

A Test of Time: Time-Aggregated Networks and Time-Ordered Networks in Behavioural Ecology



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This thesis is dedicated to my family.

To my parents, Lynn and John, for their unconditional love and support.

And to my brother, Steven, for his love, friendship, and inspiration.

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Abstract

Network theory has become a popular modelling framework within behavioural ecology. In order to use the wide range of existing tools, network practitioners typically collapse dynamic data into a static network for subsequent analysis. Temporal networks provide a relatively new framework for modelling dynamic network data, and retain either some or all of the temporal dynamics that are lost with a static network approach. This report explores two types of temporal networks in the context of behavioural ecology: (1) time-aggregated networks and (2) time-ordered networks. I stress the importance of choosing an appropriate aggregation time-window for time-aggregated networks, and introduce recurring temporal motifs as a tool to help choose appropriate aggregation time-windows. I also explore several centrality measures for time-ordered networks, and introduce two novel centrality measures (entrance centrality and exit centrality) for networks with weakly connected temporal components. As illustrative examples, I analyse small-spotted catshark social networks and movement networks using time-aggregated networks and time-ordered networks, respectively. I demonstrate that the strength of social attraction in the juvenile small-spotted catshark social networks, as measured by the mean dyadic simple ratio index, increased over time. I also identify location-specific temporal differences in the movement networks of wild adult small-spotted catsharks.

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Chapter 1

Introduction

Network theory has become a popular modelling framework for animal-behaviour research (Krause *et al.* 2007, Croft *et al.* 2008, Wey *et al.* 2008, Sih *et al.* 2009). Although first suggested over 35 years ago (Wilson 1975, as cited in Krause *et al.* 2007), recent advancements in computational power and network analysis tools has fuelled a surge of interest in network theory by behavioural ecologists (Krause *et al.* 2007). As a result, the field of animal behaviour has joined the plethora of other disciplines that have recently capitalised on network theory as a new approach for old questions (see Newman (2010) for a review).

Improving our understanding of how individual behaviours shape populations is an ongoing challenge in behavioural ecology (Sutherland 1996, as cited in Krause *et al.* 2007). Network theory is particularly well-suited for addressing this question, as both individual and group/population-level questions can be investigated simultaneously (Krause *et al.* 2007). Recent work on a variety of species (including dolphins (Lusseau 2003), guppies (Croft *et al.* 2009), elephants (Wittemyer *et al.* 2009), and many others (Wey *et al.* 2008)) has demonstrated the applicability of the social network approach for examining important questions in animal social networks.

The generality of network theory as a modelling framework adds to the attractiveness of a network approach (Krause *et al.* 2009). Although many applications of network theory in animal behaviour to date have focused on social networks (Wey *et al.* 2008), other applications have also been proposed (e.g. habitat connectivity (Lookingbill *et al.* 2010, Rayfield *et al.* 2011) and movement networks (Jacoby *et al.* 2012a)). Bascompte (2007) identified four general categories where network theory is particularly applicable for ecology: (1) networks of species interactions (e.g. food webs), (2) spatial networks (e.g. habitat networks), (3) epidemiology, and (4) evolutionary dynamics on social networks.

Most current techniques in network analysis are designed for static networks (i.e. networks that do not change in time) (Kim and Anderson 2012). A static approach assumes that a network is relatively constant in time. This assumption is too strong for many real-life applications (Kim and Anderson 2012). Nonetheless, to use the wide range of existing tools, network practitioners in behavioural ecology typically collapse temporal data into a static network prior to analysis (Blonder *et al.* 2012).

The inability of current methods to account for temporal trends is recognised as a major limitation for applications of network theory in behavioural ecology (Whitehead 1997, Blonder *et al.* 2012). Some studies have addressed this concern by dividing temporal data based on *a priori* hypotheses and aggregating the temporal data within each division (i.e. time-aggregated networks) (de Silva *et al.* 2011, Olesen *et al.* 2008, Olesen *et al.* 2011, Jacoby *et al.* 2012a). Others are using tools that directly incorporate dynamics by using time-ordered networks (Blonder and Dornhaus 2011).

The limitations of a static approach for modelling dynamic data has also been recognised within the networks community more generally. Several recent studies have proposed ideas for constructing and analysing networks that change in time (see Holme and Saramäki (2012) for a review).

The purpose of this thesis is to introduce temporal networks in the context of animal-behaviour research. By exploring both time-aggregated and time-ordered networks, I demonstrate that temporal networks are an essential tool for applications of network theory in behavioural ecology. I propose a new approach for choosing the aggregation time-window for time-aggregated networks by assessing time-scales in recurring temporal motifs. I also develop two novel centrality measures for time-ordered networks. For illustrative purposes, I investigate social and movement networks for small-spotted catsharks (*Scyliorhinus canicula*) using time-aggregated networks and time-ordered networks, respectively.

The rest of this thesis is organised as follows. In Chapter 2 I present an overview of network concepts. In Chapter 3 I provide background information for the small-spotted catshark data. In Chapter 4 I focus on time-aggregated networks, explore recurring temporal motifs and aggregation time-windows, and investigate juvenile small-spotted catshark social networks as an illustrative example. In Chapter 5 I focus on time-ordered networks, explore temporal centrality measures, and investigate wild adult small-spotted catshark movement networks. Finally, in Chapters 6 and 7, I provide concluding remarks on the relationship between time-aggregated and time-ordered networks, and general applications for temporal networks in behavioural ecology, respectively.

Chapter 2

Background - Networks

From everyday life experience, most people have a fairly intuitive understanding of what constitutes a network. From computer networks to business networks, the term ‘network’ is mainstream. But what is a network, exactly? What do people mean when they refer to networks? Is it different from the mathematical use of the word?

A mathematical network is exactly what you might expect from mainstream usage of the word - it is a mathematical description of how things are connected. For clarity, however, it is useful to define it more carefully. Below I provide a more precise definition of a network, as well as insight into the mathematics of networks and how animal behaviour networks can be constructed.

2.1 What is a Network?

A network (or a graph) is a collection of points that are joined by lines (Newman 2010). The points in a network are called ‘nodes’ (or vertices), and the lines joining the nodes are called ‘edges’ (or links). More specifically, a network G is a mathematical object consisting of two sets V and E , where V is the set of all nodes and E is the set of all edges. A simple example network is provided in Figure 2.1.

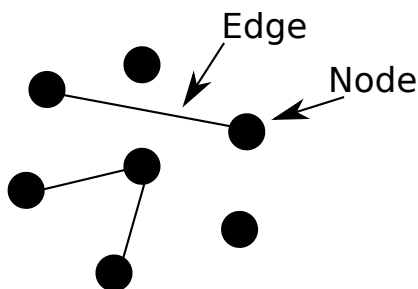


Figure 2.1: A simple network. Black dots represent nodes, and connecting lines represent edges.

2.1.1 What can be modelled as a network?

As described above, a network consists of nodes and edges. Nodes can represent any entity (e.g. individuals, groups, behaviours, particles, proteins, economies, etc.). Edges represent a relationship between a pair of nodes. Hence, a network is an appropriate modelling framework for almost any kind of pairwise relational data (Krause *et al.* 2009).

Of course, there are many different types of relationships! For example, some relationships are one-way while others are bidirectional. Some relationships are more important than others. As I explore in more detail in the next subsection, different types of relationships can be modelled by different types of networks.

2.1.2 Types of Networks

Networks can be classified into categories based on the type of relationships that the edges represent or if we restrict ourselves to a certain type of edge. Below I introduce several common network types that are used in subsequent sections of this thesis. For a more complete review of network types, see Newman (2010).

2.1.2.1 Undirected, Unweighted Networks

The simplest type of network is an undirected, unweighted network. ‘Undirected’ refers to the direction of the relationship (edge) between any two nodes and implies that the relationship goes both ways. ‘Unweighted’ refers to the relative importance of each relationship (edge) in a network and assumes that there is no hierarchy of importance among edges. An example of an undirected, unweighted network is provided in Figure 2.2a.

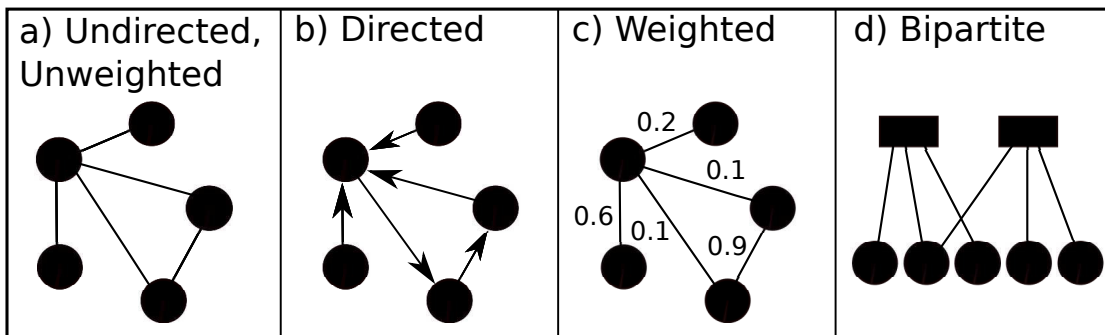


Figure 2.2: An example of four different network types: (a) undirected and unweighted, (b) directed, (c) weighted, and (d) bipartite.

2.1.2.2 Directed Networks

Relationships are not necessarily bidirectional. For example, a disease spreads directionally from one individual to another. Alternatively, an individual might move from one location to another. Any relationship that can be described as ‘to’ and ‘from’ but not vice-versa is a directed relationship. Directed relationships between two nodes can be represented in a network by a directed edge (e.g. Figure 2.2b) (Newman 2010).

In the behavioural ecology literature, relationships that are directed are referred to as ‘interactions’ (Whitehead 2009). Relationships that are undirected are referred to as ‘associations’.

2.1.2.3 Weighted Networks

Relationships are not always equal. For example, the relationship between a pair of close friends might be stronger than the relationship between a pair of acquaintances. Alternatively, the relationship between two locations that are far away might be weaker than the relationship between two locations that are closer. To reflect the relative importance of a given relationship, edges can be assigned weights (e.g. Figure 2.2c). Networks with weighted edges are called ‘weighted networks’ (Newman 2010).

2.1.2.4 Bipartite Networks

Some relationships are best described as categorical. For example, several individuals might exhibit the same behavioural trait. Alternatively, several individuals might have been observed at the same location. Data that can be classed into two categories can be represented as a bipartite network, with each category represented by a different type of node (e.g. Figure 2.2d) (Newman 2010). In a bipartite network, edges can only exist between different types of nodes.

2.1.2.5 Static Networks

A static network is a network that does not change in time. Although the data used to construct networks often does not represent static processes, most applications of network theory have traditionally collapsed dynamic data down into a static network to take advantage of the wide range of available static network analysis tools (Kim and Anderson 2012).

2.1.2.6 Temporal Networks

Temporal networks are networks that change in time (Holme and Saramäki 2012). Figure 2.3 provides an example of a temporal network and a corresponding static network. Notice that the static network suggests that all nodes are connected, whereas in fact this was not true during any of the time points.

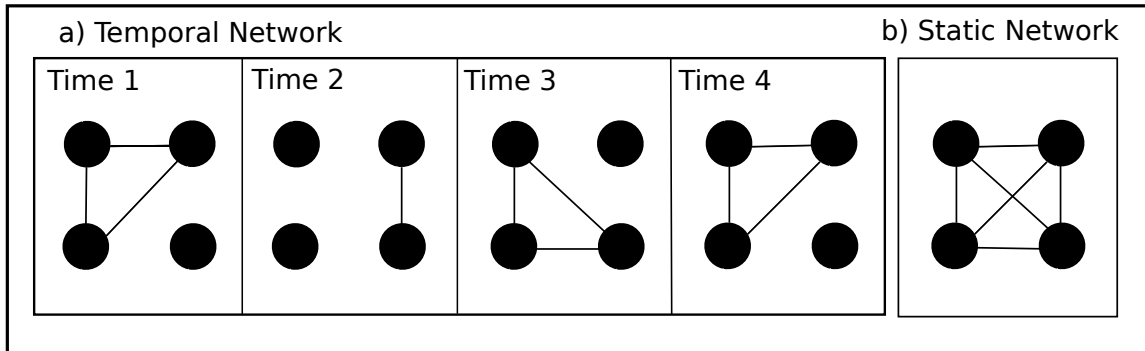


Figure 2.3: (a) A temporal network and (b) the corresponding unweighted static network.

The broad category of temporal networks can be broken down into two more specific network types (Blonder *et al.* 2012): (1) time-aggregated networks and (2) time-ordered networks. I explore both time-aggregated and time-ordered networks in more detail in subsequent sections.

2.1.3 Paths and Components

The level of connectivity can vary between networks; some networks have many edges, while others have only a few edges. For dealing with questions about connectivity, I introduce the notion of a path as sequence of nodes that are connected by consecutive edges (Newman 2010).

An undirected network with a path from every node to every other node is called a ‘connected’ network. A network that does not have a path from every node to every other node is ‘disconnected’. The disjoint networks within a larger disconnected network are called components (Newman 2010).

For directed networks, the notion of components can further be divided into two categories: (1) strong connectivity and (2) weak connectivity (Newman 2010). Strongly connected components consist of nodes with a path to and from every node in the component to every other node in the component. Weakly connected components consist of nodes with a path either to *or* from every node in the component to every other node in the component.

2.1.4 Motifs

The structure of networks based on real data is often heterogeneous across the network. Some areas might be really dense and others might be sparse. Within a network, it is sometimes possible to find recurring topologies. Such recurring isomorphic subgraphs are called ‘motifs’ (Newman 2010). A triangle (i.e. three connected nodes) is an example of one commonly-studied motif.

2.2 Mathematical Representations of a Network

Visualisations of a network are useful for developing an intuition about the system it represents. However, to do further analyses, it is useful to be able to represent a network using other mathematical objects. The following subsections introduce adjacency matrices, edge lists, and bipartite incidence matrices as three ways to represent networks mathematically.

2.2.1 Adjacency Matrices

For networks that are built on pair-wise relations, an interaction matrix is a natural way to represent a network mathematically. In mathematics, this matrix is referred to as an ‘adjacency matrix’. Other disciplines use different names - for example, behavioural ecologists often use the term ‘sociogram’ or ‘association matrix’ to describe a network and its associated adjacency matrix (Wey et al. 2008, Croft et al., 2008). For clarity, I use the term adjacency matrix throughout this report.

Suppose an undirected, unweighted network has n nodes (labelled $1, 2, \dots, n$). The associated adjacency matrix A is then an $n \times n$ matrix such that $A_{ij} = 1$ if there is an edge between nodes i and j for $i, j \in \{1, 2, \dots, n\}$ and $A_{ij} = 0$ otherwise (Newman 2010). An example of an an adjacency matrix is provided in Figure 2.4b.

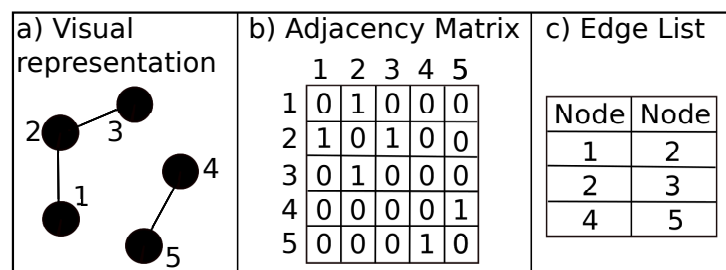


Figure 2.4: A network shown three ways: (a) visually, (b) as an adjacency matrix, and (c) as an edge list.

Notice that the main diagonal of an adjacency matrix reflects the relationship between a node and itself. Edges that link a node to itself are called ‘self-edges’.

Adjacency matrices for weighted networks can be constructed in an analogous way, placing edge weights in the matrix instead of a 1 or a 0 (Newman 2010). Additionally, the adjacency matrix for an undirected network is symmetric but this is not necessarily the case for a directed network (Newman 2010).

2.2.2 Edge Lists

Edge lists are an alternative to adjacency matrices for representing network structures (Newman 2010). An edge list is a list of all of the edges present in a network. Although edge lists are commonly used to store a network structure in a computer, adjacency matrices are more useful mathematically (Newman 2010). It is very easy to convert between an adjacency matrix and an edge list.

Figure 2.4c provides an example edge list for the undirected, unweighted network shown in Figure 2.4a. An edge list for a directed network would also account for direction, and an edge list for a weighted network would also track the edge weights.

2.2.3 Bipartite Incidence Matrices

Adjacency matrices and edge lists are effective ways of representing networks with one type of node. But what about networks with two types (i.e. bipartite networks)?

Typically, bipartite network structures are represented by a special type of adjacency matrix called an ‘incidence matrix’. Consider a bipartite network with n nodes of type 1 and m nodes of type 2. The corresponding incidence matrix B is then an $n \times m$ matrix, where $B_{ij} = 1$ if node i is connected to node j ($i \in \{1, 2, \dots, n\}, j \in \{1, 2, \dots, m\}$) and $B_{ij} = 0$ otherwise. Figure 2.5b provides an example incidence matrix for the bipartite network in Figure 2.5a.

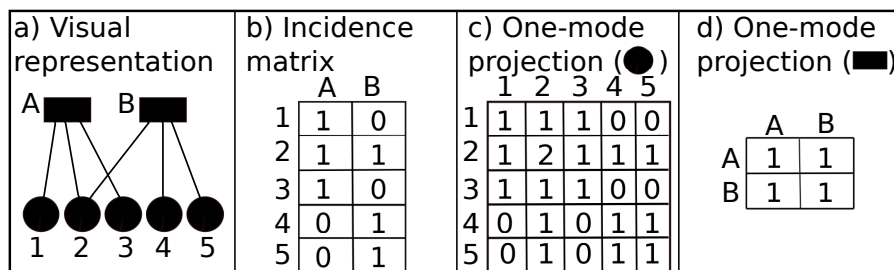


Figure 2.5: Several descriptions of the same bipartite network: (a) visual, (b) the incidence matrix, (c) a one-mode projection onto the circular nodes, and (d) a one-mode projection onto the rectangular nodes.

Relationships between nodes of the same type can be obtained from a bipartite network. All nodes of type 1 that are linked to the same node of type 2 are associated simply because they link to the same type 2 node. The same is true for all nodes of type 2 that are linked to the same type 1 node. These smaller networks that are formed by association (each with only one type of node) are called ‘one-mode projections’ of the bipartite network (Newman 2010).

The adjacency matrix of a one-mode projection of a bipartite network can be recovered by calculating BB' or $B'B$, depending on which mode is of interest (Newman 2010). Note that the diagonal entries of BB' or $B'B$ will always be non-zero, reflecting the fact that each node is inherently of the same type as itself. Figures 2.5c and 2.5d show adjacency matrices for one-mode projections of the bipartite network in Figure 2.5a.

2.2.4 Temporal Networks

There are several ways to maintain the temporal dynamics of a network in its mathematical representation. Perhaps the most obvious is to store the network as a series of adjacency matrices (i.e. one for each time-step). Alternatively, a temporal network can be represented as a bipartite network in which the two types of nodes are all possible edges and all time-steps, respectively.

Representation of a temporal network as either a series of adjacency matrices or a bipartite network is analogous to representing a static network with its adjacency matrix or its edge list. It is easy to convert from one representation to the other.

2.3 Static Network Centrality Measures

With even a moderate number of nodes and edges, networks can have very complicated structures. In these instances, descriptive measures become particularly useful for gaining insight into underlying network structures. Descriptive measures are often calculated for each node (or other structures, such as an edge) in a network, thereby allowing comparisons between nodes to help identify nodes that are somehow ‘central’. Descriptive diagnostics that try to measure the importance of network objects are called ‘centrality’ measures.

In the following section, I review two centrality measures for static networks: (1) degree centrality and (2) betweenness centrality. For brevity, I limit the discussion to the centrality measures that I use again in subsequent sections. For a detailed review, see Newman (2010).

2.3.1 Degree Centrality

One of the most basic of all centrality measures is degree (i.e. degree centrality) (Newman 2010). Although it is simple, degree centrality can be extremely useful for highlighting interesting properties in a network (Newman 2010).

The degree of each node in an unweighted network is simply the number of edges attached to it. Similarly, the degree of a weighted network is the sum of the edge weights attached to it (the conventional term for the degree of a weighted network is ‘strength’). More precisely, the degree or strength of an n -node network is

$$k_i = \sum_{j=1}^n A_{ij}, \quad (2.1)$$

where k_i is the degree of node i and A_{ij} are the elements of the adjacency matrix ($i, j \in \{1, 2, \dots, n\}$) (Newman 2010).

I provide an example of degree centrality results for an unweighted, undirected network in Figure 2.6. The degree centrality results in Figure 2.6 have been normalised by $(n - 1)$, which is the maximum possible degree for a node in a network without any self-edges.

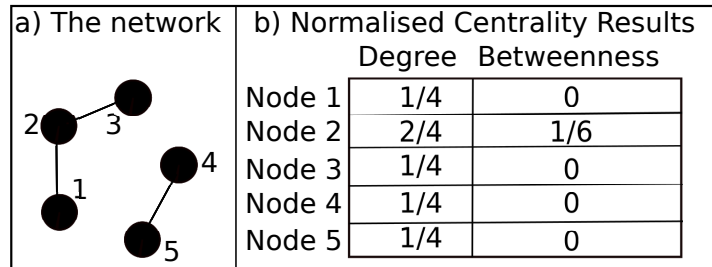


Figure 2.6: (a) A network and (b) the associated normalised degree and betweenness centrality results.

In the case of a directed network, degree can be further divided into two categories: (1) in-degree and (2) out-degree (Newman 2010). In-degree is the number of directed edges coming into a node, and out-degree is the number of directed edges going out.

2.3.2 Betweenness Centrality

Betweenness centrality is another centrality measure that is often useful for identifying important nodes in a network. The betweenness centrality of a node is a relative count of the number of times that the node lies on a shortest path between two other nodes

in the network. More specifically, ‘betweenness centrality’ of a node in an unweighted n -node network can be defined as

$$x_i = \sum_{st} \frac{n_{st}^i}{g_{st}}, \quad (2.2)$$

where x_i is the betweenness centrality of the i th node, s and t are two different nodes in the network ($s, t \in \{1, 2, \dots, n\}$, $s, t \neq i$), n_{st}^i is the number of shortest paths from s to t that pass through i , and g_{st} is the total number of shortest paths from s to t (Newman 2010). By convention, in order to accommodate infinite distances (i.e. unconnected components), $\frac{n_{st}^i}{g_{st}} = 0$ if both n_{st}^i and g_{st} are 0.

An example of betweenness centrality results for an unweighted, undirected network is provided in Figure 2.6. The betweenness centrality results in Figure 2.6 have been normalised by $\frac{1}{2}(n-1)(n-2)$ (Rubinov and Sporns 2010), which is the maximum possible betweenness for a node in an undirected network with no self-edges (i.e. it is the betweenness of the central node in a star graph (Newman 2010)).

Betweenness centrality for a directed network is calculated in an analogous way, provided that shortest paths respect the direction of the edges (Newman 2010). Betweenness centrality for a weighted network is also calculated in an analogous way, provided that the edge weights are accounted for when calculating the shortest paths (Newman 2010).

2.4 Constructing Animal Behaviour Networks

Like all models, a network is a simplification of the system it represents. To investigate meaningful questions about a system, it is extremely important to construct the corresponding network in a meaningful way (James *et al.* 2009). A network analysis is only as good as the network itself!

In subsequent sections of this thesis I focus on two specific data sets to illustrate the usefulness of temporal networks - one is a social network and the other is a movement network. Hence, the remainder of this section is focused on constructing animal social networks and movement networks, respectively.

2.4.1 Social Networks

In both human and animal social network analysis, the goal of a network model is to capture meaningful relationships between individuals. Relative to studies with human subjects, animal behaviour studies have an additional level of uncertainty

since researchers can not directly ask their subjects about the motivation for certain behaviours (Lusseau *et al.* 2008).

Animal social behaviour can typically be divided into two categories: (1) interactions and (2) associations (Whitehead and Dufault, 1999). Interactions occur when there is direct contact between two individuals (e.g. grooming, fighting, etc.). Associations occur when two individuals are members of some category by association (e.g. both in the same herd, same location, etc.). Depending on what is available and the research question of interest, networks can be constructed from either interaction data or association data (Croft *et al.* 2008).

Inferring a network from interaction data is straightforward - two individuals are connected in the network if they are interacting. Constructing a network from association data, however, is more difficult (Croft *et al.* 2008). How can one tell if two individuals are ‘associating’?

Perhaps the easiest way to define an association is through spatial proximity (Croft *et al.* 2008). If two individuals are within a pre-determined distance from each other, they are considered to be associating. This approach is called the ‘gambit-of-the-group’, and is common in behavioural ecology (Croft *et al.* 2008).

2.4.1.1 Association Indices

Once the associations in a network have been defined, animal behaviour data has the remaining complication that the entire network connectivity is not always known for each time-step (Croft *et al.* 2008). To account for missing data, association indices are typically used to determine edge weights within a network (Croft *et al.* 2008). One commonly used association index is the Simple Ratio Index (SRI)

$$SRI = \frac{X}{X + Y_{AB} + Y_A + Y_B}, \quad (2.3)$$

where X is the number of times A and B were observed in the same group (i.e. the association strength for A and B), Y_{AB} is the number of times both individuals A and B were observed but in separate groups, Y_A is the number of times A was observed without B, and Y_B is the number of times B was observed without A (Croft *et al.* 2008). Note that the SRI is equivalent to the association strength for networks in which the entire network structure is observed in each time-step.

Figure 2.7 provides an example of how a social network can be constructed from gambit-of-the-group data and the SRI.

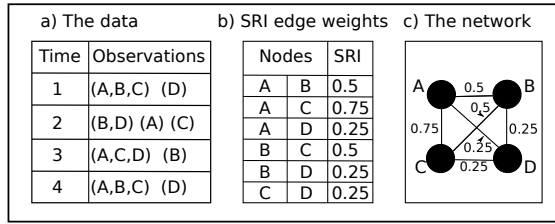


Figure 2.7: An example of how to build a network from ‘gambit-of-the-group’ data: (a) raw data (group members are shown in brackets), (b) SRI index edge weights, and (c) the resulting network.

2.4.2 Movement Networks

As discussed above, networks are useful for asking questions about how individuals interact or associate with each other. One can also ask about other relational questions in behavioural ecology. For example, how does an individual interact with its environment? Can one draw any conclusions about habitat usage or preferences?

Movement networks are one approach for using network theory to help answer such questions (Jacoby *et al.* 2012a). A movement network can be constructed by designating spatial locations as nodes, and placing an edge between nodes if an individual has moved between the corresponding locations (Jacoby *et al.* 2012a). Telemetry data (i.e. presence-absence location data obtained via radio-transmitters, GPS devices, etc.) is particularly well suited for analysis as a movement network (Jacoby *et al.* 2012a).

Edge weights in a static movement network can be chosen to reflect how often an individual has moved between two nodes, and they can be based on either absolute interaction data (AID) or relative interaction data (RID; i.e. normalised AID) (Jacoby *et al.* 2012a). However, as we will see in subsequent sections of this thesis, there is no need to assign edge weights in a time-ordered representation of a movement network. This is a major advantage of a temporal networks framework.

Figure 2.8 provides an example of a movement network based on telemetry data.

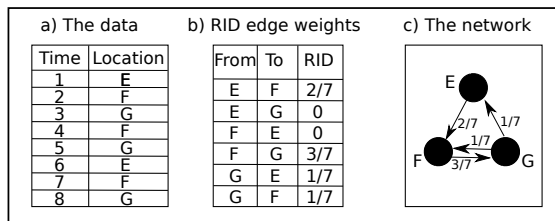


Figure 2.8: An example of how to build a network from telemetry data: (a) raw data, (b) RID edge weights, and (c) the resulting network.

Chapter 3

Background - Catshark Data

As I mentioned previously, I use both social and movement data for small-spotted catsharks (*Scyliorhinus canicula*) in subsequent sections of this thesis to demonstrate the applicability of temporal networks for animal-behaviour research. Although the methods presented in this thesis are easily transferable to data on other species, it is important to have some background on small-spotted catsharks and the respective data sets in order to help understand the results.

3.1 Catshark Biology

Small-spotted catsharks (*Scyliorhinus canicula*) are a small, bottom-dwelling species of shark (Jacoby *et al.* 2010). Found throughout both the Mediterranean Sea and the Northeast Atlantic Ocean (Compagno *et al.* 2005), small-spotted catsharks are particularly common in the English Channel (Jacoby 2012). They grow to a maximum of length of approximately one meter (Compagno *et al.* 2005), and both males and females reach sexual maturity at approximately 570 cm in length (Ford 1921).

Small-spotted catsharks demonstrate sex-specific aggregation behaviour (Sims *et al.* 2001, Sims 2005, Wearmouth and Sims 2010). Specifically, wild female small-spotted catsharks tend to aggregate in shallow-water caves with other females (Sims *et al.* 2001). There is little evidence to suggest that male-male interactions are as prevalent, although male-male interactions are plausible (Jacoby *et al.* 2012a) given that wild male home ranges sometimes overlap (Sims *et al.* 2001). Previous studies with acoustic telemetry have shown that wild male small-spotted catsharks tend to occupy deeper water during the day and warmer shallow waters at night (Sims *et al.* 2006).

3.2 Data Set 1: Juvenile Catshark Social Networks

The small-spotted catshark social network data presented in this report was collected by David Jacoby of the University of Exeter and the Marine Biological Association of the UK. He conducted experiments on juvenile small-spotted catsharks (all individuals were less than four months old) under captive conditions in the Marine Biological Association laboratory in Plymouth, UK from September to December 2010. The purpose of the experiments was to investigate social preferences between individual juvenile small-spotted catsharks based on kinship and familiarity (Jacoby 2012).

The experiments consisted of four different treatment groups, which were each replicated four times to yield a total of sixteen experiments. The four treatment groups were (1) kin and familiar (KF), (2) not kin and familiar (NKF), (3) kin and not familiar (KNF), and (4) not kin and not familiar (NKNF). Familiarity was imposed by co-habiting individuals in the same tank for 10 days prior to the experiment. Given the potential for multiple paternity (Griffiths *et al.* 2012), kinship was defined as maternal kinship (i.e. having the same mother).

Each experiment contained 12 individuals. The individuals were placed together in a tank and monitored four times a day (8:30, 11:30, 14:30, and 17:30) for five consecutive days. Individuals were considered to be interacting if they were stationary on the bottom of the tank and within one body-length (i.e. approximately 10 cm) of each other (i.e. this is ‘gambit-of-the-group’ social data).

To allow individual identification, each individual was injected with a unique color/shape combination of florescent dye just below the skin (see Figure 3.1). The experiments were conducted in a room with no windows; 12 hour day/night cycles were maintained artificially with lights on from 7:00 to 19:00 and off otherwise.

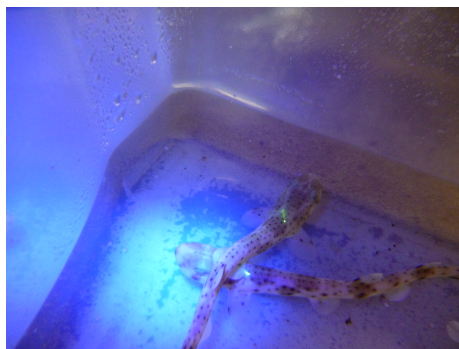


Figure 3.1: Two juvenile small-spotted catsharks with unique florescent ID tags. Photo credit: David Jacoby.

3.3 Data Set 2: Catshark Movement Networks

The small-spotted catshark movement network data presented in this report was provided by David Jacoby and David Sims of the Marine Biological Association of the UK. They collected the data using biotelemetry methods. Specifically, six static acoustic telemetry devices are located in relatively deep-waters at Whitsand Bay, Cornwall, UK, and are continually monitoring the presence of tagged small-spotted catsharks (Figure 3.2).

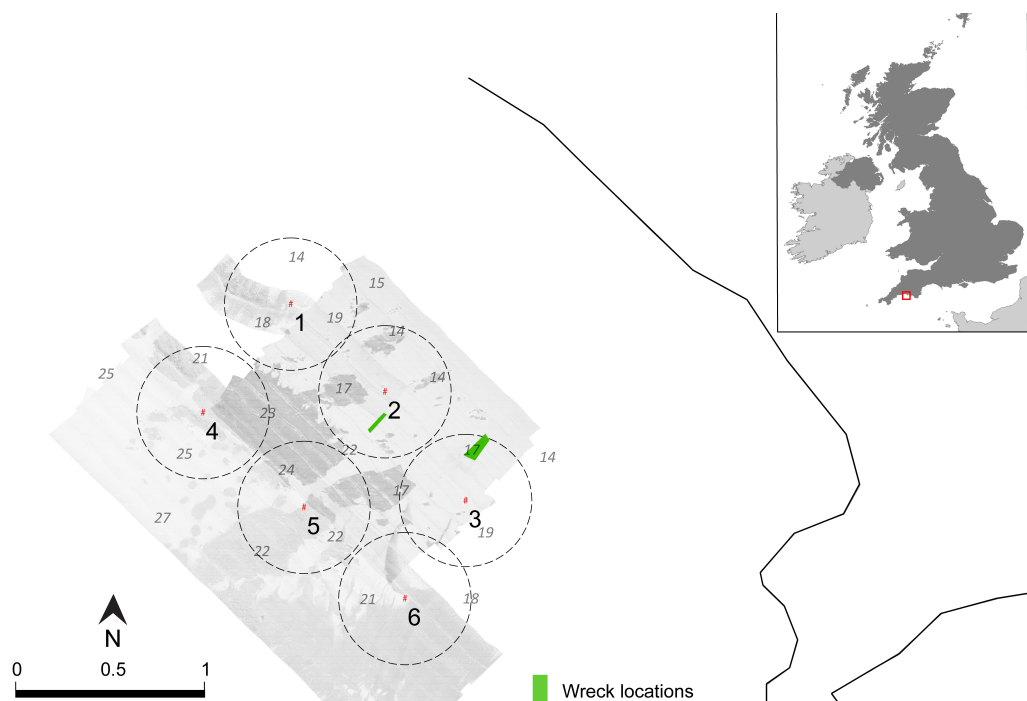


Figure 3.2: Layout diagram of the static acoustic telemetry array in Whitsand Bay, Cornwall, UK. Red dots represent an individual telemetry device. Dashed lines represent the approximate detection range of each telemetry device. Green areas identify shipwrecks located at the bottom of the ocean. The red rectangle on the map inset in the top right corner identifies the geographic location of Whitsand Bay relative to the rest of the UK. Reproduced with permission from Jacoby *et al.* (2012a).

Each telemetry device has a detection radius of approximately 350 m (manufacture specifications; confirmed up to 300 m (Jacoby 2012)); hence, the telemetry devices are placed approximately 700 m apart on the ocean floor. Data from the telemetry devices are uploaded from a boat every few months, and they consist of a series of corresponding time-stamps and individual shark identification numbers.

The data provided spans a period of approximately two years, from 27 January 2010 to 19 February 2012. During this time, 44 individuals (29 females and 15 males)

were tagged and released in the study area. Of these, 24 individuals (14 females and 10 males) moved between telemetry device locations at least once within the span of one hour.

I constructed movement networks for each catshark as suggested in Jacoby *et al.* (2012a), with nodes as spatial locations and an edge indicating that the catshark has moved between the associated locations. To investigate direct movements, movement networks included only those movements that occurred within the span of one hour. Hence, I constructed 24 movement networks (one for each individual that moved between telemetry device locations at least once within the span of one hour) for analysis in this thesis.

All individuals were not released into the study area at the same time; rather, additional individuals were added to the study as funding became available. Also, the study area is not a popular spot for commercial fishing since the ocean floor is relatively rocky and it contains two shipwrecks (Jacoby 2012).

Figure 3.3 shows a picture of an adult small-spotted catshark.

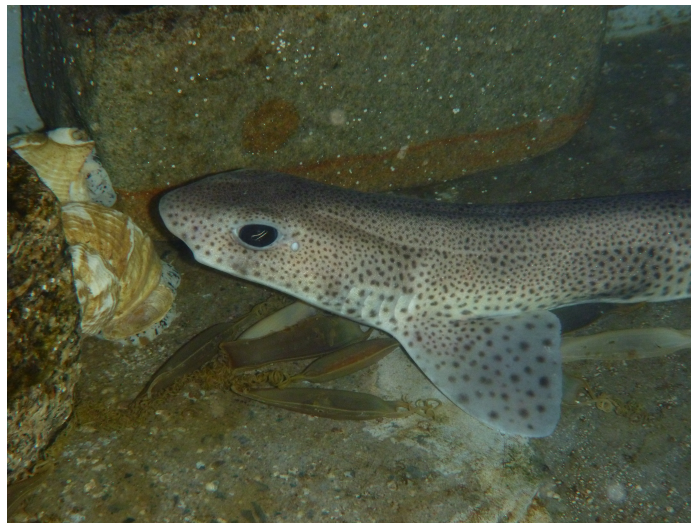


Figure 3.3: An adult small-spotted catshark. Photo credit: David Jacoby.

Chapter 4

Time-Aggregated Networks

Returning to our original goal, recall that the main purpose of this thesis is to introduce temporal networks in the context of behavioural ecology. I discuss two categories of temporal networks: (1) time-aggregated networks and (2) time-ordered networks. Time-aggregated networks are a direct extension of static networks and are therefore a natural place to start. I examine time-ordered networks in Chapter 5.

This chapter presents an overview of time-aggregated networks and introduces a new way of choosing the aggregation time-window based on recurring temporal motifs. As an illustrative example, I subsequently use time-aggregated networks to explore juvenile small-spotted catshark social networks.

4.1 What is a Time-Aggregated Network?

A time-aggregated network is a static network that is associated with a specific window of time (Blonder *et al.* 2012). Since time-aggregated networks are a type of static network, they can be analysed with the standard tools (Blonder *et al.* 2012).

Figure 4.1 provides two examples of time-aggregated networks.

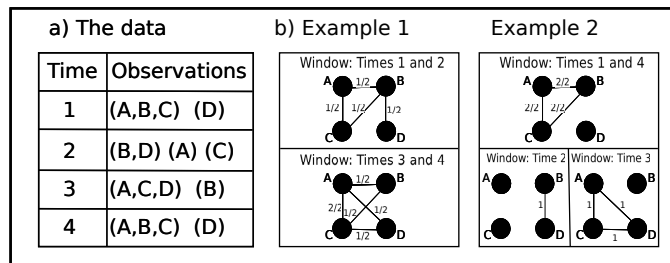


Figure 4.1: (a) ‘Gambit-of-the-group’ network data (group members are shown in brackets) and (b) two examples of time-aggregated networks (with different aggregation time-windows) constructed from (a).

4.2 Choosing an Aggregation Time-Window

Different choices for aggregation time-windows can result in different time-aggregated networks (see Figure 4.1 for an example). Hence, an appropriate choice of time window for data aggregation is of utmost importance when using time-aggregated networks (Clauset and Eagle 2007, Blonder and Dornhaus 2011, Psorakis *et al.* 2012, Hoffmann *et al.* 2012).

Empirical studies using time-aggregated networks in behavioural ecology typically choose the time window based on *a priori* hypotheses. For example, a recent analysis by de Silva *et al.* (2011) on social networks in female Asian elephants divided the data by season (wet, dry, or transitional). Similarly, investigation of flower-visitation networks by Olesen *et al.* (2008) and Olesen *et al.* (2011) used daily and annual aggregation time-windows, respectively. Jacoby *et al.* (2012a) suggested filtering temporal biotelemetry data prior to making the associated movement networks in order to tease out temporal differences in network structures.

An alternative approach is to choose aggregation time-windows based on time-scales that appear to be important in the data. In the next section, I introduce ‘recurring temporal motifs’ and suggest that they might serve as excellent indicators for identifying appropriate time-scales (and therefore aggregation time-windows) for time-aggregated networks.

4.3 Temporal Motifs as Time-Scale Indicators

4.3.1 What are Temporal Motifs?

Recall that motifs, in the static sense, are subgraphs with re-occurring topologies across the network (Newman 2010). We can easily generalise this concept to the temporal dimension - temporal motifs are simply subgraphs with topologies that re-occur in time (Holme and Saramäki 2012).

Temporal motifs can be separated into two general categories: (1) time-respecting temporal motifs and (2) recurring temporal motifs. ‘Time-respecting’ temporal motifs are repeated contact patterns between nodes in adjacent time-steps (e.g. A grooms B, and then B grooms C, etc.) (Kovanen *et al.* 2011, Holme and Saramäki 2012). ‘Recurring’ temporal motifs are subgraphs with either the same (or similar) topologies that occur at multiple (and not necessarily consecutive) points in time (Holme and Saramäki 2012). Figure 4.2 provides an example of a temporal network with both time-respecting and recurring temporal motifs.

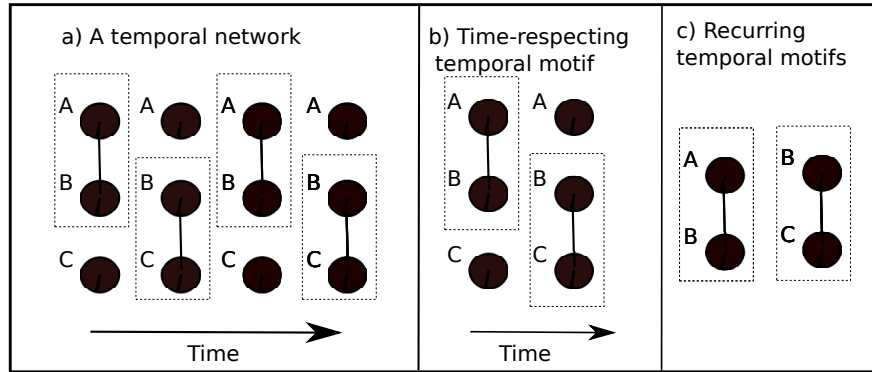


Figure 4.2: (a) A temporal network with both time-respecting temporal motifs and recurring temporal motifs. (b) The corresponding time-respecting temporal motif. (c) The corresponding recurring temporal motifs.

Within the networks community, there has been notably more work done on time-respecting motifs than recurring temporal motifs (Holme and Saramäki 2012). Nonetheless, in the following subsections, I demonstrate how recurring temporal motifs can be useful for identifying time-scales in animal-behaviour networks and propose a method for how to find them.

4.3.2 Recurring Temporal Motifs and Biological Relevance

Before delving further into finding recurring temporal motifs, let's examine what recurring temporal motifs represent and how they might be relevant to animal-behaviour networks.

Recall that a network is a modelling framework for relationships. In animal-behaviour social networks, an edge represents some sort of social relationship between two individuals (e.g. aggression, co-occurrence in a group, etc.). In animal movement networks, an edge represents relationships between two spatial locations when an individual moves between them. Subgraphs within a network represent relationships between a specific group of nodes.

Intuitively, the relative importance of relationships between a group of nodes is stronger if it is repeated in time. Recurring temporal motifs represent relationships between a group of nodes that reoccur in multiple time-steps within a temporal network. Hence, recurring temporal motifs represent relationships between groups of nodes within a larger network that are more likely to be meaningful.

By both identifying recurring temporal motifs and tracking when they occur, one can gain insight into time-scales that are important to a network.

4.3.3 Finding Recurring Temporal Motifs

There are presumably many ways that can be developed to find recurring temporal motifs. However, as previously mentioned, this is an area that has yet to be addressed thoroughly in the research literature (Holme and Saramäki 2012). The following is one viable method for finding recurring temporal motifs:

1. Step 1: Identify potential recurring temporal motifs.
 - (a) List all static motifs that occur at least once. (Note: For ‘gambit-of-the-group’ data, these are easily identified as the individual groups observed in each time-step and all subgraphs within.)
 - (b) If desired, shrink the list by grouping motifs that are sufficiently similar.
2. Step 2: Identify temporal communities for each potential recurring temporal motif.

I address each of the above steps in more detail below.

Step 1: Identifying potential recurring temporal motifs.

1a) List all static motifs that occur at least once.

Recall that, by definition, recurring temporal motifs are motifs that occur in more than one time-step. Hence, an upper bound on the number of potentially recurring temporal motifs is the total number of static motifs that occur in any of the individual time-steps.

Figure 4.3 provides an example of two motifs that occur in made-up ‘gambit-of-the-group’ data. Note that there are actually four static motifs that occur at least once in the data provided in Figure 4.3; however, for simplicity I present only those that occur at least twice.

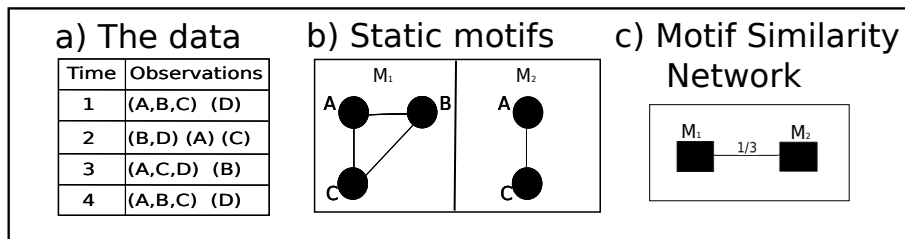


Figure 4.3: (a) An example of ‘gambit-of-the-group’ data with (b) two static motifs and (c) the corresponding motif similarity network.

The list of potential recurring temporal motifs can be minimised by relaxing the similarity requirements for two motifs to be considered the same. I explore this choice of a similarity requirement more in the remainder of this subsection.

1b) Shrink the list by grouping similar motifs.

It is tempting to assume that a recurring temporal motif should only consist of time-steps with identical motif structures. However, due to both sampling artefacts and natural variation, biological data is inherently noisy. As a result, two network structures could be slightly different and still represent the same underlying biological processes. For example, imagine a group of 1000 animals. If the group had only 999 animals, should one still consider it to be the same group?

The level of similarity between two network motifs can be calculated using an similarity function,

$$C(M_1, M_2) = \frac{|M_1 \cap M_2|}{|M_1 \cup M_2|}, \quad (4.1)$$

where M_1 the set of edges in one motif, M_2 is the set of edges in the other motif, and $C(M_1, M_2)$ is the corresponding motif similarity coefficient. Based on a pre-determined threshold, two motifs can be considered to be the same for the purposes of finding recurring temporal motifs if they are sufficiently similar. I suggest an edge-based approach (rather than a node-based approach) to allow the motif similarity to be based on the proportion of relationships (rather than the proportion of nodes involved in the relationships).

The task of comparing all possible combinations of network motifs to check their similarity coefficients may seem daunting for networks with multiple motifs. Fortunately, we can simplify the task by constructing a motif similarity network of potential recurring temporal motifs. In this new network, each node is a different potential motif and the edge between them is weighted with the motif similarity coefficient. Because we already know that each motif is exactly the same as itself, there is no need to include self-edges. As an illustrative example, Figure 4.3c presents the motif similarity network associated with two motifs identified in Figure 4.3b.

We can simplify the motif similarity network by removing all edges below a similarity threshold, which yields an undirected, unweighted network (recall that this is the simplest type of network). Different similarity thresholds will yield different networks; I discuss choosing an motif similarity threshold in more detail at the end of this subsection. Nonetheless, with our simplified motif similarity network in hand,

our task to find groups of motifs that are all sufficiently correlated with each other is reduced to finding the maximal complete subgraphs (called ‘cliques’) within the motif similarity network.

There are several ways to find the maximal complete subgraphs in a network. One way is to first identify all of the possible subgraphs in the network by listing all of the nodes that are connected by at least one edge and subsequently comparing all pairwise combinations of nodes within each list to build maximal complete subgraphs. Alternatively, maximal complete subgraphs can be identified using the algorithm proposed by Palla *et al.* (2005) as the first step in their k -clique community detection algorithm¹. I provide pseudo-code for the Palla *et al.* (2005) maximal complete subgraph algorithm in Appendix A.

Once we have identified cliques of motifs, we can seek temporal re-occurrences in our temporal network. To minimise the number of potential temporal recurring motifs (recall that this is the goal of this step), we can use only the maximal motif in each motif clique and apply the motif similarity threshold again in the next step.

Choosing a motif similarity threshold

Keeping in mind the implications of group size on our choice of a biologically meaningful motif similarity requirement level, there are many ways to determine the level of similarity that is appropriate for grouping motifs. Most simply, it can be based on professional judgement (i.e. given one’s prior experience with the research question and system of interest). Alternatively, it can be dictated by the data and based on the distribution of motif similarity coefficients. Third, the level of similarity required could be chosen proportionally to the total possible number of edges in the motif.

As an aside, a statistical approach for determining the appropriate motif similarity requirement level might be desirable. At first glance, a standard test for comparing two matrices (e.g. the Mantel Test (Croft *et al.* 2008)) seems appropriate for determining how different two adjacency matrices can be before the difference becomes statistically significant. However, a closer look reveals that our choice to focus on motifs requires that one of our networks for comparison must be a complete graph (and therefore the associated adjacency matrix has all non-zero entries except for on the main diagonal). This makes it difficult to meaningfully apply statistical methods such as the Mantel Test that are based on random permutations of rows and/or columns.

¹A k -clique is a maximal subset of nodes such that each node is at most a distance of k away from any other node in the k -clique (Newman 2010). We do not use the definition of a k -clique in this thesis, but retain the name for the k -clique community detection algorithm (Palla *et al.* 2005).

Attempting to develop a statistically-robust way to determine an appropriate motif similarity requirement is left for future work.

Step 2: Identify temporal communities for each motif.

Once we have compiled the list of potential recurring temporal motifs, the task remains to identify which ones occur multiple times in the temporal network (and, if so, the time-steps in which they occur). Specifically, what is the largest subset of time-steps containing each temporal motif?

As discussed in step 1b, our list of potential temporal recurring motifs has been trimmed down such that it now contains only the largest motifs within each clique of possible motifs for the network. I now introduce another similarity function,

$$C_M(t_1, t_2) = \frac{|M(t_1) \cap M(t_2)|}{|M|}, \quad (4.2)$$

where $C_M(t_1, t_2)$ is the time-step similarity coefficient for the motif M at time-steps t_1 and t_2 , the set $M(t_1)$ describes the edges present in the motif M at time-step t_1 , the set $M(t_2)$ describes the edges present in the motif M time-step t_2 , and M is the set of edges present in the complete motif M (i.e. it is the maximum number of edges that could exist between nodes in $M(t_1)$ and $M(t_2)$, excluding self edges).

We can now build yet another similarity network for each maximal motif M . This time, nodes are time-steps and edges are weighted with the time-step similarity coefficient C_M . More specifically, for each maximal motif M , this time-step similarity network is an undirected network with n nodes, with each node representing a time (i.e. t_1, t_2, \dots, t_n). There is an edge between nodes t_i and t_j if $C_M(t_i, t_j) > 0$ ($i, j \in \{1, 2, \dots, n\}$).

I provide an example of a time-step similarity network in Figure 4.4.

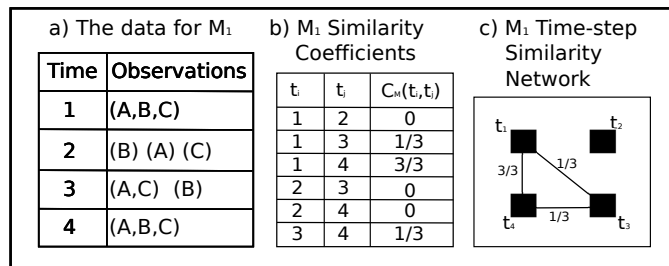


Figure 4.4: (a) The data for motif M_1 (recall Figure 4.3), (b) the corresponding time-step similarity coefficients, and (c) the time-step similarity network.

As with the motif similarity network, we can further simplify the time-step similarity network to an unweighted, undirected network by removing all edges below the motif similarity threshold. By keeping all edges greater than or equal to the motif similarity threshold, we allow motifs from the same motif clique to be represented in the time-step similarity network.

In a similar manner to which we analyse the motif similarity network, our task of finding the largest subset of time-steps containing each temporal motif is now simplified to finding the maximal complete subgraphs (i.e. cliques) within the time-step similarity network. As before, we can use any method available to find the maximal complete subgraphs (e.g. we can use the method of Palla *et al.* (2005) - see Appendix A). For the remainder of this report, I refer to these temporal cliques as ‘temporal communities’. I refer to the maximal motifs associated with each temporal community as ‘recurring temporal motifs’.

4.3.4 Seek Relevant Time-scales

Once we have identified the temporal communities and their associated recurring temporal motifs, we can proceed to identify relevant time-scales in the results. Given that our goal is to find relevant time-scales in the network, it is useful to create a list of unique temporal communities.

Each unique temporal community has one or more recurring temporal motifs associated with it. A temporal community with multiple recurring temporal motifs represents a time-scale that occurs more frequently in the temporal network, and in this sense it can be viewed as ‘stronger’. By examining the strength of the temporal communities for motifs of different sizes, one can explore the variety in time-scales that might be relevant to a network.

4.4 Example: Juvenile Catshark Social Networks

To better illustrate how time-aggregated networks can be used in animal-behaviour research, it is useful to provide an example using real data. In the remainder of this chapter, I investigate the temporal dynamics in juvenile small-spotted catshark social networks (see Section 3.2 for additional details on the data).

As mentioned previously, the juvenile small-spotted catshark social network data presented in this report was originally collected to test the effects of familiarity and kinship on grouping behaviours. A static network analysis by Jacoby *et al.* (2012b) showed that the strength of social attraction (as measured by the mean dyadic simple ratio index; recall Section 2.4.1.1) was significantly higher in treatments containing familiar individuals. In this section, I build on the findings of that static analysis and use both recurring temporal motifs and time-aggregated networks to investigate the following two questions:

1. When are social bonds between individuals particularly strong?
2. Does either familiarity or kinship play a role in the timing of social interactions?

Using the methods outlined in the previous sections of this chapter, I first use recurring temporal motifs to help identify time-scales of interest. This provides insight into our first question regarding the timing of strong social bonds, as recurring temporal motifs in a social network represent bonds that have persisted in time. I subsequently use the time-scales observed in the temporal motifs to choose aggregation time-windows and use time-aggregated networks to investigate the potential roles of familiarity and kinship on the timing of social interactions.

4.4.1 When are social bonds particularly strong?

As mentioned above, recurring temporal motifs in a social network represent relationships that have persisted in time. Hence, they are well suited for investigating questions about timing and relationship strength.

Identifying Temporal Motifs and their Temporal Communities

In order to investigate time-scales in the juvenile catshark social networks, I start by identifying temporal motifs and their associated temporal communities for each of the data sets. For simplicity, and in light of the relatively small group sizes, I

use a similarity threshold of 1 (i.e. exact similarity; each recurring temporal motif represents one network configuration only).

I provide a complete set of results for all of the datasets in Appendix B. For illustrative purposes, here I present the results for just one data set. Figure 4.5 shows the results for the NKF4 data set (i.e. not kin, familiar, replicate number 4).

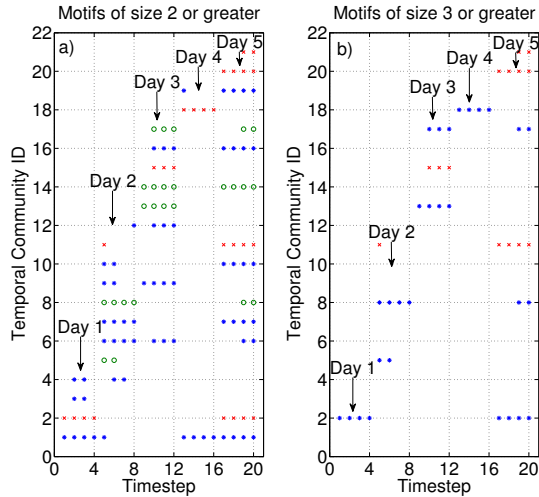


Figure 4.5: Temporal communities for recurring temporal motifs in the NKF4 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

As is shown in Figure 4.5, I identified 21 temporal communities for the NKF4 dataset. Figure 4.5a shows the results for all motifs (i.e. motifs of size two or larger). Figure 4.5b shows the results for motifs of size three or larger (i.e. with three or more individuals in a group).

In Figure 4.5a, we see that approximately half of the temporal communities have only one motif (represented by the blue asterisk). Five temporal communities have two motifs (represented by the green open circles). And the remaining temporal communities have three or more motifs. In Figure 4.5b, we see that approximately half of the temporal communities contain motifs of size 3 or larger.

The temporal communities in Figure 4.5 show a daily trend, with motifs often recurring on the same day. A similar analysis of the other 15 data sets shows variable results, with many but not all of the datasets showing daily trends (Appendix B).

Interpreting the Results

The daily pattern observed in some of the juvenile catshark social networks provides a clue into time-scales that might be important. Perhaps juvenile catshark socializing occurs at night - a feasible hypothesis, given that wild adult male small-spotted catsharks are more active at night (Sims *et al.* 2006). However, recall from the experimental design that sampling occurred four times a day at three-hour intervals between 8:30 and 17:30. Hence, the time period between samples on successive days was notably longer than the time period between samples on the same day (i.e. 15 hours overnight between samples on successive days versus 3 hours between samples on the same day). The observed daily patterns might simply be a function of the increased available time for re-assortment.

Given that there was substantially more time for individuals to re-assort between samples on different days than on the same day, it is difficult to determine if the observed daily trends are biologically meaningful or simply a product of the experimental design. A more rigorous investigation will require additional experiments. For example, a similar experimental design with additional samplings at night would be suitable for assessing the biological relevance of the observed daily trends.

Nonetheless, regardless of the cause behind the observed daily trends, it is interesting that the daily trends occurred in some of the networks but not in others. A visual inspection of the temporal communities identified for each data set (see Appendix B) suggests that networks showing relatively strong daily trends do not necessarily fit into the experimental categories of kinship and familiarity. Consequently, future investigations into the drivers of daily aggregation patterns would be warranted.

It is also interesting to note that several of the NKF4 temporal communities span multiple days, while still maintaining the daily trend. The other data sets in this study also contain ‘across-day’ temporal communities (Appendix B). These temporal communities, and the associated recurring temporal motifs, represent relationships that persisted in time even after taking into account the possible experimental bias for re-assortment time. Hence, a closer investigation of the attributes of individuals with these ‘across-day’ bonds may reveal further insight into the individual social preferences of juvenile small-spotted catsharks.

4.4.2 Familiarity, Kinship, and Timing

With our new insight into the daily aggregation patterns observed in some of the juvenile small-spotted catshark social networks, we can now proceed to investigate more specific time-related questions about familiarity and kinship using time-aggregated networks. Specifically, does either familiarity or kinship play a role in the timing of social interactions?

To investigate the effect of familiarity and kinship on the timing of social interactions, I constructed five time-aggregated networks for each data set with each aggregation time-window spanning one day. I calculated the mean dyadic simple ratio index (SRI) for each network as an indicator of social bond strength within the network. I subsequently averaged the results for familiar and not familiar treatment groups (Figure 4.6a) or kin and not kin treatment groups (Figure 4.6b). Similar results for each of the four individual treatment groups (i.e. kin and familiar, kin and not familiar, not kin and familiar, and not kin and not familiar) are provided in Appendix C.

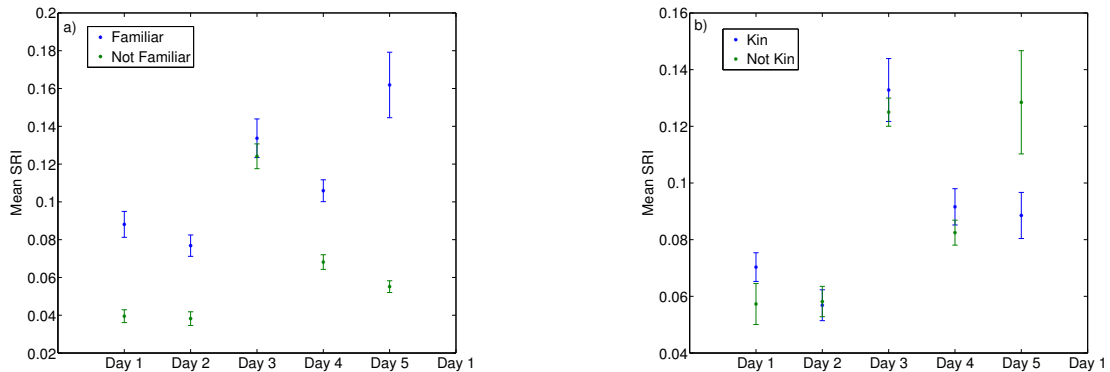


Figure 4.6: Mean simple ratio index (SRI) values for daily time-aggregated juvenile small-spotted catshark networks for (a) familiar and not familiar, and (b) kin and not kin treatment groups. There were eight experiments in each of the familiar / not familiar and kin / not kin treatment groups. Error bars represent standard error.

In agreement with the previous static social network analysis findings (Jacoby *et al.* 2012b), the results in Figure 4.6a suggest that familiarity might play a role in the social preferences of juvenile small-spotted catsharks. Specifically, all daily mean SRI values are higher for the ‘familiar’ treatment groups than for ‘unfamiliar’ treatment groups (Figure 4.6). Moreover, the mean SRI for both ‘familiar’ and ‘unfamiliar’ treatment groups tended to increase over time. The upward trend is clear for the familiar treatment group, and less pronounced but still positive for the unfamiliar

treatment group. This upward trend in time provides additional evidence for the positive effect of familiarity on social bonds within juvenile small-spotted catshark social networks.

Given the similarity in daily mean SRI values between treatment groups, the results in Figure 4.6b do not provide evidence to suggest that kinship plays a role in social preferences.

4.4.3 Limitations and Future Work

Our above investigation using time-aggregated networks allowed us to explore the temporal aspects of juvenile small-spotted catshark social networks. However, our approach is not without its limitations. Below I address some of the limitations and identify additional areas for future work.

4.4.3.1 Gambit-of-the-Group Data

The juvenile small-spotted catshark social network data presented in this thesis was collected using a ‘gambit-of-the-group’ approach, where individuals were considered to be associating if they were stationary on the aquarium floor within one body length of each other. Although this is a standard approach in behavioural ecology, the distance threshold is arbitrary (although based on a best-guess) and therefore might not represent meaningful associations (James *et al.* 2009). An alternative approach is to record the location of each individual throughout the study and subsequently use *a posteriori* methods (see Haddadi *et al.* 2011) to find relevant spatial scales.

4.4.3.2 Discrete-Time Sampling

On a similar note, the small-spotted catshark social network data was collected as discrete-time samples. Given typical logistical and financial constraints, one is hard pressed to come up with an alternative realistic sampling methodology. Nonetheless, the discrete-time sampling procedure leaves open the potential for undetected events that might have important consequences for the social structure.

4.4.3.3 Time-Aggregation

Of course, a major limitation of time-aggregated networks is the potential to lose important temporal information during the aggregation process. In this chapter, I chose aggregation time-windows *a posteriori* to reflect time-scales that I observed in recurring temporal motifs. My *a posteriori* choice of an aggregation time-window

allowed me to choose aggregation time-windows consisting of time-steps that are more likely to represent a static state in the network than if I had chosen the aggregation time-window *a priori*. Nonetheless, the approach still required an aggregation of some non-static data.

Time-ordered networks (Chapter 5) represent an alternative modelling framework that does not require data aggregation. It would be interesting to explore the juvenile small-spotted catshark social data as a time-ordered network and compare the results with the corresponding results from the time-aggregated network approach. However, given the time-limitations associated with this project, this is left for future work.

4.4.3.4 SVD of the Bipartite Incidence Matrix

Recall that temporal networks can be viewed as a bipartite network, where the two types of nodes are time-steps and edges (see Section 2.2.4). Singular value decomposition (SVD) is a matrix factorisation that can be used to find low-rank approximations for a matrix (Martin and Porter 2012). Hence, it is natural to examine a singular value decomposition (SVD) of the bipartite incidence matrix for each data set.

A list of the squares of the top seven leading singular values for each of the juvenile small-spotted catshark bipartite incidence matrices is provided in Appendix D. Several of the bipartite incidence matrices have low-rank approximations, as indicated by the high level of variance accounted for by the first few leading singular values. Given the existence of low-rank approximations for some of the bipartite incidence matrices, an SVD might be a useful tool for gaining insight into temporal variation in the temporal network. However, this observation was made relatively late in the research process and was therefore not explored further.

Chapter 5

Time-Ordered Networks

As discussed in Chapter 4, time-aggregated networks are an improvement on a purely static approach for dynamic networks. However, the data amalgamation for time-aggregated networks can still result in the loss of important temporal information.

In this chapter, we move even further away from the traditional static approach as I turn our attention to a second type of temporal network: time-ordered networks. After a brief introduction, I explore select centrality measures for time-ordered networks. I subsequently use time-ordered networks to investigate movement networks for wild adult small-spotted catsharks.

5.1 What is a Time-Ordered Network?

A time-ordered network is a network that maintains the full dynamics (i.e. order, duration, and timing) of the data it represents (Blonder *et al.* 2012). As with time-aggregated networks, time-ordered networks start with a series of static networks (one per time-step). Instead of aggregating the static networks, however, time-ordered networks can be constructed by connecting the static networks with directed edges pointing forwards in time, resulting in a larger directed network (Blonder *et al.* 2012).

Figure 5.1 provides an example of a time-ordered network.

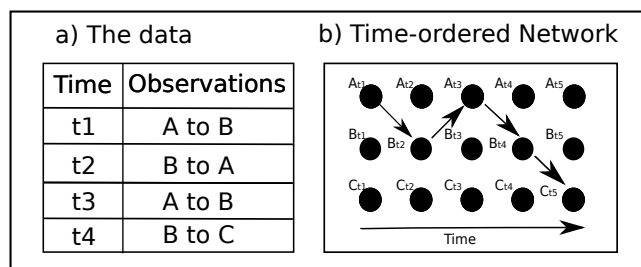


Figure 5.1: Example of a time-ordered network.

5.2 Terminology for Time-Ordered Networks

Unlike time-aggregated networks, most traditional static network analysis tools can not be directly used on time-ordered networks. Indeed, the generalisation of existing static concepts to time-ordered networks is an active area of research (see Holme and Saramäki (2012) for a review).

In Chapter 4 on time-aggregated networks, I inexplicitly introduced the concept of time-respecting paths in my discussion on time-respecting temporal motifs (see Section 4.3.1). In the following subsection, we discuss this more explicitly and subsequently introduce the concept of temporal components.

5.2.1 Time-Respecting Paths

Recall that a path in the static sense is a sequence of nodes that are connected by consecutive edges (Newman 2010). A time-respecting path is a sequence of nodes that are connected by edges in a non-decreasing order of time (Holme and Saramäki 2012).

The shortest path between two nodes is used in the definition of several static centrality measures (e.g. betweenness centrality) (Newman 2010). In time-ordered networks, the shortest time-respecting path between two nodes might vary depending on the starting point in time (Kim and Anderson 2012). Hence, as we will see later in this chapter, the temporal generalisation of a diagnostic using shortest paths must account for this potential variability in path length due to start time.

Figure 5.2 provides an example of the shortest time-respecting path lengths for a time-ordered network.

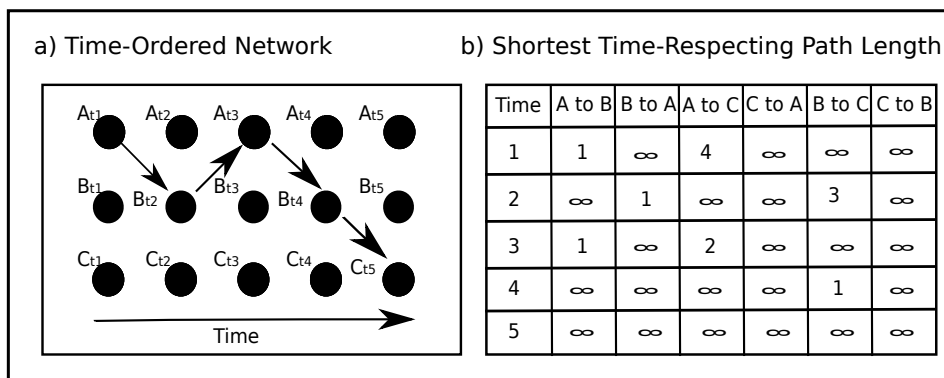


Figure 5.2: (a) A time-ordered network and (b) the corresponding shortest time-respecting path lengths.

5.2.2 Temporal Components

Just as multiple components can exist in static networks, time-ordered networks can also have multiple components in the time dimension. Recall that a component in a static network is a connected subgraph within a larger network (see Section 2.1.3). Weakly connected components are components of the undirected counterpart of a directed network. Strongly connected components are components that respect the direction of the edges.

Generalising the static definition to a time-ordered network, a weakly connected temporal component is a set of nodes that are weakly connected to all of the other nodes in the set (Nicosia *et al.* 2012). Likewise, a strongly connected temporal component is a set of nodes that are strongly connected to all of the other nodes in the set (Nicosia *et al.* 2012).

In Figure 5.2, the set of nodes $A_{t1}, B_{t2}, A_{t3}, B_{t4}, C_{t5}$ constitutes a weakly connected component. The example network in Figure 5.2 does not have a strongly connected component.

5.3 Centrality and Time-Ordered Networks

Previously we investigated two types of centrality measures for static networks: degree centrality and betweenness centrality (Section 2.3). In general, static centrality measures provide information about the relative importance of a network structure (such as a node or an edge) to the network. One can ask analogous questions about temporal networks.

In the following subsections, I examine temporal generalizations of degree centrality and betweenness centrality for time-ordered networks. I also introduce new temporal centrality measures (which I call ‘entrance’ and ‘exit’ centrality) to quantify how often each node participates in the start or end of a (weakly connected) temporal component.

5.3.1 Degree Centrality

Recall that degree centrality for a given node in a static network is defined as the number of edges attached to it (Newman 2010). A natural temporal generalization of this is the number of edges coming into and out of a node within a given time-frame of interest (Kim and Anderson 2012). Note that this is equivalent to the strength of a directed, weighted time-aggregated network, where weights in the time-aggregated

network represent the number of times each edge occurred. Hence, temporal degree for a node i is

$$k_i = \sum_{j=1}^n A_{ij}, \quad (5.1)$$

where k_i is the temporal degree, A_{ij} is the weighted adjacency matrix of the time-aggregated network for the time-frame of interest (with edges weighted by the number of times an edge occurred) and n is the number of nodes in the time-aggregated network ($i, j \in \{1, 2, \dots, n\}$). Accordingly, as for static directed networks, temporal degree can be further categorised into ‘in-degree’ and ‘out-degree’ by accounting for inbound and outbound edges separately.

5.3.2 Betweenness Centrality

Recall that the betweenness centrality of a node in a static network is a measure of how often the node lies on a shortest path between any two other nodes in the network (Newman 2010). A temporal generalisation can build on this static definition by requiring that all paths be time-respecting paths. As mentioned previously, in a time-ordered network one is faced with the added complexity that a shortest path between two nodes might be different for different starting points in time. Hence, a temporal version of betweenness centrality can be defined as follows:

$$x_i^T = \sum_{a \leq t < b} \sum_{uv} \frac{n_{uv}^i}{g_{uv}}, \quad (5.2)$$

where u and v are two different nodes in the network ($u, v \in \{1, 2, \dots, n\}$, $u, v \neq i$), a and b are the starting and ending time-steps t in the temporal network ($a \leq t \leq b$), n_{uv}^i is the number of shortest paths from u to v that pass through i , and g_{uv} is the total number of shortest paths from u to v (Kim and Anderson 2012). To accommodate infinite distances, we set $\frac{n_{uv}^i}{g_{uv}} = 0$ if both n_{uv}^i and g_{uv} are 0.

5.3.3 Entrance and Exit Centralities

Given the directed nature of time-ordered networks (i.e. forward in time), interesting questions can arise regarding the nodes that participate at either the beginning or the end of a given network. Are they the same nodes that are important in the full network, or do they play a special role in either kick-starting or concluding processes occurring on the network?

For time-ordered networks with multiple temporal components, these questions become even more tangible as each component has its own ‘beginning’ and ‘end’. To use the terminology for temporal components (Section 5.2.2), we are interested in nodes that participate in the first and last time-steps in each weakly connected temporal component.

To investigate questions surrounding nodes at the start and end of weakly connected temporal components, I developed two additional simple centrality measures: (1) ‘entrance centrality’ and (2) ‘exit centrality’. Entrance centrality is the fraction of times a given node participates at the beginning of a weakly connected temporal component within a time-ordered network. Similarly, exit centrality is the fraction of times a given node participates at the end. We can quantify the extent to which a node is ‘participating’ by its degree.

Specifically, I define the ‘entrance centrality’ for node i as

$$b_i = \sum_{c=1}^C \frac{k_{i(\text{out})}^c}{K_{\text{out}}} \quad (5.3)$$

where C is the total number of weakly connected temporal components, $k_{i(\text{out})}^c$ is the out-degree of node i in the first time-step of component c , and K_{out} is the sum of the out-degrees of all nodes in the network in the first time-step of component c .

Similarly, I define the ‘exit centrality’ for node i as

$$f_i = \sum_{c=1}^C \frac{k_{i(\text{in})}^c}{K_{\text{in}}} \quad (5.4)$$

where C is the total number of weakly connected temporal components, $k_{i(\text{in})}^c$ is the in-degree of node i in the first time-step of component c , and K_{in} is the sum of the in-degrees of all nodes in the network in the first time-step of component c .

If the first start and/or final end time of a time-ordered network is artificial in any sense (i.e. the start/end of the data collection might not necessarily reflect the start/end of a natural process), entrance and exit centralities can be adapted by omitting the first and/or last temporal components, respectively.

5.4 Example: Catshark Movement Networks

As before with the time-aggregated networks, I demonstrate the applicability of time-ordered networks with real data. In this section, I use time-ordered networks to investigate wild adult small-spotted catshark movement networks (see Section 3.3 for details about the data). Recall that each movement network consists of six nodes (representing physical locations in space), and an edge represents the movement of one catshark between locations. I label each node as $L1, L2, \dots, L6$ to match the numbering of the static acoustic array locations indicated in Figure 3.2.

To illustrate the previously-discussed centrality measures for time-ordered networks, I first investigate the movement network for two individual catsharks (one male and one female). I subsequently examine more general trends by averaging centrality results for the movement networks of multiple catsharks.

5.4.1 Two Individual Movement Networks

I now present centrality results for the movement networks of two individual small-spotted catsharks. The first is associated with a male catshark that was detected moving locations in the study area 71 times over a period of approximately fifteen months (from 6 July 2010 to 16 October 2011). Figure 5.3a shows the weighted static movement network for this catshark, with weights representing the number of times an edge occurred. The time-ordered version of this network has 35 weakly connected temporal components, reflecting the fact that this shark entered and exited the study area on 35 separate occasions. For the remainder of this report, I call this particular movement network the ‘male demo movement network’.

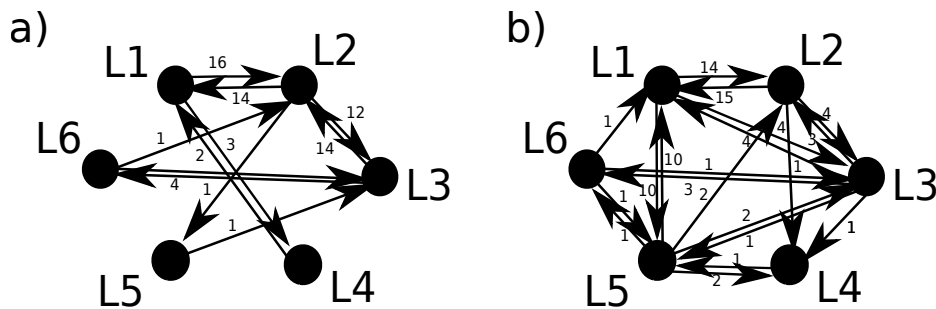


Figure 5.3: Weighted static movement networks for (a) the male demo movement network and (b) the female demo movement network.

The second movement network used in this subsection is associated with a female catshark that was detected moving locations in the study area 81 times over a period of

approximately four months (from 14 February 2010 to 6 July 2010). Figure 5.3b shows the weighted static movement network for this catshark. The time-ordered version of this network has 20 weakly connected temporal components. For the remainder of this report, I call this particular movement network the ‘female demo movement network’.

Because of the different calculations and normalisations for each type of centrality, note that only the relative rankings of each node with respect to each type of centrality are relevant (rather than comparing the centrality values for the different network types).

5.4.1.1 Degree Centrality

Given its simplicity, degree is a natural place to start for the investigation of any network. Figure 5.4 shows unweighted static, weighted static, and time-ordered degree centralities for each node in both the male and female demo movement networks. I normalised the in-degree and out-degree centralities for the unweighted static network by $n - 1$ (i.e. the maximum possible value, where n is the number of nodes). I normalised the in-degree and out-degree centralities for both the weighted static network and the time-ordered network by the sum of the in-degrees and out-degrees, respectively.

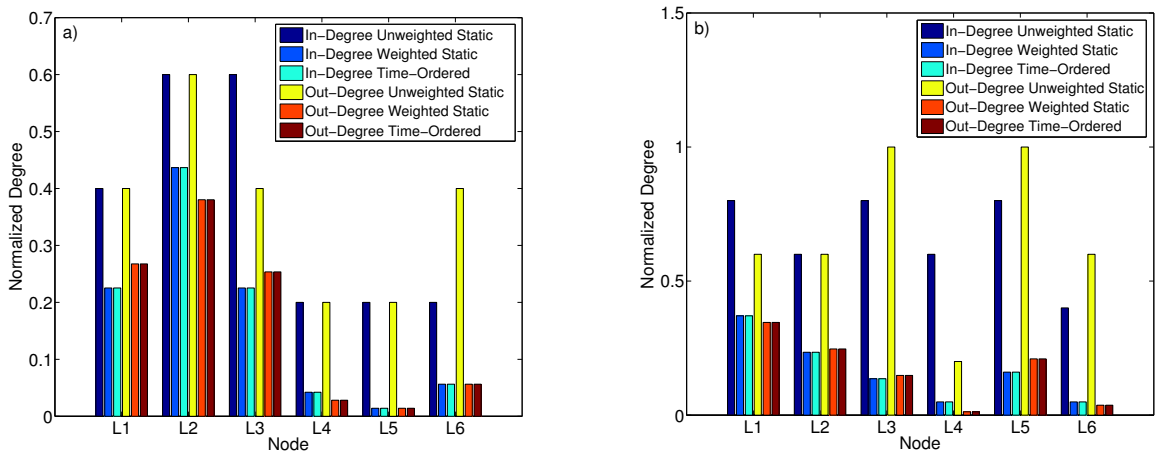


Figure 5.4: Degree centralities for the time-ordered, static weighted, and static unweighted (a) male and (b) female catshark demo movement networks.

As expected, the time-ordered network and the weighted static network have identical degree centrality results for both the male and female demo networks (Figure

5.4). However, also as expected, there are large discrepancies between the time-ordered degree centralities and their unweighted static counterparts. Specifically, because they lack the context provided by the weightings, the unweighted static degree centrality results generally overestimate the relative importance of nodes with low temporal degrees and underestimate the relative importance of nodes with high temporal degrees.

5.4.1.2 Betweenness Centrality

Figure 5.5 shows the unweighted static, weighted static, and time-ordered betweenness centralities for each node in both the male and female demo movement networks. For the weighted static betweenness centrality, the distance between two nodes (recall that we are finding shortest paths as part of the betweenness centrality calculations) was defined as the inverse weight. I used publicly available code from Rubinov and Sporns (2010) to compute the unweighted static and weighted static betweenness centralities. I normalised the unweighted static betweenness centrality by $(n-1)(n-2)$, where n is the number of nodes in the network (i.e. the maximum possible betweenness value for a directed unweighted star graph). For consistency, although it no longer represents the maximum possible betweenness value, I also normalised the weighted static betweenness centrality by $(n-1)(n-2)$. I normalised the time-ordered betweenness centralities by $(n-1)(b-a)$, where the time-steps $t \in [a, b]$.

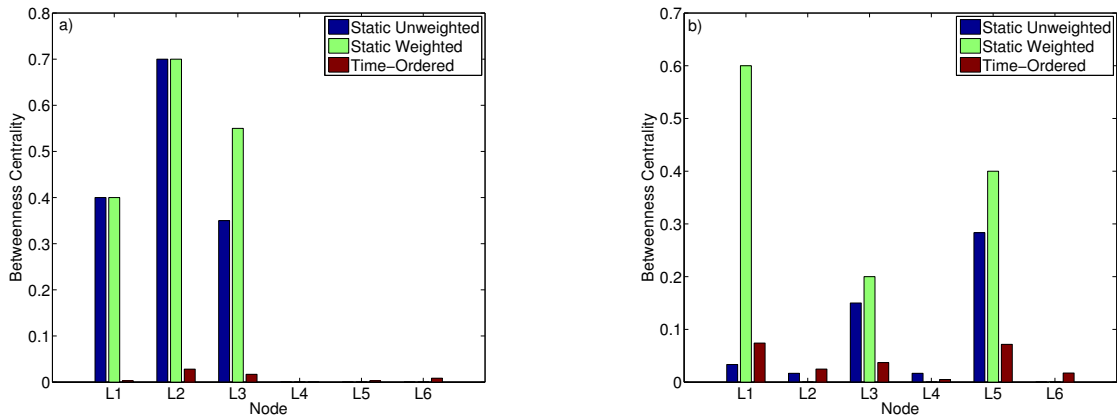


Figure 5.5: Betweenness centralities for the time-ordered, static weighted, and static unweighted (a) male and (b) female demo movement networks.

As shown in Figure 5.5, the relative rankings of each node based on betweenness centrality scores are different for each of the static unweighted, static weighted, and time-ordered networks. As with degree, the betweenness centralities for the static

unweighted networks are different than for the time-ordered networks. The discrepancy among betweenness centrality results is even more apparent when comparing the static weighted and time-ordered results, as edges with relatively low weights are ignored almost completely in the weighted network betweenness centrality calculations. Because the time-ordered betweenness centrality uses time-respecting paths, the time-ordered betweenness centralities provide a more accurate reflection of the true shortest paths (in the temporal sense) than their static counterparts.

5.4.1.3 Entrance and Exit Centralities

Figure 5.6 shows the entrance and exit centrality results for both the male and female time-ordered demo movement networks. Unlike the other centrality measures that I have discussed previously, there is not an analogous static centrality measure to compare it. I normalised both the entrance and exit centrality scores by the number of components (i.e. by the total possible score for each node).

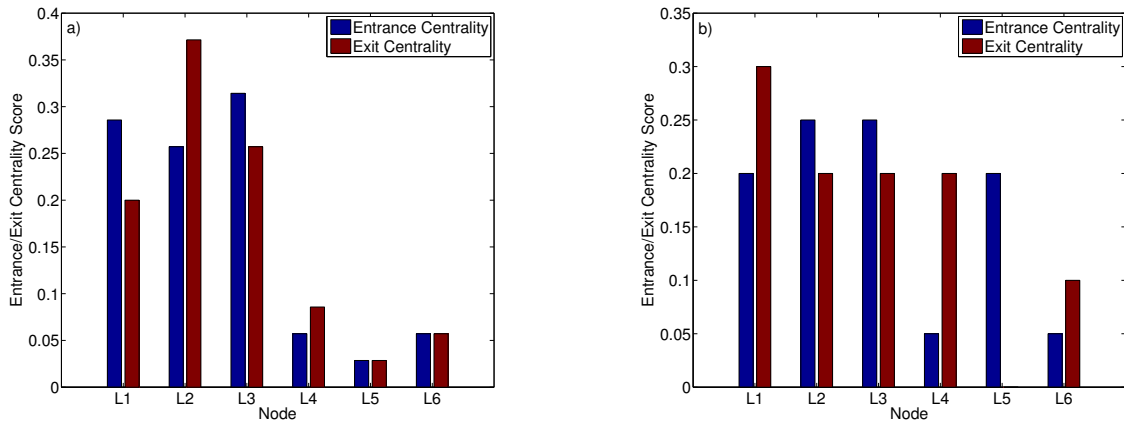


Figure 5.6: Entrance and exit centralities for the time-ordered (a) male and (b) female demo movement networks.

From Figure 5.6, we see that the the locations $L1$, $L2$, and $L3$ are popular entrance and exit locations in both the male and female demo movement networks. In the male demo movement network, locations $L4$, $L5$, and $L6$ have relatively small entrance and exit centralities. The relative entrance and exit centralities for locations $L4$, $L5$, and $L6$ in the female demo movement network are less consistent than for the male demo movement network.

It is particularly interesting to note the nodes with disparate entrance versus exit centrality scores. For example, location $L5$ in the female demo movement network has a reasonably high entrance score (relative to the other nodes in the network) but

an exit centrality score of zero. Similarly, location $L4$ in the female demo movement network has a high exit centrality score and a low entrance centrality score. Drastic differences in entrance and exit centrality scores suggests that the nodes play different roles in the time-ordered network (i.e. that different locations in the study area are used by the catsharks for different purposes).

5.4.2 Investigating Shark Habitat Usage

Using the centrality measures discussed above, I now investigate some general trends in the small-spotted catshark movement networks. As discussed previously (see Section 3.3), I use a total of 24 small-spotted catshark movement networks (14 female and 10 male). All normalisations match those previously discussed with respect to the male and female demo movement networks.

5.4.2.1 Activity Hubs

I again start with degree centrality. The temporal in-degree and out-degree of each node in a movement network provide an indication of how often each node is being visited. In other words, a high in-degree or out-degree (relative to the other nodes) implies a high level of movement activity around that node (i.e. an activity hub).

Figure 5.7 shows the mean male and female movement network temporal in-degree and out-degree for each node.

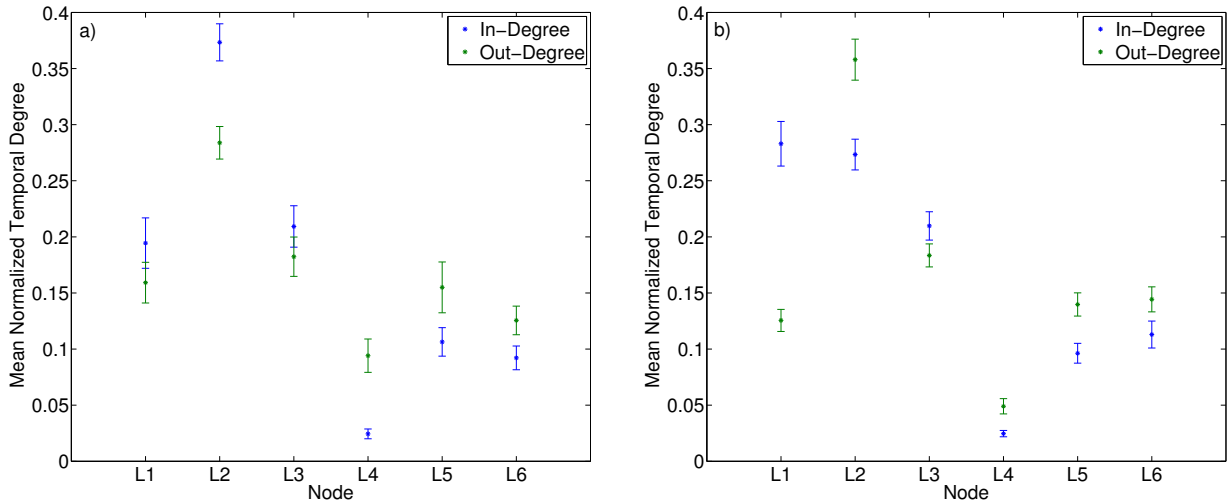


Figure 5.7: Mean normalised temporal degree centrality scores for the (a) male (10 individuals) and (b) female (14 individuals) small-spotted catshark movement networks. Error bars represent standard error.

The mean in-degree and out-degree centrality scores for each node showed similar relative trends for both the male and female movement networks (Figure 5.7). Location $L2$ has relatively high mean in-degree and out-degree centrality scores, suggesting that $L2$ is an activity hub in the study area. Location $L4$ has relatively low in-degree and out-degree centrality scores, suggesting that it did not play a major role in the small-spotted catshark movement networks.

In general, locations $L1$, $L2$, and $L3$ had higher in-degree and out-degree centrality scores than $L4$, $L5$, and $L6$. Recalling the spatial locations of each node (see Figure 3.2), $L1$, $L2$, and $L3$ are closer to shore and are in shallower waters than $L4$, $L5$, and $L6$. We know that water depth plays a role in small-spotted catshark preferences, with females typically aggregating in shallow-water caves (Sims *et al.* 2001) and males moving from deeper waters during the day to shallower waters at night (Sims *et al.* 2006). Hence, perhaps the higher degree centrality scores for $L1$, $L2$, and $L3$ reflect preferred shallow-water habitat within the study area relative to locations $L4$, $L5$, and $L6$.

Notice that the average in-degree and out-degree centrality scores for each node varied in their relative similarity to each other (Figure 5.7). For example, the mean in-degree and out-degree scores for $L1$ in the male movement networks were similar, whereas the mean in-degree and out-degree scores for $L1$ in the female movement networks are more different. Given that the sharks were able to leave the study area (and hence the network) and return at a later time, a similar mean in-degree and out-degree centrality score could reflect either a general tendency for sharks to move around in the study area upon arrival or a tendency for sharks to enter and leave the study area from the same location. Alternatively, a different mean in-degree and out-degree centrality score for a given node might suggest that the node is being used as either an entrance or an exit point.

To investigate such subtleties, we will look closer at entrance and exit points in subsequent subsections. First, however, I investigate habitat connectivity within the network using temporal betweenness centrality.

5.4.2.2 Habitat Connectivity

Network theory is well suited for asking questions about habitat connectivity (Minor and Urban 2007). Betweenness centrality lends itself naturally to these questions, as it measures how often a given node is on a shortest path between other nodes. A higher betweenness centrality score suggests that the node is important for habitat connectivity.

Figure 5.8 shows the mean male and female movement network time-ordered betweenness centrality results.

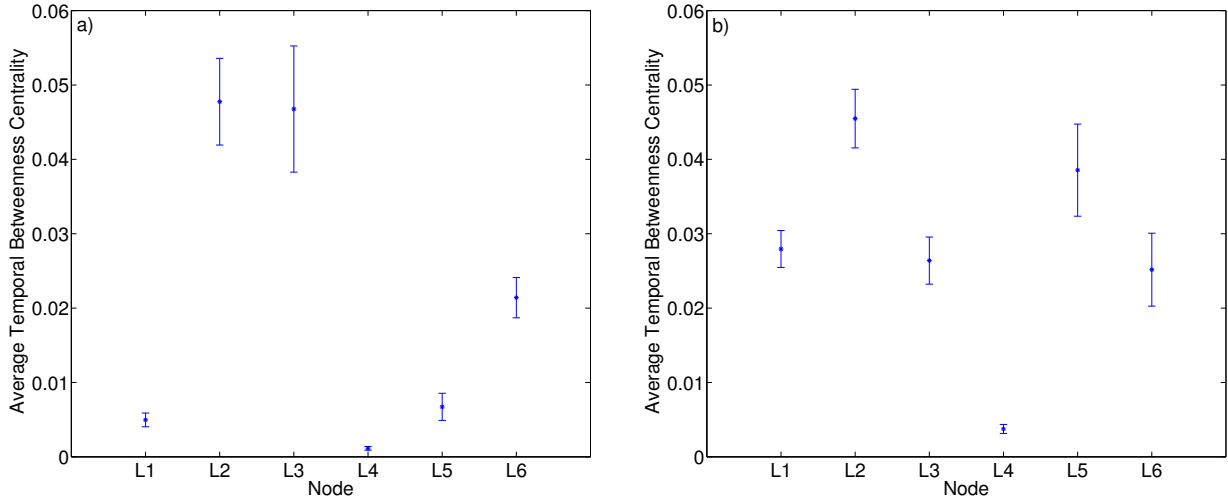


Figure 5.8: Mean normalised temporal betweenness centrality scores for the (a) male (10 individuals) and (b) female (14 individuals) small-spotted catshark networks. Error bars represent standard error.

For both the male and female small-spotted catshark movement networks, location $L2$ has the highest temporal betweenness centrality score and location $L4$ has the lowest temporal betweenness centrality score. These results suggest that $L2$ is relatively important for habitat connectivity, whereas $L4$ is not. These results agree with the findings from the earlier in and out-degree centrality scores, suggesting that $L2$ plays a more important role in the network than $L4$. Together, the high betweenness and degree centrality scores for $L1$ suggest that its relative importance for habitat connectivity is a function of frequent visitation.

Temporal betweenness centrality results for the remaining nodes in the network (i.e. $L1$, $L3$, $L5$, and $L6$) are less consistent between genders and in comparison with degree centrality results, suggesting that they have more subtle roles. Of particular interest are the nodes that had low relative degree centrality rankings but have high relative betweenness centrality score rankings. These nodes represent locations that were visited infrequently but are on many temporal shortest paths. For example, $L5$ has a relatively low degree centrality ranking but a high betweenness centrality ranking for the female movement networks. This suggests that $L5$ might be important for habitat connectivity in the female movement networks.

5.4.2.3 Entrance and Exit Points

The temporal degree and betweenness centrality results presented in the previous two subsections allowed us to speculate on the relative importance of each node. In this subsection, I use the entrance and exit centralities to explicitly investigate entrance and exit points within the small-spotted catshark movement networks.

Figure 5.9 shows the mean entrance and exit centrality scores for each node for the male and female small-spotted catshark movement networks. Nodes with high entrance or exit centrality scores represent locations where sharks have frequently entered or left the study area, respectively. Correspondingly, nodes with low entrance or exit centrality scores represent locations that were rarely used as entrance or exit points to the study area.

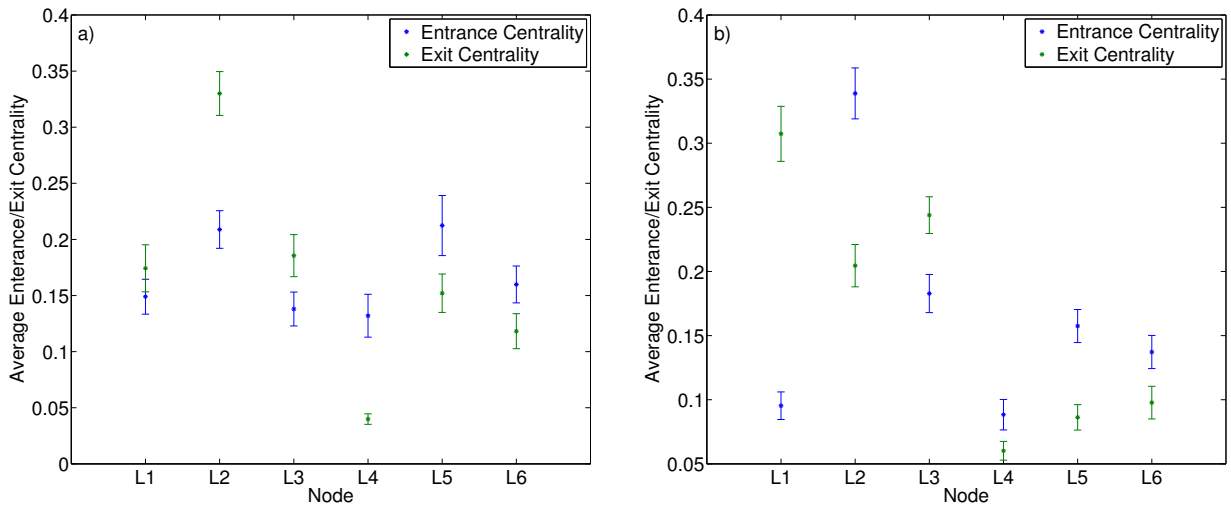


Figure 5.9: Mean normalised temporal entrance and exit centrality scores for the (a) male (10 individuals) and (b) female (14 individuals) small-spotted catshark networks. Error bars represent standard error.

As with the temporal degree and betweenness centrality results, the entrance and exit centrality results for both the male and female small-spotted catshark movement networks reflect the relatively high importance of location $L2$ (Figure 5.9). Interestingly, the $L2$ entrance centrality score is higher than the exit centrality score for the male catshark movement networks, whereas the opposite is true for the female catshark movement networks. A further investigation into gender-specific timings within the network would be interesting - one intriguing possibility is that female catsharks might tend to leave when the males arrive.

The mean entrance and exit centrality scores for location $L1$ in the male movement networks were relatively similar and not particularly high or low relative to the other nodes in the network. Hence, $L1$ might serve as a casual entrance and exit point for male small-spotted catsharks in the study area.

In contrast to the male results, the mean entrance and exit centrality scores for location $L1$ in the female movement networks were notably different. Specifically, the mean exit centrality for $L1$ is notably higher than the corresponding mean entrance centrality for $L1$ in the female movement networks. This result suggests that female small-spotted catsharks are much more likely to leave the study area from $L1$ than they are to enter from $L1$.

5.4.3 Limitations and Future Work

There are a multitude of questions that can be investigated using a time-ordered networks approach to model animal movements. The analyses presented in this section for the small-spotted catshark movement networks provide only a glimpse into the possibilities. However, as with all models, a movement network is a simplification of the actual system. An understanding of the modelling limitations is important for accurate analyses and interpretations.

Below I identify several cautionary notes for the interpretation of the wild adult small-spotted catshark movement network results presented previously. I also outline additional ideas that would be insightful to pursue, both for addressing the limitations of my current modelling assumptions and for investigating additional questions.

5.4.3.1 Explicit Investigations of Time

One of the most attractive aspects of time-ordered networks is that they can track all of the dynamics of a system, including the explicit timing of events. Questions pertaining to biologically meaningful time-scales (e.g. daily, seasonal, etc.) are often of particular interest in behavioural ecology, and time-ordered networks are well-equipped as a framework for investigating these questions. For example, male small-spotted catsharks are known to rest in relatively cool and deep waters during the day, and move to shallow warmer waters for hunting at night (Sims *et al.* 2006). Do the male movement networks in our study area reflect this?

Due to both difficulties with accurate time-stamp importing into MATLAB and general time constraints associated with this thesis, I did not investigate questions involving explicit time-stamps. However, this could be an extremely fruitful endeavour for the future.

5.4.3.2 Time-Respecting Motifs

Extending from the general topic of questions that address time explicitly, it would be interesting to know if small-spotted catsharks move throughout the study area in a habitual way. Do they visit locations in a predictable sequence? If so, is it specific to a certain time of day, season, etc.?

I introduced time-respecting motifs earlier in this thesis in our discussion regarding time-recurring motifs for the juvenile small-spotted catshark social networks. Recall that time-respecting motifs are repeated contact patterns between nodes in adjacent time-steps. Hence, an investigation of time-respecting motifs in catshark movement networks could shed light onto habitual movement patterns within the network.

5.4.3.3 Movement Network Subtleties

Network Construction and Robustness

The small-spotted catshark movement networks investigated in this thesis were constructed from movements that occurred within a time-span of one hour. The choice of one hour as a threshold for inclusion or exclusion in the network was arbitrary, although it was based on a general suggestion in Jacoby *et al.* (2012a).

A different threshold choice would have undoubtedly resulted in different movement networks, and one needs to check whether our conclusions still hold in that case. To get a sense of the effect of threshold choice on time-ordered network analysis results, it would be desirable to repeat the analyses for networks constructed using different thresholds.

Given that the general purpose of this thesis is to introduce temporal networks in the context of animal-behaviour, the analyses presented are sufficient for demonstrative purposes. However, the effect of threshold choice on the resulting time-ordered network topologies should be investigated further before reaching more concrete conclusions about small-spotted catshark movement patterns within the study area.

Temporal Components

For the analyses presented in this thesis, weakly connected temporal components within each movement network were defined based on both movements that originated at a different node than previously detected and on movements that occurred after a time-lapse of more than one hour. Information regarding detections at the same node were not accounted for; therefore, a temporal component might not accurately reflect the coming and going of a catshark from the study area (i.e. it could have stayed

in one spot in the study area for a long time before moving on, therefore having a movement that occurred after a time-lapse of more than one hour). Hence, some of the temporal components identified with the current approach might be artificial. As a result, both the betweenness centrality results and the entrance and exit centrality results should be interpreted with caution.

In the future, information regarding detections at the same node should be included when detecting temporal components. Allowing self-edges within the movement network, as discussed in the next paragraph, would mitigate this problem.

Self-Edges

The movement networks presented in this thesis were constructed from movements between nodes. I did not include detections at the same node (i.e. self-edges). By not including self-edges, dynamics within the movement network could be lost (for example, see the discussion above regarding weakly connected temporal components).

An inclusion of self-edges would also expand the depth of questions that can be asked of the movement networks. For example, one could ask about the length of time a catshark stayed at one location, or how long a catshark typically spends at each location before moving on.

5.4.3.4 Potential Data Uncertainty

The above discussion has centred primarily on limitations associated with representing the small-spotted catshark biotelemetry data as a time-ordered movement network. In addition, one is inevitably also limited by the data itself. Specifically, the biotelemetry data is limited by the detection range of the acoustic array. If a shark has left the study area, we can not tell how far it has gone. Likewise, barriers within the study area (e.g. rocks, shipwrecks, etc.) might prevent accurate detection (Jacoby 2012).

Chapter 6

Integrating Time-Aggregated and Time-Ordered Networks

Recall that the purpose of this thesis is to introduce temporal networks in the context of animal-behaviour research. Hence, in addition to a general introduction on static networks, previous chapters of this report have investigated both time-aggregated and time-ordered networks. Given the progression in apparent complexity (i.e. static networks to time-aggregated networks to time-ordered networks), it is tempting to assume that time-ordered networks are the best approach. However, if this is the case, why not model all dynamic network data as a time-ordered network?

In years to come, it might turn out that time-ordered networks are indeed superior to time-aggregated networks. In the meantime, however, the current suite of available tools for time-ordered networks is substantially smaller than that for static (and therefore also for time-aggregated) networks. Further, the discrete-time sampling used to gather some animal-behaviour data does not necessarily lend itself well to time-ordered networks (depending on the question of interest). Additionally, the trade-off between the added complexity of a temporal network (relative to a static approach) and the benefit for insight into dynamic network processes is question-specific and may not always be justified (Holme and Saramäki 2012).

Time-aggregated networks can easily be constructed from their time-ordered counterparts (Blonder *et al.* 2012). Hence, animal-behaviour data can be analysed using both time-aggregated and time-ordered networks without too much extra effort. By making use of both time-aggregated and time-ordered networks, animal-behaviour network practitioners have a much wider set of tools at their disposal.

Chapter 7

Conclusions

There are many interesting questions in behavioural ecology that involve an aspect of time. For those that lend themselves to a networks approach (i.e. relational questions), temporal networks provide a framework for investigating dynamics within the data. Time-aggregated and time-ordered networks are two complementary tools within the realm of temporal networks, and can be used to give complementary insight.

Time-aggregated networks are a series of static networks constructed from condensed temporal data. Provided that an appropriate aggregation time-window is used, time-aggregated networks allow insight into network dynamics while still maintaining accessibility to the wide range of existing tools for static network analysis. As demonstrated in this thesis, an analysis of the time-scales demonstrated by recurring temporal motifs can help network practitioners to choose appropriate aggregation time-windows.

Time-ordered networks maintain all of the dynamics of the data they represent, and therefore avoid the potential pitfalls of data aggregation associated with time-aggregated networks. Although analysis tools for time-ordered networks are not yet as heavily developed as their static counterparts, even basic measures such as temporal degree centrality and betweenness centrality can provide useful insights. In this thesis I also introduced the notions of entrance centrality and exit centrality as additional diagnostics for examining time-ordered networks.

I used juvenile small-spotted catshark social networks and wild adult small-spotted catshark movement networks to demonstrate the applicability of time-aggregated and time-ordered networks, respectively. In both cases, the temporal networks approach was able to provide insight that would not have been obvious from a static network analysis. Specifically, I showed that the strength of social attraction in juvenile small-spotted catshark networks (measured by the mean dyadic simple ratio index)

increased over time. I also identified location-specific temporal differences in the habitat usage of wild adult small-spotted catsharks within the study area.

This thesis has only scratched the surface regarding applications for temporal networks in behavioural ecology. Given the potential for insight into patterns and processes in dynamic data, both time-aggregated networks and time-ordered networks will surely be explored more widely in the future as tools are developed. However, several outstanding issues remain. For example, given that most association indices are fundamentally based on an average over time, how can one generalise association indices to time-ordered networks? Development of statistical methods for networks, including temporal networks, is another area that needs attention (Croft *et al.* 2011). Of course, the generalisation of existing static centrality measures (or the development of new ones) for temporal networks would also be a useful contribution.

In summary, temporal networks are a useful modelling framework for dynamic relational animal-behaviour data. By incorporating dynamics into the modelling framework, temporal networks can contain more information about the systems they represent than their static counterparts. Hence, both time-aggregated and/or time-ordered networks can provide additional insight compared to the traditional static networks approach. Like all disciplines that use network theory, applications of temporal networks in behavioural ecology is relatively new. It promises to be an exciting area of research in the years to come.

Appendix A

Clique Finding Pseudo-Code (Palla *et al.* 2005)

The method for finding recurring temporal motifs that is presented in the main body of this thesis requires an algorithm for finding all maximal complete subgraphs (i.e. cliques) within a given network. The clique-finding algorithm presented in Palla *et al.* (2005) is well suited for this problem. Full details of the algorithm are provided in the supplementary information that accompanies the Palla *et al.* (2005) publication. I give a brief summary of the algorithm below in the form of pseudo-code.

Algorithm 1 Find all maximum complete subgraphs in a network

Identify the largest possible clique size k as the largest degree in the network.

for $s = \max k : -1 : 2$ {i.e. for each clique size, starting with the largest} **do**

$M = A$ (i.e. the adjacency matrix for the network)

for $i = 1 : n$ {i.e. for each node in the network} **do**

 Find all neighbours of node i .

if node i and its neighbours are a subset of nodes in an already-found clique **then**

 Break

else

 Find all cliques of size s containing node i by checking all possible combinations of size s of node i and its neighbours.

end if

 Then delete node i from the network (i.e. $M(i,:) = []$, $M(:,i) = []$)

end for

end for

MATLAB code for the Palla *et al.* (2005) k -clique community detection algorithm, which can be easily modified to find only cliques, is publicly available on MATLAB Central ([www.http://www.mathworks.co.uk/matlabcentral/](http://www.mathworks.co.uk/matlabcentral/)) (Nguyen 2011).

Appendix B

Juvenile Catshark Social Networks: Temporal Community Results

The juvenile catshark social network temporal community results presented in the main body of this thesis were selected for illustrative purposes. Here I present the temporal community results for all of the available data sets. The results are below are presented by treatment group category: (1) kin and familiar, (2) kin and not familiar, (3) not kin and familiar, and (4) not kin and not familiar. Each treatment group consists of four replicated experiments.

B.0.4 Kin and Familiar

Replicate 1 (KF1)

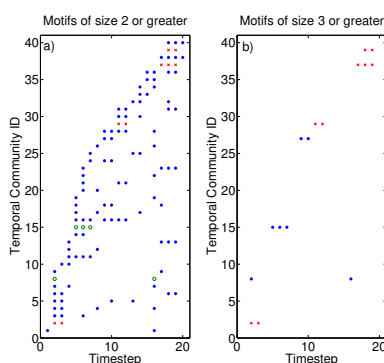


Figure B.1: Temporal communities for recurring temporal motifs in the KF1 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

Replicate 2 (KF2)

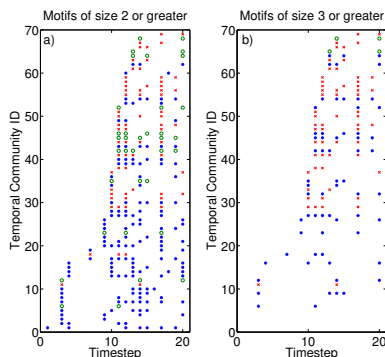


Figure B.2: Temporal communities for recurring temporal motifs in the KF2 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterix ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

Replicate 3 (KF3)

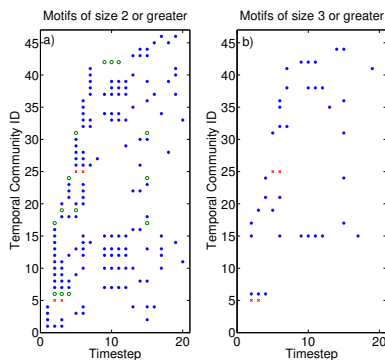


Figure B.3: Temporal communities for recurring temporal motifs in the KF3 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterix ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

Replicate 4 (KF4)

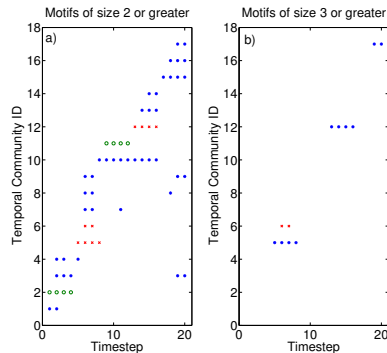


Figure B.4: Temporal communities for recurring temporal motifs in the KF4 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

B.0.5 Kin and Not Familiar

Replicate 1 (KUF1)

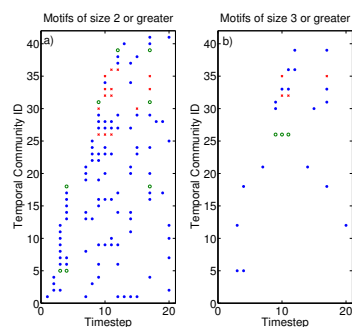


Figure B.5: Temporal communities for recurring temporal motifs in the KUF1 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

Replicate 2 (KUF2)

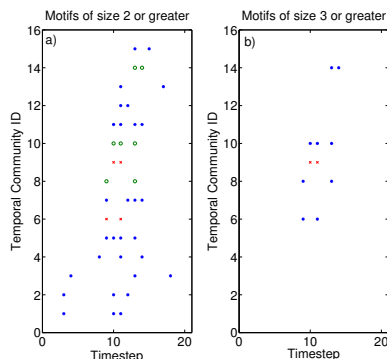


Figure B.6: Temporal communities for recurring temporal motifs in the KUF2 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterix ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

Replicate 3 (KUF3)

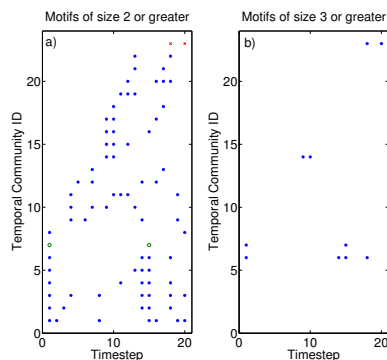


Figure B.7: Temporal communities for recurring temporal motifs in the KUF3 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterix ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

Replicate 4 (KUF4)

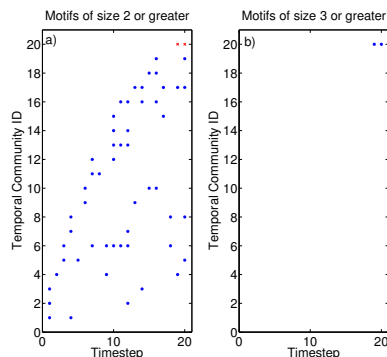


Figure B.8: Temporal communities for recurring temporal motifs in the KUF4 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

B.0.6 Not Kin and Familiar

Replicate 1 (NKF)

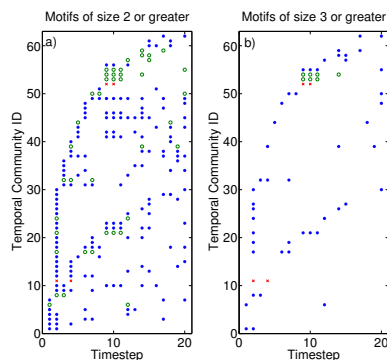


Figure B.9: Temporal communities for recurring temporal motifs in the NKF1 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

Replicate 2 (NKF2)

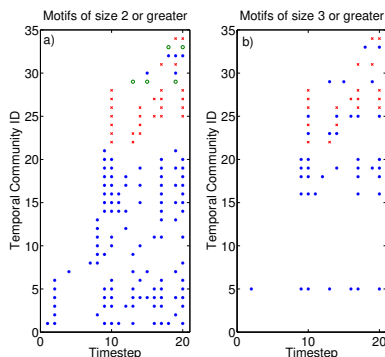


Figure B.10: Temporal communities for recurring temporal motifs in the NKF2 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

Replicate 3 (NKF3)

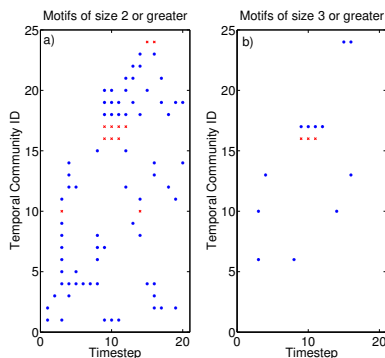


Figure B.11: Temporal communities for recurring temporal motifs in the NKF3 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

Replicate 4 (NKF4)

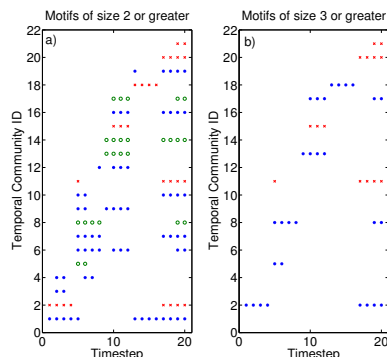


Figure B.12: Temporal communities for recurring temporal motifs in the NKF4 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

B.0.7 Not Kin and Not Familiar

Replicate 1 (NKUF1)

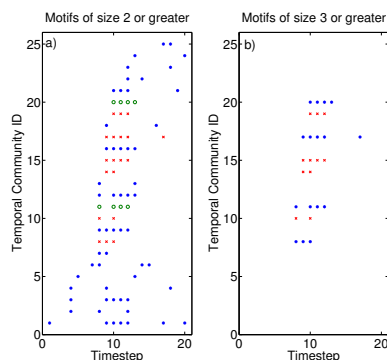


Figure B.13: Temporal communities for recurring temporal motifs in the NKUF1 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk ‘*’ indicates one motif, a green open circle ‘o’ indicates two motifs, and a red ‘x’ indicates three or more motifs.

Replicate 2 (NKUF2)

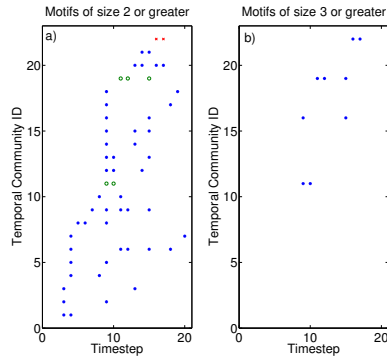


Figure B.14: Temporal communities for recurring temporal motifs in the NKUF2 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk '*' indicates one motif, a green open circle 'o' indicates two motifs, and a red 'x' indicates three or more motifs.

Replicate 3

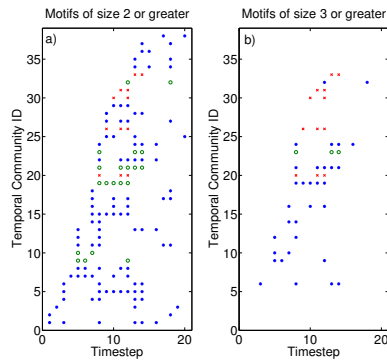


Figure B.15: Temporal communities for recurring temporal motifs in the KNKUF3 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk '*' indicates one motif, a green open circle 'o' indicates two motifs, and a red 'x' indicates three or more motifs.

Replicate 4

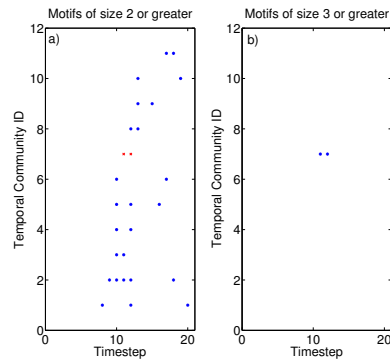


Figure B.16: Temporal communities for recurring temporal motifs in the NKUF4 juvenile small-spotted catshark social network (with a similarity threshold of 1). (a) Motifs with two or more nodes (i.e. $n \geq 2$). (b) Motifs with three or more nodes (i.e. $n \geq 3$). The number of motifs in each temporal community is indicated by different symbols as follows: a blue asterisk '*' indicates one motif, a green open circle 'o' indicates two motifs, and a red 'x' indicates three or more motifs.

Appendix C

Mean Dyadic SRI Results by Treatment Group

As discussed in Chapter 4 of this thesis, daily patterns observed in the recurring temporal motifs of some of the juvenile small-spotted catshark social networks prompted subsequent analysis using time-aggregated networks with daily aggregation time-windows. In Figure C.1 I present the mean dyadic simple ratio index (SRI) results for the time-aggregated networks in each treatment group (i.e. kin and familiar, kin and not familiar, not kin and familiar, and not kin and not familiar).

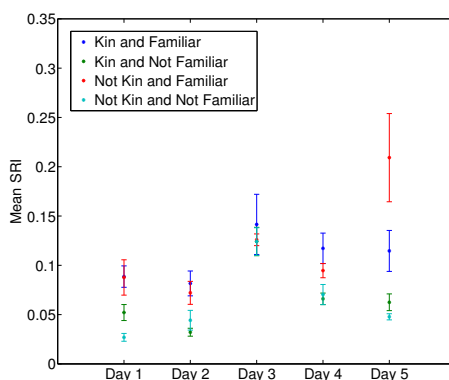


Figure C.1: Mean simple ratio index (SRI) values for daily time-aggregated juvenile small-spotted catshark networks for each of the four treatment groups: kin and familiar, kin and not familiar, not kin and familiar, and not kin and not familiar. There were four replicates in treatment group. Error bars represent standard error.

Appendix D

SVD of Bipartite Incidence Matrices

As discussed in Section 4.4.3 of this thesis, singular value decomposition (SVD) might be a useful tool for investigating temporal networks. In Table D.1 I show the squares of the top seven leading singular values for each of the juvenile small-spotted catshark social network bipartite incidence matrices. I have normalised the values by dividing by $\sum_{k=1}^n \sigma_k^2$, where n is the total number of singular values σ (Porter *et al.* 2007).

Table D.1: The seven leading normalised squared singular values for each of the temporal bipartite incidence matrices associated with the different small-spotted catshark social networks.

Data set	σ_1^2	σ_2^2	σ_3^2	σ_4^2	σ_5^2	σ_6^2	σ_7^2
KF1	0.2195	0.1524	0.1265	0.0849	0.0806	0.0600	0.0541
KF2	0.4545	0.1184	0.0840	0.0619	0.0539	0.0429	0.0358
KF3	0.3032	0.1375	0.1125	0.0775	0.0654	0.0545	0.0403
KF4	0.2482	0.1975	0.1539	0.1191	0.1051	0.0580	0.0333
KFUF1	0.2705	0.1238	0.0991	0.0942	0.0773	0.0741	0.0586
KFUF2	0.3530	0.1585	0.1101	0.0941	0.0686	0.0469	0.0284
KFUF3	0.2281	0.1208	0.0883	0.0816	0.0725	0.0696	0.0563
KFUF4	0.2057	0.1426	0.0936	0.0833	0.0706	0.0581	0.0525
NKF1	0.2595	0.1288	0.0782	0.0746	0.0647	0.0606	0.0489
NKF2	0.4035	0.1357	0.0897	0.0666	0.0568	0.0545	0.0424
NKF3	0.2461	0.1551	0.1128	0.0974	0.0795	0.0633	0.0474
NKF4	0.5921	0.1294	0.0778	0.0678	0.0441	0.0339	0.0198
NKUF1	0.4100	0.1031	0.0912	0.0667	0.0556	0.0526	0.0410
NKUF2	0.2506	0.1407	0.1023	0.0869	0.0721	0.0589	0.0553
NKUF3	0.3278	0.1635	0.0944	0.0722	0.0545	0.0473	0.0418
NKUF4	0.3065	0.1243	0.1038	0.0777	0.0708	0.0488	0.0488

Appendix E

Social Butterfly Index

I developed the following diagnostic, coined the ‘social butterfly index’, during the course of this thesis as part of my investigation of the juvenile small-spotted catshark social data. The purpose of the social butterfly index is to identify individuals who move from group to group and would therefore be important for the spread of disease or information in a network. Although it did not prove to be particularly insightful for the juvenile small-spotted catshark social data, I include it here as an appendix as it is an interesting concept that could prove useful for other applications.

Specifically, I define the social butterfly index as

$$s_i = \sum_{t=a}^b \delta(i, t) g_i, \quad (\text{E.1})$$

$\delta(i, t) = 1$ if node i is in a group at time t and $\delta(i, t) = 0$ otherwise, and g_i is the number of individuals in the group with node i who have not been in a group with node i for the previous m time-steps. One can compare the results for different values of m .

The social butterfly index of a given node reflects both how often it was in a group and the number of new nodes with which it has some relationship. A relatively high social butterfly index indicates that an individual (represented by a node) frequently socialised with new individuals. A lower social butterfly index indicates that an individual spent relatively more time either alone or in the same group.

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