely to engage in aggression later. This finding may provide insight into the “LL” phenomenon identified by Turner et al (2017), where certain pigs are capable of avoiding aggression at both times points. Potentially a large clique may enable a large enough proportion of the pen to establish their position without the need for low aggressive pigs to get involved. Alternatively, the personality traits present in a pen with a large clique may allow certain individuals to establish their social position without the need for overt aggression, for example by readily displaying submission.

High eigenvector centralization was found to be the pen level trait most associated with a decrease in anterior lesions at 24hr post mixing. This suggests that a pen with a greater disparity in individual eigenvector centrality had pigs with the fewest lesions in this body region. Yet at the individual level, individuals with high eigenvector centrality had the highest lesions. A high individual eigenvector centrality indicates that an animal did not fight with individuals in the pen equally, but instead fought with other aggressive individuals. The fact that the presence of a highly aggressive subset
of animals in a group is most predictive of a low level of lesions at the pen level appears contradictory.

While the reason for this is unclear, one interpretation of these results is that highly aggressive individuals exert an inhibitory effect on the remainder of the group. This may also be the case in terms of betweenness centralization. In both eigenvector centralization and betweenness centralization we see a highly aggressive individual engaging in a considerably higher proportion of fights than the remaining group. The key difference is that betweenness centralization detects a significant division within the group, whereas in pens with high eigenvector centralization this may not be the case. The continued aggression in stable groups in highly centralized pens may be due to the inability to express aggression towards others in the hours following mixing without becoming the target of the hyper aggressive individual. Alternatively, individuals in the presence of an extreme aggressor may be too pre-occupied with fighting the aggressor to have time or energy to establish other dominance relationships. Therefore, the difference between individuals who do not engage in fights in pens with large cliques and those in pens with a centralized aggressor may be a matter of choice; whereby pigs in pens with large cliques (non-members) are non-aggressive by nature and have no desire to engage, pigs that are in the presence of an extreme aggressor may be deprived of establishing dominance relationships with the remainder of the group. Whilst further research is required to test the validity of this theory, the results do suggest that an even distribution of aggression is more beneficial than an uneven distribution. However further research is also required to determine the causation of this uneven distribution (see section 5.6 for further research suggestions).
In Chapter 4, the difference in hierarchy formation suggested that pens with large cliques had made better progress in establishing a hierarchy than pens with high betweenness centralization, as indicated by linearity and steepness. This is despite a large proportion of dyads in pens with large cliques not reaching a significant threshold, and many being two-way or tied. In contrast, betweenness centralization had higher rates of directional consistency than pens with large cliques. Whilst the individual(s) responsible for the directed attacks were not investigated further in Chapter 4, this feature in pens with high betweenness lends some credence to our hypothesis regarding the presence of an aggressor that may be causing disruption.

5.5 Limitations

5.5.1 Limitations of identified traits.

Very few studies have looked at the social networks formed exclusively from aggressive behaviour, less so in pigs, and none in a predictive capacity with pigs. This posed a challenge in identifying a priori which network traits would be most important in terms of predicting lesion scores. Our approach of using a stepwise regression to objectively test model fit was a necessary first step in understanding how (if at all) indirect network measures related to short and long term lesion scores.

While ‘the largest clique’ was identified as the best predictor, as a trait it is prone to misinterpretation and may not be an optimal trait for reflecting the true nature of what is occurring within the pen. To clarify, “size of the largest clique” only reflects how many individuals make up the largest clique but does not reflect how many cliques of this size exist (See Figure 5.2).
Figure 5.2. Model network depicting 5 nodes. The largest clique in this network contains 4 nodes, but there are two cliques of this size, (1,2,3,4) and (2,3,4,5). Therefore, in this network all 5 nodes are members of the largest clique, despite the largest clique containing 4 individuals. Nodes 2-4 are members of both cliques, whereas nodes 1 and 5 are members of different cliques and are not directly connected.

Even though the models accounted for any effect due to the number of interactions, we did not account for any effect that may have resulted from being associated with multiple cliques. The results from the current study simply highlight that pens with larger cliques are better at reducing long term lesions than pens that do not form a clique. If the clique effect actually measures cohesion, further research is needed to understand the variability within clique formation in pigs and determine whether other network measures would provide more precision than simply the size of the largest clique. Likewise, we are unable to determine whether there is an effect due to the number of large cliques that exist in a pen. For example, two pens of 15 individuals may both have a largest clique size of 5 pigs. However, hypothetically there may be 4
cliques of this size in one pen, and only 1 in another. This is a variable that was not included in the model, but potentially could have an effect. Furthermore, it is highly likely that there is a ceiling effect to this measure. Previous studies have found that only ~40% of animals fight each other upon mixing (Arey and Edwards, 1998), and this coincides with our results. However, if the clique size exceeded this, we cannot conclude that this would result in a further reduction in lesions.

Based on the results of the current study, we suggest that the ‘size of the largest clique’ as a global measure appears to reflect the degree of cohesion at the network level, which in turn is associated with evenly distributed aggression and establishment of dominance relationships across the group. This pattern of behaviour likely leads to a higher proportion of pigs recognising their position and leads to lower chronic aggression. A repeat of this study would include the identification of number of large cliques, and over-lapping cliques (individuals that belong to multiple large cliques) to see whether this exerts any influence on long term aggression. Ultimately, further research is required to understand the variability in cohesion at the group level in pigs and whether other network traits that measure cohesion would be a more appropriate trait in future research.

5.5.2 Lack of other social interactions

Another limitation to this study was the lack of data on wider social behaviour. Pigs are known to have a wide repertoire of behaviours and social relationships that were not included in this thesis. Pigs have shown preference for particular conspecifics, which is reflected in their proximity patterns and positive social interactions (Newberry and Wood-Gush, 1986; Stookey and Gonyou, 1998, Camerlink and Turner, 2013, Camerlink et al., 2014). It is possible that two pigs may show very similar
aggressive behavioural patterns but differ considerably in affiliative behaviour. Such additional behaviours may explain remaining variation in long term social outcomes, and why certain individuals fare better than others despite similar levels of aggressive engagement at mixing. A number of studies have demonstrated that network positions derived from other social behaviours have important consequences for the individual in other contexts. For example, Boogert et al., (2014) noted that the spread of information regarding new food sources could be predicted by associations birds made during perching, but not while foraging. Potentially, individuals that are central in pro-social behaviours may benefit from reduced aggression compared to those that do not engage in the same degree of affiliative behaviours.

5.5.3 Future research

Whilst this thesis has identified structural differences at the group level, and different outcomes at the individual level, we still do not yet know why such variation exists in group level network structures. In the majority of network studies, populations exist in different environments with unique combinations of demographics, group size, and resource availability which likely play a fundamental role in shaping the social interactions. However, in commercial animals, such as our study sample, control of the abiotic environment removes this variability. What remains is a combination of individuals that each have their own approach to coping with the disruptive event of mixing.

Sequential analysis would be the first step in understanding the various social processes that shape network structure, and this would also be valuable in understanding how certain positions become established and would identify individuals that disrupt or aid the formation of certain network structures. For example,
individuals with high betweenness centrality appear to hold an important role in their network. Yet without analysing the order of events it is hard to determine whether these pigs are aggressive in nature and inhibit pigs from interacting with others, or that the remainder of the group is already divided and high betweenness pigs are actually responsible for creating cohesion. Previous studies have identified betweenness to be highly associated with current dominance rank (e.g. in male chimpanzees, Gilby et al, 2011), and also predictive of ascension in social rank (McDonald et al, 2007). The final dominance rank of individuals was not studied in this thesis, and therefore the association between rank and network position is not verified, however the lower lesion counts of high betweenness individuals at mixing may reflect higher dominance status at 24hrs-PM.

Sequential analysis would also be a valuable asset in identifying how individuals respond to aggressive behaviour. For example, some pigs might be more likely to attack another pig sooner after a defeat or a win than other pigs. We may also be able to detect variation in temporal patterns of aggressive behaviour that may relate to fighting strategies. For example, two individuals may engage in the same number of fights, but one individual may engage in aggression right at the start of the mixing process whereas others may wait until a proportion of the dominance relationships have already been established. This could affect lesion outcomes, as possibly fewer injuries are accrued when fighting an animal that is already tired from previous fights. Such sequential analysis could be carried out using dynamic dominance ranking systems such as Elo-rating or its refinement in the form of the Glicko rating (Albers and de Vries, 2001).
Another area that ought to be researched further is the consistency of network structures and individual position over time. However, one challenge that has been experienced a number of times is the fact that once a hierarchy has been established aggression can be rare and collecting enough interactions to recreate a network may prove challenging. An alternative to this would be testing whether network position can be predicted by other personality or behavioural traits. The effect of personality on network structure has been studied in fish and has demonstrated that different personality types create significantly different networks. Other research has also shown the disruptive effect hyper aggressive individuals can have on the entire group (Sih and Watters, 2005). Yet this has not been tested in pigs and is a promising area of future study. Experimental grouping of different personality types may identify individuals who form cohesive group structures, and other individuals who are disruptive. One method of testing this would be the removal of a high betweenness or high eigenvector individuals from the pen to see if the remaining individuals start to form a more cohesive network structure.

A method that could be useful in testing this hypothesis is agent-based modelling (ABM). ABM allows researchers to simulate behaviour under different internal and external conditions and observe the outcomes from these different conditions. This method has the advantage that it enables researchers to test a variety of hypotheses without the need for large and costly animal trials. ABM has already been successfully utilised in applied ethology to test whether redirected behaviour motivation and stress can elicit tail-biting behaviour in pigs (Boumans et al., 2016). In a later study Boumans et al. (2018) demonstrated that coping style (see Bolhuis et al., 2004) as a model variable exerted considerable influence on feeding and social interaction patterns.
As a continuation of the research in this thesis, ABM’s could enable us to set and test the effect of certain criteria (e.g. aggressive personality types) and observe whether different combinations lead to different social network structures and different lesion outcomes in both the short and long term. If such personality traits proved to be a reliable method of predicting short and long term lesion outcomes, the next step could be investigating the heritability of these traits as they may be a valuable inclusion to future breeding programs.

Research into the indirect genetic effects, i.e. the effect an individual exerts on to its group members (Rodenburg et al., 2010), may also yield valuable information regarding the formation of beneficial group structures (such as cliques). One method of using indirect genetic effects would be to select for the desired behavioural outcomes. For example, selecting for birds that engaged in a low number of feather pecking bouts was shown to reduce feather pecking and improve plumage in three generations (Kjaer et al., 2001). However, individual behaviour may depend on both the genotype of the focal animal and that of its social partner, as found in the case of cannibalism in laying hens (Ellen et al., 2008). Furthermore, recording of behavioural data (e.g. bouts of feather pecking or aggressive interactions) is time consuming and impractical. Another challenge of researching indirect genetic effects of behavioural traits is that it requires a large sample of animals (~20,000) in multiple groups that have been formed in the correct way (small group size, and with the right balance of relatedness within and between pens). Alternatively, we can select for indirect genetic effects on growth which can be used to indirectly select for beneficial behaviours (Camerlink et al., 2013; Rodenburg et al., 2010). This approach of selecting for indirect genetic effects for growth has the advantage that growth and pedigree data is
recorded by breeding companies, and in many cases a record of what pigs shared a pen is also available.

5.6 Based on the findings of this thesis we may expect cliques to form in pens containing pigs with high IGE for growth, however as Camerlink et al. (2014) noted, it is likely that indirect genetic effects on growth targets a behavioural strategy, rather than one individual trait. Therefore, it is possible we may see changes to a wider variety of behaviours as a result of this selection pressure. Furthermore, as growth rate is usually measured over a prolonged period of time, behavioural traits that are acute (e.g. mixing aggression) may not be influenced by indirect genetic effects for growth as their effect on growth is fairly transient. However, chronic aggression which develops over a prolonged period of time are more likely to benefit from indirect genetic effects for growth. Conclusion

These findings have provided the first step into uncovering the relevance of indirect social connections in relation to short and long term lesion outcomes in newly mixed pigs. Our results suggest that cohesive network structures are a beneficial structure at mixing, and lead to a reduction in lesions in stable groups without causing excessive injury at mixing. One of the key findings that emerged from Desire et al (2015) research was the inverse relationship between lesions at mixing and in stable groups. It presented the challenge of identifying a behavioural phenotype that would not lead to excessive injury at each time point. This thesis has made progress in the identification of a promising phenotype, which can serve as a starting point for further research to develop our understanding and ability to manage post-mixing aggression in pigs. Primarily, the results indicate that at the individual level we ought to identify
individuals who tend to form cliques with others, and evenly distribute aggression through the group without showing excessive aggression that is disproportionate in relation to the rest of the group.

Furthermore, our research will contribute to the field of social network analysis, as to date there is a limited amount of social network analysis applied to commercially reared species. It is anticipated the methodology applied in this thesis may be of use to other applied ethologists wishing to apply SNA to replicate pens of commercially reared animals.

As far as the author is aware, this study contains the highest number of replicate networks derived from large cognitively advanced mammals in a controlled physical environment. The findings from this study demonstrate the variation in social structure than can exist even without environmental variation, which ought to be of interest to any researcher studying the variation in network structure and the associated consequences.
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Melo


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Appendix A

Table S1. Network properties estimated from the behavioural networks and entered in the stepwise regression.

<table>
<thead>
<tr>
<th>Network properties</th>
<th>Behavioural Networks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bully</td>
</tr>
<tr>
<td>Clustering-coefficient</td>
<td>x</td>
</tr>
<tr>
<td>Largest Clique</td>
<td>x</td>
</tr>
<tr>
<td>Degree</td>
<td>x</td>
</tr>
<tr>
<td>Eigenvector</td>
<td>x</td>
</tr>
<tr>
<td>Betweenness</td>
<td>x</td>
</tr>
<tr>
<td>Closeness</td>
<td>x</td>
</tr>
<tr>
<td>In-degree</td>
<td>x</td>
</tr>
<tr>
<td>Out-degree</td>
<td>x</td>
</tr>
<tr>
<td>In-closeness</td>
<td>x</td>
</tr>
<tr>
<td>Out-closeness</td>
<td>x</td>
</tr>
</tbody>
</table>

Separate networks were created using fighting only and bullying only and these behaviours combined. Directed versions of degree and closeness were applied to bullying networks only.


### Table S2. Summary of key terms and network properties.

<table>
<thead>
<tr>
<th>Terminology</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Graph</td>
<td>A set of nodes and the set of relationships between them.</td>
</tr>
<tr>
<td>Node</td>
<td>An individual in a network with known interactions to other individuals within the network.</td>
</tr>
<tr>
<td>Behavioural network</td>
<td>Each pen has a network comprised of either only bullying or fighting, or both behaviours combined.</td>
</tr>
<tr>
<td>Dyadic traits</td>
<td>Behavioural traits based on dyadic interactions that do not take account of third party interactions.</td>
</tr>
<tr>
<td>Network traits</td>
<td>Umbrella term to refer to all quantitative descriptors of network properties derived from network measures.</td>
</tr>
<tr>
<td>Edge</td>
<td>The interaction between two nodes</td>
</tr>
<tr>
<td>Edge direction</td>
<td>Edges can be directed based upon the nature of the interaction. The edge direction travels from the ‘sender’ towards the ‘receiver’.</td>
</tr>
<tr>
<td>Path length</td>
<td>A path is the number of edges that lie between two nodes.</td>
</tr>
<tr>
<td>Individual measures</td>
<td>An individual measure quantifies the position of individual nodes in a network</td>
</tr>
<tr>
<td>Global measures</td>
<td>A global measure quantifies the network as a whole.</td>
</tr>
<tr>
<td>Centrality</td>
<td>A category of approaches which are used to identify which nodes occupy a ‘central’ or an influential position within a network.</td>
</tr>
<tr>
<td>Centralisation</td>
<td>Freeman’s equation of centralisation describes the inequality in centrality within a network.</td>
</tr>
</tbody>
</table>

**Definitions of network traits used in this paper**

<p>| Degree centralisation | A centralised network is one in which one individual has considerably more direct connections than all others in the network. Degree can also be calculated as ‘in-degree’ or ‘out-degree’. Directed degree centralisation informs us whether certain individuals within a network receive or give substantially more interactions than other individuals in the network. |</p>
<table>
<thead>
<tr>
<th>Concept</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvector centralisation</td>
<td>Eigenvector centrality takes account of the number and quality of the indirect connections an animal has. A centralised network is one in which highly connected individuals tend to interact with each other. Betweenness calculates the extent to which a node is present on the shortest path (geodesic) between other nodes. A centralised network has one or a few individuals that interact with nodes that they themselves do not interact directly. A node that has high closeness has a short distance to all other nodes in the network. A centralised network has one or a few individuals with shorter paths to all individuals in the pen than the rest of the animals. In this paper we present the largest clique as the number of individuals that belong to the largest clique.</td>
</tr>
<tr>
<td>Betweenness centralisation</td>
<td></td>
</tr>
<tr>
<td>Closeness centralisation</td>
<td></td>
</tr>
<tr>
<td>Largest clique</td>
<td></td>
</tr>
<tr>
<td>Clique</td>
<td>A group of fully connected nodes.</td>
</tr>
<tr>
<td>Clustering coefficient</td>
<td>The probability that a node’s connections are also connected. E.g A is connected to B and C. If B and C are also connected, this leads to a higher clustering co-efficient.</td>
</tr>
</tbody>
</table>
Appendix C

Table S3. Descriptive statistics of network properties in fighting, bullying and combined networks

<table>
<thead>
<tr>
<th>Network Property</th>
<th>Behavioural network</th>
<th>Median</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Largest clique</td>
<td>Fight</td>
<td>4.00</td>
<td>3.00</td>
<td>7.00</td>
</tr>
<tr>
<td></td>
<td>Bully</td>
<td>4.00</td>
<td>3.00</td>
<td>7.00</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>5.00</td>
<td>4.00</td>
<td>8.00</td>
</tr>
<tr>
<td>Clustering Co-efficient</td>
<td>Fight</td>
<td>0.46</td>
<td>0.14</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>Bully</td>
<td>0.39</td>
<td>0.08</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>0.58</td>
<td>0.36</td>
<td>0.80</td>
</tr>
<tr>
<td>Closeness</td>
<td>Fight</td>
<td>0.16</td>
<td>0.07</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>Bully</td>
<td>0.34</td>
<td>0.07</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td>Bully (In)</td>
<td>0.06</td>
<td>0.01</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>Bully (Out)</td>
<td>0.24</td>
<td>0.04</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>0.39</td>
<td>0.13</td>
<td>0.77</td>
</tr>
<tr>
<td>Betweenness</td>
<td>Fight</td>
<td>0.15</td>
<td>0.06</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>Bully</td>
<td>0.21</td>
<td>0.08</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>0.14</td>
<td>0.01</td>
<td>0.53</td>
</tr>
<tr>
<td>Degree</td>
<td>Fight</td>
<td>0.30</td>
<td>0.17</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>Bully</td>
<td>0.35</td>
<td>0.12</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>Bully (In)</td>
<td>0.20</td>
<td>0.09</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td>Bully (Out)</td>
<td>0.39</td>
<td>0.12</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>0.33</td>
<td>0.14</td>
<td>0.61</td>
</tr>
<tr>
<td>Eigenvector</td>
<td>Fight</td>
<td>0.51</td>
<td>0.32</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>Bully</td>
<td>0.52</td>
<td>0.30</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>0.40</td>
<td>0.16</td>
<td>0.60</td>
</tr>
</tbody>
</table>
## Appendix D

<table>
<thead>
<tr>
<th>Combined degree</th>
<th>Fighting eigenvector</th>
<th>Fighting betweenness</th>
<th>Size of the largest clique</th>
<th>Average duration of bullying and fights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Combined degree</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fighting eigenvector</td>
<td>0.17</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fighting betweenness</td>
<td>0.21</td>
<td>0.54**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Size of the largest clique</td>
<td>-0.17</td>
<td>-0.46**</td>
<td>-0.35*</td>
<td></td>
</tr>
<tr>
<td>Average duration of bullying and fights</td>
<td>-0.27*</td>
<td>-0.21</td>
<td>-0.13</td>
<td>0.10</td>
</tr>
<tr>
<td>Proportion of injurious fighting</td>
<td>-0.15</td>
<td>-0.24*</td>
<td>-0.06</td>
<td>0.26*</td>
</tr>
</tbody>
</table>

*** p<0.001   ** p<0.01   * p<0.05