Variability of Factors Shaping Animal Social Networks

Ph.D. Dissertation

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List of abbreviations

Abbreviation	Meaning	Page
ANTs	Animal Network Toolkit software	27
APL	Average Path Length	24
C	Cleaner	31
CC	Clustering Coefficient (or Transitivity)	23
CV_{TI}	Coefficient of Variation in Topological Importance	24
D	Node Degree or Degree	21
DI	Out -and In -Strength differences	34
EF	Edge Formations	25
ERGM	Exponential Random Graph Models	25
F	Forager	31
GS	Group Size	30
H1	First hypothesis in the Thesis Question 1	35
H2	Second hypothesis in the Thesis Question 1	35
H3	Third hypothesis in the Thesis Question 1	35
H4	Fourth hypothesis in the Thesis Question 1	35
H5	Fith hypothesis in the Thesis Question 1	35
H6	Sixth hypothesis in the Thesis Question 1	35
HC	Hierarchical Clustering	36
IS	In-Strength	22
LMM	Linear-Mixed-Models	27
N	Nurse	31
NCI	Network Centralization Index	23
NLPM	Node-Label Permutation Models	26
NM	Null Model	27
NQ	No- Queen-Network (network not containing the Queen)	31
NS	Node-Strength	22
OD	Out-Degree	22
OS	Out-Strength	22
PCA	Principal Component Analysis	36
Q	Queen-Network (network containing the Queen)	31
SNA	Social Network Analysis	9
TI	Topological Importance	22
TS	Territory size	30
WI	Weighted Topological Importance	22

Table of Contents

1. Preface

In my PhD dissertation, I summarize the scientific activities conducted during my four years of doctoral studies, focusing on animal social network analyses and their application and modeling approaches using various modeling and statistical methods typical of this scientific field. As a generalist, I present the network modeling techniques learned during these four years across four completely different model species.

In the first third of the thesis, I will provide a methodological (Chapters 2.2-2.3), statistical (Chapters 2.4, 3.1-3.7), and literature overview (Chapter 2.5) of animal social networks, with particular attention to the terminology of network approaches and the composition of network models. I conducted a systematic literature review (Chapter 2.5) to categorize animal social network research studies and identify which taxonomic groups are represented in the literature, highlighting the significance and diversity of this scientific topic today.

In the second third, I introduce the various methodological variations of network analysis on four different model species (Chapter 3.8), independent of location, time, and other factors, using three different statistical methods. I explore the general questions of animal social network research by addressing a common query: *What do the networks look like in these animal groups under different environmental conditions?* The selection of these species was subjective and based on my interests and passion, data availability, collaborative opportunities, and fieldwork capacities over the four years.

Finally, in the third part of my work, I compare the network properties of the four species, searching for trends and characteristic patterns among them.

The dissertation was primarily written in the first-person singular and focused on the results obtained from studies published (or in progress) either solely by myself under supervision or occasionally as a corresponding author. However, each of these works was accomplished through teamwork with colleagues and supervisors, for which I would like to express my gratitude. The results could not have been achieved without our collective efforts.

2. Introduction

Recognizing that addressing questions about animal behavior often leads to endless discussions due to diverse perspectives and approaches, I narrow my focus to a specific aspect of this topic to demonstrate how generalist ecologists adopting a network perspective, can approach the study of social behavior in animals. In this chapter, I begin with a brief overview of social behavior in animals and then narrow my focus to the establishment of direct or indirect connections between them. Following these introductory subchapters, I demonstrate how these animal connections can be quantified using a network approach to achieve the main objective of this dissertation: modeling animal social networks. Here, I establish the basic mathematical terms, methods, and tools to facilitate a clearer understanding of this scientific topic. Before concluding this chapter and addressing my thesis points, I aim to position animal social network studies within the broader context of scientific literature for the reader. To achieve this, I conducted my systematic review of published studies on this topic to contextualize my case studies and aid the reader in following my line of reasoning.

2.1. Social behavior in animals

Social behavior characterizes a wide variety of animal species, accompanied by associated population dynamics (Krebs, 1978). Understanding the evolution of sociality is one of the central questions in behavioral and evolutionary biology (Wilson, 1975; Maynard Smith and Szathmáry, 1995). Sociality serves critical functions affecting fitness. For instance, animals with higher social ranks often exhibit greater reproductive success within populations (Armitage, 1986; Pusey and Packer, 1997). In several species, the social environment influences the physiological reactions of individuals. For example, the existence of familiar conspecifics mitigates the impact of stress in rats, mice, goats, and monkeys (House et al., 1988; Seeman and McEwen, 1996). Social dynamics are also connected to decreased levels of basal cortisol (Sapolsky et al., 1997), and the characteristics of closer social bonds between males and females reduce stress responses in baboons (Beehner et al., 2005; Engh et al., 2006). Sociality may be influential beyond the intraspecific level to the biogeographic patterns by influencing species movement between islands in mixed-species bird flocks (Martinez et al., 2023). Furthermore, social behavior can be essential for long-term survival in predator-prey dynamics, encompassing defensive and hunting strategies (Fryxell et al., 2007). While specific behavioral interactions are readily observable like male dog fighting events or territory marking (Gosling et al., 1982), others are more indirect and complex to define like affiliative connections (for example, friendship or cooperation) between animals (Seyfarth and Cheney, 2012). The intensity and characteristics of these behavioral interactions hinge upon dynamic environmental conditions (e.g., migratory bird behavior influenced by seasonal changes). To comprehend these nuances, undertaking extensive and prolonged observations becomes essential, allowing for discernment of disparities both among and within species or populations. For instance, the reproductive rates of the Great Tit (*Parus major*) were explored in urban and rural habitats within the same region (Seress and Liker, 2015). While some factors shaping group behavior, such as temperature, territory size, and available water, can be assessed using relatively straightforward methods like visual observations, GPS locations, and databases, others prove more challenging to quantify and standardize. These factors include sex ratio, predation pressure, food availability dynamics, and effective population size. In my thesis, I aimed to investigate the predictors and determinants of network structures in four animal species. This facilitated a comparative understanding of social network properties across the phylogenetic tree, highlighting the importance of measuring diversity in animal social behavior for a better understanding of adaptation and social evolution processes.

2.2. Animal social relation types

Defining relationships between individuals can be challenging due to the wide variety of connections, requiring various approaches to differentiate among them. One helpful approach can be to define relationships between individuals using ethograms in different species. Ethograms are the most common catalogs with behavioral data in ethnological research, which contain the complete set of animal patterns (Brockmann, 1994). After decades of over-emphasizing dominance interactions, ethograms are becoming now increasingly richer for a number of species, making more complete and holistic (e.g. multinetwork) approaches possible.

In this thesis, I use the terminology of Social Network Analysis to describe social structure (Wasserman and Faust, 1994). Therefore, animal social relations between individuals can be distinguished into two types: associations and interactions (Croft, 2008).

Associations have been quantified by many authors based on observations of spatial proximity between individuals, and they can be measured using two approaches. First, within the population, some subgroups are defined by an individual attribute. This approach is called group membership, and members are associated (Croft, 2008). Second, the definition of association can be based on space use. In this case, all individuals are associated within the same territory, habitat, or area, with particular attention to setting the spatial scale (Croft, 2008).

Interactions can be categorized into agonistic interactions and affiliative interactions. Agonistic interactions are frequently used synonymously with aggressive interactions. It includes every behavior that is intended to harm another animal (intra-and interspecifically), for example, threats, displays, retreats, and fights (Young et al., 2022). Affiliative interaction can also display a wide range of types. It is often defined as a friendly connection among individuals (Jasso and Nekaris, 2022). Affiliative behavior is commonly observed primarily among birds and mammals. The specific forms of affiliative interactions may differ across species. It can be observed as grooming in mammals, allopreening in birds, playing interactions, and sharing food with other individuals (Jasso and Nekaris, 2022). These associations and interactions shape the whole group dynamics and function in a population and determine the characteristics of the information flow between individuals (Sueur, 2012).

2.3. Measuring animal behavior

Researchers study behavior in various ways and for various reasons. One of these reasons is the concept of sociality. When several individuals live together, multiple interaction patterns may develop, resulting in complex social structures and relationships (Wey et al., 2008). One of the basic measures of social patterns, for example, the mating system or population size, showed many proofs of sociality (Brown and Brown, 1996). These approaches aim only at the individuals and only indirectly focus on their interactions; therefore, some homogeneity of effect on the given population is implicitly assumed. The network approach to studying animal behavior will provide an opportunity to study social complexity in greater detail by measuring interactions directly (Wey et al., 2008). One of the best benefits of the animal social network approach is that we can study the populations at different levels (i.e., individual, group, and population) and for different connection types (e.g., sexual, aggressive, affiliative, cooperative, etc.) (Krause et al., 2009). Connections between individuals create a social environment at the group level, which selects behavioral attributes at the individual level (Krause et al., 2009). The universal methods of social networks allow us to study systems ranging from social insects to primates (Krause et al., 2009).

When examining the diverse array of approaches and methodologies applied to questions concerning animal social networks, an inevitable question arises: Are these approaches comparable, and if so, which approach is the most precise or which one should be used under specific circumstances? It is important to remember the inherent limitations of animal social networks. To synchronize methods between different species and populations is nearly impossible. Observing finer scales of group dynamics reveals more issues in comparing social characteristics among species, populations, or groups.

2.4. Introduction to animal social networks

2.4.1. Graph theory

A graph is defined by a set of nodes, a set of edges and a relation. Nodes represent entities (e.g. individuals), and edges link nodes with the observed relation. The arrangement of nodes and edges determines the structure of the graph. In 1736, Euler's demonstration of the insolvability of the "Königsberg bridge problem" served as an essential moment of graph theory. He demonstrated that where land (graph nodes) connected by bridges (graph edges) have an odd number of degrees, it is impossible to traverse the area by using each bridge only once. Throughout my work, the terms "graph" and "network" will be used interchangeably (Dale, 2017). Graph theory has since expanded into various interdisciplinary fields, including epidemiology (Meyers, 2007), social sciences (Wasserman and Faust, 1994), ecology (Bascompte and Jordano, 2007), and animal behavior by using Social Network Analysis tools (Wey et al., 2008).

2.4.2. Social Network Analysis (SNA)

Social network analysis (SNA) methods originated from social and behavioral sciences (Wasserman and Faust, 1994). In social networks, the nodes represent the social entities, such as an individual, a group, or a habitat, depending on the question being asked. The edges symbolize the social ties or relationships between these entities (Wasserman and Faust, 1994). Networks can be unweighted (binary) or weighted when a number is associated with the edge. The edges can be undirected (symmetric connections) or directed (actor and receiver). SNA quantifies interaction data using edge lists as a simple table with columns like actor, receiver, edge weight, etc., or adjacency matrices, where the row and column names are the same, and the matrix entries are the edge weights (Krause et al., 2015). The properties of individuals are called node attributes, and the elements of a network can be used as network configurations (edge, dyad, triad, degree, etc.) (Silk and Fisher, 2017). While in most cases, the edges represent the same type of interaction between two individuals, networks can be constructed as multilevel networks when the set of edges has multiple definitions by interaction types between the same set of individuals (Krause et al., 2015). As more data are collected continuously in time, time-aggregated or temporal networks are becoming more frequent (Blonder et al., 2012). The terms "*network structure*" and "*network topology*" are used here synonymously (Krause et al., 2015).

2.4.3. Network topology levels

At the outset of the network study, the scale of the measures has to be selected. These scales focus on different topology levels of a network (Croft, 2008). This chapter is only introductory, the formulas and definitions of all presented indices will be discussed in detail in the Methods chapter.

Node-based measures, also known as local or individual measures, pertain to the network characteristics of an individual within a given social network. The primary objective is to determine the social role of a member through the use of local network indices (Borgatti et al., 2013). Among these indices, centrality calculations are predominant, and there exist many centrality indices to choose from. The main family of centrality measures includes (1) path-following measures, among which the most commonly employed is Degree (D) in the context of unweighted and undirected networks (Wasserman and Faust, 1994). For directed but unweighted networks, the Out-Degree (OD) and In-Degree (ID) become relevant, where the prefixes "out-" and "in-" denote the number of edges originating from and leading to a node, respectively (Krause et al., 2015). The underlying concept behind all degree measures is that the nodes with the highest number of connections are considered the most central within the network. A closely related group of measures is the $node_i$ reach, which quantifies the number of nodes that are located at a distance i away from a specific node (Krause et al., 2015). Additional path-following node centrality measures encompass Betweenness Centrality, Closeness Centrality, Flow Centrality and Information Centrality. In essence, these measures tally the paths between pairs of nodes that traverse through the node of interest (Wey et al., 2008). Second is the (2) matrix-derived measure method. In this category, two prominent ones are Katz Centrality and Eigenvector Centrality (Borgatti et al., 2013). Katz Centrality evaluates the influence of a node based on the total number of paths that connect it to other nodes, considering both direct connections and indirect connections through intermediate nodes. Eigenvector centrality, on the other hand, assigns importance to a node based on the centrality of its neighbors, emphasizing connections to well-connected nodes (Borgatti et al., 2013). These measures have found extensive use in analyzing social networks to understand the significance and influence of individual nodes within the network (Borgatti et al., 2013).

In the case of intermediate measures, two familiar indices are used to describe the subgrouping within networks. The Clustering Coefficient is used to localize network areas of high and low density (Watts and Strogatz, 1998). The Transitivity or Global Clustering Coefficient (CC) is measured by triad network configurations. If the network's Transitivity is higher (more transitive) the information flow is more „barrier-free" through the network (Borgatti et al., 2013). Cliquishness tells us how the network can be divided into cliques (cohesive subgroups), which are sets of nodes directly connected (Wey et al., 2008).

In network-level measures (also called global network measures), the Network Centralization Index (NCI), is used to show how centralized the networks are. Highly centralized networks look more like a star, where some nodes have significantly more edges than others, forming a center (Borgatti et al., 2013). Furthermore, to measure the „speed" of information between nodes, the Average Path Length (APL) can be calculated (Borgatti et al., 2013). These path lengths can be interpreted as the time required to pass information from one randomly chosen individual to another (Borgatti et al., 2013).

The network measures and indices basically describe the direct effects of interactions between nodes. However, in the 19th century, some studies dealt with the significance of indirect effects on ecology (Wootton, 1994). In trophic networks, it is crucial to determine the spread of the effect of one species to another, both directly and indirectly. Describing positional (also called topological) importance in the network can be useful by calculating Topological Importance (TI) and Weighted Topological Importance (WI) indices to locate keystone species and quantify these indirect effects, as well as the influence of a species on another within the group (Jordán et al., 2006). These indices are defined for the undirected networks but can be measured by weighted or unweighted networks as well (Jordán et al., 2006).

The terms of topological importance of trophic networks can be useful in animal social network measures in many ways. In animal social networks the most commonly used indices to determine network positions were introduced above. However, there is no study of animal social networks that used TI or WI indices to calculate the indirect effects of social interactions in a group of animals. Topological Importance can be crucial, for example, in agonistic networks to locate dominant individuals who lead the group or in the affiliative networks to see which individuals are essential in cooperating or able to take care of the others.

There are more local, intermediate, and global networks used, but this thesis focuses only on those, that were used in the case studies: Network Centralization Index, Average Path Length, and Coefficient of Variation of Topological Importance at the global network level, and Transitivity in the intermediate network level, and Out-Degree, In-Degree, Out-Strength, In- Strength, Topological and Weighted Topological Importance indices in the local network level (Table 2).

In this thesis, my objective is to use topological indices to describe the network properties of multiple animal species (see Chapter 2.6).

2.5. Classification of animal social network studies

This subchapter focuses on the documentation of animal social networks from the years 1997 to 2023. The purpose of this review was to identify the observed and modeled species using various types of social networks, without delving into detailed calculations or specific questions. I established four general categories to filter the vast volume of published papers on this topic to help follow the logical structure of the thesis. These categories are described in the following:

(1) Describing the observed properties of social networks, such as indices, positions, dynamics, and more.
(2) Exploring the relationship between various environmental conditions and social network topology, including seasonal change, infection threats, habitat change, and every condition, which cannot be related to the individuals of the given groups.
(3) Effects of individual behavioral characteristics (moving behavior, foraging habits, caste behavior, etc.) on social network properties.
(4) Statistical predictors (individual’s sex, age, size, etc.) of social network positions and structural characteristics.

All categories are somehow related to the properties of network topology, which is the main focus of this thesis, along with case studies. To gather relevant papers, I used the Web of Science online database, with the search of *animal* and *social network* keywords. The steps of the filtering process are summarized in Figure 1.

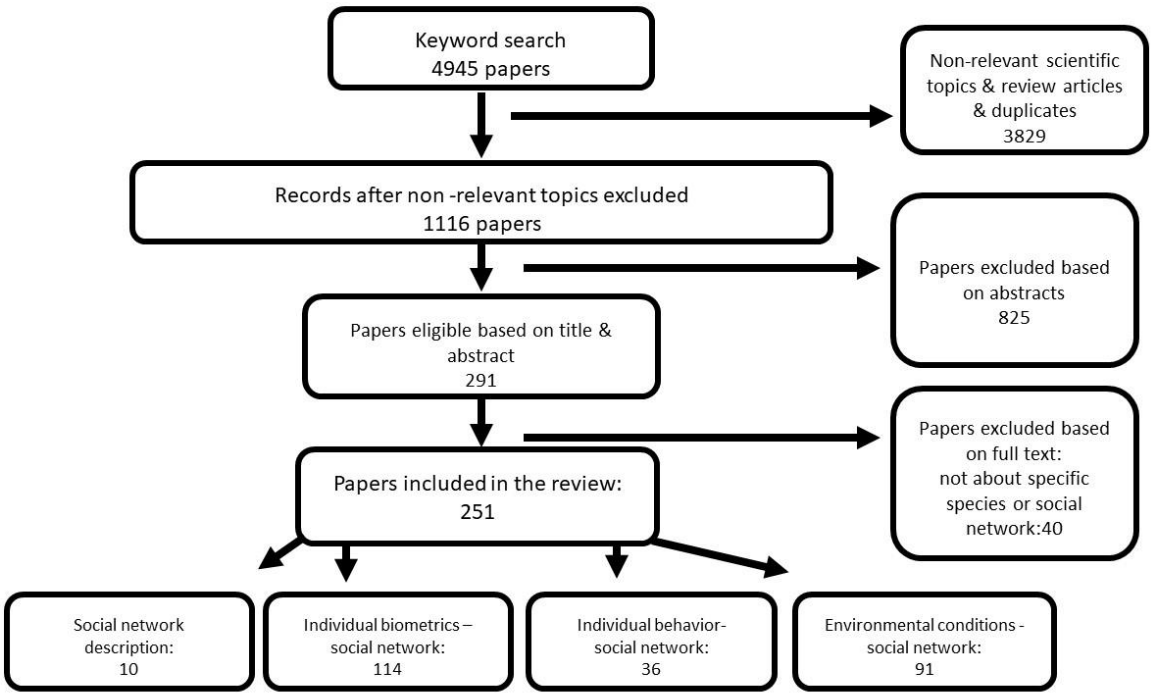

Figure 1 Filtering process of systematic review in animal social network studies.

First of all, I excluded all papers that did not meet the criteria of behavioral ecology, ethology, and evolutionary biology. These publications were mainly related to veterinary, agricultural, or medical sciences. Additionally, genetic and molecular biological experiments were excluded from this review, along with review articles, duplicates, and simulated data.

Secondly, I examined the abstracts of the papers and then excluded all methodological, multi-species, and landscape-related research. The selection of papers was thoroughly inspected by reading the full text of studies using the aforementioned four groups, and any non-relevant papers were once again excluded.

251 papers remained after the filtering process, with 10 papers in group (1), 91 in group (2), 36 in group (3), and 114 in group (4). The case studies of the thesis were not included in this review.

From these 251 publications and 4 groups, the distribution of species in taxonomical classes is presented in Figure 2, and the full list of species are presented in Appendix 1.

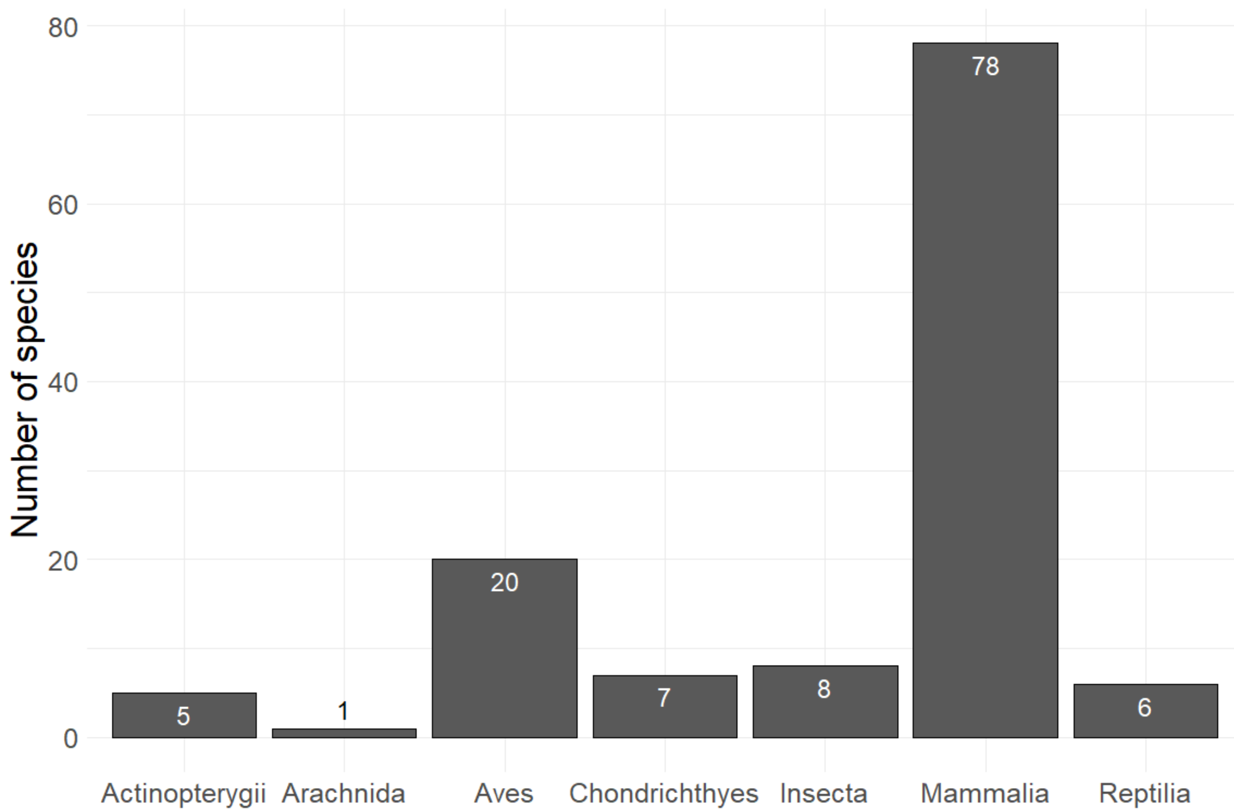

Figure 2 The number of published social networks for various taxa between 1997-2023.

Due to the focus of this thesis, detailed discussions of mammals, birds, and insects are presented here. The majority of species within the mammal group are primates, and among these 25 species, 14 belong to the family of Old-World Monkeys. Carnivores and Ungulates occupied the second and third positions, comprising 12 and 9 species respectively. Furthermore, when examining bird species, passerines were well-represented, with 14 out of 20 species falling under this category. Lastly, among the 8 insect species, the Hymenoptera order accounted for 6 of them. In summary, the diversity of species among the published papers from the year 1997 to 2023 in social networks is relatively high. However, the availability of these studies is highly biased towards mammals, with a primary focus on monkeys. Among these 251 publications, the representation of reptiles, insects, spiders, and fishes is limited to fewer than 10 species. These findings highlight a significant opportunity for shaping future research in this field.

The thesis objects are based on the structure of this review. Each case study corresponds at least to one of the four categories mentioned above.

2.6. Thesis objective

In the first part, my research is about modeling multiple social networks of animal species (*Parus major, Cynomys gunnisoni, Camponotus fellah, Spheniscus demersus*) based on data from collaborations, literature, and the field. As I mentioned above, I followed the idea in Chapter 1.5 about the four categories in social networks, which I defined: (1) Descriptive measures of the social networks: patterns, dynamics, topology, and characteristics, and (2) The relationship between changing environmental conditions and social network topology; for example, the group size or effect of food availability on network structures. (3) How individual behavioral characteristics affect network topology: castes behavior, foraging habits, and different rearing histories in captivity, and (4) the influence of individual attributes on social network structures in individuals: sex, age, and body size.

Second, I aim to compare these networks only on the scale of global and intermediate network metrics (Network Centralization Index, Transitivity, Average Path Length, and Coefficient of Variations in the Topological Importance Index) without edge type and direction to show the fundamental differences between network topologies among species.

2.6.1. Thesis Question 1

How do the individual attributes, environmental, and behavioral conditions shape the social network topologies in Great Tits (Parus major), Prairie Dogs (Cynomys gunnisoni), Carpenter Ants (Camponotus fellah), and African Penguins (Spheniscus demersus)?

Concerning Great Tits, I sampled the data from the field in the winter season at Laczkó-forrás near Veszprém. My aim in this study is to explore the winter behavior of wild Great Tits via social network analysis by two different approaches: the proximity of individuals on the feeders, and agonistic interactions. I use Exponential Random Graph Models to calculate homophily between sexes. Finally, I have only one summarized network in each case. These networks are time aggregated.

Regarding Prairie Dog networks, I received collaboration data from Jennifer Verdolin from Arizona, who has been working with this species for a long time. These 14 networks were affiliative, based on undirected edges called „groom-kisses". I use Node Label Permutation Correlation Models to find the connection between Group Size, Territory Size (m^2), and food availability (Biomass/m^2), and three global measures like Network Centralization Index, Transitivity, and Average Path Length. These network variables cover all the basic topological traits of a social network properly.

In the case of Carpenter Ants, I collected six colonies and sixteen network data sets from the literature by Mersch et al. from 2013. I focus in this study on the role of the queen in a colony and how the working castes (Nurse, Forager, Cleaner) differ from each other in a network aspect. I model only ten days of each colony. I create networks for every day and castes. I define two new artificial categories called subnetworks among individuals: ants directly linked to the queen (Queen Networks, Q) or not (No-Queen networks, NQ). I use Linear-Mixed-Models to test the relationship between the castes and subnetworks and global network indices.

Finally, I collaborated with Budapest Zoo & Botanical Garden to collect behavioral data on African Penguins. In this study, I focused on feeding events when I collected agonistic and food competition network interactional data. The main question is, similarly to Great Tits, how does the individual data affect the network positions. I defined agonistic and food competition categories to describe individuals by networks. I assume that sex, age, and different rearing procedures shape the network topologies in agonistic and food competition networks as well. I use the Node Strength and Weighted Topological Importance local indices to measure network positions. As in Great Tits, I use permuted correlations on local measures and Linear -Mixed -Models for categorical comparisons. I work with 97 sampled days from April to November in 2022.

2.6.2. Thesis Question **2**

How do the social network structures compare to each other? Are there any shared or opposing patterns between the network topologies?

To compare these strictly different species by networks in detail seems quite impossible. Too many specific conditions appear, like taxonomy, wild-captive habitat, interaction definitions, and so on. For that reason, I analyzed the edges without directions, only on a global scale with the same as above the four basic network indices to cover the general topological traits of all social networks: Network Centralization Index, Transitivity, Average Path Length, and Coefficient of Variation in Topological Importance Index.I investigated the relationship between these network indices and the Group Sizes of the species in case studies, to reveal the sensitivity of network topologies from the sizes of the given populations These results may open new directions in the future study of these species and the animal social network topic as well.

3. Methods

In this dissertation, I distinguish between two main categories within my datasets. The first category includes all data with non-network, some external meaning (Chapter 3.1). This includes individual-level variables such as sex, body size, and behavioral characteristics, as well as environmental-level variables like territory size, food availability, and group size. The second category comprises all network-related variables (Chapter 3.2), including network indices, nodes, and edges. Given that each of my four case studies employs distinct data sampling methods, I present them separately to facilitate interpretation (Chapters 3.2.1–3.2.5). Each case study investigates the relationships between these two categories in various ways. Additionally, different populations, networks, and associated questions often necessitate different statistical approaches. Thus, in the subsequent Chapter 3.7, I introduce three different statistical models from existing literature and previous studies for analyzing animal social networks.

3.1. Individual and environmental data

In ecology, individual attribute data (variables) can be collected on four scales (Anderberg, 1973): (1) Nominal data. In this case, the categories are strictly discrete. The only operation meaningful with its values is equality or inequality, and the frequency is allowed to be measured. Examples of nominal scale are color, shape, or any text-based data. A specific case on the nominal scale is binary, which allows only two state levels, 0 or 1 (for example, presence-absence of an attribute). (2) On the ordinal scale, the data have a strict order among the states, for example, the competition results. On this scale, the >, < logical operators are allowed, but there are no numerical differences between the categories for example between the first and second place in a running contest. (3) Interval data scales allow calculating differences between categories, which can be interpreted between defined limits (intervals). The most trivial interval scale is the temperature degrees. (4) All operators can be used on the ratio scale. These values are continuous, like body size, speed, or acceleration. Every calculation, statistic, and analysis depends on these data scales and should be set carefully at the beginning of the research (Podani, 2000).

In this thesis the nominal scales appear in Carpenter Ants as caste definitions of behavioral categories (Nurses, Foragers, Cleaners), sex of individuals, in African Penguins as rearing procedures (handed, parental, mixed), the ratio scale as ages, and in all the network measures will be presented in the following chapters (see data in Appendix 2).

3.2. Network data

The first step in network analysis is to define the edges in the network. Generally, the edge definitions are based on animal interactions or associations (Castles et al., 2014). For example, observing agonistic hierarchies requires aggressive interactions between individuals. Edges represent the associations or interactions between nodes (individuals). Besides the accurate collection of interaction data, the directions and edge weights are essential to set. Thus, they can be either directed or undirected, and symmetrical (unweighted) or asymmetrical (weighted). After collecting the field data, and before the analyses the next step is the conversion of datasets. Two main input data types are used in common. First, the converted data table is called an adjacency matrix or sociomatrix, where the columns and rows represent the same set of individuals, and the matrix entries correspond to network edges. Second, the data table contains 3 columns. The first and second columns are the individuals who are the participants in the given interactions. In directed cases, the first column is the interaction source individual the second column is the target individual and the third column is always the interaction weight column.

3.2.1. Observational network data for wild Great Tits *(Parus major)*

I collected network data of Great Tits in the field. I distinguish two different social network models via interaction and association types in this study. These multiple-edge definitions are based on the interactions during foraging events. The first is the agonistic interactions between birds, which contains every aggressive behavior displayed, chases, and pecks. The edges here are directed and weighted by the frequency of the interactions. The second is the proximity associations. The edges come from the co-occurrence of two birds simultaneously on the feeder for at least one second (common space use associations). Edges in the proximity network are undirected but weighted by frequency. I modeled two networks, agonistic and proximity, by summarizing the given edges over the study period.

3.2.2. Collaboration network data for wild Gunnison's Prairie Dogs *(Cynomys gunnisoni)*

In the study of this animal, I use all occurrences of greet-kissing interactions between individuals as network edges. This interaction is an easily visible, distinct behavior that indicates group membership (King, 1955, Travis and Slobodchikoff, 1993, Verdolin et al., 2014). The edges within the networks are undirected and weighted. I received network data from Jennifer Verdolin, who was the head of this study and I worked with her as a collaborator.

3.2.3. Literature network data for Carpenter Ants *(Camponotus fellah)*

This research is based on a published database on social networks of the ant species *Camponotus fellah* (Mersch et al., 2013). I aim for a time window of the first ten days from 41 days in this study (Mersch et al., 2013). This period is essential for the organization of the colony. The dataset contains six colonies of Carpenter Ants. Edges are associations of proximity (Mersch et al., 2013, Supplementary Materials). Therefore, they are not directed but weighted by frequency.

3.2.4. Observational network data for African Penguins *(Spheniscus demersus)*

Network data on African Penguins came from observing a population in the Budapest Zoo & Botanical Garden. I define two categories of edges: (1) Agonistic interactions. Like Great Tits, it contains all the aggressive behavior events like display, chase, and peck. (2) Food competition interactions. Here, the individuals went for fish during feeding events, and the edges mean who steals or tries to steal the fish from another. Both network types, agonistic and food competition are directed and weighted. The edge weight is the frequency of interactions.

All interaction and association types are summarized in Table 1.

3.2.5. Network data for comparative analyses

For this analysis, I converted daily networks to time-aggregated networks for Carpenter Ants and African Penguin groups. Moreover, I dropped all of the networks with node numbers lower than 5, to avoid sample size bias during analysis. That issue appeared only in Prairie Dog networks. Due to the high level of heterogeneity among species and their networks, I only measured the networks without directions and weights, regardless of the network types, focusing on the presence or absence of a relation between individuals within groups to model and compare information flow dynamics through the social networks.

Table 1. Interactions, associations and edge definitions in case studies.

Species	Interaction/ association	Edge	Network	Data source
Gunnison's Prairie Dog	Greet-kisses	Undirected Weighted	Greet-kiss (Grooming)	Collaboration: Jennifer Verdolin
Carpenter Ants	Touching another individual's antenna	Undirected Weighted	Communication	Literature: Mersch et al., 2013
Great Tit	Agonistic display, chase, peck	Directed Weighted	Agonistic	Field data Laczkó-forrás, Veszprém
	Feeding together on the feeder	Undirected Weighted	Proximity	
African Penguin	Agonistic display, chase, peck	Directed Weighted	Agonistic	Field data Budapest Zoo & Botanical Garden, Budapest
	Get the fish, steal the fish from another, or try.	Directed Weighted	Food competition	

3.3. Local network indices

3.3.1. Node Degree (D)

The simplest network index is the Node Degree, which is also called Degree. The Degree is the number of direct edges an individual has:

$$D_i = \sum e_i$$

where e_i is the number of edges connected to node i. The directional version of Degree is Out-Degree, which is the source of the interaction, and In-Degree is a target of the same interaction (Wasserman and Faust, 1994):

$$OD_i = \sum oe_i \quad \text{and} \quad ID_i = \sum ie_i$$

where, oe_i and ie_i are the summary of directed edges connected to node i (Wasserman and Faust, 1994).

3.3.2. Node Strength (NS)

The weighted versions of Degrees provide a summary of the edge weights in each node. As I mentioned above, in the case of Degrees, they can also be represented by directed indices, namely Out-Strength and In-Strength, which represent the source and target of weighted edges from and to a node, respectively (Borgatti et al., 2013):

$$NS_i = \sum we_i$$

where we_i is the sum of edge weights in node i, and

$$OS_i = \sum owe_i \quad \text{and} \quad IS_i = \sum iwe_i$$

are the directed versions with owe_i and iwe_i directional edges (Borgatti et al., 2013).

3.3.3. Topological and Weighted Topological Importance (TI,WI)

WI has demonstrated its suitability in modeling agonistic hierarchies and competitive scenarios (Jordán et al., 2006). It assesses the centrality of individuals without taking edge directions into account. Furthermore, WI has been established as a measure of the topological significance of node i Within networks that incorporate weighted edges:

$$WI_i^n = \frac{\sum_{m=1}^{n} \sum_{j=1}^{N} a_{m,ji}}{n}$$

Here $a_{m,ji}$ is m-step effect from a node i to node j, which in this case is 2 steps. Parameter a comes from the formula $a = \frac{we_{ij}}{\mu_i}$, where e_{ij} is the edge weight between nodes i and j, and μ_i represents the sum of the edge weights of node i. It calculates the importance of an individual in the social network and calculates how one individual's effect spreads to others indirectly. The nonweighted case of WI is TI, the Topological Importance Index (Jordán et al., 2006).

3.4. Intermediate network indices

3.4.1. Transitivity (CC)

Also called the Clustering Coefficient. The CC gives information on how cliquish information is spread in the network. High CC means the individuals are tightly linked to small groups with relatively poor connections to each other (Borgatti et al., 2013). Low CC means a larger diversity of edges, less cliquish structure, and information potentially spreading more freely in the network (Borgatti et al., 2013). The CC of node (NCC) i equals the density of the subnetwork composed of the neighbors of node *i* (Borgatti et al., 2013). This is the probability that its two neighbors *j* and *k* will be directly linked to each other. It can be defined as:

$$NCC_i = \frac{2 \text{ x } |E(G_i)|}{D_i \text{ x } (D_i - 1)}$$

where *Gi* is the subgraph composed of the nodes that are directly linked to node *i*, |*E(Gi)*| is the number of edges in this subgraph and D_i is the degree of node *i*. The whole network can be characterized by the Transitivity, which is the average calculated NCC for all nodes (Borgatti et al., 2013).

3.5. Global Network Indices

3.5.1. Network Centralization Index (NCI)

The NCI quantified the overall shape of the network. It shows how hierarchical are the given networks (Wasserman and Faust, 1994). If the Degree for node i is D_i and the largest Degree is denoted by D_{max}, then the value of NCI is:

$$NCI = \frac{\sum_i^N D_{\max} - D_i}{(N-1)\ x\ (N-2)}$$

The values of NCI range from 0 (every individual has the same number of connections) to 100 (perfect star, absolute hierarchy with one individual directed to all others). In the directed networks there is a centrality for outgoing edges (Out-NCI) and for the ingoing edges to a node (In-NCI) as well.

3.5.2. Average Path Length (APL)

The APL between two nodes *i* and *j* in a network (d_{ij}) is the minimal edge number connecting them:

$$APL = \frac{\sum_i \sum_j d_{ij}}{2N}$$

This quantifies how long (and slow) is the spread of information between any pair of individuals in the network. It is averaged for all of the path lengths between each pair of nodes, and the path length for nodes *i* and *j* is the minimum number of steps connecting them in the network (it equals 1 for directly linked neighbors) (Wasserman and Faust, 1994, Wey et al., 2008). This can be an indication of the general speed of communication between individuals.

3.5.3. Coefficient of Variation in Topological Importance (CV_{TI})

In addition to all the indices mentioned above, CV_{TI} provides specific information about the social network: the topological influence rates among individuals. It is calculated from the regular coefficient of variation:

$$CV_{\mathrm{TI}} = \frac{\sigma_{\mathrm{TI}}}{\mu_{\mathrm{TI}}}$$

where σ_{TI} is the standard deviation of TI values, and μ_{TI} is the mean of all TI values in nodes.

All used network indices are summarized in Table 2.

Table 2 All used network indices in different topology levels

Topology level	**Index name**
Global	Network Centralization Index (NCI) Average Path Length (APL) Coefficient of Variation of Topological Importance (CV_{TI})
Intermediate	Transitivity (CC)
Local	Out-Degree (OD) Out- and In- Strength (OS, IS) Topological Importance (TI) Weighted Topological Importance (WI)

3.6. Visualization

There are several tools available to visualize social networks. I used two softwares to model my networks. First, I used UCINET software (Borgatti et al., 2002). A good feature of UCINET is the efficient handling interface. The leading network indices can be quickly calculated. It can transform, edit, normalize, and convert network data (Borgatti et al., 2002). In the last few years, UCINET seemed old-fashioned and limited compared to the new tools, but the general SNA calculations are accurate. UCINET is perfect for visualizing Stochastic Network Models (Borgatti et al., 2002). Second, I visualized some of my networks via Gephi (Bastian et al., 2009). With Gephi, the visualization can be more detailed. Considerable edge variability is available, like thickness, color, and shape. In the case of directional networks, the arrows can be personalized as well. The shape, size, color, and position can be easily changed with Gephi. It has the general SNA methods as well, but it breaks down under complicated models. Compared to UCINET, the benefit of Gephi is the Dynamic Network Model method to visualize the dynamic network as well (Bastian et al., 2009). I used UCINET for the studies to model Prairie Dog and Carpenter Ant networks, and Gephi to visualize Great Tit and African Penguin networks.

3.7. Hypothesis testing in studies of animal social networks

Statistical analysis of social network data presents multiple challenges. One of these, the non-independent nature of the data excludes the assumptions of numerous statistical approaches. At present, null models based on data randomizations are the strongest and most adaptable method for network data characteristics (Farine and Whitehead, 2015). However, when comparing network-level measures among populations or species, one potential solution involves studying replicated populations. Each population would generate an independent network-level metric that can be subjected to conventional statistical analysis (Farine and Whitehead, 2015). In this thesis, I present three statistical models through the case studies: *Linear-Mixed-Models (LMM), Exponential Random Graph Models (ERGM),* and *Node-label Permutation Models (NLPM).*

3.7.1. Exponential Random Graph Models (ERGM)

ERGM is a model family for calculating the processes between local network measures and network configurations (Lusher et al., 2013). These network configurations can be any part of the network structure, where the most basic is the Edge Formations (EF). The model computes potential edges between nodes as stochastic variables arranged within an adjacency matrix. The response variables involve the probability of matching the observed network, while the explanatory variables consist of various potential network characteristics (Silk and Fisher, 2017). The mathematical formula of the ERGMs is:

$$P(N) = ce^{\theta_1 z_1(N)+\theta_2 z_2(N)+\cdots\theta_n z_n(N)}$$

Here *P(N)* represents the probability of getting a given network, z is a network configuration, which is weighted by θ external parameter, which can be for example the biometrics of individuals, and *c* is a constant parameter of the model. Edges in a network are formed considering the traits of the connected nodes and the values of nearby edges. This also means that the ERGM framework takes into account how edge values can depend on neighboring edges or other features of the network structure. As a result, the ERGM framework deals with the way the network's structure emerges in specific areas, which helps handle the issue of dependence related to this (Lusher et al., 2013). In practice, we established ERGM in an R studio environment with packages *stanet* and *ergm* (Hunter et al., 2008).

This model can be used for static and time-aggregated single networks. It was the reason why I chose this method for modeling stochastic agonistic and proximity networks in Great Tits.

3.7.2. Linear- Mixed-Models (LMM)

I measured caste effects on global network metrics in six ant colonies with Linear-Mixed-Models (McCulloch and Searle, 2004), where castes (Forager, Nurse, Cleaner) were set as fixed effects and colony was set as random effect. Moreover, to identify and observe variations in network metrics among three zookeeper rearing procedure categories, I employed LMM as well to tests across zoo-housed African Penguin population. Here the rearing categories were used as fixed effect and age categories were used as random effect. To build the models, the 'stats' R package (R Core Team, 2012) was used.

3.7.3. Node Label Permutation Models (NLPM)

To deal with the problem of dependent characteristics of the network data we applied Node Label Permutation Models in Prairie Dog and African Penguin measures. The package *Animal Network Toolkit Software or ANTs* was created specifically for R studio users who are dealing with animal social networks (Sosa et al., 2020). This global package helps users to compute multiple things to figure out different ways to measure networks as a whole, between pairs, and for individual parts.

The Null Model (NM) approach using permutation is one way to test hypotheses statistically. This method lets users analyze data by making random sets from the actual data. They then compare the measured value of interest, like a correlation coefficient, with a distribution of values made from the random sets. This helps determine if the observed value is significantly different from what's expected by chance. The NM approach can be used in different ways. In ANTs, this is possible by adjusting the permutations based on the kind of data collected (either associations or interactions). It also considers the research question – for instance, shuffling nodes when looking at individual network measures or shuffling links when studying individual polyadic or overall measures (Sosa, 2020). In ANTs, there are several statistical tests available under the *'stat'* group in the function family. These tests encompass the correlation test (*'stat. cor'*), t-test (*'stat.t'*). I performed permuted correlation tests to look for relationships between the external variables and network structures.

In a study about Prairie Dogs, I ran the test between global metrics NCI, CC, and APL and environmental conditions territory size, available biomass, and group size. On the other hand, we ran these correlation tests on the local scale of the network in African Penguins as well. Here the external variables were the individual data like sex, and age in captive conditions. In this case the age variables were continous. From the local indices in this measure, we used NS and WI metrics to calculate the network positions of penguins. No transformation is needed in these analyses. In contrast to the Great Tit study, these measures are based on multiple social networks; therefore, ERGMs were not used here.

3.8. Thesis Question 1 – Case studies

In addition to the results and conclusions of the analyses, another important objective of the dissertation is to demonstrate the diversity of animal social analysis methods and the varying availability of these methods for different species, all within the constraints of time and capacity.

I made an effort to present these opportunities with four distinctly different species, each with its unique context and conditions. For example, in Case Study I, I explored the social structures of a wild and rural habituated little songbird, the Great Tit group from Hungary. Moreover, I demonstrated the influence of environmental conditions on the social topology of Prairie Dogs from Arizona. I examined caste differences via SNA in Carpenter Ants from Tel Aviv and for an African Penguin species in a zoo. I conducted all these analyses using three different statistical approaches to demonstrate the various ways that can be employed when dealing with animal social networks.

3.8.1. Case Study I: Great Tit *(Parus major)*

Study site and data sampling

The idea behind this study arose from a gap in knowledge regarding the winter season behavior of wild great Great Tits. Since 2011, the HUN-REN-PE Evolutionary Ecology Research Group has been conducting nestbox monitoring work in both rural and urban habitats within Veszprém city, Hungary with approximately 200 artificial nestboxes in all areas around the city. These data sampling methods were initially focused on the breeding season and the breeding behavior of Great Tits. During the winter season, these songbirds form mixed-species flocks for foraging purposes. As a result, the appearance and availability of food patches play a crucial role in Great Tits throughout the entire winter period (Nakamura and Shindo, 2001). To observe behavioral interactions among individual Great Tits, I installed an artificial bird feeder (see Appendix 3) within a rural forest area in Veszprém known as Laczkó-forrás (Figure 3) in Veszprém.

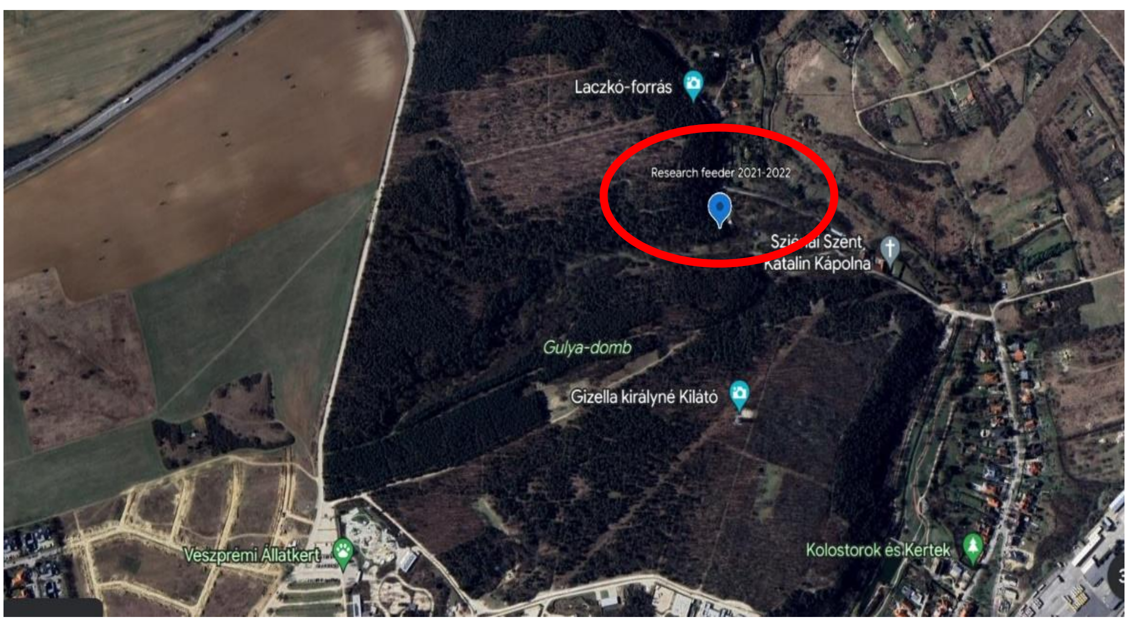

Figure 3 Study site and the artificial feeder (red circle, Veszprém, Hungary, 47^{0}05'38''N, 17^{0}53'0''E).

The observation period lasted from November 7, 2021 to February 22, 2022. I sampled 37 days in these months focusing on the active foraging period on a given day. The behavior of birds was recorded by 4 GoPro cameras hidden inside the feeder (see Appendix 3). I recorded two periods of a day for one hour. The morning session started at 09:00 AM, and the afternoon session started at 14:00. In summary I recorded 74 foraging sessions and 296 hours with four cameras.

Data

In every social network study, the identification of individuals is inevitable. Alongside the nest box monitoring, the research group mentioned above has also been conducting bird ringing since 2011. Therefore, I used their color ring identifications to gather network data from the birds. Each metal-ringed bird has a specific combination of color rings to aid in distinguishing the individual within the video recordings (Appendix 2 (1)). All ring and individual data were accessible within the OpenBiomaps database of the HUN-REN-PE Evolutionary Ecology Research Group (Appendix 2 (1)). I was looking for network-shaping effects of sex, age, and tarsus length attributes. I choose tarsus length as an indicator of body size, which was used in many studies, for example Kölliker et al. (1999). From the 230 relational data, I modeled two time-aggregated networks, based on the two types of edges: agonistic network and proximity network. In this study, I calculated Degree (D) for proximity network, and Out-Degree (OD) for agonistic network as a network metric. All of the relational and network data are summarized in Table 2.

Hypotheses and statistical models

In Case Study I, I posited two primary hypotheses: (1) The sex, age, and tarsus length of individuals have an impact on the Edge Formations (EF) and Out-Degree configurations (OD) of the agonistic network, implying that these individual data factors shape the agonistic network's topology. (2) The sex, age, and tarsus length of individuals also influence the EF and D configurations of the proximity network. To test my hypotheses, I conducted Exponential Random Graph Models (ERGM) to estimate the external factors' influence on these time-aggregated networks (Hunter et al., 2008). A previous study concerning brown capuchin monkeys (*Cebus apella*) and hamadryas baboons (*Papio hamadryas*) used ERGM to quantify the effects of individual attributes on EF (Lutz et al., 2019). The findings indicated a tendency for individuals within these species to form edges with others possessing similar attributes, and these EF were sensitive to age differences (Lutz et al., 2019).

3.8.2. Case Study II: Prairie Dog *(Cynomys gunnisoni)*

Study site and data sampling

Gunnison's Prairie Dogs are diurnal and socially active species of ground squirrels, inhabit exclusively the grasslands of the Colorado Plateau (Hall and Kelson, 1959). The data used for the analyses conducted in this study were derived from behavioral and vegetation observations gathered from two colonies (HS and CC) from March to August 2004. These data pertain to three distinct, non-overlapping populations: CCI, HSI, and HSII. Both colonies were situated within the municipal boundaries of Flagstaff, Arizona (see details in Verdolin et al., 2014).

Data

In this research, previously published social networks (Verdolin et al., 2014) are employed. These networks were established based on all instances of greet-kissing, aiming to assess the impact of aboveground resource biomass on shaping overarching network characteristics. To provide a succinct overview, the networks were formulated by including adult and yearling males and females, encompassing all potentially reproductive individuals. These networks were unweighted and undirected. Verdolin et al. (2014) previously showed that greet-kissing constitutes a dependable behavior, suitable for constructing social networks within the context of Gunnison's Prairie Dogs. To provide a comprehensive depiction of the networks, I calculated the Network Centralization Index (NCI) to capture the overall structure of networks, taking into account all connections that individuals hold within the group. Additionally, I evaluated the Transitivity (CC) as an indicator of the likelihood that an individual's immediate neighbors are interconnected. I also computed the Average Path Length (APL) for the minimal number of links connecting two individuals (Table 2). All the modeled networks were weighted and undirected. Multiple ecological variables were used in this study. Aboveground foraging Biomass (biomass/m2) was calculated during a previous study on these Prairie Dog populations. This research focused on exploring the relationship between resources and social structure (Verdolin, 2007). Territory Size (TS), measured in square meters (m^2), was determined through the utilization of a fixed kernel density estimator, relying on the positional data of social group members. Subsequently, the mean dry weight of food plant samples was derived by procuring samples of 100 cm^2 from fifteen arbitrarily selected 100 m^2 quadrants quadrats within each territory. Finally, the Group Size (GS) variable was calculated by taking simply as the number of individuals within groups.

Hypotheses and statistical models

In this study, I focused only on the global and intermediate network levels. My hypothesis aimed to explore the relationship between ecological variables (group size, territory size, and biomass/m2) and selected network metrics (NCI, CC, and APL). To answer my question, I used Node Label Permutated Models to correlate the variables.

3.8.3. Case Study III: Carpenter Ant *(Camponotus fellah)*

Study species and data

My research relies on information from a published database about social interactions among ants of the species *Camponotus fellah* (Mersch et al., 2013). This particular ant species is commonly found in dry and warm regions of North Africa and the Middle East. They have different types of worker ants, each with its own tasks. Younger ones are Nurses, middle-aged ones are Cleaners, and older ones are Foragers. Their roles depend on age rather than size, which is called age polyethism. When worker ants are isolated, they lose weight, change their behavior (moving more), and have a shorter lifespan. This happens because they eat less when they're they are alone, which is a result of losing social interactions. One key ants interact is by sharing food through trophallaxis, which helps the group stay united. I was focusing on the first 10 days of a 41-day experiment (Mersch et al., 2013) because this initial period seems to be very important for how the ant colony organizes itself.

Network models

In the networks of this study networks, nodes represent ant individuals and edges represent associations by proximity (Mersch et al., 2013, Supplementary Materials). Associations are not directed and not signed but weighted by interaction frequency (data also exist for the duration of interactions, not used here). I studied six ant colonies with three castes: Nurses (N), Foragers (F), and Cleaners (C). I modeled networks for each day for each colony and castes as well (Appendix 4 (3). In addition, I established two further groups, individuals linked to the Queen (Q), and those not linked to the queen (NQ). I labeled these new groups as subnetworks, and they were modeled with networks for each day and colonies as well. I measured these temporal network topologies to follow colony dynamics during this short period. In summary, I modeled and studied 360 timeordered networks (6*6*10= six colonies* whole networks- N, F,C castes - Q, NQ subnetworks* 10 days).

Hypotheses and statistical models

After all the network models across all colonies castes and subnetworks types, my focus shifts to comparing the castes using global and intermediate network measures (NCI, CC, and APL). I employed Linear-Mixed-Models to identify the castes and subnetwork effects on metrics above. Each statistical analysis was conducted using R Studio software (R Studio Team, 2020). The main hypotheses in this study: The castes and subnetworks are the predictors of the NCI, CC, and APL indices. I set colony categorical variable as random factor in this models.

3.8.4. Case Study IV: African Penguin *(Sphensicus demersus)*

Study site and data sampling

The sampling of behavioral data took place at the penguin enclosure of the Budapest Zoo & Botanical Garden in, Budapest, Hungary. The enclosure covered a space of approximately 15 m x 15 m meters, without a specific geometric shape, and included a central pool. Adjacent to the enclosure, there was an elevated viewing point that offered a comprehensive view of the feeding area, where the animals assembled before feeding. The penguins were fed twice daily. The African Penguin group consisted of 29 members, comprising 16 males, and 13 females. Nearly all the birds were outfitted with distinct combinations of colorful identification bands on their wings, enabling individual recognition. In situations where birds lacked these bands, unique physical characteristics allowed for identification. One bird had experienced blindness from a young age. The ages of the birds ranged from 1 year to 28 years.

Data

All the individual data variables are listed in Appendix 2 (4), and were obtained from the Zoo's database. I rounded up juveniles for 1 year, exhibiting different gray fledgling colors and distinct behavior from mature birds, other age variables were rounded to whole years as well. In addition, to measure the effect of juveniles I established a categorical variable for age with two classes: adult and juvenile The caretakers of the Zoo defined three rearing categories: reared by parents, reared by zookeepers, reared by both parents and zookeepers. I used parent, hand, and mix names for these variables, respectively.

The observation took place between the 8th of April and 18th of November, 2022. The morning feeding started between 9:30 and 10:00, depending on the season, while the afternoon feeding started at 16:00. The observation started 30 minutes before the feeding and lasted until no more fish remained, and the keeper left the area; therefore, the observation lasted approximately 45 min in total, and I merged two feeding events into one sampling day. During the study, 97 sampling days were recorded in total. My study focused on agonistic food competition behaviors; therefore, just the following interactions were recorded (Eggleton and Siegfried, 1979): displays, chasing events, pecks, successfully stealing fish, going for the same fish, and successful and unsuccessful fish stealing. I presented a summary of the interactions and edge definitions about penguins in Table 3.

Table 3 Definition of networks and edges in the Case Study IV

Network	Type	Interactions	Edge weight 1	Edge weight 2	Edge weight 3
Agonistic: behavior with the absence of food	Directed and weighted	Point threat, gape, sideways stare, alternate stare ,chase, peck	Bird A exhibits an aggressive display to bird B	Bird A is chasing bird B without pecking	Bird A pecks or starts a fight with Bird B
Food competition: Behaviour with the presence of food	Directed and weighted	Fight for the fish at the same time and win the fish, unsuccessfully try to steal the fish, successfully try to steal the fish	Bird A attempts to steal a fish from bird B, but does not succeed	Bird A attempts to steal a fish from bird B, and succeeds or wins the fight for the food and eats the fish	

In agonistic networks, the edge weights were determined based on the categorical range of physical effort invested by individuals, ranging from (1) displays, where no physical contact is exhibited, to (2) chasing, where there is no physical contact but more aggression invested, and finally to (3) actual fights. Regarding food competition networks, the edge weights were determined based on the success of getting food more effectively than others, ranging from (1) attempting to steal to (2) successfully stealing or winning the fish.

Network data

I constructed an agonistic network and a food competition network for each of the 97 days (194). In this study, the network positions were determined by two network metrics. First, I utilized the Out- and In-Node Strength (OS and IS) (Squartini et al., 2013), and then I calculated the OS and IS differences (DI = OS - IS). It can be used to calculate aggression and food competition rates expressed by signed integers or zero. Strong aggressors and competitors are assigned large positive numbers, while non-aggressive and weak competitor individuals are assigned small negative numbers. Second, I measured Weighted Topological Importance (WI), which proved to be the most appropriate for modeling agonistic hierarchies and food competition conditions (Jordán et al., 2006). The DI index was used to calculate aggression rates with edge directions among individuals. However, WI indicated the centrality positions of individuals without considering edge directions.

Hypotheses and statistical models

This study aimed to determine which individual variable significantly affect network topoligies in African Penguins. My hypotheses were as follows: (1) Network indices are determined by rearing categories in both agonistic and food competition networks. (2) Sex and age discrete categories significantly differ from each other, and continuous age variables significantly correlate with network index values in both agonistic and food competition networks.

I employed the Linear-Mixed-Models to assess the rearing procedure effect on the DI and WI network indices within both network types. To calculate sex and age categorical differences I used NLPM t-test. For the correlation tests, I conducted NLPM correlations to uncover relationships between variables. In cases where DI or WI exhibited significant differences or correlations, I identified these individual variables as influential factors shaping the given network structure.

All of the hypotheses over the case studies are summarized in Table 4.

Table 4 All of the set hypotheses concerning Thesis question 1 distinguished into the three category of the systematic review in Chapter 2.5. To facilitate interpretation, these hypotheses have been assigned capital letter codes for further use.

Category	**Case study**	**Hypothesis**	**ID**
Individual attributes and network structures	I	The sex, age, and tarsus length of individuals have an impact on the EF and OD configurations of the agonistic network, implying that these individual factors shape the agonistic network's topology.	H1
Individual attributes and network structures	I	The sex, age, and tarsus length of individuals also influence the EF and D configurations of the proximity network.	H2
Environmental conditions and network structures	II	NCI, CC, and APL correlate with GS, TS, and biomass/m^2 environmental variables	H3
Individual behavior and network structures	III	The global and intermediate network indices, NCI, CC, and APL differ significantly between castes and subnetworks.	H4
Individual behavior and network structures	IV	Network indices are determined by rearing categories in both agonistic and food competition networks.	H5
Individual attributes and network structures	IV	Sex and age discrete categories significantly differ from each other, and continuous age variables significantly correlate with network index values in both agonistic and food competition networks.	H6

3.9. Thesis Question 2 – Comparison of global network properties of the case studies

In all of the social networks created, global and intermediate network metrics were calculated. The networks were modeled as undirected and unweighted, and calculations were performed using RStudio software (RStudio Team, 2020). All networks were time-aggregated within a given case study window. Each network's NCI (Network Centralization Index), CC (Transitivity), APL (Average Path Length), and CV_{TI} (Coefficient of Variation in Topological Importance Index) were calculated using RStudio, with the R script for TI values available on GitHub (https://github.com/hidasandris/Network-scripts).

Considering the potential influence of group sizes within the networks, Group Size (GS) was included as a new variable among the global metrics. Multivariate analysis was performed to measure all social networks at the global and intermediate levels (including GS), encompassing 2 Great Tits, 11 Prairie Dogs, 6 Carpenter Ants, and 2 African Penguin time-aggregated social networks. All global and intermediate indices were calculated for each network.

For the analysis, only 11 Prairie Dog networks were used, as networks with fewer than 5 nodes could cause a sample size bias and were considered outliers and thus removed from the data. The focus was solely on the presence of any connection, regardless of interaction and association types (agonistic, proximity, food competition). To ensure comparability among various networks, the index data were normalized, constraining values between 0 and 1.

Standardized Principal Component Analysis (PCA) (Karl, 1901) was performed on the data matrix of the results of 126 objects and 5 variables based on the 21 networks in 4 species. Subsequently, an effort was made to distinguish network indices and GS data into clusters using Hierarchical Clustering (HC) with the single-link method (Sneath, 1957) to observe how social network data can be separated based on species.

4. Results: Thesis Question 1 – Case studies

4.1. Case Study I: Great Tit *(Parus major)*

All of the ERGM results are summarized in Table 5. The results show that tarsus length, as an indicator of body size has a negative significant effect on EF, D and OD network configurations in networks. However, sex has not shown any significant influence on any network configurations in both networks. Besides the tarsus length, the ages of the birds negatively affected the OD and EF only in agonistic networks. The network graphs are visualized on Figure 4.

Table 5 Results of ERGMs in the case study I, Great Tits *(Parus major)*.

External variable	**Network variable**	**Network**	**Estimated parameter**	**P value**
Sex	OD	Agonistic	-0.089	0.521
	EF		0.141	0.269
Age	OD		-0.141	**0.026**
	EF		0.123	0.043
Tarsus length [cm]	OD		-0.091	**<0.001**
	EF		-0.312	**0.005**
Sex	D	Proximity	-0.064	0.735
	EF		0.109	0.51
Age	D		-0.051	0.505
	EF		0.133	0.054
Tarsus length [cm]	D		-0.091	**<0.001**
	EF		-0.312	**0.005**

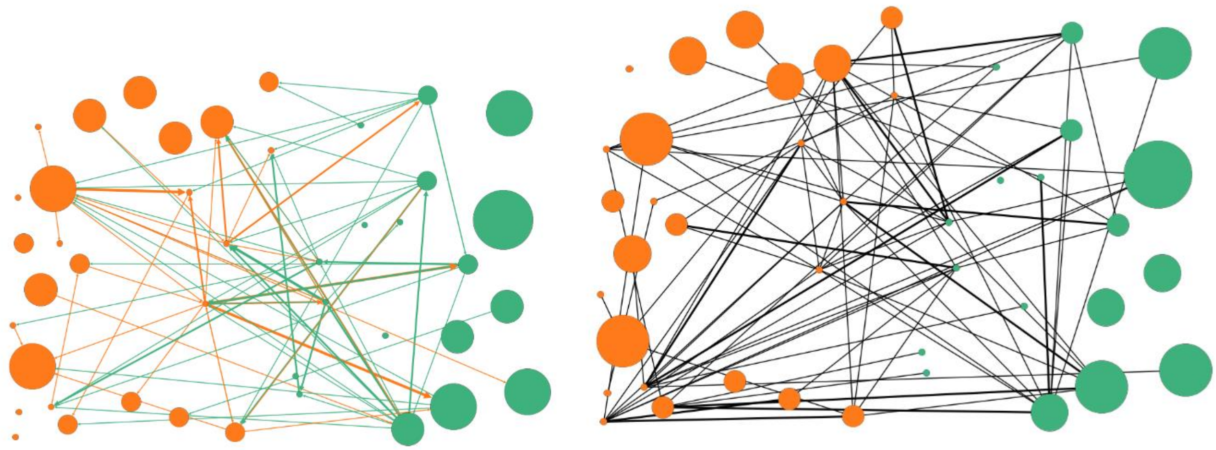

Figure 4 Visualization of social networks in Great Tits via Gephi software. The agonistic (left) and proximity (right) network are shown. Orange nodes represent the female, and green nodes the male birds. The edge colors in the agonistic network show the affector node in the given edge, and node sizes show the age of individuals.The proximity network has no direction, therefore, black edges represents the undirected connections between nodes The thickness of edges represents the edge weights.

4.2. Case Study II: Prairie Dog *(Cynomys gunnisoni)*

14 social network graphs were modeled (example: Figure 5), and the results of the statistical analyses are presented in Table 6. The CC remains relatively stable in this case, exhibiting no significant relationship with GS, TS, or available Biomass within the territory. However, the NCI exhibits a statistically significant negative correlation, while the APL displays a statistically significant positive correlation with both GS and TS. Conversely, no significant correlation was observed between Biomass and the network indices.

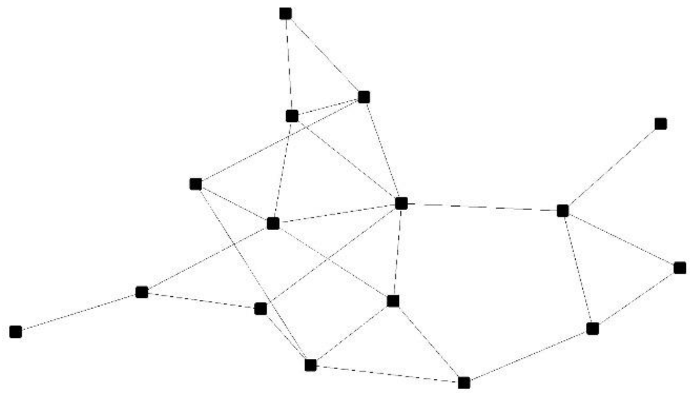

Figure 5 An example of one Gunnison's paririe dog „greet-kiss" affiliative social network. Nodes represent the individuals, and edges are positive „greet-kiss" interactions among them. These networks are undirected and unweighted.

Table 6 Results of NLPM correlation tests between environmental and network variables in Prairie Dog grooming social networks.

Environmental variable	Network variable	Estimated parameter	P value
Group size	NCI	-0.766	**<0.001**
	CC	-0.296	0.131
	APL	0.856	**<0.001**
Territory size	NCI	-0.692	**0.001**
	CC	-0.259	0.233
	APL	0.511	**0.049**
Biomass	NCI	-0.138	0.313
	CC	-0.004	0.466
	APL	0.061	0.397

4.3. Case Study III: Carpenter Ant *(Camponotus fellah)*

The individual centrality (TI) values of nodes change over time (Figure 6). At the level of nodes, there is extreme turnover in the identity of the most and least central ants, but the variability of TI indices shows quite consistent trends over the colonies. All colonies become more dense during these 10 days. My analysis showed significant differences in the NCI and CC values among castes when compared to the reference category (C values): networks of F and N castes have significantly higher NCI and CC values. For APL, the C castes' networks show higher values than those of the F and N castes (Table 7). I visualized networks in one day in colony I on Figure 6

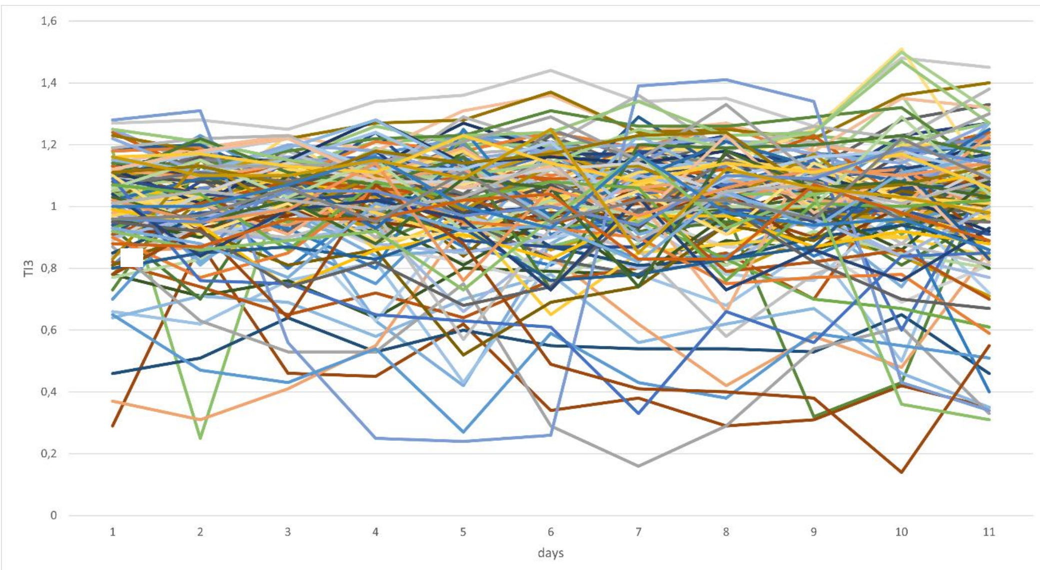

Figure 6 TI values for all nodes over 10 days in Carpenter Ants.

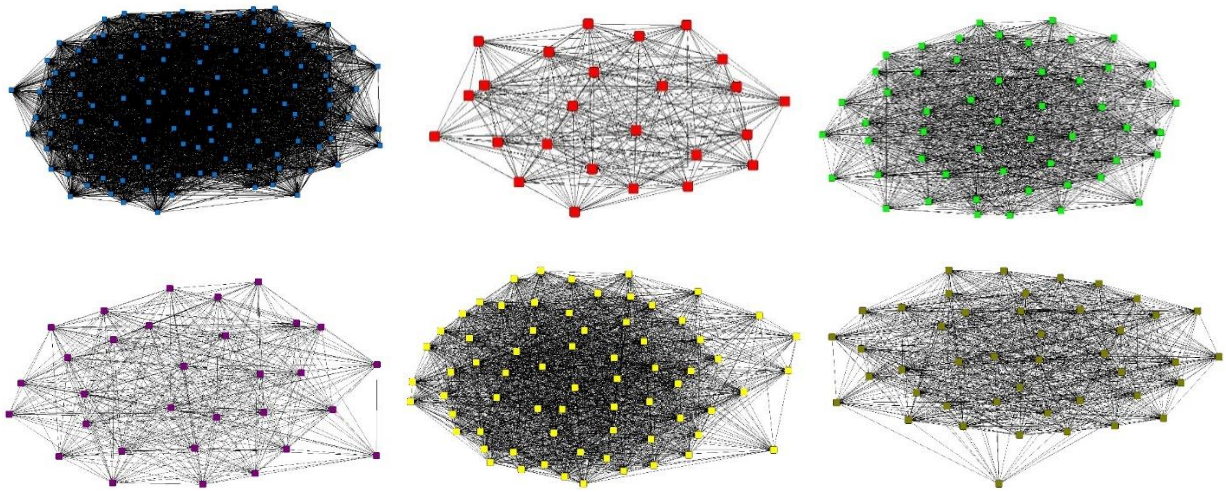

Figure 7 Social network graphs of Carpenter Ants of colony I in day 1 in all network, caste and subnetwork levels. Node-colors: blue-Whole Network, red-Nurses, green-Foragers, purple-Cleaners, yellow-Queen-subnetwork, lightbrown-No-Queen subnetwork.

Table 7 Caste and Subnetwork effect on NCI, CC, and APL global and intermediate network indices First column represents the estimated coefficients of the model. The results of the predictors (columns) are from bivariate LMM models The stars represents the categorical rates of p-values: * = p<0.05; ** = p<0.01; *** = p<0.001.

Castes and subnetworks	NCI	CC	APL
C (reference level)	11.151	7.785	1.157
F	2.672**	5.064***	-0.085***
N	2.314*	0.987*	-0.070***
NQ	-1.411	0.037	0.083***
Q	-0.377	-0.294	-0.017

4.4. Case Study IV: African Penguin *(Spheniscus demersus)*

The network graphs of the first day in both cases as an examples are visualized on Figure 8.

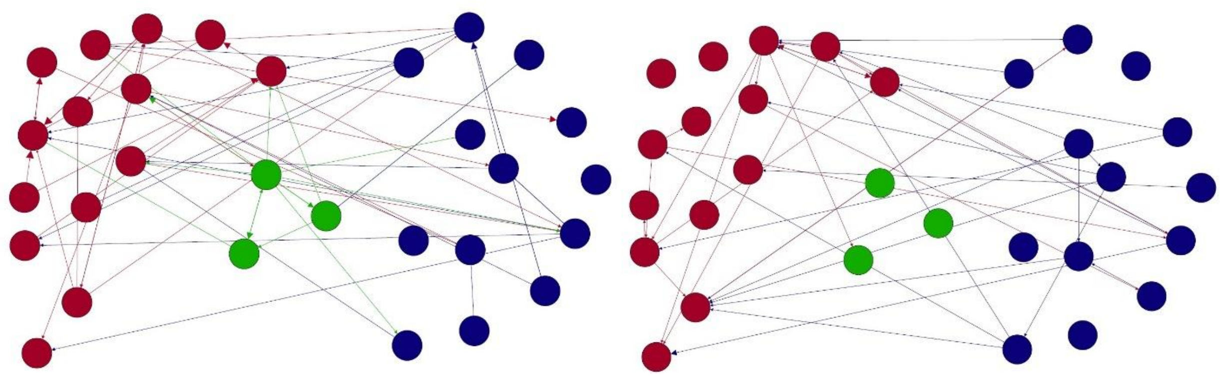

Figure 8 Visualization of agonistic (left) and food competition (right) networks on day 1 in African Penguins via Gephi software (green nodes: juvenile (age < 1 year), blue nodes: adult male, red nodes: adult female, edge color represents the source of the interaction).

I calculated local network indices WI and DI. All three, rearing history, sex, and age individual data showed a shaping effect on network positions. Table 8 presents the results of NLPM t-correlations between age and network indices.

Table 8. Results of NLPM correlation tests between individual age and network variables in African Penguin social networks.

External variable	Network variable	Network	Correlation coefficient	P-value
	DI	Agonistic	-0.324	**<0.001**
Age	WI		-0.449	**<0.001**
	DI	Food competition	0.03	0.106
	WI		-0.049	0.099

The results show that during foraging, the age of individuals does not affect the success of the food competition network. However, a negatively significant correlation was found in the agonistic network between the age and network variables.

Moreover, DI values were significantly higher for males than females in both networks, but female WI values in food competition networks were higher than male WI values. In the tests of age category comparisons, juvenile DI was significantly higher in agonistic and food competition networks as well. However, adult WI in the food competition network was also higher than juvenile WI, meanwhile, juvenile WI was significantly higher in agonistic networks. All results are summarized in Table 9.

Table 9 NLPM t-test results in African Penguin agonistic and food competition networks between sexes.

Network	**Differences**			**Network Index**	**T parameter**	**P value**
Agonistic	Male	>	Female	DI	-14.576	**<0.001**
Food competition	Male	>	Female		-6.719	**<0.001**
Agonistic	Male	>	Female	WI	-5.801	**<0.001**
Food competition	Male	<	Female		7.218	**<0.001**
Agonistic	Adult	<	Juvenile	DI	-18.664	**<0.001**
Food competition	Adult	<	Juvenile		-4.148	**<0.001**
Agonistic	Adult	<	Juvenile	WI	-21.229	**<0.001**
Food competition	Adult	>	Juvenile		7.218	**<0.001**

Finally, the rearing procedures also shaped the network positions significantly. In agonistic networks mix and parental-rearing categories have significantly higher DI values than hand-rearing categories (Table 10). Mix has also higher DI values than hand-rearing categories as well (Table 10). In food competition networks parent and mix values were also higher than hand-rearing values (Table 10).

Table 10 Rearing effect on DI and WI network indices The first column represents the estimated coefficients of the model. The results of the predictors (columns) are from bivariate LMM models The stars represent the categorical rates of p-values: * = p<0.05; ** = p<0.01; *** = p<0.001.

Network	**Rearing type**	**DI**	**WI**
Agonistic	Hand (Reference)	6.182	1.167
	Parent	1.245	0.432***
	Mix	4.290***	0.286***
Food	Hand (Reference)	0.121	0.535
Competition	Parent	0.269	0.429***
	Mix	0.287	0.352***

4.5. Conclusion – Thesis Question 1 – Case studies

Concerning the relationship between individual data and network structures four hypotheses were answered.

H1 and H2: *The sex, age, and tarsus length as body size indicators of individuals have an impact on the Edge Formation and Out-Degree configurations of the agonistic network, implying that these individual data shape the agonistic network's topology.*

Sex had no effect on network structures on both proximity and agonistic social networks as well. However, age was considered a good predictor of Out-Degree and Edge Formation in the agonistic network as a negative effect. Tarsus length was also a good predictor variable in both proximity and agonistic networks negatively.

H3: *NCI, CC, and APL correlate with Group Size, Territory Size, and Biomass/m^2 environmental variables.*

Global network index relationships were found in testing the hypothesis of Gunnison's grooming social networks.Available Biomass on the group territories has not shown any relationship with network indices. Territory Size with NCI exhibited a negative correlation and with APL a positive correlation. NCI and APL showed negative correlations with the Group Size values. In summary, NCI and APL about the Group and Territory Sizes can be used as a predictor of group structures on global and intermediate network levels.

H4: *The global and intermediate network indices, NCI, CC, and APL differ significantly between castes and subnetworks.*

Concerning the relationship between individual behavior and social structure, castes and subnetwork differences emerged in the answers to the hypothesis in the case of Carpenter Ants. Caste effects were found in NCI and CC, where forager (F) and nurse (N) castes exhibited higher NCI values than cleaner (C) castes. Opposite results appeared in APL, where C values were higher. Moreover, the subnetworks No-Queen related (NQ) APL values were higher than C APL values.

H5*: Network positions are significantly different between rearing categories in both agonistic and food competition networks.*

The network positions, characterized by DI and WI indices, were influenced by the rearing history of individuals. Within agonistic networks, individuals raised in mixed environments exhibited a significantly higher level of DI compared to those reared by parents or through hand-rearing processes. Conversely, within food competition networks, the influence of rearing type appeared less pronounced, with no significant differences observed between rearing categories. Regarding WI, both parent and mixed rearing categories showed significantly higher results than the hand-reared category in both agonistic and food competition networks.

H6*: Sex and age discrete categories significantly differ from each other, and continuous age variables significantly correlate with network position values in both agonistic and food competition networks.*

Male-biased differences were found in DI indices in both agonistic and food competition networks. However, WI indices were also higher in males in agonistic networks, but in food competition networks females had higher WI. That is, DI and WI-generated network positions were highly sensitive to the sex of the individuals. Concerning age categories, juveniles reached the highest DI and WI values in agonistic networks, but adults were more central (WI) in food competition networks. DI values in food competition networks were still juvenile-biased. Like the sex variables, age also serves as a robust predictor of network positions in this context. The correlations between age as a continuous variable and the DI and WI indices further substantiate these findings. These correlations reveal a significant relationship that favors younger penguin individuals, demonstrating a negative correlation.

5. Results: Thesis Question 2 – Comparison of global network properties of the case studies

Analyses of 2 Great Tits, 11 Prairie Dogs, 6 Carpenter Ants, and 2 African Penguin time-aggregated social networks are demonstrated here. Except for Carpenter Ants, these are the first modeled social networks in their respective contexts. My study here focuses solely on the global and intermediate scales of network topologies presented above, describing trends and connections between network indices among the case study species.

Numerous global and intermediate network indices have been introduced in Chapter 2.5.1 (NCI, CC, APL, CV_{TI}). Furthermore, these indices were assessed across all study species in this section. Given the considerable variance observed among network samples within species, our current objective primarily involves delineating trends and patterns, abstaining from drawing enduring conclusions. Before embarking on any comparisons, I conducted a Principal Component Analysis (PCA) to calculate the correlations among all the aforementioned indices and Group Size (GS) of all studied species (Figures 9-10).

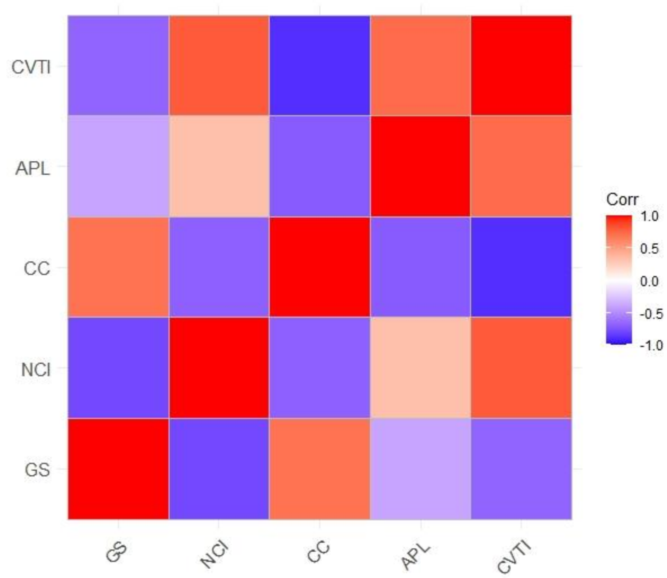

Figure 9 Results of Spearman rank correlation using 4 network indices and GS values from 21 time-aggregated networks. The correlation coefficients range between red (1) and blue (-1).

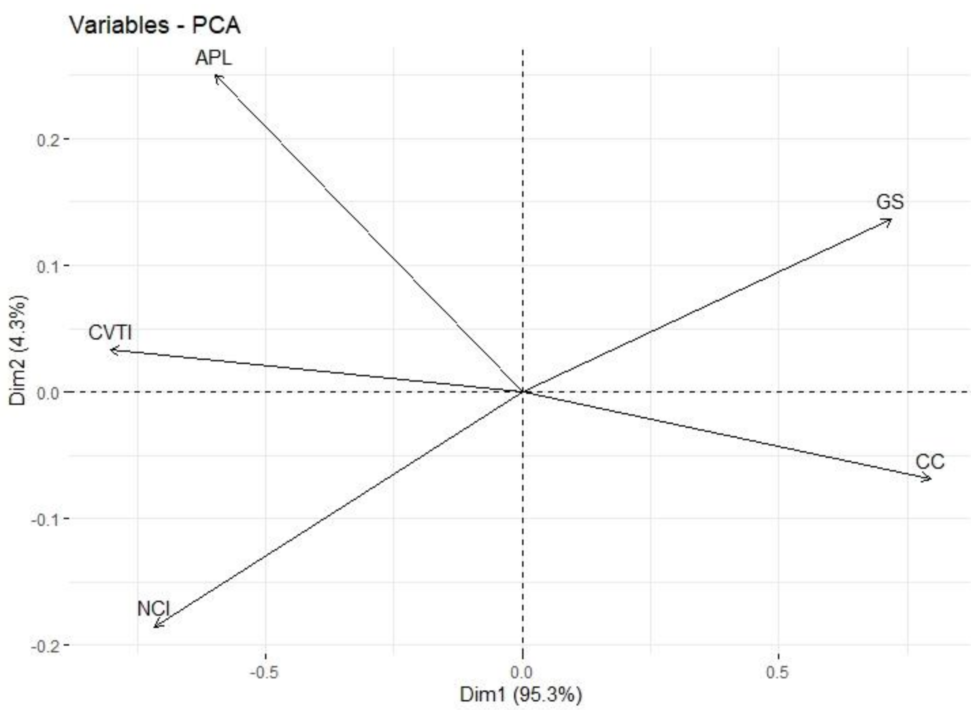

Figure 10 Biplot of standardized PCA with two dimensions based on 4 indices and GS values in 21 social networks.

The PCA results in terms of GS, negative correlations were observed between the NCI and CV_{TI} indices (Figures 11 and 14). However, GS has not exhibited any visible trends in relation to CC (Figure 12), nor APL (Figure 13). Moreover, NCI showed no strong negative relationship (corr > 0.5, Figure 9) with CC (Figure 15), and APL (Figure 16). CC showed negative correlations with CV_{TI} (Figure 19) and APL (Figure 18) as well. Positive relationship pattern appeared between APL and CV_{TI} indices as well (Figure 20). NCI and CV_{TI} also exhibited a strong positive relationship trend (Figure 17).

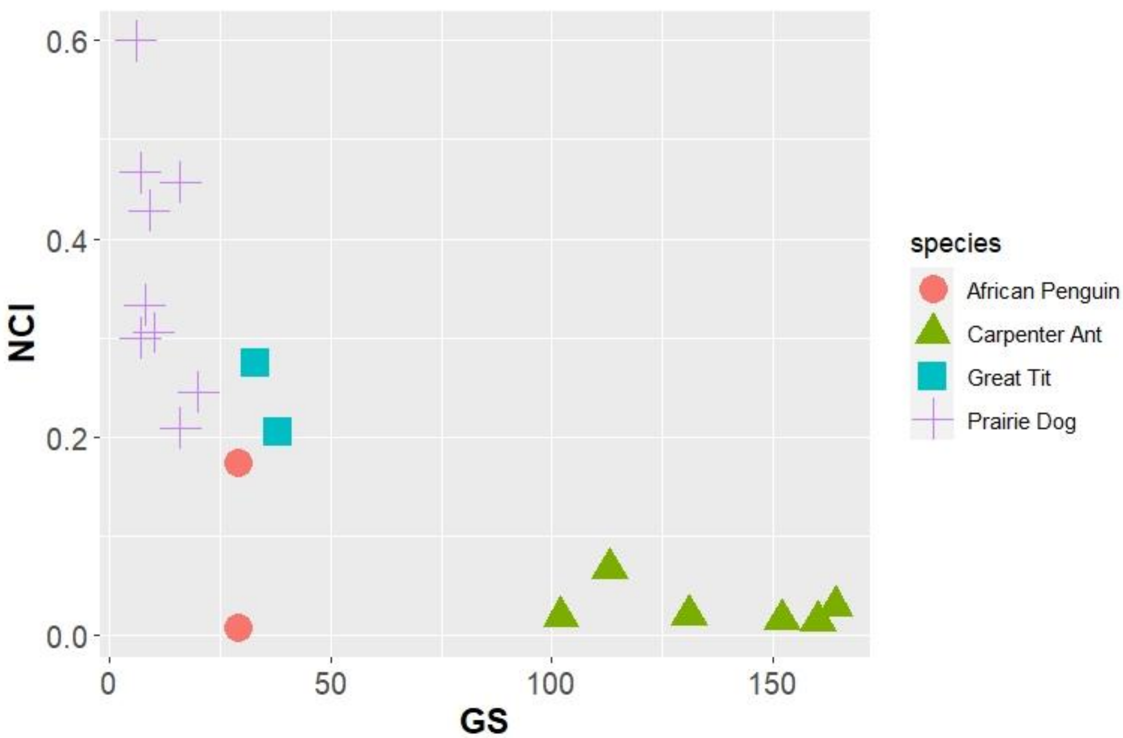

Figure 11 Scatterplot of Group Size (GS) and Network Centralization index (NCI) within study species.

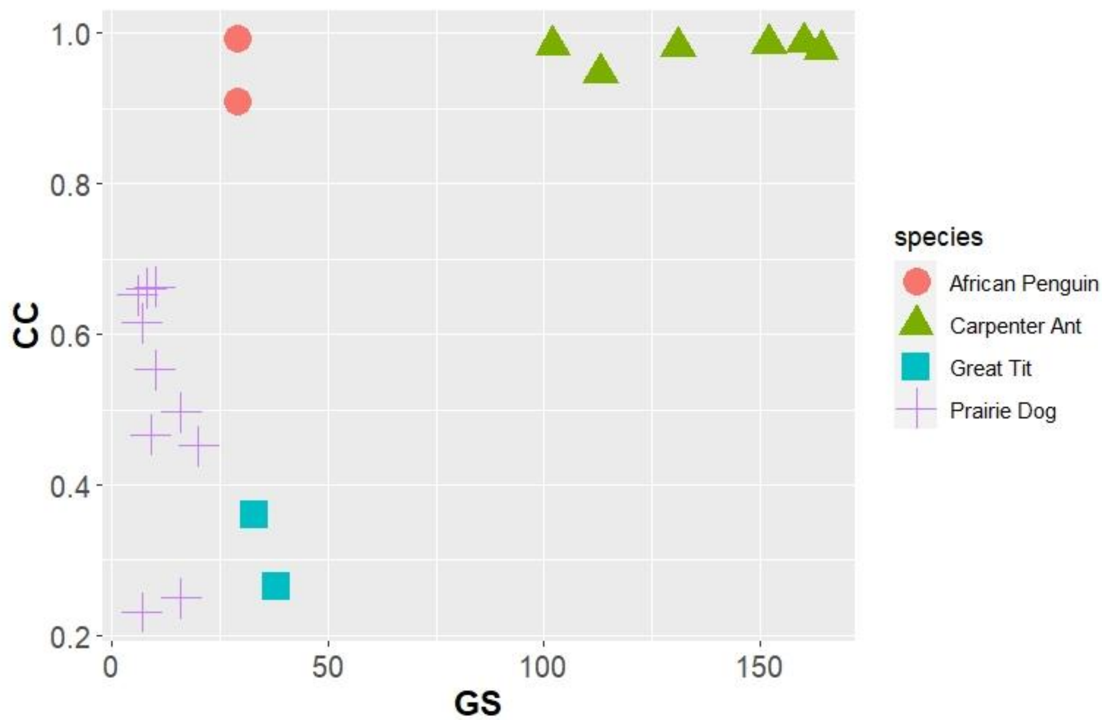

Figure 12 Scatterplot of Group Size (GS) and Transitivity (CC) within study species.

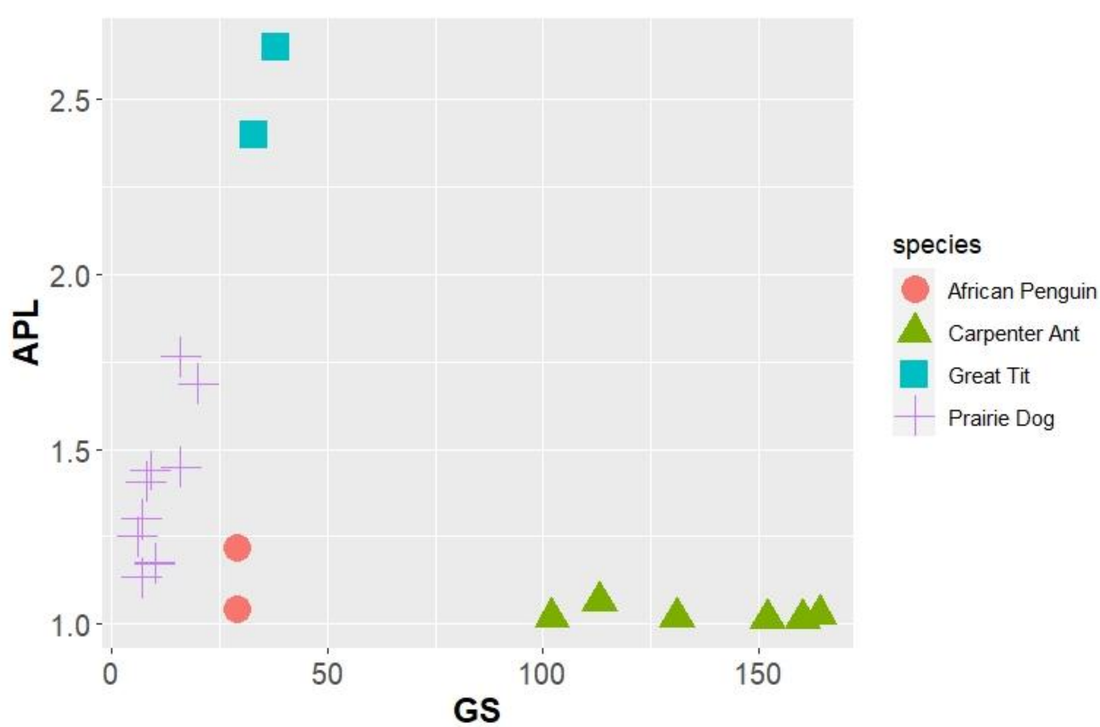

Figure 13 Scatterplot of Group Size (GS) and Average Path Length (APL) within study species.

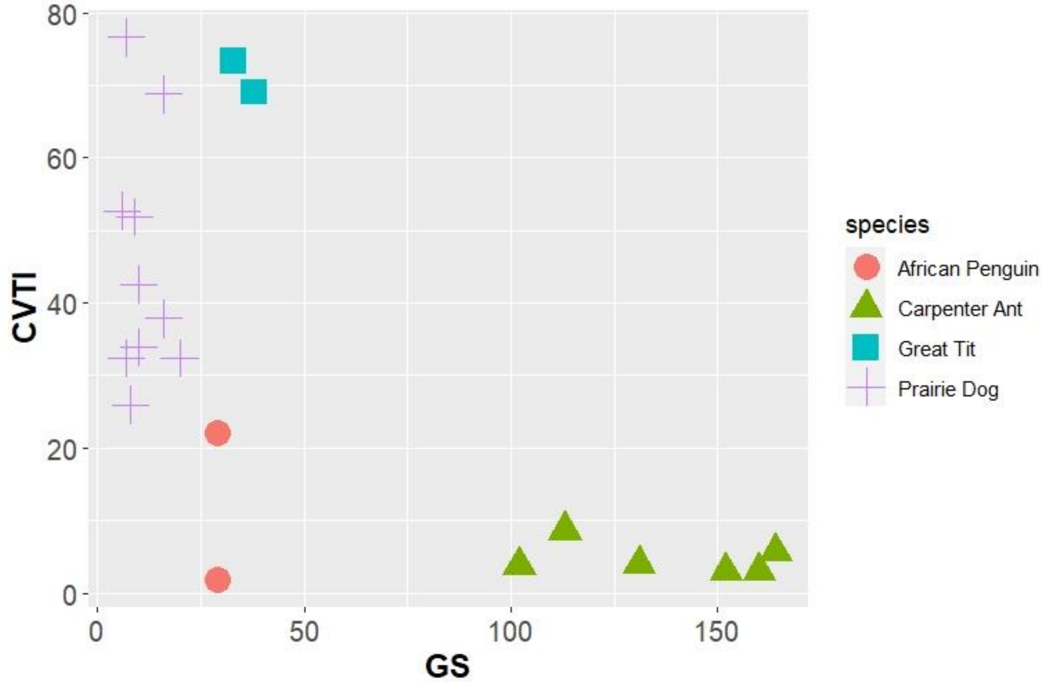

Figure 14 Scatterplot of Group Size (GS) and Coefficient of Variation in Topological Importance (CV_{TI}) within study species.

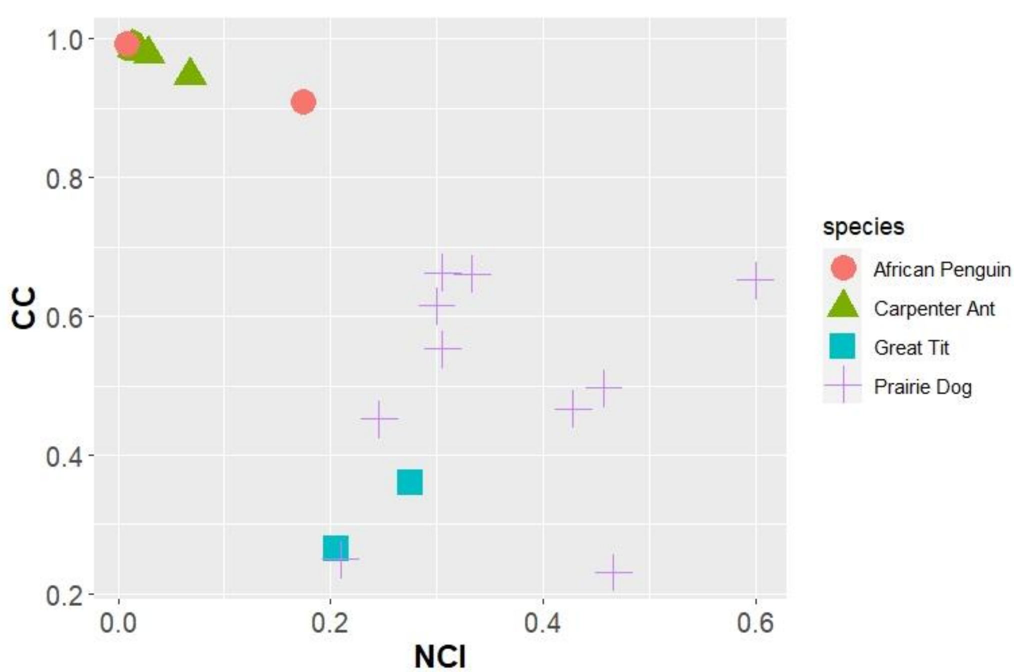

Figure 15 Scatterplot of Network Centralization index (NCI) and Transitivity (CC) within study species.

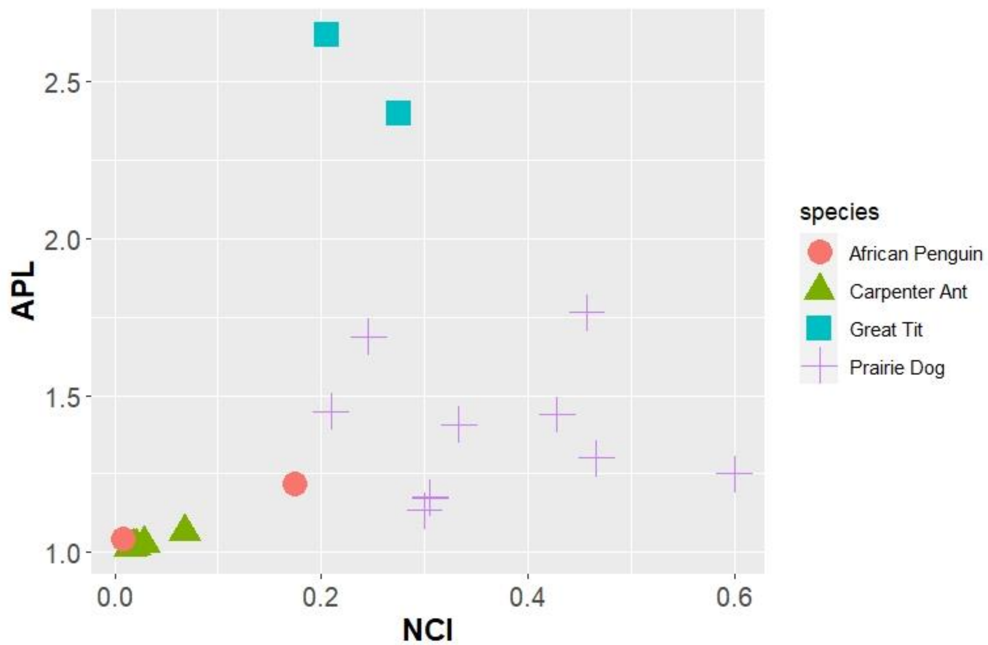

Figure 16 Scatterplot of Network Centralization index (NCI) and Average Path Length (APL) within study species.

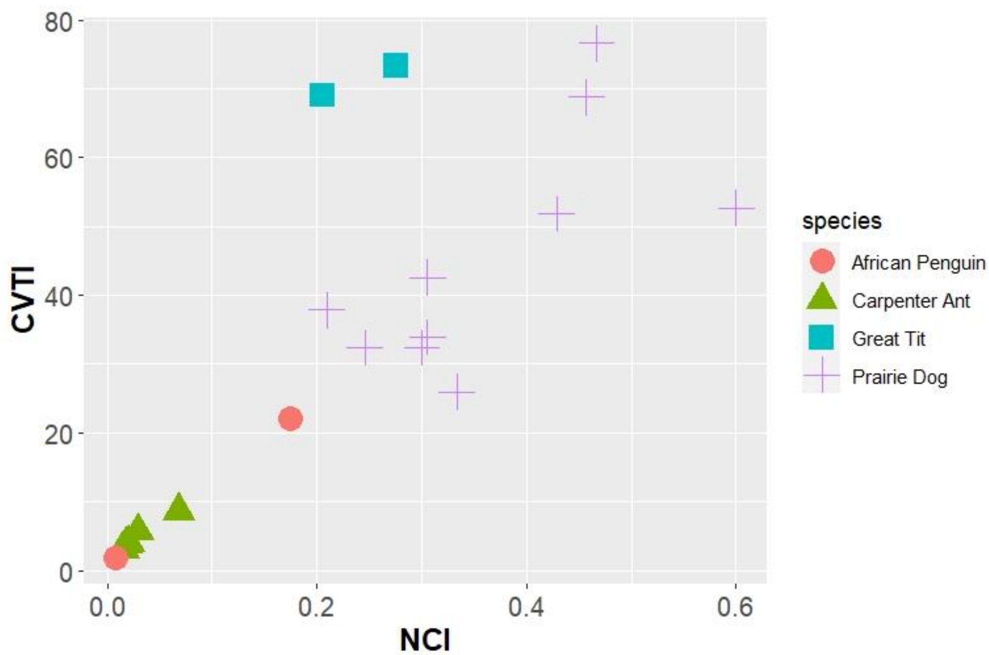

Figure 17 Scatterplot of Network Centralization index (NCI) and Coefficient of Variation in Topological Importance (CV_{TI}) within study species.

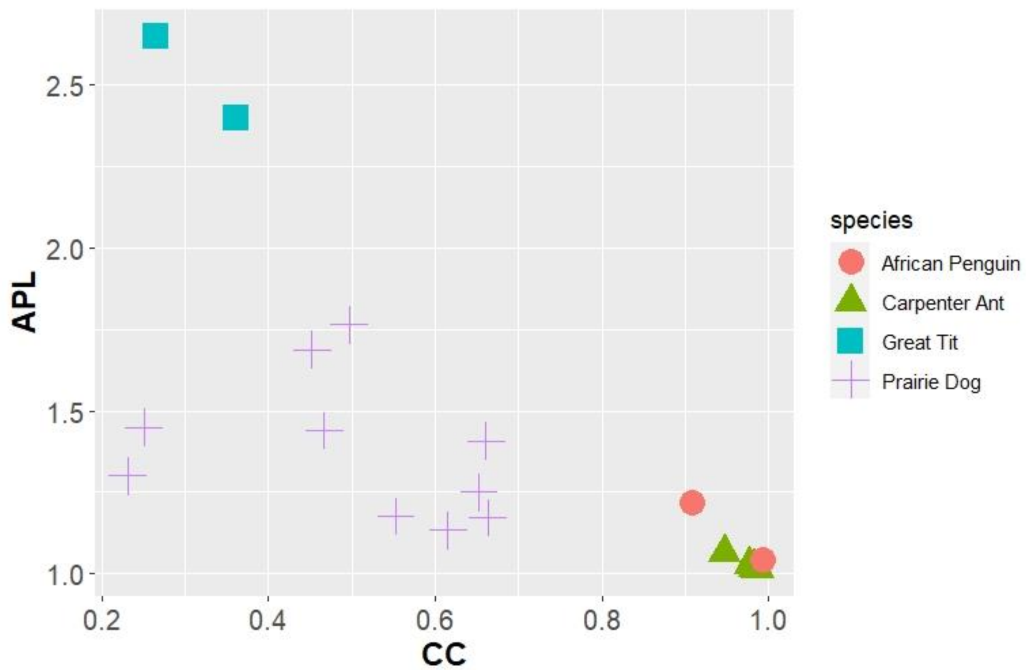

Figure 18 Scatterplot of Transitivity (CC) and Average Path Length (APL) within study species.

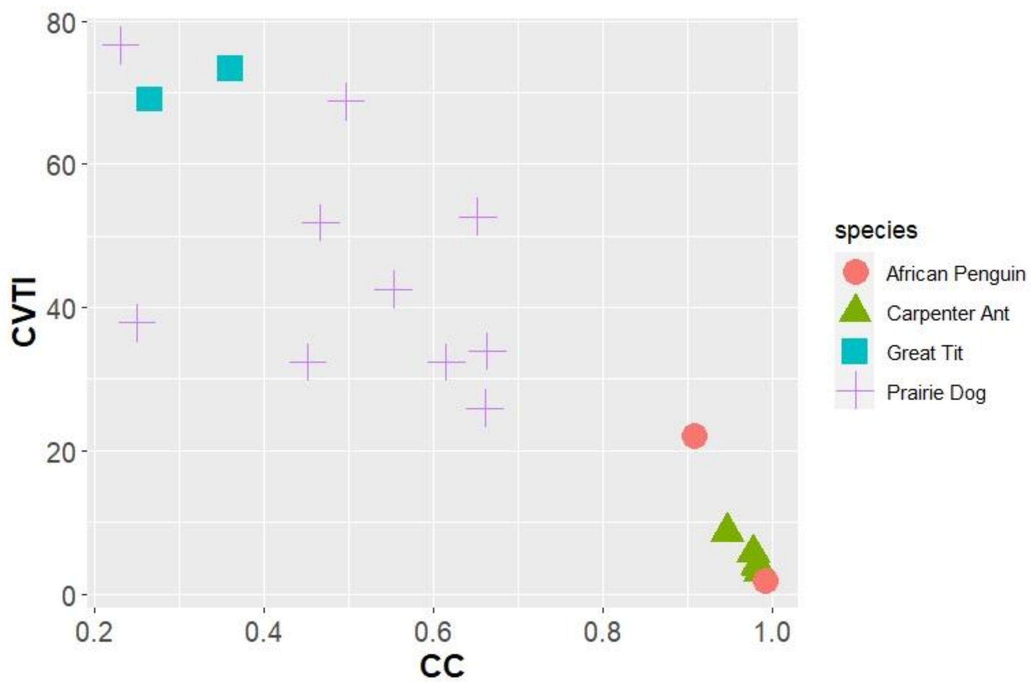

Figure 19 Scatterplot of Transitivity (CC) and Coefficient of Variation in Topological Importance (CV_{TI}) within study species.

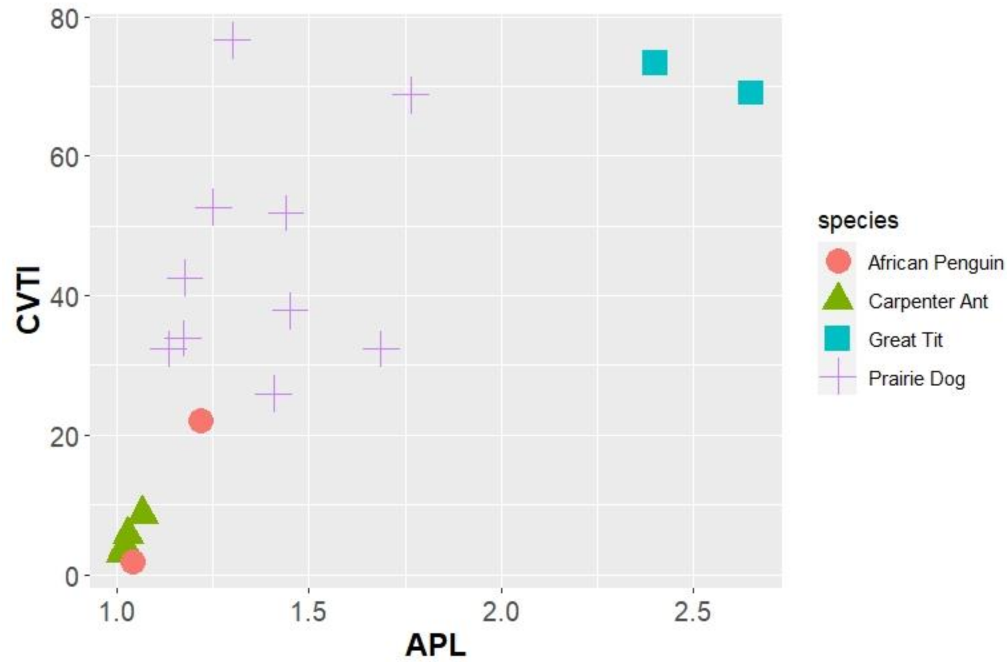

Figure 20 Scatterplot of Average Path Length (APL) and Coefficient of Variation in Topological Importance (CV_{TI}) within study species.

In the hierarchical clustering single-link process, the four species were separated into two clusters strictly at a height of about 2. One cluster included the two Great Tit networks, while the other cluster comprised all remaining networks (Prairie Dog, African Penguin, and Carpenter Ant) (Figure 25). At a height of 1.5, three additional clusters were established: one containing all Prairie Dog networks, another with only one African Penguin network, and a third with all Carpenter Ant networks along with an African Penguin network. Overall, based on hierarchical clustering using the single-link method, Great Tit network indices appeared to be the most distant from the others.

However, it must be emphasized that these results only describe these four specific cases. The methodology of the four cases is very different, making it difficult to draw any concrete and far-reaching conclusions from such a comparison. I merely attempted to compare them in the simplest way possible based on the data I collected.

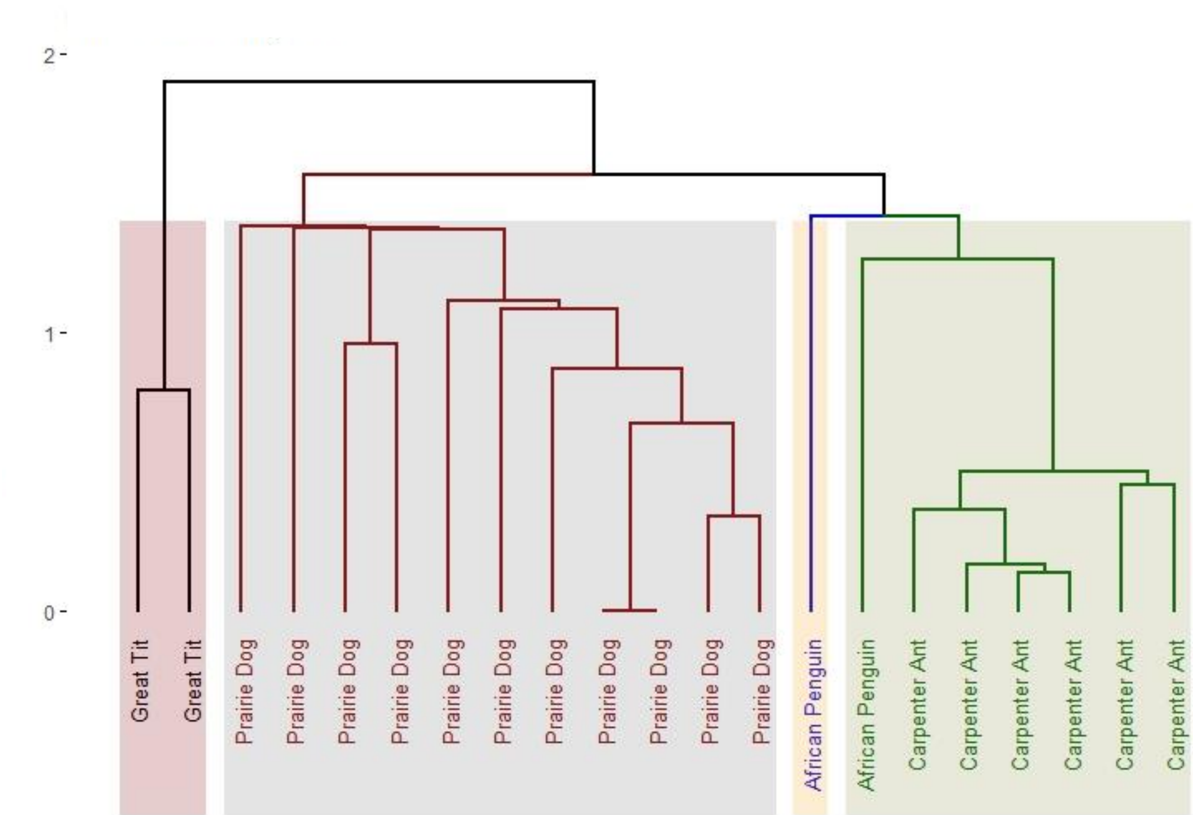

Figure 21 Dendogram of single link hierarchical clustering based on euclidean distances between networks using 5 network indices and Group Size (GS) values. Four clusters are separated by colored boxes.

6. Conclusion – Thesis Question 2 – Comparison of global network properties of the case studies

Findings for Thesis Question 2: *How do the social network structures compare to each other? Is there any shared or opposite pattern between the network topologies?*

The results of the principal component analyses reveal visible trends in network indices across species. By observing pairwise correlations through PCA (Figures 9-10) for GS, NCI, CC, APL, and CV_{TI} metrics, it becomes evident that species in case studies can be strictly separated from a social network structure perspective. The negative correlation trends between NCI, CV_{TI}, and GS can be observed in Figures 11 and 14. Notably, GS has not shown any trends with CC and APL, which indicates that information may flow independently of the number of given populations. As could be expected, with higher CC scores, APL tended to be lower, because more connections mean "faster" pathways within networks in general.

In addition, species can be distinguished based on each index. Great Tits exhibited the most "longest" networks, with the the highest APL scores. Additionally, these networks were less transitive and had the highest CV_{TI} score. Notably, the network data of Great Tits established a strictly distinct cluster in hierarchical clustering, separate from the others. Concerning Prairie Dog networks, they had the most centralized (NCI) networks with moderated CC, APL, and CV_{TI} scores. It is important to note that prairie dogs were the species with the most networks and the highest variability in the size of these networks, ranging from 6 to 20.

The comparison of metrics among species are visualized in Figure 26.

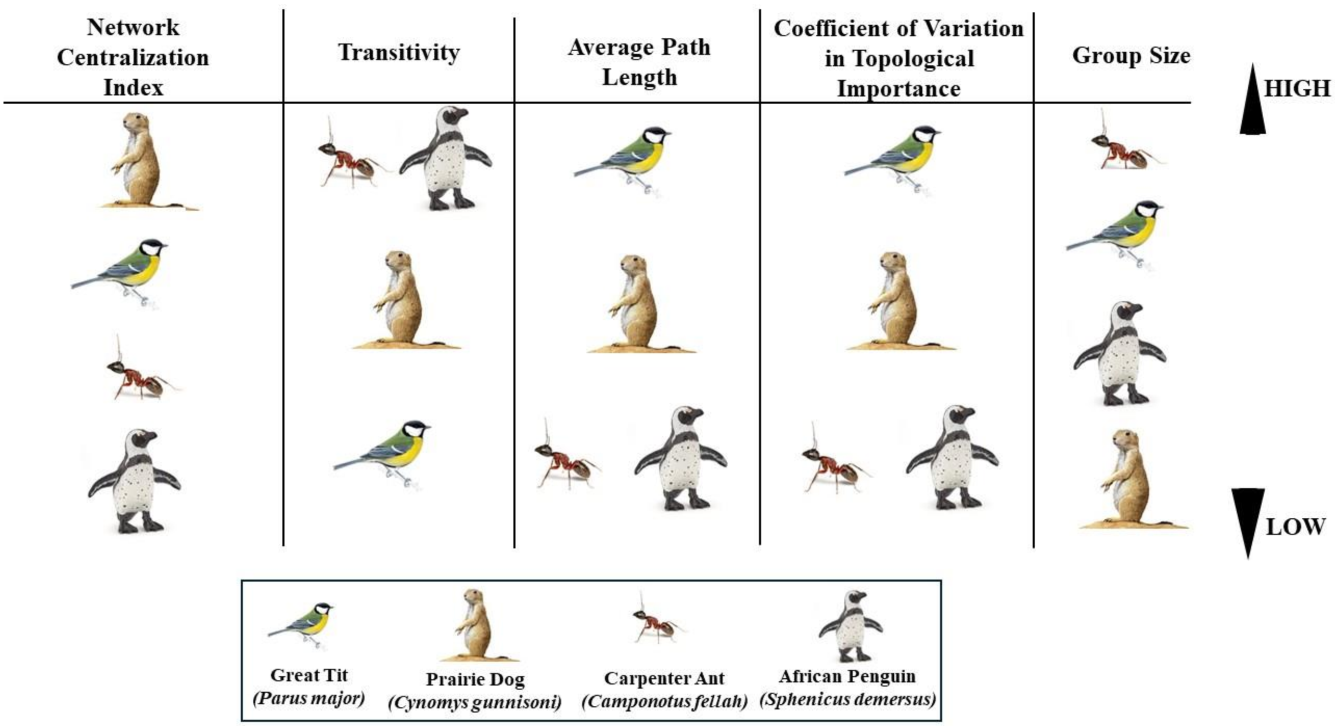

Figure 22 Visualization of NCI, CC, APL, CV_{TI}, and GS metric scores amoung case study species, where arrows with HIGH label represents the high scores, LOW label represents the low scores of the given metric.

7. Discussion

In recent decades, various methodologies have been employed to assess the social behavior of animals. While some approaches are centered on individuals, aiming at their surroundings and conduct, the network terms seek to quantify interactions or affiliations within a group of animals. Social Network Analysis (SNA) emerges as a valuable tool to describe and compute interaction or association patterns between individuals. The period spanning from the late 1990s to 2023 has witnessed the publication of over a thousand research articles featuring social networks in animal species, particularly in the context of animal behavioral ecology. Upon a closer look, it becomes evident that these investigations have predominantly concentrated on mammals, particularly primates, whereas other taxonomic groups remain under-represented. Multiple criteria can be used to classify these papers. In this study, I have refined my focus to relevant publications categorized into four groups: 1) offering a general description of animal social networks devoid of specific hypotheses or statistical tests, 2) probing the impact of individual attributes on network structures like sex, age, and body size, 3) assessing the influence of individual behaviors on network topologies like castes in ants, and 4) investigating the impact of environmental conditions on network structures. Besides the considerable number of publications, statistical models are also represented with high diversity. Two specific statistical models were used here. The Exponential Random Graph Models (ERGMs) can be employed to estimate the impact of an external factor on the probability of specific network configurations, such as Edge Formations or Degrees (Silk and Fisher, 2017). Meanwhile, Node Label Permutation Models (NLPM) utilize random permutations to mitigate the issues of dependent data within graphs (Sosha et al., 2020). In this thesis, I applied both of these methodologies to assess the influence of individual data on the topologies of social networks in Great Tits and African Penguins. Furthermore, I employed to examine the associations between environmental conditions and global as well as intermediate indices in the study of Prairie Dogs.

In my research in Case Study I, I observed outgoing aggressive interactions (OD) and the sensitivity of Edge Formations (EF) in wild Great Tits (*Parus major*) during the winter season. I noted a higher intensity of aggression exhibited by younger birds. Interestingly, no age effects were discerned in the proximity network. Surprisingly, sex differences did not affect any network metrics on any network type. This observation could potentially indicate the lack of significance of sex-related attributes during the non-breeding season. Additionally, I identified a negative impact of tarsus length on all network configurations, implying that the assumption of younger birds being more socially active than their older counterparts may not hold. These findings collectively suggest that Great Tits uphold complex social systems even during the winter season. This study first explored agonistic and proximity social networks in Great Tits during the non-breeding season.

I modeled 14 grooming social networks in Gunnison's Prairie Dog (*Cynomys gunnisoni*) using collaborative data (Case study II). I aimed to find out the potential impact of environmental factors on network topologies. I assessed the network topology using global and intermediate metrics: the Network Centralization Index (NCI), Clustering Coefficient or Transitivity (CC), and Average Path Length (APL). These metrics were contrasted with environmental variables such as Group Size, Territory Size, and available Biomass per unit area. Several studies measured familiar environmental conditions' influences on network structures. Agonistic networks were examined for family size, which is analogous to Group Size in blue tits (*Cyanistes caeruleus*) (Garcia et al., 2023). In blue tits, these authors found that the Degree and Density of the networks remained independent of family size. Another study explored changes in resource availability affecting network connections in wood ants (*Formica lugubris*) (Burns et al., 2021). Moreover, Wilson et al. (2015) identified how changes in habitat influenced Network Density in Trinidadian guppies (*Poecilia reticulata*). My research in Gunnison's Prairie Dog social dynamics revealed the critical role of Group Size. As Group Size increased, the flow of information within the network slowed down, as evidenced by an increase in Average Path Length (APL). Simultaneously, the centralization of information decreased with larger group sizes. This phenomenon could potentially lead to a slower response to predatory threats or the transmission of essential information within the group. My findings were supported by a negative correlation between APL values and territory sizes. This suggests that not only group size, but also the shape and size of the territory, significantly influence the social network's topology. Surprisingly, the availability of biomass resources did not exhibit any relationship with network metrics.

In Case Study III, I investigated how the individual behavior attributes affect the network on global and intermediate topology levels in Carpenter Ants (*Camponotus fellah).* To accomplish that, I constructed 60 daily proximity social networks from six colonies (10 networks per colony) of Carpenter Ants *(Camponotus fellah)* based on data from the literature (Mersch et al., 2013). Moreover, I set behavioral variables as individual worker castes, which were the worker castes within colonies: Nurses (N), Foragers (F), and Cleaners (C). In addition, I established two extra subnetworks based on a direct link with the queen: Queen-Networks (Q) and No Queen-Networks (NQ).

The distinctive topological variations of caste subnetworks became evident through the outcomes. Specifically, the Forager and Nurse castes exhibited a more centralized topology comparison to the Cleaner networks. The same pattern appeared in the case of Transitivity (CC), Cleaners maintained less “cliquish” networks than Foragers and Nurses. However, Cleaners exhibited the longest pathways (APL) among the castes. This observation could reflect the significance of swift information transmission between Nurses attending to offspring or searching for food in Foragers. Only NQ subnetworks showed longer pathways (APL) than Cleaners. Suggesting, that this phenomenon leads to a deceleration in information flow in the absence of the queen.

In Case Study IV, I investigated and presented the primary shaping factors of the topologies of agonistic and food competition social networks in zoo-kept African Penguins *(Spheniscus demersus)*. Previous studies showed that the high rate of aggressive behavior, including even nest usurpation is a key component of the group dynamics and structure by affecting breeding success (Traisnel and Pichegru, 2018). Moreover, another study demonstrated male-biased territory aggressive displays (Figel et al., 2023). However, no study discussed agonistic behavior patterns focusing on a whole group via networks. I found that high aggression rates emerged by juveniles (less than 1 year old, with gray feathers) within the group. Both network position indicator (DI and WI) indices were the highest in juveniles in agonistic networks. Moreover, the males occupied more central (WI) and more aggressive (DI) network positions than females, which supports the observations in the wild based on the results of Figel et al. (2023) mentioned above.

Different results were exhibited in food competition networks. Earlier research has delved into individual data characteristics, specifically boldness, and how they forecast food competition-related foraging behavior in the natural habitat. Notably, these studies revealed that boldness influences foraging success in females (Traisnel and Pichegru, 2019). In contrast, my study focused on modeling food competition social networks within a distinctly different zoo environment. The primary aim is to determine whether individual indicators play a role in shaping the food competition network dynamics among penguins. In the context of my study, it was observed that juveniles displayed higher positive values in the disparity between won and lost food-related fights (referred to as DI) compared to adults. However, their WI was lower, indicating a scenario where juveniles engage in fewer but more impactful foraging competitions compared to adults. To investigate the broader influence of age on network dynamics, I employed permuted correlations involving continuous age variables instead of simply categorizing individuals into juvenile and adult groups. My findings revealed that both the rate of aggression (DI) and centrality (WI) were negatively correlated with age, specifically within agonistic networks. Remarkably, food competition networks displayed no connections with age, thereby extending the previously mentioned results. This suggests that while juvenile individuals influence the dynamics of food competition, the impact of age on food competition dynamics among adults is negligible.

Additionally, to contribute to conservation efforts within zoo environments, I explored the effect of rearing procedures on the two aforementioned networks. This human-mediated activity directly interacts with a particular population, as discussed by Williams et al. (2016). For instance, the behavior of captive parrots was found to be influenced by their rearing history. Parrots that were hand-reared and kept in solitary conditions exhibited fewer normal behaviors compared to their parent-reared counterparts within a group (Williams et al., 2016).

In the context of my study, individuals with a combination of hand-rearing and parental-rearing procedures displayed the highest levels of aggression, centrality, and central food competitiors, as evidenced by elevated DI and WI values in agonistic networks, and higher WI values in food competition networks. Conversely, those subjected solely to hand-rearing exhibited the lowest values. These findings can offer valuable guidance to zookeepers, assisting them in providing more attentive care for African Penguins in captivity.

Each of the presented case studies shows the significance and value of assessing animal social networks through diverse perspectives and methodologies. Nevertheless, while the tools of social network analysis hold promise for investigating and quantifying animal populations, limitations tend to arise primarily within wild populations. In such scenarios, individuals may conceal themselves or prove challenging to track, potentially resulting in data collection with noticeable gaps. The exponential advancement of technology, however, has ushered in fresh prospects for data collection and the observation of animal behavior, surpassing previous capabilities.

The limitations of SNA methods are nearly as varied as the multitude of species that exist on Earth (different space, time, environment, number of individuals, etc.). Using the networks without direction, sign, or weight, only the absence or presence of interactions can be a way to conduct comparisons across species without delving into deeper intricacies. Another important issue is the observation periods. In my Case Study, I examined a winter period from November to February 2021 for Great Tits, a summer period from March to August 2009 for Prairie Dogs (Case study II), and a breeding period from April to November in 2022 for African Penguins (Case study IV). Data encompassed Carpenter Ants observed for 10 days (Case Study III). Given that these are invertebrates with significantly shorter lifespans, I deemed their "season" in life comparable. By utilizing seasonally time-aggregated networks, I selected Group Sizes (GS) of the presented species above and global and intermediate network metrics to characterize network topology (NCI, CC, APL, CV_{TI}). These metrics formed the basis for cross-species comparisons in social behavior network studies.

Cross-species sociality measures appeared in the same mixed group, for example in Savi's bats (*Hypsugo savi) and* Kuhl's pipistrelles *(Pipistrellus kuhlii)*, when they demonstrated occurrences of social bonds between species (Ancillotto et al., 2014). Another study discussed two distinct social network properties between Grevy's zebras and onagers (Sundaresan et al., 2007). However, these observations were somehow connected in time, space, or with specific conditions. In this dissertation, I first made efforts to compare strictly distinct and independent randomly chosen studies across species using SNA methods. The network metrics in general among species showed strong correlations with each other.

Among all of these five indices, a negative correlation emerged between the NCI index and GS, indicating how hierarchical characteristics within populations can increase in smaller groups, as observed in my model species, Prairie Dogs, and African Penguins. Another index, CV_{TI}, which can be used as an indicator of influence within a population between individuals, also exhibited a similar negative correlation with GS. This and the positive relationships between NCI and CV_{TI} provides further evidence to support the assumption that smaller groups tend to maintain a more centralized social environment.These patterns of centrality was previously studided, for example Feral Goats *(Capra hircus)* were observed, where smaller groups has individuals with higher centrality, and bigger groups tended to been unstable and collapsed (Stanley and Dunbar, 2013). Suprisingly, GS has not showed any trends with CC and APL, which indicates that information may flow independently from the number of the given populations.

Based on network intermediate and global topologies, the social systems of the Great Tits exhibited the most distinctive characteristics from each other. From the perspective of information flow, APL shows the speed, and CC describes the "blockades," NCI gives the ratio of "leadership," and CV_{TI} demonstrates how individuals influence each other (Wasserman and Faust, 1994). Great Tits represent the most slowest social system, while the African Penguins and Carpenter Ants showed the opposite pattern.The indices related to social hierarchy exhibit non-linear patterns, except the positive relation with each other. The ant colonies and penguins represent the less hierarchical social structures with higher cluster rates. The variety of influences on individuals within the networks emerged in Great Tits but diminished in penguins and ants. The ant and penguin similarities in multiple indices are interesting. The outlier results of CC, APL and CV_{TI} in ants could be interpreted as a reflection of a high level of eusociality, but in penguins these index patterns may indicate a contrast between wild and captive states in these groups. Under natural conditions, the larger available space, specific foraging strategies, and relatively infrequent contact with other group members can lead to more sparse (low CC, and high APL) and more random (high variety of socially important group members, CV_{TI}) social network patterns compared to controlled environments in captivity with a steady food supply and absence of predators. However, in light of other measures, explaining these patterns is hindered by the lack of more data and information about other eusocial species. Further exploration through detailed studies in the future is necessary.

This thesis, along with the main questions it addresses, highlights the importance and relevance of animal social network approaches in several taxa, in a comparative way (as much as possible), for numerous social-related behavioral and ethological inquiries. In addition to the network-shaping factors of individual data, behavioral characteristics, and changing environments discussed here, more areas within animal science await exploration through social networks for example with a major focus on conservation efforts or human-wildlife conflicts.

8. Summary

My research aims to use network analysis methods to examine the external influencing factors on the social behaviors of four different species - the Great Tit *(Parus major)*, Gunnison Prairie Dog *(Cynomys gunnisoni)*, Carpenter Ant *(Camponotus fellah)*, and African Penguin *(Spheniscus demersus)*. The primary focus was on uncovering external factors that influence the topology of their social networks under different variable conditions. Furthermore, I compared the network models among species to identify similar or different trends and patterns among them. I demonstrated that individual age negatively correlates with network indices indicating the level of aggression (OD, DI) in both Great Tits and African Penguins. The sex of individuals did not influence the social network topology of Great Tits, but in the case of African Penguins, males were more aggressive and efficient foragers within the networks. Tarsus length, as an indicator of body size, seemed to be a good predictor for Great Tits in both proximity and agonistic networks, where smaller birds showed higher aggression and affinity to interact with others. Among the global network indices of Prairie Dogs, I found a negative correlation between NCI and Group Size, NCI and Territory Size, and a positive relationship between APL and Group Size, as well as APL and Territory Size. I did not find a relationship between Biomass and network index variables. The castes and subnetworks of Carpenter Ants also showed significant differences. The NCI and CC values of Cleaners were lower than Foragers and Nurses, but their APL values were higher. Additionally, the No-Queen related subnetwork had higher APL values than the Cleaner caste. In the second part of my study, I compared the above-mentioned relational networks at global and intermediate network topological levels. Great Tits formed networks with long peaks. In contrast, African Penguins had the most clustered and shortest networks, while Carpenter Ants exhibited intermediate values between the two. Prairie Dog networks did not show visible trends, with data points showing large variations when comparing indices. Regarding NCI, a non-linear pattern emerged among species with high centrality and moderate transitivity (CC) in ants, and low NCI in birds with low clustering. CV_{TI} emerged as a unique indicator here, derived from food web methodology, reflecting the diversity of positional importance of peaks in the networks, which was highest in Great Tits and lowest in African Penguins.

9. Összefogalás

Kutatásaim célja a kapcsolathálózatelemzési módszerek felhasználása, hogy megvizsgáljam, milyen külső befolyásoló tényezői vannak négy különböző faj – széncinege *(Parus major)*, Gunnison prérikutya *(Cynomys gunnisoni)*, harcias lóhangya *(Camponotus fellah)* és afrikai pingvin *(Spheniscus demersus)* – társas viselkedéseinek. Összehasonlítottam a hálózati modelleket a fajok között, hogy azonos vagy különböző trendeket és mintákat fedezzek fel közöttük. Kimutattam, hogy az egyedek kora mind a széncinegéknél és az afrikai pingivneknél is negatívan korrelál az agresszió mértékét mutató hálózati indexekkel (OD, DI). Az egyedek neme nem befolyásolta a széncinege társas hálózatának topológiáját, de az afrikai pingvinek esetében a hímek agresszívebbek voltak és hatékonyabb táplálékszerzők a hálózatokban. A csüdhossz, mint testméretindikátor, jó befolyásoló tényezőnek bizonyult a széncinege mind közelségi, mind az agonisztikus hálózataiban, ahol a kisebb madarak nagyobb agressziót és hajlandóságot mutattak másokkal való interakcióra. A prérikutya globális hálózati mutatói közül negatív korrelációt találtam a NCI és a csoportméret között, a NCI és a területméret között, és pozitív kapcsolatot az APL és a csoportméret között, valamint az APL és a területméret között. Nem találtam kapcsolatot a biomassza és a hálózati mutatóváltozók között. A harcias lóhangyák kasztjai és alhálózatai is szignifikáns különbségeket mutattak. A takarítók NCI, CC értékei alacsonyabbak voltak, mint a táplálékszerző és utódgondozó kasztokéi, de APL értékei magasabbak. Ezen felül a királynőhöz nem kapcsolódó egyedek alhálózatának APL értékei nagyobbnak bizonyultak, mint a takarító kasztéi. A kutatásom második részében összehasonlítottam a fent említett kapcsolati hálózatokat globális és köztes hálózat-topológiai szinteken. A széncinegék hosszú csúcsok közötti úthosszal rendelkező hálózatokat hoztak létre. Ezzel szemben az afrikai pingvinek a legzsúfoltabb és legrövidebb hálózatokkal rendelkeztek, míg a harcias lóhangyák a kettő közötti értékeket vettek fel. A prérikutya hálózatok nem mutattak látható trendeket, az adatpontok nagy szórást mutattak az indexek összehasonlításakor. Az NCI tekintetében nem lineáris mintázat alakult ki a fajok között magas centralitással és mérsékelt tranzitivitással (CC) a hangyáknál, és alacsony NCI a madaraknál alacsony klasztereződéssel. A CV_{TI} itt egyedülálló mutatóként jelent meg, ez a táplálékhálózatok módszertanából származik. Tükrözi a csúcspontok pozícionális fontosságának változatosságát a hálózatokban, amely a legmagasabb volt széncinegeknél és a legalacsonyabb afrikai pingvineknél.

10. References

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11. Publications

Publications related to PhD dissertation

Jordán, F., **Kovács, B**., & Verdolin, J. L. (2021). Resource availability influences global social network properties in Gunnison's prairie dogs (Cynomys gunnisoni). Behaviour, 159(3-4), 321-338. DOI: 10.1163/1568539X-bja10118

Kovács, B., & Jordán, F. (2024). Emergence of keystone individuals in the social networks of the ant Camponotus fellah. Insectes Sociaux, 1-9. DOI: 10.1007/s00040-024-00963-6.

Submitted

Bálint Kovács, Péter Kollár, Borbála Kocsis. Rearing procedure influences on agonistic and competition social network sturctures in captive African Penguins *(Spheniscus demersus)*. Applied Animal Behaviour Science, submitted.

In preparation:

Bálint Kovács, Boglárka Bukor, Krisztina Sándor, Gábor Seress, András Liker, Ferenc Jordán. Exploring social network dynamics in wild Great Tits *(Parus major)*. In preparation

Conference talks

Kovács B., Jordán F., Liker A., Modeling and Measuring Temporary Animal Social Networks in Wild Great Tits *(Parus major)*. 24th Symposium of Biology Students in Europe.Portugal, Lisbon2021, 27-31 of July, Book of Abstracts, page 72.

Kovács B., Jordán F., Liker A., Szociális kapcsolathálózatok modellezése téli időszakban vadon élő széncinegéknél *(Parus major)*. 12. Magyar Ökológus Kongresszusz, Hungary, Vácrátót, 24-26 of August, Book of Abtracts, page 71.

Publications not related to Phd dissertation

Vincze, E., & **Kovács, B.** (2022). Urbanization's effects on problem solving abilities: A meta-analysis. Frontiers in Ecology and Evolution, 10, 834436. DOI: 10.3389/fevo.2022.834436.

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13. Appendix

Appendix 1. Published social networks for 4 groups of species: (1) Descriptive measures of social networks, including indices and dynamics.(2) Measures examining the effects of changing environmental conditions on social network topology, such as seasonal changes, temperature, habitat, food availability, and infections. (3) The influence of individual social behavior characteristics on social network positions. (4) The influence of individual biometric variables on social network positions.

Species	*Scientific name*	Group
beef cow	*Bos taurus*	(4)
sulphur-crested cockatoo	*Cacatua galerita*	(2)
Gambel's quail	*Callipepla gambelii*	(4)
feral goat	*Capra aegagrus hircus*	(2)
elk	*Cervus canadensis*	(2)
spotted hyeana	*Crocuta crocuta*	(2)
Konik horse	*Equus ferus caballus*	(4)
onager	*Equus hemionus khur*	(2)
forest elephant	*Loxodonta cyclotis*	(2)
European badger	*Meles meles*	(4)
Australasian gannet	*Morus serrator*	(3)
Tasmanian devil	*Sarcophilus harrisii*	(4)
long-tailed tits	*Aegithalos caudatus*	(4)
giant panda	*Ailuropoda melanoleuca*	(4)
lizard	*Ameiva corax*	(4)
small-clawed otter	*Aonyx cinerea*	(4)
Geoffroy's spider monkey	*Ateles geoffroyi*	(3)(4)
brown spider monkey	*Ateles hybridus*	(2)
fungus beetle	*Bolitotherus cornutus*	(2)(3)
bumble bees	*Bombus impatiens*	(2)
sulphur-crested cockatoos	*Cacatua galerita*	(4)
California quail	*Callipepla californica*	(4)

common marmosets	*Callithrix jacchus*	(4)
Carpenter Ant	*Camponotus fellah*	(3)
house dog	*Canis lupus familiaris*	(3)
Alpine ibex	*Capra ibex*	(4)
blacktip reef sharks	*Carcharhinus melanopterus*	(4)
reef Sharks	*Carcharinus perezi*	(2)
white sharks	*Carcharodon carcharias*	(4)
Colombian white-faced capuchin	*Cebus capucinus*	(4)
brown capuchin monkey	*Cebus Sapajus apella*	(4)
red deer	*Cervus elaphus*	(3)
Gould's wattled bats	*Chalinolobus gouldii*	(2)
vervet monkey	*Chlorocebus pygerthrus*	(1)(2)(4)
colobus monkey	*Colobus angolensis ruwenzorii*	(2)
old world monkey	*Colobus gelada*	(4)
old world monkey	*Colobus guereza*	(4)
Eurasian jackdaws	*Coloeus monedula*	(4)
saltwater crocodile	*Crocodylus porosus*	(2)
spotted hyeana	*Crocuta crocuta*	(4)
blue tit	*Cyanistes caeruleus*	(2)(4)
Gunnison's Prairie Dog	*Cynomys gunnisoni*	(1)
common carp	*Cyprinus carpio*	(3)
vampire bat	*Desmodus rotundus*	(2)(4)
downy woodpecker	*Dryobates pubescens*	(2)
tree skink	*Egemias triolata*	(2)
big brown bat	*Eptesicus fuscus*	(2)
Przewalski's horse	*Equus ferus przewalskii*	(4)
Grevy's zebra	*Equus grevyi*	(2)
feral horse	*Equusferus caballus*	(3)
common waxbill	*Estrilda astrild*	(1)
common waxbill	*Estrilda astrild*	(2)

red-bellied lemur	*Eulemur rubriventer*	(2)
collared flycatcher	*Ficedula albicollis*	(4)
wood ant	*Formica lugubris*	(2)
red junglefowl	*Gallus gallus*	(4)
threespine stickleback	*Gasterosteus aculeatus*	(2)(3)(4)
giraffe	*Giraffa camelopardalis*	(2)(4)
field cricket	*Gryllus campestris*	(2)
Savi's bat	*Hypsugo savii*	(4)
African elephant	*Loxodonta africana*	(4)
stump-tailed macaque	*Macaca arctoides*	(4)
long-tailed macaque	*Macaca fascicularis umbrosus*	(2)(4)
Japanese macaque	*Macaca fuscata*	(2)(4)
rhesus macaque	*Macaca mulatta*	(2)(3)(4)
black macaque	*Macaca nigra*	(3)
bonnet macaque	*Macaca radiata*	(2)
barbary macaque	*Macaca sylvanus*	(2)(4)
Eastern grey kangaroos	*Macropus giganteus*	(3)
yellow-bellied marmot	*Marmota flaviventer*	(3)(4)
acorn woodpecker	*Melanerpes formicivorus*	(2)
Mongolian gerbil	*Meriones unguiculatus*	(4)
prairie vole	*Microtus ochrogaster*	(2)(4)
elephant seal	*Mirounga angustirostris*	(4)
reef manta ray	*Mobula alfredi*	(3)
brown-headed cowbird	*Molothrus ater*	(2)(4)
banded mongoose	*Mungos mungo*	(1)
house mouse	*Mus musculus musculus*	(1)
Bechstein's bat	*Myotis bechsteinii*	(4)
Natterer's bat	*Myotis nattereri*	(4)
lemon shark	*Negaprion brevirostris*	(3)
cichlid	*Neolamprologus pulcher*	(2)
cichlid	*Neolamprologus pulcher*	(4)

Western black-crested gibbon	*Nomascus concolor*	(4)
hihi	*Notiomystis cincta*	(4)
giant noctule bat	*Nyctalus lasiopterus*	(2)
degu	*Octodon degus*	(4)
white-tailed deer	*Odocoileus virginianus*	(2)
trapjaw ants	*Odontomachus hastatus*	(4)
Otago skink	*Oligosoma otagense*	(4)
Australian snubfin dolphin	*Orcaella heinsohni*	(3)
killer whale	*Orcinus orca*	(2)(4)
mountain goat	*Oreamnos americanus*	(4)
sharks	*Orectolobus maculatus*	(2)
European rabbit	*Oryctolagus cuniculus*	(2)(3)
ground squirrel	*Otospermophilus beecheyi*	(2)(3)
chimpanzee	*Pan troglodytes*	(2)(4)
African lion	*Panthera leo*	(2)
leopard	*Panthera pardus*	(3)(4)
baboon	*Papio anubis*	(4)
baboon	*Papio ursinus*	(3)
Great Tit	*Parus major*	(1)(2)(3)(4)
weaver	*Philetairus socius*	(2)
Wood warbler	*Phylloscopus sibilatrix*	(4)
red colobus monkey	*Piliocolobus tephrosceles*	(4)
Kuhl's pipistrelle	*Pipistrellus kuhlii*	(4)
wire-tailed manakin	*Pipra filicauda*	(4)
black-capped chickadee	*Poecile atricapillus*	(2)(4)
mountain chickadee	*Poecile gambeli*	(2)
Trinidadian guppie	*Poecilia reticulata*	(2)(3)(4)
wasp	*Polistes gallicus*	(3)
Hanuman langur	*Presbytis entellus*	(4)
common racoon	*Procyon lotor*	(2)(4)

Yunnan snub-nosed monkey	*Rhinopithecus bieti*	(2)(4)
Sichuan snub-nosed monkey	*Rhinopithecus roxellana*	(4)
wasp	*Ropalidia marginata*	(4)
peacock blenny	*Salaria pavo*	(3)
capuchin monkey	*Sapajus apella*	(3)(4)
small spotted catshark	*Scyliorhinus canicula*	(2)
white-breasted nuthatche	*Sitta carolinensis*	(2)
Guiana dolphin	*Sotalia guianensis*	(1)(2)(4)
Australian humpback dolphin	*Sousa sahulensis*	(4)
squirrel monkey	*Saimiri sciureus*	(3)
African social spider	*Stegodyphus dumicola*	(2)(3)
meerkat	*Suricata suricatta*	(2)(4)
wild boar	*Sus scrofa*	(2)
bluetongue lizard	*Tiliqua adelaidensis*	(2)
sleepy lizard	*Tiliqua rugosa*	(1)(2)(4)
Indo-Pacific bottlenos dolphin	*Tursiops aduncus*	(1)(2)(3)(4)
common bottlenose dolphin	*Tursiops truncatus*	(2)(4)
Columbian ground squirrel	*Urocitellus columbianus*	(3)
ruffed lemur	*Varecia variegata*	(4)
Galapagos sealion	*Zalophus wollebaeki*	(2)(4)

Appendix 2

Individual attributes, environmental, and behavioral data of Case studies: (1) Great Tit (*Parus major)*, (2) Gunninson's Prairie Dog *(Cynomys gunnisoni)*, (3) Carpenter Ant *(Camponotus fellah)*, (4) African Penguin *(Spheniscus demersus*)

(1)

ID	**Sex**	**Age**	**Tarsus length [cm]**
apcb	male	3	19.20
apcl	male	1	20.00
apcy	male	2	20.40
apkc	male	3	20.00
bbba	female	1	18.20
bfba	female	1	19.20
blba	female	1	19.30
capp	female	2	20.50
cbaz	male	1	20.70
cfba	female	1	19.90
cfza	female	2	20.30
cpaz	female	1	19.00
craz	female	2	20.10
crka	female	4	20.00
csal	female	1	19.50
frna	male	4	20.50
frsa	female	2	20.10
fsra	male	4	20.20
kral	male	1	19.20
krba	female	1	19.90
lsal	female	1	19.30
nanr	male	1	20.40
nasc	male	1	19.00
nasr	male	1	20.30
nbra	female	3	20.10
ncka	female	3	19.90
panr	female	2	19.60
pcna	female	3	19.30
pcsa	female	3	19.90
pfar	female	2	19.50
plar	female	1	20.00
praz	female	2	19.40
rkba	male	2	19.70

rlra	male	5	19.80
rpaz	male	2	19.80
rsba	female	1	20.20
rzba	female	1	19.60
zacl	female	4	19.20
zalc	male	3	20.80
zazc	male	4	19.50
zfar	male	1	19.40
zfra	female	3	18.30
zrba	male	1	21.10

(2)

Network	**Colony**	**Network size**	**Territory**	**Biomass/m^2**
CC	3	20	2142.94	8.05
HS2	2	16	1170.96	5.60
HS2	3	16	1211.02	4.27
CC	2	11	1450.76	5.53
HS1	1	10	1586.29	3.74
HS1	3	9	1161.82	2.75
HS2	4	8	493.18	0.43
CC	1	8	1461.50	7.76
CC	4	8	1729.00	7.62
HS2	5	7	997.39	3.09
HS1	5	6	550.12	3.79
HS1	4	4	559.59	5.59
HS2	1	4	442.25	1.36
HS1	2	3	375.18	3.60

(3)

Colony	**Caste**	**Size**
I	T	113
I	N	25
I	F	53
I	C	31
II	T	131
II	N	70
II	F	22
II	C	35
III	T	160

III	N	54
III	F	59
III	C	43
IV	T	102
IV	N	38
IV	F	25
IV	C	35
V	T	152
V	N	67
V	F	39
V	C	41
VI	T	164
VI	N	81
VI	F	46
VI	C	35

(4)

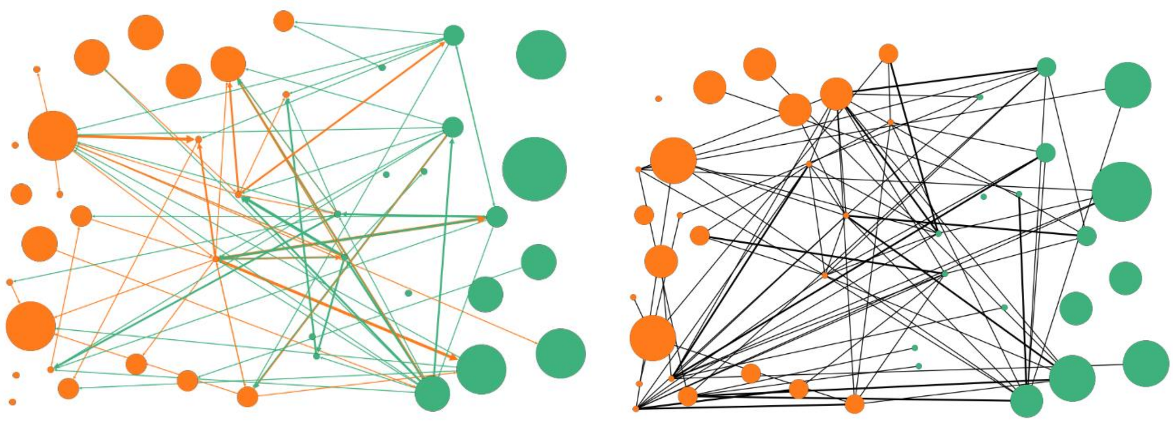
ID	**Sex**	**Age**	**Age class**	**Rearing**
AUGUSTUS	f	3	adult	parent
BARNA	f	23	adult	mix
BERISZLO	f	3	adult	mix
BOLDIZSAR	f	2	adult	parent
BPFEH	f	27	adult	parent
BRIAN	m	1	juvenile	mix
CHARLIE	f	15	adult	hand
CRYSTALL	m	16	adult	parent
DOMOTOR	f	3	adult	parent
ELZA	m	8	adult	mix
EUME	m	10	adult	parent
FANNI	f	4	adult	mix
HILDA	m	1	juvenile	mix
IVY	m	22	adult	hand
IZAURA	m	1	juvenile	mix
JOY	f	15	adult	hand
JUNIOR	m	9	adult	parent
KAMILLA	m	17	adult	hand
MAZSOLA	f	10	adult	parent
POFATLAN	m	10	adult	parent
PULCSI	f	4	adult	mix
RICO	m	8	adult	mix
ROSIE	f	7	adult	mix

SANYI	m	1	juvenile	mix
SISU	m	6	adult	mix
SKIPPY	m	6	adult	mix
STAN	m	2	adult	parent
SUMMER	f	2	adult	parent
ZENO	m	18	adult	parent

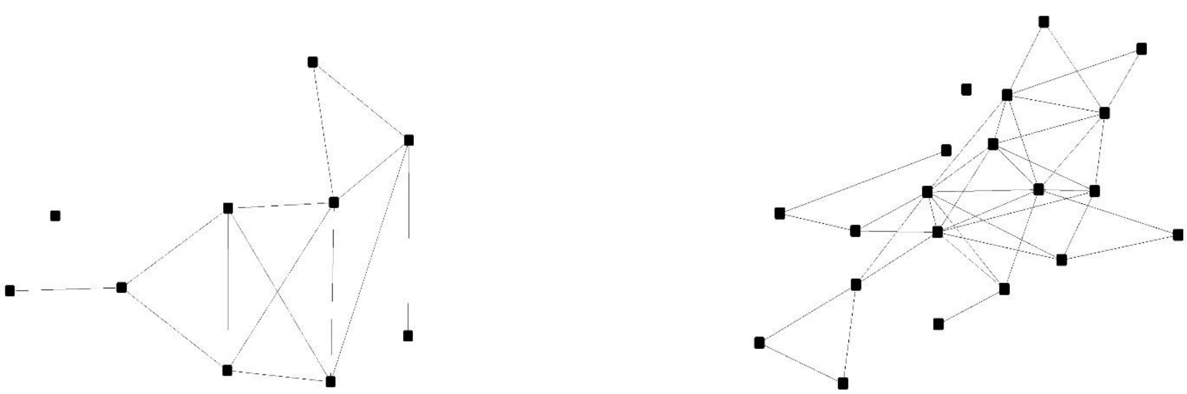
Appendix 3 The used feeder with 4 GoPro cameras, and a demonstration of color codes on Great Tits in Case Study I

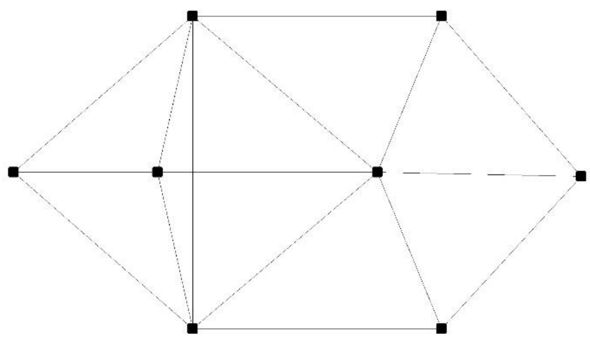
Appendix 4 Modelled social networks in Case Studies

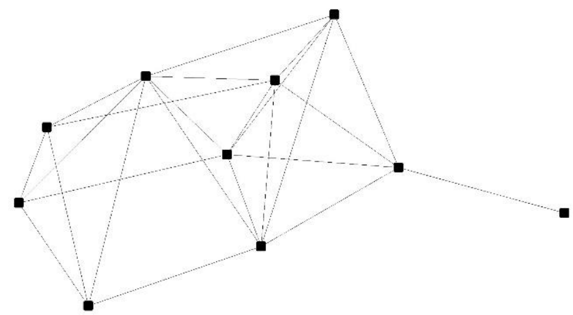
(1) Visualization of social networks in Great Tits via Gephi software. From left to right- agonistic and proximity networks. Orange nodes represent the female, and green nodes the male birds. The edge colors in the agonistic network show the interaction source node in the given dyad, and node sizes show the age differences between individuals.

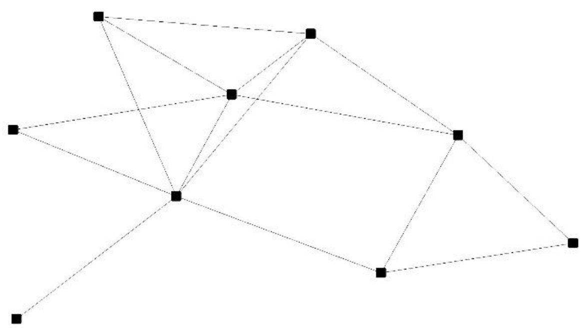


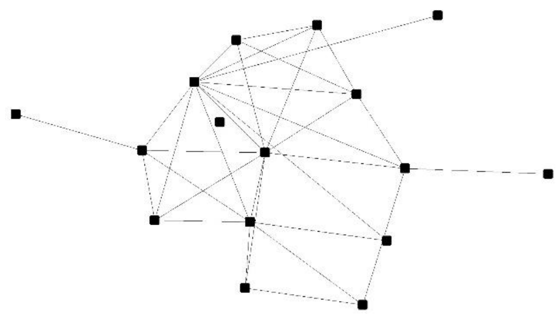
(2) Visualization of 14 social networks in Prairie Dogs via Ucinet & Netdraw software. Nodes represnets the individuals and edges represents the greet-kiss interactions between them.

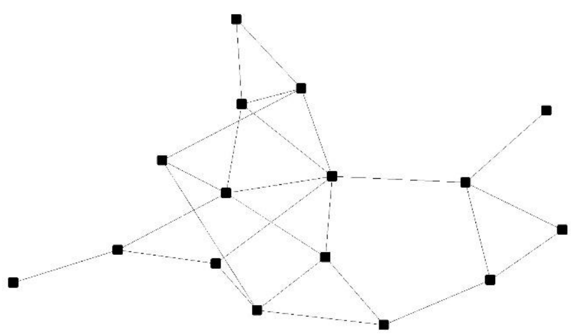


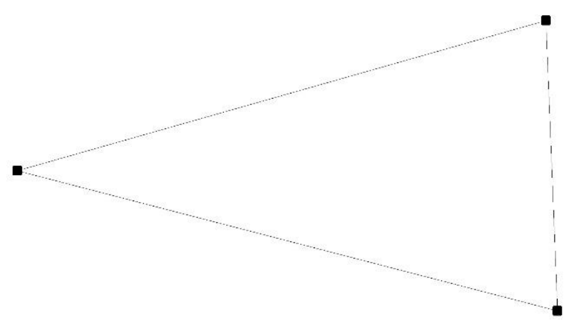


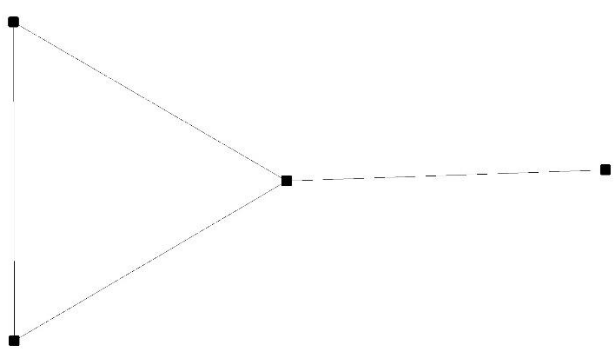


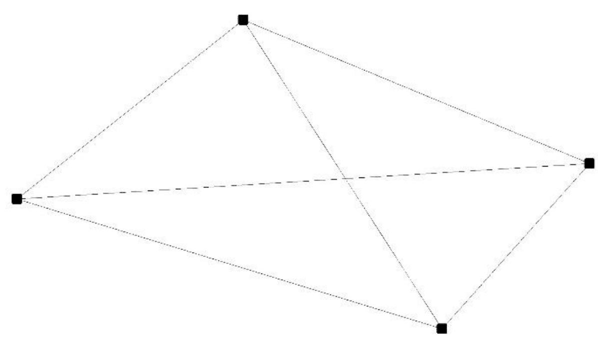


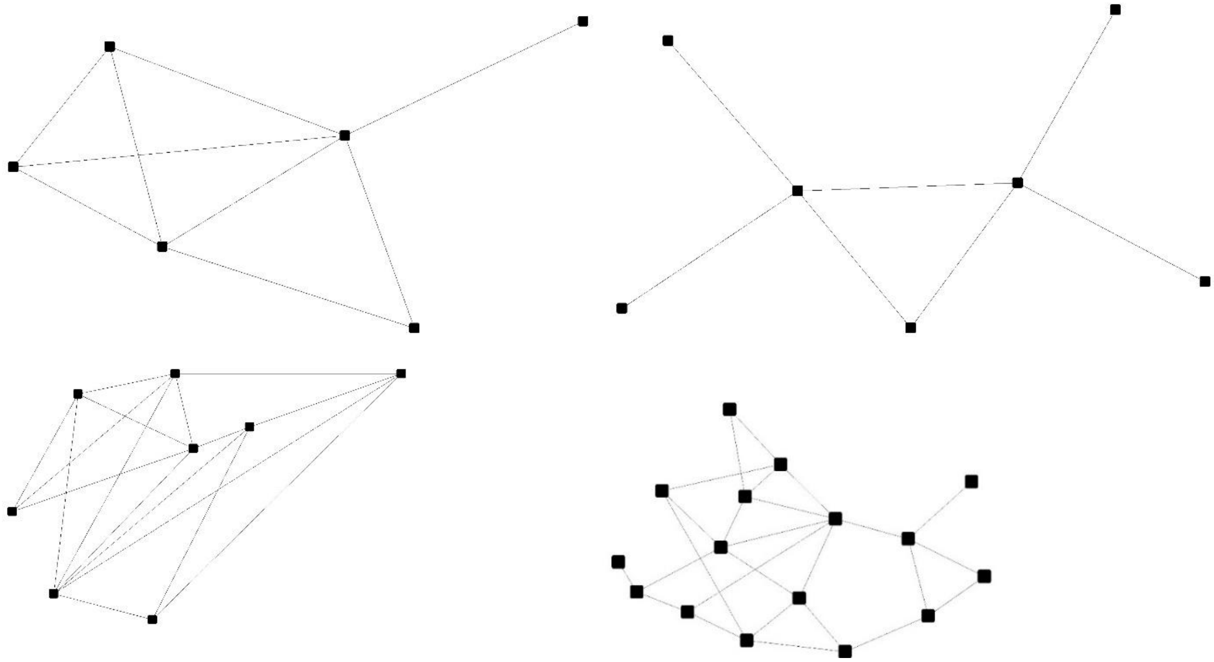






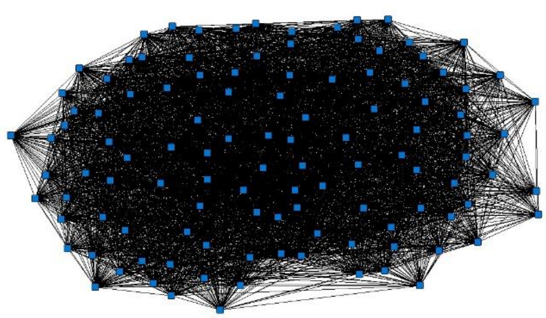






(3) Visualization of social networks in Carpenter Ants via Ucinet & Netwdraw software. The graphs represent the first day of all colonies in all Castes and Subnetworks. From left to right and up to down colonies I-VI. Node color codes: blue- whole network, red-nurses, green- forages, purple-cleaners yellow-queen-related, olive-no queen-related

I



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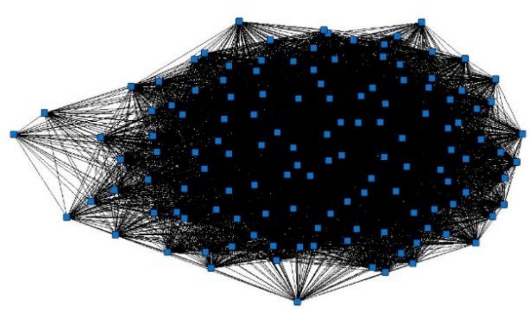

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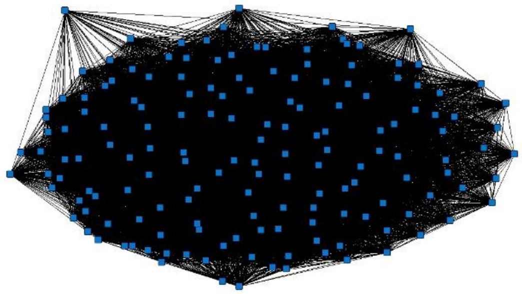

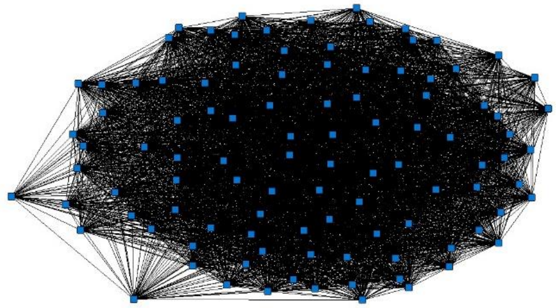

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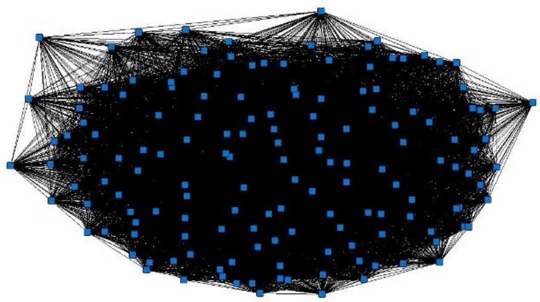

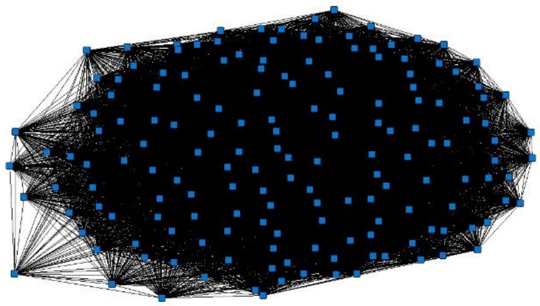

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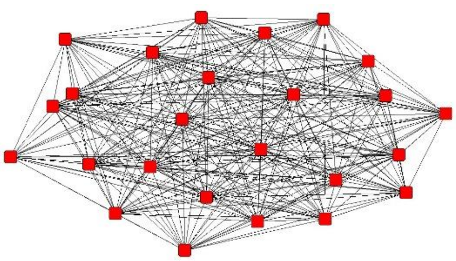

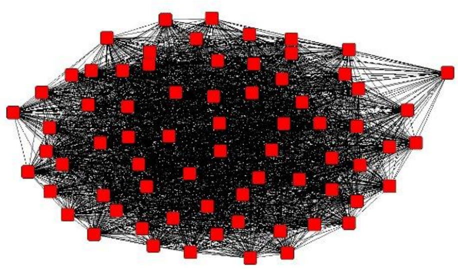

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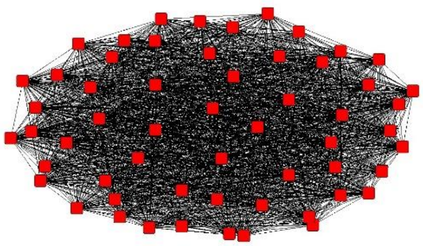

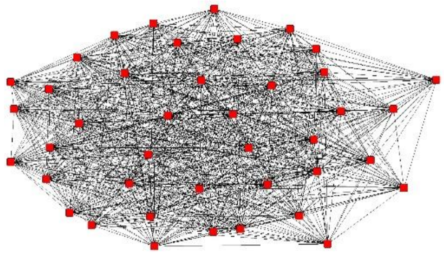

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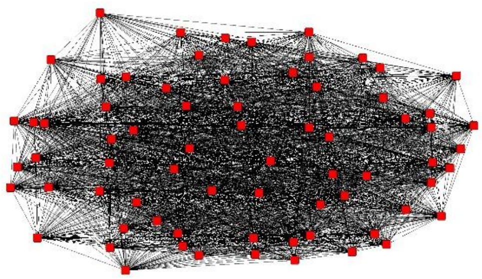

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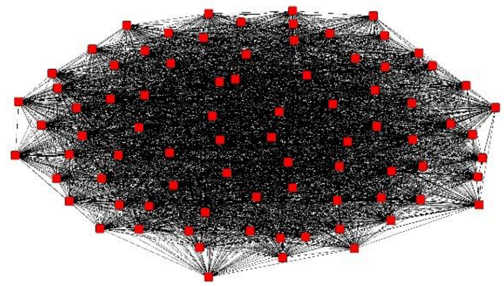

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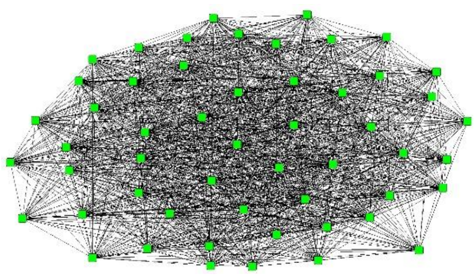

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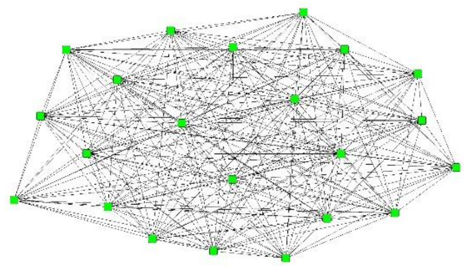

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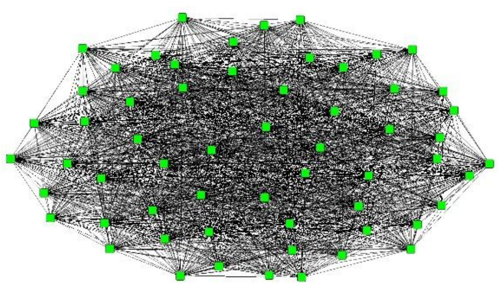

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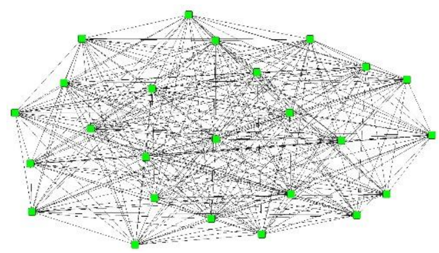

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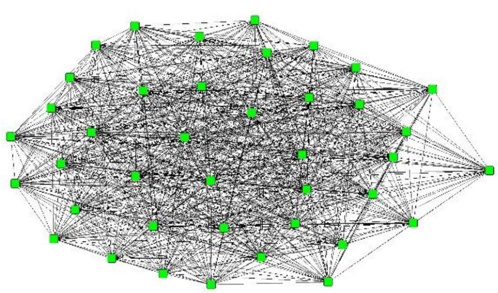

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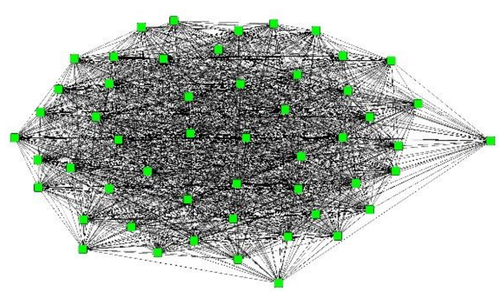

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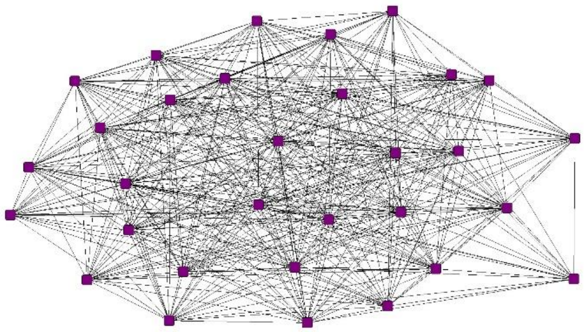

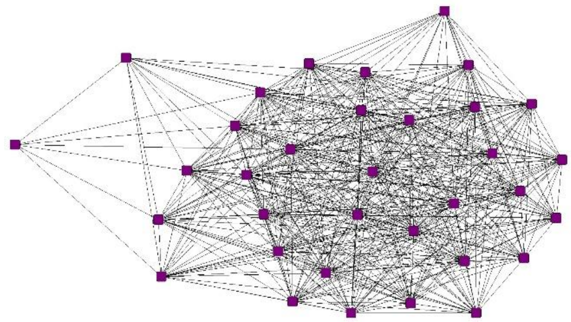

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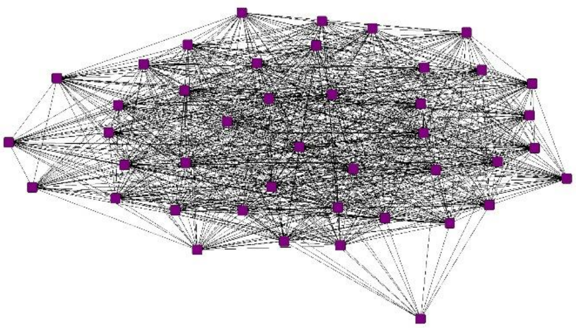

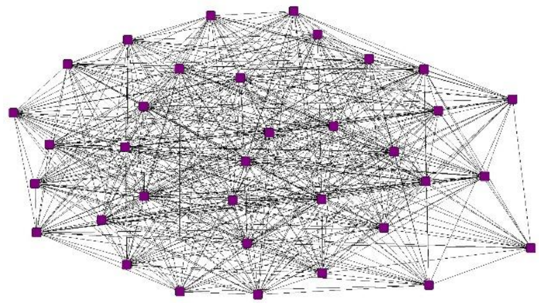

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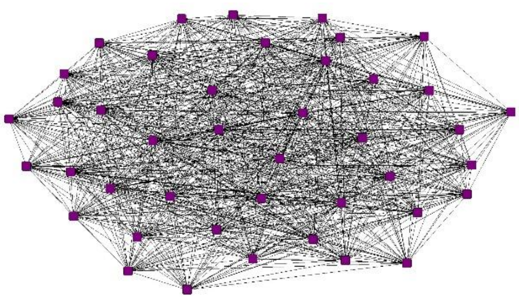

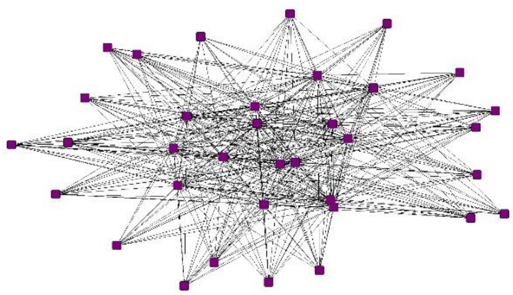

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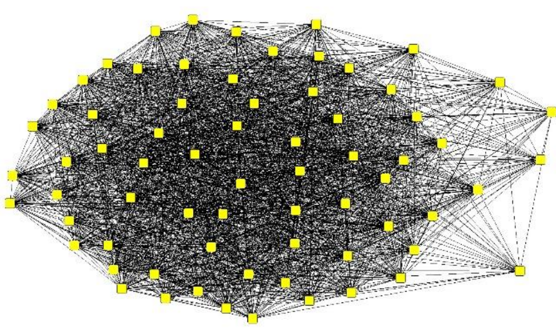

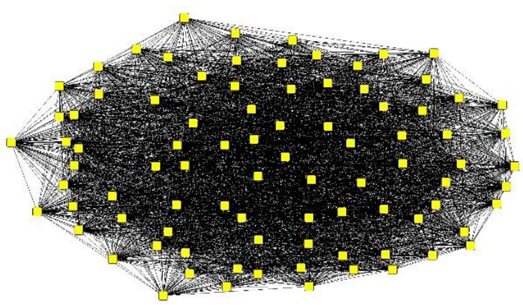

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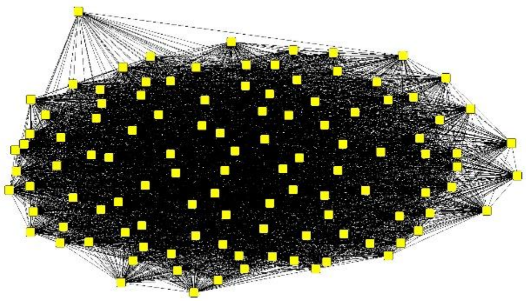

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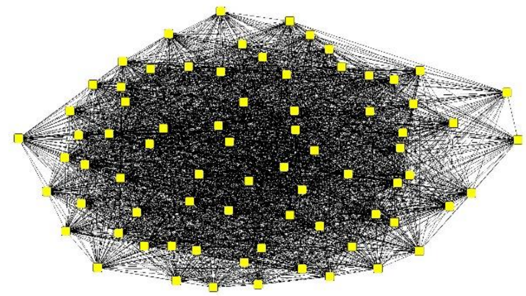

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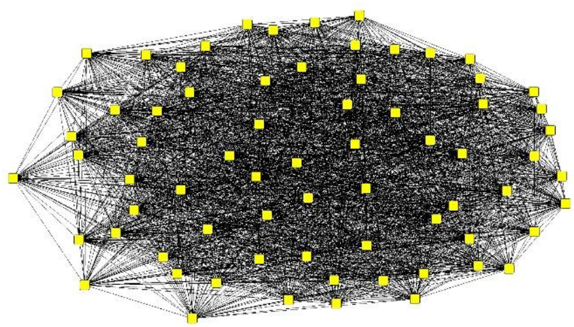

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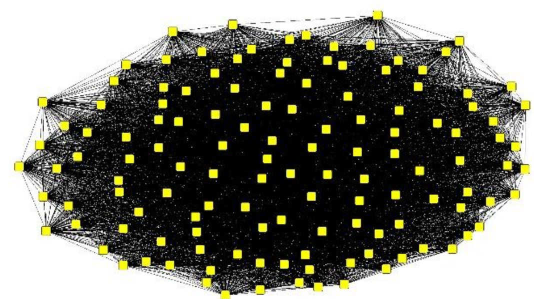

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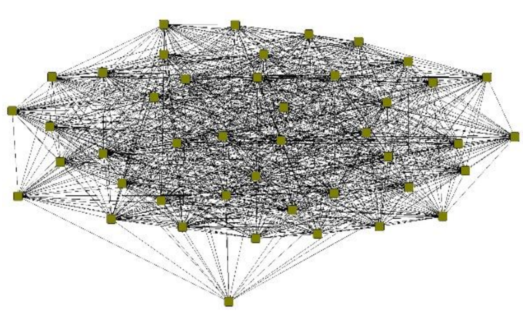

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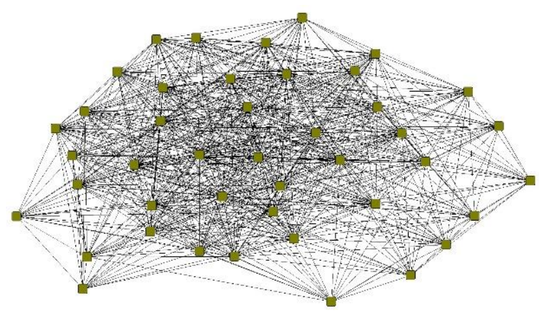

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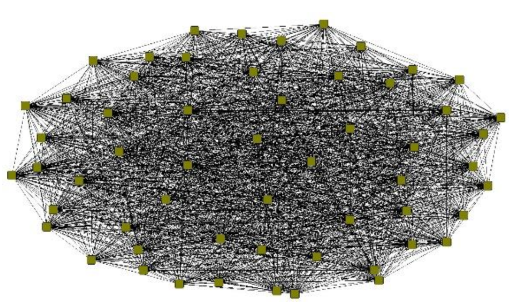

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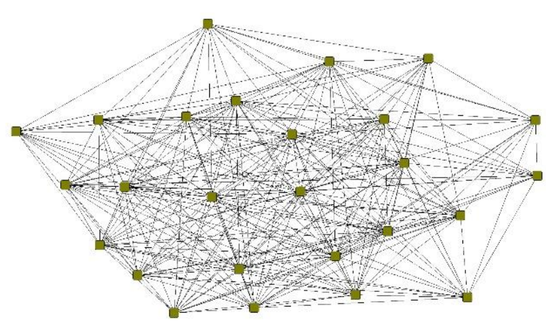

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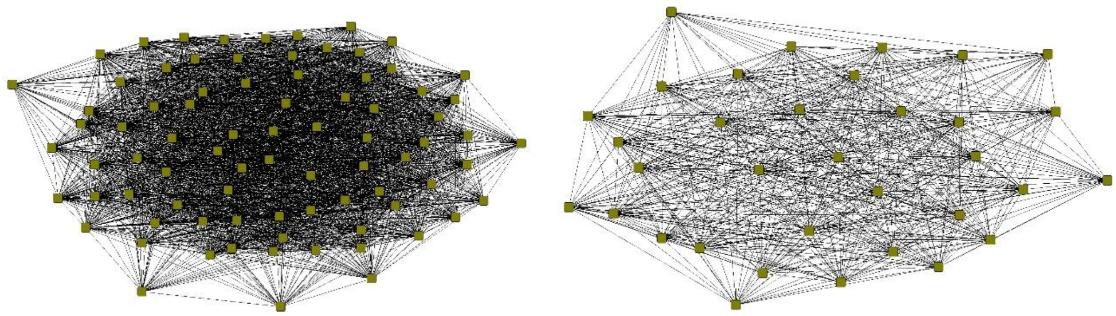

(4) Visualization of agonistic (left) and food competition (right) aggregated networks African Penguins via Gephi software. Color codes: green-juvenile (age < 1 year), blue-adult male, red-adult female. The edge color represents the source of the interaction.