

**University of South Bohemia
Faculty of Science**

**Relationship between personality and
social network characteristics**

Master thesis

Bc. Klára Valentová

Supervisor: Mgr. Martina Konečná, Ph.D.

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Annotation:

This thesis investigated whether an individual's personality (assessed on four personality dimensions: Friendliness, Activity/Excitability, Confidence, Openness) can be related to its social network position in Barbary macaques (*Macaca sylvanus*). The effect of sex and rank was also evaluated. The network position of individuals was described by individual network characteristics values generated via social network analysis. Additionally, the phenotypic based assortment within the studied group was examined. The results showed that personality is related with the position of the individual in its social group and assortment based on several personality dimensions was found in studied networks.

Declaration:

I declare that I am the author of this Master thesis and that I worked out my Master thesis on my own and only using the cited literature.

Prohlášení:

Prohlašuji, že jsem autorem této kvalifikační práce a že jsem ji vypracovala pouze s použitím pramenů a literatury uvedených v seznamu použitých zdrojů.

V Českých Budějovicích dne

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1. INTRODUCTION

1.1 Individual and its social group

Each individual creates its own unique social environment through its interactions with others. Within the social group, this contributes to the formation of an emergent social structure of relationships which can influence various processes on both individual and global levels (Cantor et al., 2021).

Social network analysis (SNA) is a relatively new method invented for studies of social structure. It provides a unified conceptual framework which enables to study social structure at various levels – from individuals to the entire population (Krause et al., 2009). Although the method of SNA is based on the relatively simple principle of graphs, originally developed to study the social interaction patterns of human society (Kasper & Voelkl, 2009), it is now a widely established method applicable in many areas of animal behaviour research (Cantor et al., 2021).

Social structure of a group can significantly affect the evolution and ecology of given species. The way social ties are formed in the group can fundamentally affect the flow of information (Cantor et al., 2021), genes, or the spread of pathogens in a group (Kurvers et al., 2014). Furthermore, the social structure of the group may be involved in social evolution, culture (Kurvers et al., 2014) or cooperation (Cantor et al., 2021). From an individual point of view, the social structure of a group can influence an individual's access to resources or level of predation risk of an individual and thus influence the individual's fitness (Watts & Strogatz, 1998 in Pike et al., 2008).

The SNA enables researchers to deal simultaneously with the questions of how individual behaviour influences what happens at the level of whole group and how the structure of the whole group can influence the behaviour of a given individual. Furthermore, it offers the opportunity to study the role of a particular individual within a group, community or population (Krause et al., 2010), which can be especially useful when studying the relationship between individual's personal characteristics and its position within social group.

1.2 Animal personality

Stable individual differences in behaviour, emotions, and cognitive predispositions that are consistent over time and across situations are referred to as animal personalities (Weiss et al., 2020). It means that each individual is unique and has a certain personality type characterised by its ranking on particular personality traits. The knowledge of personality types can help researchers predict or explain an individual's behaviour (Barrick & Mount, 2005). The studies of stable behavioural differences between individuals can provide important information when we are interested in social dominance (David et al., 2011), partner choice (Schuett et al., 2010), wildlife conservation (reviewed in Roche et al., 2016) or social structure (Pike et al., 2008).

Current literature includes a large number of animal personality traits, such as friendliness, curiosity, aggression, or a willingness to take a risk (Réale et al., 2007; Pacheco, 2020) when describing an animal personality. Nevertheless, Boldness is one of the most commonly measured personality traits (e.g., Pike et al., 2008; Croft et al., 2005; Croft et al., 2009; Ilany & Akçay, 2016; López, 2020). On the contrary, Sociability was relatively neglected trait, but is gaining some prominence now (e.g., Pacheco, 2020).

The individual's personality significantly contributes to the formation of its social interactions (e.g., Pike et al., 2008; Croft et al., 2009; Aplin et al., 2013; Snijders et al., 2014; López, 2020). Personality may influence the decision with whom the individual will interact and how often will the others interact with the individual, the type of social interactions, the stability and strength of its relationships or the number of social partners. Personality may also influence the extent to which individual considers previous experiences during its interactions (Pike et al., 2008; Wolf & Krause, 2014).

Therefore, personality differences between individuals might play an important role in shaping the fine social structure of a group (Wolf & Krause, 2014). And similarly, the social structure of the whole group can significantly influence an individual's personality development and its resulting personality type (Krause et al., 2010; Webster & Ward, 2011).

1.2.1 Social network analysis and personality assessment

Although the analysis of personality assessed by SNA is not the goal of my thesis, the method of SNA can bring some interesting benefits to the study of animal personality as

it potentially broadens the options how to measure personality traits relevant to social context.

Individuals of various personality types differ in the number and frequency of interactions with others as well as in the type and direction of their interactions with respect to previous experience (Wolf & Krause, 2014). However, there was no suitable analytical framework capable of creating a meaningful description of aspects of animal social behaviour, until the advent of SNA. Consequently, an individual's personality has been examined purely on the basis of its dyadic interactions (Wilson et al., 2013). Thanks to the SNA, the position of an individual in social group can be statistically characterized, which provides new knowledge in terms of personality research that would not be possible to study using traditional techniques (Wilson et al., 2013). SNA allows to take into account the number, strength, direction and as well as the stability of social ties of each individual in the group.

A significant benefit of the SNA is the possibility of studying the indirect ties of an individual (whether and how are the individuals with whom the focal individual interacts connected?). For the complete understanding of the ecology and development of personality, it may be useful to consider not only direct interactions, but also indirect relationships with other group members to visualize the individual's personality in the context of the whole group (Krause et al., 2010).

Across three years, Aplin and colleagues (2015) examined repeatability in social behaviour of great tits (*Parus major*) quantified by a range of social network characteristics. Their study demonstrates stability, which is one of the defining components of personality. Significant individual consistency in group size and in several social network characteristics including betweenness were found. Betweenness informs about how often the studied individual forms a “bridge” between different individuals in the network. Individuals with a high betweenness can, for example, significantly influence the spread of diseases or the transmission of information within group. In the previous study Aplin and colleagues (2013) also found that betweenness may be related to the level of explorative behaviour. Great tits with higher level of explorative behaviour achieved higher betweenness score more often compared to less explorative individuals.

Many authors suggest that description of an individual's position within social group through network characteristics offers the opportunity to characterize an individual's

personality based on its social interactions and to derive its social significance in a given social structure (Krause et al., 2010; Wilson et al., 2013; Kulahci et al., 2018).

2. WHAT IS THE POSITION OF THE DIFFERENT PERSONALITY TYPES IN THE SOCIAL GROUP

Currently, there is only a small number of the animal studies that focuses on the relationship between personality and the role of individual in a social group. Larger number of studies have been performed with humans, so in this chapter, I pay attention to them as well.

For better orientation in the following text, Table I summarizes the definitions of the most frequently used individual social network characteristics.

Tab. I: The table summarizing the definitions of the most frequently used network characteristics in the method of SNA.

NETWORK CHARACTERISTIC	WHAT DOES IT TELL?	DEFINITION**
Degree*	How many social partners does an individual have?	The number of social ties (relationships) the focal individual participates.
Strength*	What is the total number of ties of focal individual? Or how many and how strong ties does the individual form with other members of the group?	Weighted characteristic of the degree determined by the strength of social ties of the individual. The strength value increases when an individual interacts with a higher number of partners or interacts with its partners with a higher frequency.
Betweenness	How often does the study individual form a “link“ between the other group members?	The number of shortest paths defined by the lowest number of connections between different pairs of individuals that pass through the studied individual.
Closeness*	How close is the study individual to the other individuals in the group?	The average length of all the shortest paths connecting the studied individual and all other members of the studied social group.
Eigenvector centrality	Does the studied individual form ties with highly central individuals in the group?	Represents the interconnection of an individual within a network depending on the number and strength of ties that the individual has, with respect to the centrality of the individuals to which he is connected.

Node transitivity	Is the studied individual part of a closely connected subgroup in the network? Are the individual's social partners also social partners?	The number of observed ties between the neighbours of the studied individual divided by the maximum possible number of ties between them.
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* In the directed networks the network characteristics degree, strength, and closeness can consider only outgoing ties of focal individual (out), only incoming ties (in), or all ties of individual (all).

** The definitions of individual network characteristics are based on Wey et al. (2008).

2.1 Personality and position within the human social group

The literature on human behaviour includes variety of studies dealing with the relationship between an individual's personality traits and its position within social networks. The five-factor model, or the Big Five, is the most widely used tool for personality assessment (e.g., Kafner & Tanaka, 1993; Wehrli, 2008; Schaefer et al., 2008; Klein et al., 2004). The main personality components of this model are Openness to experience, Conscientiousness, Extraversion, Agreeableness, and Neuroticism. Both personality and network characteristics are usually based on completed questionnaires.

In his study, Wehrli (2008) focused on the environment of Internet social networks. He concluded that the level of Extraversion plays an important role in creating social ties. People with a high level of Extraversion more often registered on social networks and gathered more friends on the contact list of their online profile. Within the network of friendly relations, they reached more central positions, when Extraversion was positively correlated with degree, betweenness, closeness and eigenvector centrality. People with a high level of Conscientiousness, on the other hand, tended to refrain from participating in social networks and achieved lower values of degree betweenness and closeness. Problem is that all the network characteristics used in this study correlated with the degree network characteristic.

The personality also plays an important role in how the individual is perceived by others during a common interaction. In Kafner & Tanaka (1993) students with low levels of

Neuroticism and high levels of Extraversion reached high indegree values, which means that they were the most preferred partners for interaction. In the same study the authors also showed that people with high level of Agreeableness achieved high outdegree values. They more often established social interactions with other students and thus showed a tendency to occupy central positions within the seminar group (Kafner & Tanaka, 1993). Similarly, Klein and colleagues (2004) found that people with low levels of Neuroticism achieved higher indegree value in the friendship network and were therefore more preferred companions within the working group and were often the ones that other members of the working group went to for an advice. Contrary to the results of the previous study (Kafner & Tanaka, 1993), Klein and colleagues (2004) demonstrated that people with a high level of Extraversion achieved higher indegree values in the adversarial network, and were therefore more often referred to by others as those who are difficult to get along with and those who are better to avoid. This incompatibility between studies may be due to the fact that Kafner & Tanaka (1993) studied social interactions between students, whereas Klein and colleagues (2004) focused on the interactions within working groups, where individuals solved the task and were thus exposed to more demanding conditions.

Furthermore, other studies found relationship between network characteristics and other personality characteristics. For example, people who achieved high values of betweenness and thus more often formed ties between different subgroups were independent, open to changes, and seeking responsibility (Burt et al., 1998) or had a high level of self-control in terms of appearing in front of other (Mehra et al., 2001).

In summary, human studies show that personality can have a major impact on people's role within various social groups.

2.2 Personality and position within the animal social group

Animal studies have most often focused on the relationship between social network characteristics and personality trait Boldness. In three-spined sticklebacks (*Gasterosteus aculeatus*), individuals rated as bolder had lower strength and thus achieved a lower number of social interactions in comparison with shy individuals. In terms of node transitivity, bolder individuals tended to distribute their interactions more equally among all group members, while shyer individuals preferred to form stronger ties with lower number of social partners (Pike et al., 2008). Also in Trinidadian guppies (*Poecilia reticulata*), shyer individuals achieved higher strength and degree values compared to bolder ones, and thus

they had the higher number of social partners on average and their ties were stronger (Croft et al., 2009).

A seemingly contradictory result came from a study of the relationship between network characteristics and Boldness - Shyness in wild bottlenose dolphins (*Tursiops truncatus*) (Díaz López, 2020). The Boldness scale was based on the reactions to the novel object and the novel situation. The results showed that in the proximity network, bolder individuals (showing more novelty-seeking behaviour) achieved higher strength and thus occupied more central positions within their social network and formed stronger ties with others compared to shyer individuals (showing more novelty-averse behaviour). For other network variables (degree, node transitivity, closeness, and betweenness), no relationship with Boldness was found (Díaz López, 2020).

The inconsistent results of previous studies may be caused mainly by different methods of personality assessment and by differences in biology of studied species. For example, Boldness assessment of dolphins was based on novelty seeking behaviour, while Boldness assessment of three-spined stickleback on latency to feed following a mild startle and assessment of Trinidadian guppies on predator inspection tendency and shoaling tendency. Vast methodological differences make comparison of the results complicated and inconclusive.

On the other hand, the finding that bolder three-spined sticklebacks achieve lower node transitivity values and thus distribute their interactions more equally among others compared to shyer individuals are in agreement with the results of a modelling study by Ilana & Ackay (2016). These authors used a different approach to explain how personality can affect the social structure of a group and thus the network position of individuals. Through their generative model, they represent a fictitious population in which the probability of ties between a newborn individual and other group members is affected by the Boldness value of the newborn. The outcomes of the study demonstrate that individuals with low Boldness were more likely to form coherent groups, which was reflected in their higher node transitivity (so call clustering coefficient). On the contrary, bolder individuals achieved lower node transitivity and less often were part of clusters within the group. Moreover, they achieved higher betweenness, which means that they more often formed links between different subgroups of individuals.

Exploratory behaviour is another personality trait that has been studied in the context of the individual's social network position. Great tits (*Parus major*) with lower exploratory

behaviour scores had lower degree and higher strength values compared to high exploratory tits (Aplin et al., 2013). Thus, less exploratory birds formed stronger and relatively long-term ties with a smaller number of social partners compared to more exploratory birds. In addition, more exploratory birds moved more frequently between different subgroups and reached higher betweenness, which means that they more often formed links between different subgroups. As a result, individuals with higher exploratory behaviour scores occupied more important positions within the social network, especially in terms of the spread of diseases and information flow (Aplin et al., 2013).

Snijders and colleagues (2014) also examined the relationship between the level of exploratory behaviour of male great tit (*Parus major*) and their position within the social network. Nonetheless, in this study, individuals with lower exploratory behaviour scores achieved both lower degree and lower strength values. Thus, they spent less time in proximity to other males compared to individuals with higher exploratory behaviour scores, which was also related to the small number of their social partners. These individuals subsequently achieved lower eigenvector centrality and occupied more peripheral positions in the network compared to individuals with higher exploratory behaviour scores.

The discrepancy of the results concerning the strength variable between the two studies may be due to the different method and period of data collection. Aplin and colleagues (2013) observed winter encounters of nonterritorial great tits visiting artificial feeding stations (gambit of the group approach) but Snijders and colleagues (2014) followed social encounters during the territorial period. Interactions during a territorial period are more likely to reflect interactions based on space competition and reproductive opportunities (Snijders et al., 2014). Moreover, Aplin and colleagues (2013) focused on individuals of both sexes, whereas Snijders and colleagues (2014) included only males.

Other personality traits and domains have been investigated less often. For several groups of meerkats (*Suricata suricatta*), Pacheco (2020) analysed the relationships between personality dimension Friendliness and Aggression and individual network characteristics generated from grooming, dominance and foraging competition networks. The results showed that personality was not a consistent predictor of an individual's position within the social network across studied groups. Only in the networks of foraging competition, positive relationship was found between Friendliness and node transitivity, which means that friendlier individuals were more often part of a more interconnected subgroup in the foraging competition networks. The study found more significant relationships between

personality dimensions and network characteristics; however, the relationships were not significant across multiple groups. This study illustrates how important is to take into consideration what kind of behaviours are used for creating social networks and the group characteristics.

An individual's network characteristics can play an important role in the individual's options of exploiting social information and similarly social information flow might affect the network characteristics. Thus, it is interesting to investigate relationship between network characteristics and cognitive performance of an individual. For example, individuals who form social ties with a higher number of other group members may have better access to social information due to their position within the social network. Knowledgeable individuals with a tendency to exploratory behaviour can in turn more easily obtain new information from the environment. Because of that, they may be the preferred partners for others to interact and occupy central positions in the network as well. A study of ring-tailed lemurs (*Lemur catta*) showed that individuals who successfully solved novel task subsequently had higher number of incoming social interactions and thus became more central in social network (Kulahci et al., 2018).

The animal and human studies support the prediction that personality of individual can influence its social strategies and thus contributes to the fine structure of its social networks. In human studies, personality has been mostly assessed using five-factor model and both personality and network characteristics have been assessed by questionnaires. Animal studies have been predominantly focused on only one aspect of personality which has been mostly assessed by observations or experiments (Pike et al., 2008; Darren P. Croft et al., 2009; Aplin et al., 2013; Snijders et al., 2014; Díaz López, 2020). Moreover, social ties between individuals are often defined only by spatial proximity or subgroup affiliation (Pike et al., 2008; Croft et al., 2009; Aplin et al., 2013; Snijders et al., 2014; Díaz López, 2020) or the authors work only with non-direct ties (Ilany & Akçay, 2016) instead of focusing on specific and directed interaction.

Given the above mentioned issues it is complicated to vigorously compare the results of the studies as well as to draw some general conclusions.

3. SOCIAL NETWORK ANALYSIS AS A TOOL FOR PERSONALITY BASED ASSORTMENT DETECTION

Individuals in many social species show strong preferences for certain individuals within their social group (Massen & Koski, 2014). Assortment, or homophily, refers to the non-random tendency of individuals to associate with individuals with similar phenotypic or genotypic characteristics. If an individual prefers to associate with individuals with different traits, it is called disassortment.

Assortment is another structural phenomenon that can be well studied through the SNA. Network analysis enables to study the extent to which individuals with similar phenotypic traits are interconnected within a social network (Krause et al., 2010). A preference for social ties with a similar individual may for example support partner's predictability in social interaction (Massen & Koski, 2014). Assortative ties can thus bring important adaptive benefits to individuals, especially in terms of cooperation.

3.1 Why does an individual prefer specific members of the group?

In many cases, the strong relationship between individuals can be explained by their kinship or by their similarity in age and status (reviewed in Massen & Koski, 2014). In rhesus macaques (*Macaca mulatta*), strong bonds are mostly formed among members from same matriline; however, strong affiliative bonds are also formed between unrelated individuals of different ages and positions (Massen & Sterck, 2013). Likewise, Barbary macaques (*Macaca sylvanus*) are characterized by friendships between individuals from different matrilines (Thierry & Aureli, 2006; Roubová et al., 2015). Similarity in personality traits can explain maintenance of such strong social bonds between unrelated individuals in the groups.

Because strong associations with others represent an investment of energy, time and trust, it is evolutionarily advantageous to form strong relationships with more trustworthy individuals. Individuals with similar personality traits are more likely to behave similarly in certain situations, which may increase their mutual compatibility and trust (Massen & Koski, 2014). In chimpanzees (*Pan troglodytes*), individuals who were more often in close proximity were found to have more similar personality traits related to cooperative and socio-positive behaviours (Massen & Koski, 2014). In chacma baboons (*Papio ursinus*), a

phenotypic assortment based on the propensity to generate and exploit information was found (Carter et al., 2015). Furthermore, an assortment based on network characteristic degree was found in three-spined stickleback (*Gasterosteus aculeatus*). Stickleback, who had a higher number of social partners, interacted with each other more often, than with other individuals in the group (Croft et al., 2005). On the other hand, other studies found no individual preference for individuals with a similar level of Boldness in bottlenose dolphins (*Tursiops truncatus*) (Díaz López, 2020) or an assortment based on Friendliness and Aggressiveness in meerkats (*Suricata suricatta*) (Pacheco, 2020).

Also studies that have not directly measured assortment can offer some interesting insights to non-random distribution of social interactions. In their study, Verspeek and colleagues (2019) focused on partner compatibility and found a higher probability of certain partner combinations. Bonobos (*Pan paniscus*) who were more similar in the personality dimension Activity had lower compatibility in their relationships (Verspeek et al., 2019). Although the study did not directly focus on assortment, it could be assumed that individuals associated less with each other and disassortment based on the Activity was therefore present.

Assortative ties based on similarity in personality can be important determinants of a group's social structure. Consequently, the knowledge whether the studied individuals show a tendency to associate with individuals with similar personality traits can contribute to a better understanding of the association processes of individuals and thus the functioning of the group as a whole.

4. BARBARY MACAQUES

Macaques represent a species rich primate group. They live in multimale-multifemale groups with male dispersion. Females mostly remain in their natal group. Within the group, matriline are formed in which several generations of females coexist and strong bonds are maintained within these matriline (Thierry, 2007).

Macaques can be classified on a scale from tolerant to despotic species, based on their different level of kinship preference and inequality in dominance rank (Thierry & Aureli, 2006; Thierry, 2007). Barbary macaques are rather tolerant species of macaques. In terms of social ties, kinship and dominance are not among the major determinants of their relationships. Strong social ties often arise even between unrelated individuals. For example, the proportion of support provided to an unrelated individual during aggressive interactions is particularly high for Barbary macaque (Paul 2006).

Due to the fact that in Barbary macaque kinship and position in dominance do not have such a significant effect on social bond (compared to for example rhesus macaques), Barbary macaques are a suitable species for studying the influence of personality on individual's social ties and for studying personality-based assortment.

5. MAIN GOALS

The aim of this work is to test whether the position of an individual in a group may be related to its personality traits and whether there is an assortment based on personality traits in the study group via method of SNA.

Specifically, I will test whether the four personality dimensions (Friendliness, Activity/Excitability, Confidence and Openness) determined in the previous study (Konečná et al., 2012) are related to the social network characteristics generated from two types of behavioural data, sitting in contact and grooming.

Furthermore, within the two types of social networks based on the two types of behavioural data, I will analyse the assortment based on the four personality dimensions, sex and rank.

6. METHODS

6.1 Data collection

The data for analysis came from semi-free-ranging group of Barbary macaques living in the Upper Rock Natural Reserve, Gibraltar. The study group was provisioned daily and in contact with the public.

Individuals were observed over two mating seasons (November 2007 - February 2008; October 2008 - February 2009). The data collection was performed by Martina Konečná and Veronika Roubová using the method of focal continuous sampling together with focal instantaneous sampling and occasional ad libitum sampling (Altmann, 1974). During the first season, the group consisted of 17 adult females, 6 adult males, and up to 15 juveniles and infants who were not included in the analyses. In the second season, three males immigrated to the group. The age of the individuals was derived from a pedigree administered by the Gibraltar Ornithological and Natural History Society (GONHS).

Observations always took place from 8:00 to 18:00 and for each individual, data were collected evenly throughout the day and throughout the season. Observers recorded over 50 predefined behaviours covering a range of daily macaque activities.

More information about data collection, localities and individuals can be found in the original studies (Roubová 2011; Konečná et al., 2012; Roubová et al., 2015).

6.2 Personality rating

Personality rating was performed and analysed in study by Konečná and colleagues (2012). Personality was measured through personality questionnaires by two observers. The questionnaire contained 51 items. Each item consisted of an adjective supplemented by one to three clarifying sentences that defined the adjective with respect to primate behaviour. For example, FRIENDLY: *“An individual often seeks friendly contact with others. An individual seldom initiates hostile behaviour toward others.”*. The items were rated by the observers on a seven-point scale, where “1” indicating the absence of the personality trait and “7” the fully developed personality trait.

For the purposes of this thesis, the personality scores of individuals from the second season were used because it includes data from higher number of individuals. As could be find in the study by Konečná and colleagues (2012), personality ratings showed great

agreement between observers and between seasons. Using principal component analysis, four personality dimensions were obtained. Subsequently, for each individual was calculated a weighted score on each dimension. The weighted score then entered into further analyses.

Found personality dimensions were labelled Friendliness, Activity/Excitability, Confidence, and Opportunism.

- Personality dimension **FRIENDLINES** included items related to friendliness (e.g., sympathetic, helpful) and sociability or extraversion (e.g., sociable, popular, friendly, playful).
- Personality dimension **ACTIVITY/EXCITABILITY** included items related to activity (e.g., active, excitable), reactivity (e.g., alert), and exploratory behaviour (e.g., curious, exploratory).
- Personality dimension **CONFIDENCE**, after multiplying -1, positively loaded items related to dominance, confidence or intelligence and negatively loaded with items related to the submission (e.g., submissive, dependent, shy).
- Personality dimension **OPPORTUNISM** included items such as jealous and opportunistic, items related to low friendliness (e.g., manipulative, irritable, bullying) and items related to the ability of individuals to meet their needs (e.g., greedy, picky, persistent).

6.3 Social network analysis

I included behavioural data from the second season collected by the method of focal instantaneous sampling into the analysis of social networks. The total observed time for each individual averaged 13.8 ± 1.2 SD hours (Konečná et al., 2012).

The data for network analysis were based on two types of observed behaviours: sitting in contact and grooming. These behaviours were chosen because they are well observable and common, which is important for the network analysis (Farine & Whitehead, 2015). In addition, each of these behaviours represents one of two types of data commonly used in SNA.

For the proximity type of data (in this case sitting in contact, from here referred to as contact), the association ties between individuals are typically based on spatial proximity. The ties are non-directed, which means that it is not possible to determine the initiator and recipient of the interaction. The interaction type of data (in this case grooming) is based on directed interactions, for which the initiator and the recipient of the interaction are known. Directed ties between individuals can be symmetrical, if the tie directs to both individuals, or asymmetrical, where only one individual in the pair exhibits behaviour towards the other.

Contact data were recorded during the instantaneous sampling every 2 minutes whenever two or more individuals were in such proximity, that they were touching with any part of the body. Other behaviours such as an embrace or grooming were not observed. The relationship of each pair of individuals was determined by the ratio of the samples where two individuals were sitting in contact and the sum of the minute samples (records) for each pair. Thus, contact data include information about the strength of the interaction and are referred to as weighted. Since this type of data does not contain information about the initiator and recipient of the interaction, the matrix created from the contact data is symmetric.

For the grooming data, both initiated (a situation where a focal individual groomed another individual) and received (a focal individual was groomed by another individual) interactions were recorded. An asymmetric matrix was subsequently created from the data of these directed interactions. Finally, the strength of the association between each pair of individuals was calculated as the ratio of the number of grooming interactions and the sum of the minute samples of each pair. Grooming data are also weighted. Since they carry information about the initiator and recipient of the interaction, the final network is asymmetric.

In total, two weighted association matrices based on two different types of behaviour were included in the analysis. All network and statistical analyses were performed in R 3.5.1. (R Core Team, 2020).

6.3.1 Individual network characteristics selection

The network properties of an individual can be studied through various network characteristics. Some network characteristics indicate the number (degree) and strength (strength) of the individual's ties. Others take into account the degree of centrality and social significance of the individual (closeness, betweenness, eigenvector centrality), or measure the individual's tendency to be part of some subgroup in the network (node transitivity).

Using the igraph package (Csardi & Nepusz, 2006), six network characteristics for contact (degree, node transitivity, strength, closeness, betweenness, eigenvector centrality) and ten network characteristics for grooming (strength in, strength out, node transitivity, eigenvector centrality, betweenness, closeness all, closeness in, closeness out, indegree, outdegree) were generated from matrices of two types of behaviour.

Subsequently, Pearson correlation of these network characteristics was run. This procedure was chosen in order to reduce the number of network characteristics entered into subsequent analyses and thus reduce the probability of type I error and so-called metric hacking (Webber et al., 2020). The results of the correlations are shown in Table II and Table III. Uncorrelated characteristics, strength, node transitivity and betweenness were chosen for contact and strength in, strength out, node transitivity and betweenness for grooming data. These characteristics capture various aspects of an individual's position in the network and were used in the subsequent analysis.

Tab. II: Correlation values of network characteristics generated from the network of contact. Values highlighted in bold indicate significant correlations ($p < 0.05$).

SITTING IN CONTACT						
Correlation						
	degree	node transitivity	strength	closeness	betweenness	eigen_centrality
degree	1					
node transitivity	0.12	1				
strength	0.58	0.34	1			
closeness	0.19	-0.24	-0.37	1		
betweenness	0.35	-0.22	0.06	0.56	1	
eigen_centrality	0.69	0.38	0.87	-0.18	0.13	1

Tab. III: Correlation values of network characteristics generated from the grooming network. Values highlighted in bold indicate significant correlations ($p < 0.05$).

GROOMING										
Corellation										
	strength_in	strength_out	node transitivity	eigen_centrality	betweenness	closeness_all	closeness_in	closeness_out	indegree	outdegree
strength_in	1									
strength_out	-0.11	1								
node transitivity	0.38	-0.07	1							
eigen_centrality	0.9	0.05	0.36	1						
betweenness	-0.01	-0.15	0.02	0.13	1					
closeness_all	-0.06	-0.61	0.15	-0.03	0.69	1				
closeness_in	-0.57	-0.15	-0.16	-0.45	0.49	0.4	1			
closeness_out	0.06	-0.49	0.39	-0.02	0.58	0.75	0.35	1		
indegree	0.52	-0.23	0.17	0.43	0.56	0.44	0.15	0.37	1	
outdegree	-0.07	0.57	0.07	0.14	0.45	0.1	0.15	0.25	0.07	1

6.4 Definitions of selected network variables

6.4.1 Strength

The network characteristic degree is given by the number of ties (relationships) of any strength in which the individual participates. Strength is a weighted characteristic of degree and takes into account the strength of the ties (the total number of interactions of each individual). In directed networks, there are usually three types of strength: strength in (incoming ties), strength out (outgoing ties), and total strength. Outdegree expresses the number of outgoing ties of an individual and often reflects the sociability or companionship of the individual to others. Indegree is given by the number of incoming ties of an individual and can indicate, for example, its popularity (Csardi & Nepusz, 2006; Wey et al. 2008; Clifton & Webster, 2017). The difference between degree and strength is depicted in Figure 1. The difference between strength in and strength out is depicted in Figure 2.

degree x strength

- individual A: degree = $1 + 1 = 2$, strength = $4 + 2 = 6$

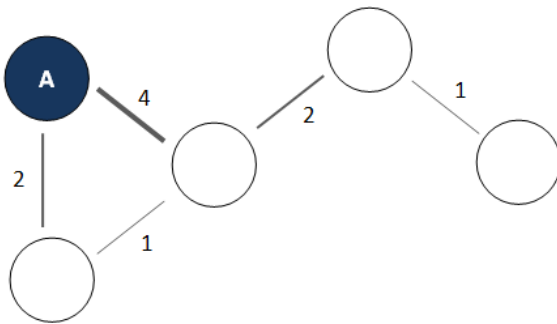


Fig. 1: The figure illustrates the difference between the degree and strength values of the individual A. Individual A forms ties with two other individuals in the network. The degree value of individual A = $1 + 1 = 2$. The strength value of individual A is given by the sum of the strength of the ties it has. Thus, the strength value of individual A = $4 + 2 = 6$.

Figure based on Cantor, M., Workshop on Animal Social Networks. YouTube. Oceans Research (2016).

strength in x strength out

- individual A: strength in = 1 + 3 + 3 = 7, strength out = 1 + 2 = 3

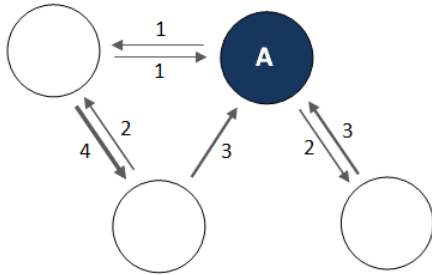


Fig. 2: The figure illustrates the differences between the strength in and strength out values of the individual A. The value of strength in is given by the sum of the incoming ties of an individual. The value of the strength in of the individual A = 1 + 3 + 3 = 7. The value of the strength out of an individual is given by the number of outgoing ties of the individual. The strength out value of the individual A = 1 + 2 = 3.

Figure based on Cantor, M., Workshop on Animal Social Networks. YouTube. Oceans Research (2016).

If the directionality of interactions were not considered, an individual might be, for example, perceived more popular within a group than he would be in reality. Focusing separately on incoming and outgoing interactions would reveal that the individual initiates more associations than receives.

6.4.2 Node transitivity

Node transitivity or "node level clustering coefficient" is based on the tendency of individuals to form subgroups within a network. It is given by the number of observed ties between the partners of the studied individual divided by the maximum number of possible ties between them (Fig. 3). It measures the tendency of nodes to cluster to other nodes while capturing network cohesion. High values of node transitivity indicate that the individual interacts more with certain members of the group and that the "friends" of the studied individual are often "friends" as well. This can lead to subgroups within the network, which can significantly limit the flow of information in the group or diffusion processes (Csardi & Nepusz, 2006; Wey et al., 2008).

node transitivity

- node transitivity of the individuals $A = 1/6 = 0,16$ and $B = 1/1 = 1$

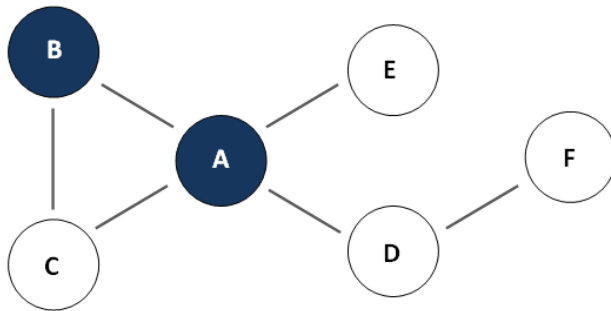


Fig. 3: The figure illustrates the different node transitivity values of individuals A and B. In the network, individual A forms ties with four other individuals: B, C, D, and E. Among these individuals another 6 potential ties may form. However, the tie occurs only between B and C. Therefore, the value of the node transitivity of the individual $A = 1/6 = 0.16$. Individual B is connected only with individuals A and C, between whom the tie also occurs. Node transitivity value of individual $B = 1/1 = 1$.

Figure based on Cantor, M., Workshop on Animal Social Networks. YouTube. Oceans Research (2016).

6.4.3 Betweenness

Betweenness is defined by the number of shortest paths (the path length is given by the number of ties) between different pairs of individuals that pass through the studied individual (Fig. 4). In other words, betweenness says how many times a given individual forms a link between other individuals. Individuals with high betweenness usually form links between two subgroups within the network and can thus influence the dynamics of information flow and other diffusion processes in the group. They may or may not pass on the information (Csardi & Nepusz, 2006; Wey et al., 2008).

betweenness

- betweenness of the individuals $D = 1/2 + 1/2 = 1$ and $E = 0$

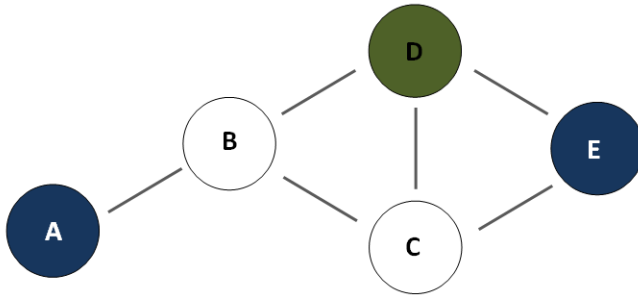


Fig. 4: In the figure, individuals C, D and E are interconnected within the network. There are two possibilities of the shortest path between individuals A and E, one of them leads through individuals D ($D = 1/2$). Equally, there are the two possibilities of the shortest path between individuals B and E ($D = 1/2$). The betweenness value of the individual $D = 1/2 + 1/2 = 1$. The individual E does not form a single tie between other individuals in the network. The betweenness value of the individual $E = 0$.

Figure based on Cantor, M., Workshop on Animal Social Networks. YouTube. Oceans Research (2016).

6.5 Predictions

Based on the found personality dimensions (Friendliness, Activity/Excitability, Confidence, Openness) and chosen network characteristics (strength, node transitivity, betweenness), I formulated the specific predictions about the relationships between these variables. The formulated predictions are summarized in Table IV.

Personality dimension Friendliness

- Friendliness will be positively related to strength in the contact and the grooming network. Individuals with high level of Friendliness will have a large number and especially more strong social ties, due to their sociability and popularity. They will

be often initiators and recipients of grooming interaction. Likewise, due to their tolerant and friendly nature, they will be favoured social partners and thus will be more often in contact with other individuals.

- Friendliness will not be related to node transitivity in the contact network and the grooming network. Individuals with a similar level of friendship can restrict their interactions to a certain subgroup or form social ties across the entire group.
- Friendliness will be positively related to betweenness in the contact network and grooming network. Individuals with high Friendliness score are sociable and do not like loneliness. It means that it will be easier for them to form ties between different individuals, and therefore subgroups. Their role as “linkers” may also be a consequence of their high popularity and tolerance.

Personality dimension Activity/Excitability

- The individual's score for Activity/Excitement will not show a linear relationship to strength in the grooming network. Individuals with both above-average and below-average scores in Activity/Excitability can be expected to have a lower number of grooming interactions than individuals with an average score. The tendency of highly active individuals toward higher physical activity and their greater propensity for exploratory behaviour suggest that they prefer to invest their energy to other activities than maintaining social ties and time-consuming grooming. Low-rated individuals, on the other hand, lack energy and are inactive, and thus they will probably not often engage in social interactions as well.
- Activity/Excitability will be positively related to strength in the contact network. Individuals with higher Activity/Excitability score will have a higher number of total interactions in the contact network compared to less active individuals. They are inquisitive explorers, so they can often be in close proximity to others in order to gain some interesting information. Likewise, due to their nature, they can be good generators of information from environment, so others can search for their company and benefit from generated information.

- Activity/Excitability will be positively related to betweenness in the contact network. Compared to less active individuals, individuals with high Activity/Excitability score will often move between different members of the group, and due to their inquisitive nature, they will spend more time in their close proximity and observe them. This will make it easier for them to create links between different individuals and subgroups in the network.
- No predictions were made for the relationship between Activity/Excitability and node transitivity in the contact network and grooming network, and for the relationship between Activity/Excitability and betweenness in grooming network.

Personality dimension Confidence

- Confidence will be positively related to strength in the grooming network. Individuals with a high Confidence score are dominant and confident and, in addition, often occupy preferred places and resources. Their high level of Confidence can bring them benefits as preferred partners (recipients) of grooming interactions. Others will groom them in order to maintain good relationship with them.
- Confidence will be negatively related to strength out in the grooming network. Due to the fact that individuals with high Confidence scores are dominant, confident and independent, they do not need to strengthen their social ties through grooming interaction or trade grooming for coalition support or access to resources (Carne et al., 2011). These are the reasons why highly confident individuals will have a lower number of total outgoing interactions in the grooming network compared to less confident ones.
- Confidence will not be related to strength in the contact network. The dominance and self-confidence of individuals with high Confidence score may be the reason why they are more common in the proximity of others. They do not need to stay away, and are often close to preferred locations and resources. On the other hand, other individuals will not stay in close proximity to individuals with high Confident score

for long time. They might rather avoid highly Confident individuals due to their dominance and aggression, and want to avoid possible conflict.

- Confidence will not be related to node transitivity. Individuals may prefer to associate with individuals within a particular subgroup, regardless of their assessment in the personality dimension Confidence.
- No predictions were made for the relationship between Confidence and betweenness in the contact network and grooming network.

Personality dimension Opportunism

- Opportunism will be positively related to strength out in the grooming network. Individuals with high Opportunism score, who are manipulative and insistent, will more often initiate grooming interactions with other members of the group as they try to take every chance to mate or to gain the favour of other individuals.
- Opportunism will not be related to node transitivity. It may be assumed that individuals with high Opportunism score will seek beneficial social interactions both across the whole group and within its subgroup. The tendency of individual to be part of some subgroups will therefore be independent of its Opportunism score.
- Opportunism will be positively related to the betweenness in the grooming network. Individuals with a high Opportunism score will more often create links between different individuals and subgroups in the network. Opportunistic females could interact with individuals from different matriline and try to secure the necessary support to shift in the dominant hierarchy, while males are look for opportunities to mate.
- In general, relationships could be assumed rather in the grooming networks. One of the functions of grooming interactions is the tactical trading so the tendency of individuals towards Opportunism could be present more in grooming network than in the contact network.

Tab. IV: Table summarizing the predictions about the relationships between personality dimensions and social network characteristic.

PERSONALITY DIMENSION	NETWORK	NETWORK CHARACTERISTIC	PREDICTION
FRIENDLINESS	GROOMING	STRENGTH IN	POSITIVE RELATIONSHIP
		STRENGTH OUT	POSITIVE RELATIONSHIP
		NODE TRANSITIVITY	NO RELATIONSHIP
		BETWEENNESS	POSITIVE RELATIONSHIP
	CONTACT	STRENGTH	POSITIVE RELATIONSHIP
		NODE TRANSITIVITY	NO RELATIONSHIP
BETWEENNESS		POSITIVE RELATIONSHIP	
ACTIVITY/EXCITABILITY	GROOMING	STRENGTH IN	NO RELATIONSHIP
		STRENGTH OUT	NO RELATIONSHIP
		NODE TRANSITIVITY	-
		BETWEENNESS	-
	CONTACT	STRENGTH	POSITIVE RELATIONSHIP
		NODE TRANSITIVITY	-
BETWEENNESS		POSITIVE RELATIONSHIP	
CONFIDENCE	GROOMING	STRENGTH IN	POSITIVE RELATIONSHIP
		STRENGTH OUT	NEGATIVE RELATIONSHIP
		NODE TRANSITIVITY	NO RELATIONSHIP
		BETWEENNESS	-
	CONTACT	STRENGTH	NO RELATIONSHIP
		NODE TRANSITIVITY	NO RELATIONSHIP
BETWEENNESS		-	
OPPORTUNISM	GROOMING	STRENGTH IN	-
		STRENGTH OUT	POSITIVE RELATIONSHIP
		NODE TRANSITIVITY	NO RELATIONSHIP
		BETWEENNESS	POSITIVE RELATIONSHIP
	CONTACT	STRENGTH	-
		NODE TRANSITIVITY	-
BETWEENNESS		-	

(-) – the relationship without prediction

6.6 The analysis of relationship between personality and social network characteristics

All analyses in this thesis were run in R 3.5.1. (R Core Team, 2020). Using the stats package (R Core Team, 2020), linear models were run to determine whether an individual's personality affects its position within the social network. Individual network characteristics based on either grooming data (strength in, strength out, betweenness, node transitivity) or contact data (strength, betweenness, node transitivity) were used as response variables. Individuals personality scores on four dimensions (Friendliness, Activity/Excitability,

Confidence, Opportunism), sex (M, F) and rank (continuous) entered the model as predictors.

Because network characteristics are not independent (network characteristics of one individual depend on network characteristics of other individuals in the network) and because data independence is a prerequisite for many statistical tests, it was necessary to compare the resulting test statistics calculated from observed data with the distribution of test statistics generated from randomized social networks (Farine, 2017). For each model, 100 randomized networks were created using the sna package (Butts, 2008) and then 100 linear models based on data from these networks were calculated. To determine whether the analysis based on the observed data differs significantly from the analysis performed on the basis of randomized networks, one tailed p-values were calculated (Wooddell et al., 2020). Example can be found in supplementary material S1.

To assess correlations between the explanatory variables, I created correlation matrix using Pearson correlations (see Tab. V).

Tab. V: Correlation matrix of the six phenotypic traits.

PHENOTYPES	Friendliness	Activity/Excitability	Confidence	Opportunism	Sex	Rank
Friendliness	1					
Activity/Excitability	-0.34	1				
Confidence	-0.18	0.32	1			
Opportunism	-0.42	0.40	0.31	1		
Sex	0.24	-0.06	-0.18	-0.01	1	
Rank	0.00	0.08	-0.76	-0.16	0.00	1

Using the regclass package (Petrie, 2016) I also calculated the variance inflation factors (VIF) for individual variables within the linear models (see Tab. VI).

Tab. VI: Variance inflation factors values of the six phenotypic traits.

Variance inflation factors					
Friendliness	Activity/Excitability	Confidence	Opportunism	Sex	Rank
1.361	1.7713	3.9761	1.4245	1.1710	3.4950

The multicollinearity values of all phenotypic attributes tested by VIF were less than 3.98. If the VIF value is less than 5, there should be no significant deterioration in the model's ability to estimate the relevant coefficients (Petrie, 2016).

6.7 Assortment analysis

I also tested whether an assortment based on personality dimensions (Friendliness, Activity/Excitability, Confidence, Opportunism), sex and rank can be detected in studied networks. In other words, I tested, whether the studied individuals prefer to associate with individuals of similar/dissimilar phenotype.

To test the assortment, I used the assortnet package (Farine, 2014). I calculated assortment coefficients, which indicate the extent to which associations between individuals with a similar phenotype occur within the studied networks. The assortment coefficient ranges from “-1” (observed individuals never associate with individuals with a similar phenotype) to “1” (observed individuals always associate with individuals with a similar phenotype) (Farine, 2014). Discrete assortment was calculated for sex, continuous assortment for personality dimensions and rank.

In this study, the effect of each phenotype was assessed independently (there is no statistical technique to examine the effects of multiple phenotypes on the assortativity of a weighted network). Standard errors were calculated using jackknife simulation. If the standard error of the assortment coefficient does not exceed 0, a significant preference of individuals for individuals with a similar phenotype can be assumed within the network (Farine, 2014).

7. RESULTS

7.1 Do individuals with a certain phenotype occupy characteristic positions within the social group?

In the networks based on two types of behaviours (contact and grooming), several significant relationships between phenotypic traits and selected network characteristics were found (Tab. VII and Tab. VIII). Furthermore, several insignificant trends were found, which I decided to also comment given the small size of the sample (Tab. VII and Tab. VIII).

Predictors of contact network characteristics

Tab. VII: Table is summarizing the results of the linear models. Significant relationships ($p < 0.05$) and relationship trends ($p < 0.1$) between network characteristics generated from contact networks and studied phenotypic traits are highlighted.

SITTING IN CONTACT						
STRENGTH	Predictor	Estimate	SE	t-value	Pr (> t)	p-value
	Intercept	-0.0868	0.0641	-1.355	0.191	
	Friendliness	0.0127	0.0076	1.682	0.109	0.06
	Activity/Excitability	0.0040	0.0093	0.427	0.674	0.34
	Confidence	0.0174	0.0119	1.467	0.159	0.05
	Opportunism	0.0027	0.0070	0.394	0.698	0.33
	Sex (M)	-0.0045	0.0135	-0.336	0.714	0.31
	Rank	0.0095	0.0116	0.817	0.424	0.19
NODE TRANSITIVITY	Predictor	Estimate	SE	t-value	Pr (> t)	p-value
	Intercept	0.2225	0.2176	1.023	0.319	
	Friendliness	0.0500	0.0257	1.948	0.066	0.02
	Activity/Excitability	-0.0018	0.0316	-0.057	0.955	0.48
	Confidence	0.0109	0.0403	0.269	0.791	0.44
	Opportunism	-0.0074	0.0237	-0.312	0.758	0.3
	Sex (M)	-0.0007	0.0460	-0.015	0.988	0.32
	Rank	-0.0270	0.0393	-0.688	0.500	0.33
BETWEENNESS	Predictor	Estimate	SE	t-value	Pr (> t)	p-value
	Intercept	0.1385	2.7131	0.051	0.960	
	Friendliness	-0.2854	0.3200	-0.892	0.383	0.18
	Activity/Excitability	0.6308	0.3940	1.601	0.126	0.09
	Confidence	0.1113	0.5027	0.221	0.827	0.41
	Opportunism	0.2064	0.2951	0.699	0.493	0.21
	Sex (M)	-0.4603	0.5729	-0.803	0.432	0.15
	Rank	-0.1347	0.4901	-0.275	0.786	0.36

In contact network, a non-significant trend of the relationship between Friendliness and strength ($p = 0.06$) and a positive relationship between Friendliness and node transitivity ($p = 0.02$) were found.

This means that individuals with high Friendliness score had more frequent and stronger associations with other members of the group and more often associated with members within a certain subgroup compared to less friendly individuals.

Next, a non-significant trend of the relationship between Activity/Excitability and betweenness was found in the contact network ($p = 0.09$). Thus, individuals with high Activity/Excitability score had a higher tendency to form links between different group members compared to individuals with lower Activity/Excitability score.

A significant relationship between Confidence and strength ($p = 0.5$) was also found in the contact network. Individuals with higher Confidence score had more frequent and stronger ties with others in the group compared to less confident individuals (Fig. 5a).

Predictors of grooming network characteristics

Tab. VIII: Table is summarizing the results of the tested linear models. Significant relationships ($p < 0.05$) and relationship trends ($p < 0.1$) between network characteristics generated from grooming networks and studied phenotypic traits are highlighted.

GROOMING						
STRENGTH IN	Predictor	Estimate	SE	t-value	Pr (> t)	p-value
	Intercept	-0.0418	0.0664	-0.630	0.536	
	Friendliness	0.0142	0.0078	1.817	0.085	0.05
	Activity/Excitability	-0.0011	0.0096	-0.112	0.912	0.51
	Confidence	0.0100	0.0123	0.814	0.426	0.16
	Opportunism	0.0069	0.0072	0.958	0.350	0.22
	Sex (M)	-0.0125	0.0140	-0.892	0.383	0.23
	Rank	-0.0129	0.0120	-1.078	0.295	0.1
STRENGTH OUT	Predictor	Estimate	SE	t-value	Pr (> t)	p-value
	Intercept	-2.4244	1.2213	-1.985	0.062	
	Friendliness	0.1390	0.1440	0.966	0.346	0.19
	Activity/Excitability	0.0919	0.1773	0.518	0.610	0.33
	Confidence	-0.212	0.2263	-0.964	0.347	0.09
	Opportunism	-0.0385	0.1329	-0.290	0.775	0.47
	Sex (M)	0.1054	0.2579	0.409	0.687	0.44
	Rank	-0.1361	0.2206	-0.617	0.545	0.21
NODE TRANSITIVITY	Predictor	Estimate	SE	t-value	Pr (> t)	p-value
	Intercept	0.2053	0.2511	0.818	0.424	
	Friendliness	0.0208	0.0296	0.702	0.491	0.25
	Activity/Excitability	-0.0288	0.0365	-0.789	0.440	0.15
	Confidence	0.0501	0.0465	1.076	0.295	0.12
	Opportunism	0.0352	0.0273	1.288	0.213	0.06
	Sex (M)	-0.0816	0.0530	-1.539	0.140	0.08
	Rank	0.0462	0.0454	1.018	0.321	0.13
BETWEENNESS	Predictor	Estimate	SE	t-value	Pr (> t)	p-value
	Intercept	2.7610	2.2497	1.227	0.235	
	Friendliness	-0.0737	0.2651	-0.278	0.784	0.29
	Activity/Excitability	0.1834	0.3267	0.561	0.581	0.23
	Confidence	-0.3996	0.4168	-0.959	0.345	0.22
	Opportunism	0.4478	0.2447	1.830	0.083	0.09
	Sex (M)	0.8915	0.475	1.835	0.082	0.01
	Rank	-0.2860	0.4034	-0.704	0.490	0.29

A positive relationship was found between Friendliness and strength in ($p = 0.05$) in the grooming network. Thus, friendly individuals received more grooming interactions from other members of the group compared to individuals with a lower Friendliness score.

Next, a non-significant trend of a negative relationship between Confidence and strength out was found ($p = 0.09$). It means that in grooming network, confident individuals had a meaningfully lower number of outgoing interactions compared to less confident group members.

A non-significant trend of the relationship between Opportunism and the network characteristics node transitivity ($p = 0.06$) and betweenness ($p = 0.09$) was also found. Compared to less opportunistic individuals, individuals with high Opportunism score were more likely to form strong ties with members within a particular subgroup and were also more common “linkers” between different individuals in the network (Fig 5b).

A non-significant trend of a negative relationship between sex and node transitivity ($p = 0.06$) and a significant relationship between sex and betweenness ($p = 0.01$) were also found in the grooming network. Compared to males, females more often formed strong ties with members of a certain subgroup. Males, on the other hand, were more common “linkers” between different individuals in a network compared to females.

The results of the analysis confirmed 12 of 20 predictions (Tab. IX). No relationship was found between the pairs of personality dimensions and network characteristics for which no prediction was made. Results of the tested relationships between sex and rank and the seven network characteristics are summarized in Table X.

Tab. IX: The table summarizing the predictions about the relationships between four personality dimensions and seven network characteristics and the results of the analyses among these variables. No relationship was found between the pairs of personality dimensions and network characteristics for which no prediction was made.

PERSONALITY DIMENSION	NETWORK	NETWORK CHARACTERISTIC	PREDICTION	RESULT
FRIENDLINESS	GROOMING	STRENGTH IN	POSITIVE RELATIONSHIP	POSITIVE RELATIONSHIP ✓
		STRENGTH OUT	POSITIVE RELATIONSHIP	NO RELATIONSHIP ×
		NODE TRANSITIVITY	NO RELATIONSHIP	NO RELATIONSHIP ✓
		BETWEENNESS	POSITIVE RELATIONSHIP	NO RELATIONSHIP ×
	CONTACT	STRENGTH	POSITIVE RELATIONSHIP	POSITIVE RELATIONSHIP ✓
		NODE TRANSITIVITY	NO RELATIONSHIP	POSITIVE RELATIONSHIP ×
BETWEENNESS		POSITIVE RELATIONSHIP	POSITIVE RELATIONSHIP ×	
ACTIVITY/EXCITABILITY	GROOMING	STRENGTH IN	NO RELATIONSHIP	NO RELATIONSHIP ✓
		STRENGTH OUT	NO RELATIONSHIP	NO RELATIONSHIP ✓
		NODE TRANSITIVITY	-	NO RELATIONSHIP -
		BETWEENNESS	-	NO RELATIONSHIP -
	CONTACT	STRENGTH	POSITIVE RELATIONSHIP	NO RELATIONSHIP ×
		NODE TRANSITIVITY	-	NO RELATIONSHIP -
		BETWEENNESS	POSITIVE RELATIONSHIP	POSITIVE RELATIONSHIP ✓
CONFIDENCE	GROOMING	STRENGTH IN	POSITIVE RELATIONSHIP	NO RELATIONSHIP ×
		STRENGTH OUT	NEGATIVE RELATIONSHIP	NEGATIVE RELATIONSHIP ✓
		NODE TRANSITIVITY	NO RELATIONSHIP	NO RELATIONSHIP ✓
		BETWEENNESS	-	NO RELATIONSHIP -
	CONTACT	STRENGTH	NO RELATIONSHIP	POSITIVE RELATIONSHIP ×
		NODE TRANSITIVITY	NO RELATIONSHIP	NO RELATIONSHIP ✓
		BETWEENNESS	-	NO RELATIONSHIP -

OPPORTUNISM	GROOMING	STRENGTH IN	-	NO RELATIONSHIP	-
		STRENGTH OUT	POSITIVE RELATIONSHIP	NO RELATIONSHIP	×
		NODE TRANSITIVITY	NO RELATIONSHIP	POSITIVE RELATIONSHIP	×
		BETWEENNESS	POSITIVE RELATIONSHIP	POSITIVE RELATIONSHIP	✓
	CONTACT	STRENGTH	-	NO RELATIONSHIP	-
		NODE TRANSITIVITY	-	NO RELATIONSHIP	-
		BETWEENNESS	-	NO RELATIONSHIP	-

(-) – relationship without prediction; (✓) – prediction was confirmed; (x) – prediction was not confirmed

Tab. X: A table summarizing the tested relationships between sex and rank and the seven network characteristics generated from the data of two types of behaviour.

PHENOTYPIC TRAIT	NETWORK	NETWORK CHARACTERISTIC	RESULT
SEX	GROOMING	STRENGTH IN	NO RELATIONSHIP
		STRENGTH OUT	NO RELATIONSHIP
		NODE TRANSITIVITY	POSITIVE RELATIONSHIP
		BETWEENNESS	POSITIVE RELATIONSHIP
	CONTACT	STRENGTH	NO RELATIONSHIP
		NODE TRANSITIVITY	NO RELATIONSHIP
		BETWEENNESS	NO RELATIONSHIP
RANK	GROOMING	STRENGTH IN	NO RELATIONSHIP
		STRENGTH OUT	NO RELATIONSHIP
		NODE TRANSITIVITY	NO RELATIONSHIP
		BETWEENNESS	NO RELATIONSHIP
	CONTACT	STRENGTH	NO RELATIONSHIP
		NODE TRANSITIVITY	NO RELATIONSHIP
		BETWEENNESS	NO RELATIONSHIP

7.2 Is the study group assorted by the phenotypic traits?

In my analysis, the phenotypic assortment occurred in four of the six studied phenotypes in the contact network (Tab. XI) and in five of the six studied phenotypes in the grooming network (Tab. XII).

Assortment in contact network

Tab. XI: The table shows the assortative coefficients and standard errors of the six phenotypic traits in a social network based on contact data. Statistically significant assortment is highlighted in colour.

SEZENÍ V KONTAKTU		
	Assortativity coefficient	SE
Friendliness	0.382	0.113
Activity/Excitability	-0.244	0.072
Confidence	0.329	0.067
Opportunism	0.07	0.101
Sex (M)	0.448	0.088
Rank	0.07	0.102

Assortment in grooming network

Tab. XII: The table shows the assortative coefficients and standard errors of the six phenotypic traits in a social network based on grooming data. Statistically significant assortment is highlighted in colour.

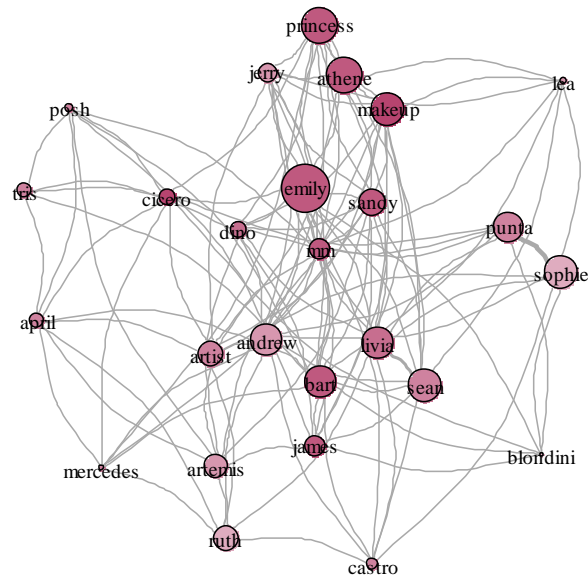
GROOMING		
	Assortativity coefficient	SE
Friendliness	0.146	0.11
Activity/Excitability	-0.146	0.071
Confidence	0.268	0.08
Opportunism	-0.009	0.102
Sex (M)	-0.179	0.089
Rank	0.408	0.08

In both types of networks, individuals showed positive assortment based on Friendliness and Confidence and disassortment based on Activity/Excitability. Thus, individuals similar to each other in the Friendliness and Confidence dimensions associated

more with each other. In contrast, individuals were more often associated with individuals with different score on Activity/Excitability dimension.

In the contact network, individuals of the same sex preferred to associate together, while in the grooming network, individuals of the opposite sex preferred to associate together. In addition, the grooming network was assorted according to the rank, thus individuals of a similar rank established grooming interactions more often than those with dissimilar rank.

a)



b)

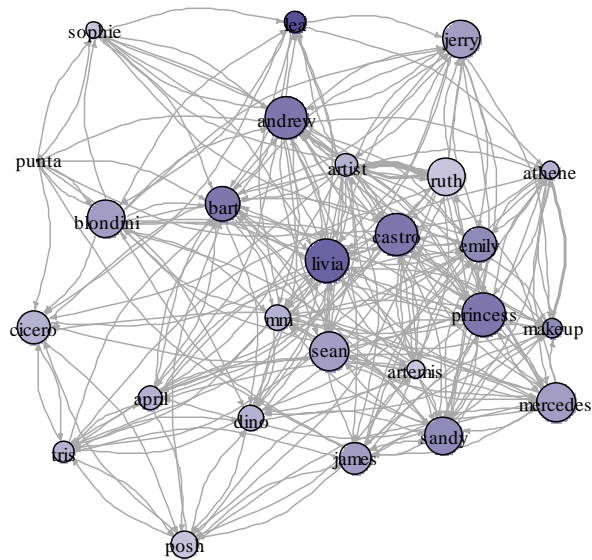


Fig. 5: a) The relationship between Confidence and node transitivity in the contact network. b) The relationship between Opportunism and betweenness in the grooming network. The size of the node represents the network characteristic value (the bigger = the higher the rating), the shadows of the colour represent the personality dimension value (the darker = the higher the rating). More networks presenting the relationship between phenotypic traits and social network characteristics can be found in supplementary material S2.

8. DISCUSSION

The results confirmed that personality is indeed related to the individual's position in its social group. Based on personality, we can infer which individuals in the group are more likely to have higher number of social contacts or to form links between different subgroups. This conclusion can contribute to a further understanding of the advantages or disadvantages of each personality type.

In addition, in both types of networks, I found a positive assortment based on the personality dimensions Friendliness and Confidence and disassortment based on the personality dimension Activity/Excitability. The results illustrate that social interactions between individuals are not randomly distributed in the social group and that the personality type of an individual may determines the type of individuals with whom it interacts most often.

Friendliness

Individuals with high Friendliness score had higher strength in the contact network, i.e. a higher number and stronger ties, compared to less friendly individuals. It means that friendly individuals were often in close proximity to many members of their social group. In the grooming network, individuals with higher Friendliness score had higher strength in and thus they received grooming interactions more often and from a higher number of different group members compared to less friendly individuals. These findings are partly consistent with my prediction that individuals with higher Friendliness score, will be more likely near other group members and will be more likely involved in grooming interactions due to their popularity and friendly, social, and tolerant nature.

A general similarity with my results can be found in the study by Kafner & Tanaka (1993). People with higher Agreeableness score more often established social interactions with others and tended to occupy central positions within the social group. On the other hand, people with a high score in Extraversion and a low score in Neuroticism were more preferred partners for interactions.

Results of a study on meerkats (*Suricata suricatta*) by Pacheco (2020) are also consistent with my results. The author concluded that in the dominance network and the foraging competition network, individuals with a higher Friendliness score achieved lower strength out and outdegree. It means that friendly individuals less often initiated weighted and unweighted dominant and competitive interactions compared to less friendly individuals.

This between study comparison illustrate how important it is to take into account the type of data on which the studied network is based (affiliate network versus network of dominant and competitive interactions). In both cases, Friendliness is related to the strength (weighted degree), but in the networks of affiliate interactions (contact and grooming) positive relationships have been found between the variables, while in networks of agonistic interactions (dominant interaction, competition) negative relationships have been found.

In the contact network, it was found that individuals with a high Friendliness score had high node transitivity and thus they had tendency to be in close proximity to certain members of the group, who also show mutual preference. This finding is inconsistent with my prediction that individuals can be just as friendly whether their relationships are limited to a subgroup or they establish relationships across an entire social group. The same relationship between Friendliness and node transitivity was also found across the studied groups of meerkats in the foraging competition networks (Pacheco, 2020).

It seems that for friendly individuals it is more typical to maintain more intense ties within the subgroup, which can also lead to increased mutual interactions between the partners of individuals with higher Friendliness score. The observed phenomenon may also be related to the functioning of the matriline, when the females, for example, stay close to relatives during the resting time. The study on yellow baboons (*Papio cynocephalus*) by Silk and colleagues (2003) shows that strong social ties between females can have an adaptive function. The authors found that infants of females, who spent more time by mutual grooming and in close mutual proximity and thus formed strong and lasting social ties, had a higher chance of survival compared to infants of less socially integrated females. Another possible explanation may be the phenotypic assortment based on Friendliness. Friendly individuals may simply prefer the company of other friendly individuals and thus tend to form subgroups.

The prediction that individuals with higher Friendliness score will through their social ties create links between different parts of the network, especially in the contact network, was not confirmed in the network of any type of behaviour. This was probably caused by preference for friendly individuals to maintain and create social ties within the subgroup and matriline, as mentioned above.

Activity/Excitability

Consistent with my prediction, strength did not depend on the Activity/Excitability score. An active and inquisitive personality with a tendency to exploratory behaviour suggests that individuals may prefer investing their energy to other activities to maintaining social ties. Similarly, individuals with low Activity/Excitability score lacking spontaneity and being inactive unlikely to engage in frequent social interactions with others.

Nonetheless, different results were obtained in studies on great tits (Aplin et al. 2013, Snijders et al 2014). Aplin and colleagues (2013) found that during the non-territorial season tits with a higher level of exploratory behaviour (which is included in macaque's personality dimension Activity/Excitability) achieved higher degree and lower strength, and thus established weaker and relatively shorter ties with a higher number of partners. Snijders and colleagues (2014) based their network analysis only on data from males collected during the breeding season. They found that male tit with a higher level of exploratory behaviour achieved higher degree and higher strength and therefore spent more time in close proximity with higher number of other males.

The reason for the discrepancy between my results and the results of these studies may be the different social system of both study species as well as the different methods of data collection (see previous text). Another reason may be that the majority of individuals were females in my study, whereas the study by Aplin and colleagues (2013) had balanced data from both sexes and study by Snijders and colleagues (2014) focused only on males.

Furthermore, my results showed that individuals with high Activity/Excitability score had higher betweenness in contact network. Compared to less active individuals, they more often connected other individuals in the group through their social ties, and thus created links between different parts of the group. These results are in consistency with my prediction. More active individuals move between different subgroups in the network more often, and thus come into close proximity with different members of the group. Due to their curiosity, they more often come into contact with a wider range of individuals.

My findings are consistent with the results of a study on great tits by Aplin and colleagues (2013) examining the relationship between exploration and betweenness. Tits with a higher level of exploratory behaviour had weaker and relatively shorter ties with a higher number of social partners. Moreover, they moved between different subgroups more often and easily formed connections between different individuals, and therefore different parts of the group. Identifying those individuals who form ties with a high number of other

group members and often move between different subgroups can be crucial when studying the spread of communicable diseases, pathogens or information transfer. The literature and my study showed that candidates for these crucial roles will be rather among the more active individuals.

Confidence

In the contact network, the more Confident individuals achieved higher strength. This result is not consistent with my prediction. In addition, it contradicts the results of studies on three-spined sticklebacks (*Gasterosteus aculeatus*) (Pike et al., 2008) and Trinidadian guppies (*Poecilia reticulata*) (Croft et al., 2009) where negative relationships between Boldness (in my case it corresponds to Confidence) and strength were found in networks of proximity interactions. This discrepancy can be caused by different methods of personality assessment (see introduction, questionnaires vs behavioural observations) as well as different biology of the studied species. For Barbary macaques, the positive relationship between Confidence and strength in the contact network may be caused by the need of Confident individuals to have an overview of the other group members and their behaviour. Confident individuals may often interfere in the social interactions of others (Flack et al., 2006; McCowan et al., 2011). Another reason may be the tendency of individuals to gather around the confident group members in order to develop positive relationship with them and to secure their tolerance (Henzi & Barrett, 1999; Carne et al., 2011) and protection and support in conflicts (Schino, 2007; Carne et al., 2011).

This may also be related to the finding that highly confident individuals rarely initiated grooming interactions compared to individuals with low Confidence score (negative trend between Confidence and strength out in the grooming network). This result is in consistency with my assumption. Confident individuals achieve a high level of dominance, are independent of others, self-sufficient, and therefore do not need to use the trading for social support. In contrast, individuals with low Confidence score are often submissive and they are relying on the guidance and support of others. Often they have to initiate grooming interactions with others in order to gain their favour and support.

My assumption that individuals with high Confidence score will also accept a higher number of grooming interactions was not confirmed. It is possible that high-ranking individuals receive grooming from a higher number of individuals, but these interactions are

not as regular. In contrast, individuals with lower rank may have fewer grooming partners, but their interactions are stronger.

Furthermore, the results confirmed my predictions that Confidence does not affect the node transitivity values, and thus the tendency of individuals to associate more with members of a certain subgroup, in both networks. My findings are inconsistent with a study based on a fictitious population by Ilana & Akçay (2016). The results of their study of non-directional networks show that individuals with a low Boldness score are more likely to form coherent groups, which is reflected in their higher node transitivity values. The difference in the results can be attributed to the existence of matriline in macaques. More confident as well as less confident females more often interact with individuals from one subgroup/matriline.

Opportunism

Strength (the number and strength of social ties of individuals) did not relate to the Opportunism score in the networks of both types of behaviour. Thus, the prediction that individuals with higher Opportunism score will initiate grooming interactions with other members of the group more often than individuals with lower score was not confirmed.

Further, it was found that in the grooming network, more opportunistic individuals achieved higher node transitivity values, which means that they had a higher tendency to interact with group members who also show mutual preference, compared to less opportunistic individuals. This finding is not consistent with my prediction.

The tendency of opportunistic individuals to interact intensively with members of particular subgroup may be due to their strategy of limiting grooming interactions to individuals who themselves show the ability to strategically establish social relationships. Opportunistic individuals thus use interactions with one individual to interact with other members of its subgroup. In addition, they prefer interactions with well-networked subgroups than with more solitary individuals, which is more advantageous in terms of the benefits of social ties.

Furthermore, in the grooming network, more opportunistic individuals had higher betweenness values and thus, through their social ties, more often connected other individuals in the group and formed links between different parts of the group. This result is consistent with my hypothesis. Opportunistic females (as the sample is female biased) can try to interact with individuals from different matriline in order to secure the necessary

support in the case of conflicts or foraging tolerance. For males in the study group, this result may be caused by the fact that their grooming interactions were limited to females (males did not groom each other), so opportunistic males may more often interact with females from multiple subgroups/matrilines.

Sex and Rank

In the grooming network, males achieved higher betweenness values and thus, compared to females, moved more often between different subgroups and formed links between different parts of the group. Females, on the other hand, achieved higher node transitivity values and, compared to males, showed a higher tendency to associate only with certain members of the group and thus form subgroups in the network. These results are logical and completely consistent with the functioning of the macaque group. Males distribute and receive their grooming interactions across different matriline, while females limit their grooming interactions mostly to members of their own matriline.

The individual's position in the social hierarchy did not in any way affect its position in grooming and contact networks. Nevertheless, I assume that, for example, in networks of antagonistic interactions or in networks of competition, the influence of an individual's position in the individual's hierarchy would be noticeable. As was the case of the network of agonistic interactions of Barbary macaque (*Macaca sylvanus*) (Sosa 2016), where high ranking individuals had higher outdegree values and thus more often initiated agonistic interactions while achieving lower indegree values and therefore they less often accepted interactions compared to low ranking individuals. Similarly, in meerkats (*Suricata suricatta*) in the network of dominant interactions, higher ranking individuals were more likely to initiate dominant interactions (achieving higher outdegree values) compared to lower ranking members of the group (Madden et al., 2011). The non-significant influence of the rank in my study could be also due to the fact that the personality dimension Confidence included in the models was positively correlated with rank.

A study on chimpanzees (*Pan troglodytes*) by Kanngiesser et al. (2011) found in the network of unweighted grooming interaction a positive relationship between rank and network characteristics betweenness and eigenvector centrality. However, when they focused on a weighted grooming network (including information about strengths of the ties between individuals) the relationship between rank and betweenness was not significant.

This result is another example of how important it is to take into account the data on which the social network is based.

A study by Sueur and colleagues (2011) assessed the relationship between rank and eigenvector centrality in two intolerant (*Macaca mulatta*, *Macaca fuscata*) and two tolerant species (*Macaca nigra*, *Macaca tonkeana*) of macaques. Eigenvector centrality indicates the interconnection of an individual within the network. This characteristic depends on the number and strength of ties the individual has, with respect to the centrality of the individuals to which study individual is connected. In intolerant macaque species, high-ranking individuals achieved higher Eigenvector centrality values compared to lower-ranking group members in the network of body contacts (non-directional). Similarly, in a study by Wooddell and colleagues (2020) on intolerant rhesus macaques (*Macaca mulatta*), high-ranking individuals achieved higher eigenvector centrality values and occupied more central positions compared to lower-ranking individuals in the network of social contact and the network of grooming.

In contrast, in tolerant species of macaques (including Barbary macaques studied in this thesis) no relationship was found between the rank and the network centrality of an individual (Sueur et al., 2011). Once more, these results illustrate the influence of different biology of the studied species on the function and thus the structure of social network of the social group. In the case of intolerant species of macaques, rank may have a greater influence on the patterns of individual social interactions (and thus on the position of individual within the social network) than in the case of tolerant species. The higher centrality of higher-ranking intolerant macaque species may be due to both the need of higher-ranking individuals to have control over lower-ranking individuals and the tendency of the lower-ranking individuals to seek contact with the higher-ranking individuals for personal benefits like tolerance, protection, or access to resources (Sueur et al., 2011).

Assortment

The phenotypic assortment based on the personality dimension Friendliness was found in the contact network as well as grooming network, however, in the contact network the effect was stronger. Positive assortment based on personality traits related to sociality and cooperative behaviour was also found in chimpanzees (Massen & Koski, 2014). In contrast, in meerkats no tendency of individuals to interact with individuals with similar

Friendliness score was found in the networks of grooming, dominant interactions, and foraging competition (Pacheco, 2020).

An interesting finding is disassortment based on the personality dimension Activity/Excitability, which was found in the networks of both types of behaviour. It could be caused by both the active, excitable and exploratory nature of individuals with the high Activity/Excitability score and the dejected, gloomy and conventional nature of individuals with a low rating in this dimension. Similar results were obtained in the study of the bonobos (*Pan paniscus*) (Verspeek et al., 2019). The study monitored the compatibility index of relationships between individuals, indicating the level of their mutual tolerance. Bonobos, who had more similar score in the personality dimension Activity had lower compatibility in their relationships and thus more often behaved more aggressively towards each other (Verspeek et al., 2019).

Assortment based on the personality dimension Confidence was also found in networks of both types of behaviours. Individuals with a similar Confidence score were sitting in mutual contact and groomed each other more often than with other individuals. This phenomenon could be caused by a social hierarchy, where individuals usually interact with individuals close to them in the hierarchy and interactions between the lowest and highest-ranking individuals are generally not common (Roubová et al., 2015). This is true especially in grooming networks as is shown in this thesis via rank-based assortment.

Neither the contact network nor the grooming network was assorted according to the personality dimension Opportunism. Individuals did not prefer or deny to interact with similarly opportunistic individuals. They are probably looking for benefits from association ties regardless of the interaction partner's personality.

The results of the sex-based assortment showed that in the contact network, individuals with the same sex preferred to associate with each other, while in the grooming network the trend was the opposite. The difference between the contact network and the grooming network may be caused by the mating season during which the group was observed. During mating season, a significant part of the grooming interactions take place in the sexual context (Lhota et al., 2019). When resting, and thus sitting in close contact, females prefer the company of other females rather than males. Staying close to a male could with higher probability lead to harassment and conflict caused by mating competition.

The rank-based assortment was found in the grooming network, when individuals of a similar rank more often established grooming interactions. Preference for individuals with

a similar social position can be found in a number of primates (e. g. Roubová et al., 2015; Sosa, 2016). Kinship could also play a role, as positions in the hierarchy are inherited from mother to daughter and female interactions are influenced by their belonging to the matriline. The pair of mother and daughter or the pair two sisters is thus often more similar in terms of rank than the pair of unrelated individuals (Paul 2006).

9. CONCLUSION

The aim of my theses was to find out whether an individual's personality can be related to its social network position. Besides the four personality dimensions (Friendliness, Activity/Excitability, Confidence, Openness), I also included the sex and the rank among studied phenotypic traits. The network position of individuals was assessed by their individual network characteristics values from networks based on two types of data (contact and grooming). I also studied the question whether there was the phenotypic-based assortment within the studied group.

The results suggested that personality of individual may be related to its position in social group. Several significant relationships and insignificant trends between studied phenotypic traits and selected network characteristics were found in grooming and contact networks. 12 of my 20 predictions about the relationship between individual's personality and its position within social networks defined by selected network characteristics were supported. Positive assortment based on the personality dimensions Friendliness and Confidence and disassortment based on the personality dimension Activity/Excitability were also found in studied networks. These findings demonstrate that knowledge about individual's personality may allow a better understanding of the role of the individual in its social group as well as the knowledge about the group position of individual may allow better understanding of its personality.

Among other things, my work points out that the social network structure properties differ according to the data entering the analysis. Therefore, it is always important to specify the form of interaction on which the social network is establish, as the position of an individual in the network and its association partner choice may differ depending on the type of interactions. For example, in a network of affiliate interactions (i.e. grooming), individuals with certain personality traits (i.e. Friendliness) are more likely to occupy different social positions than they would occupy in a network of agonistic interactions. Future research should consider that individuals with certain phenotypic traits may occupy characteristic positions in their social group, but it is necessary to consider the type of behavioural data entering the analysis as well as the biology of the studied species.

Furthermore, I consider it important to remind that the results of my thesis are based on the data collected during one mating season from one studied group of Barbary macaques

and the results thus cannot be generalized. For a given group, however, they allow a better understanding of the association processes of individuals and the functioning of the group as a whole. SNA provided a picture of a specific group based on a specific type of behavioural data.

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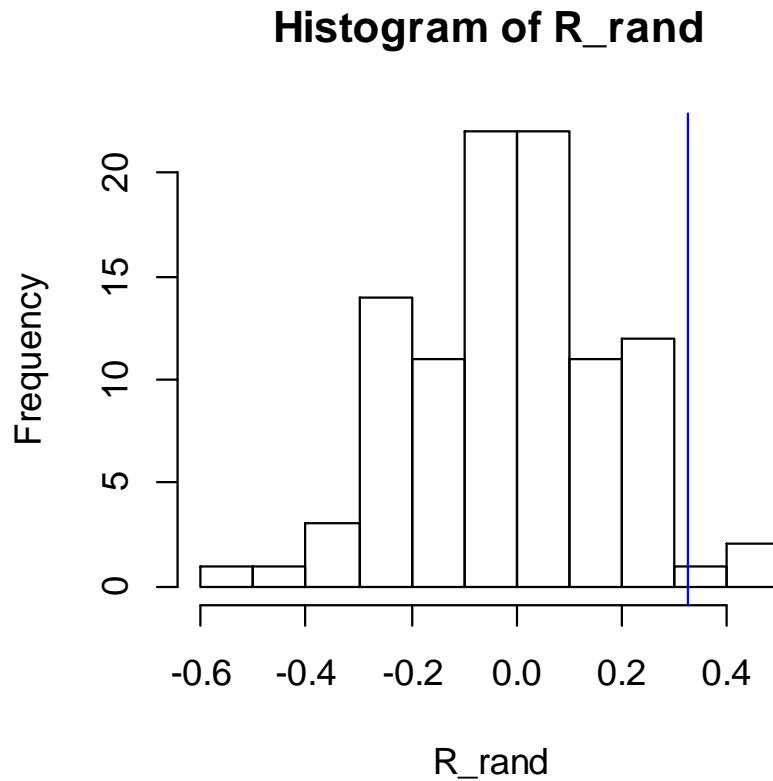
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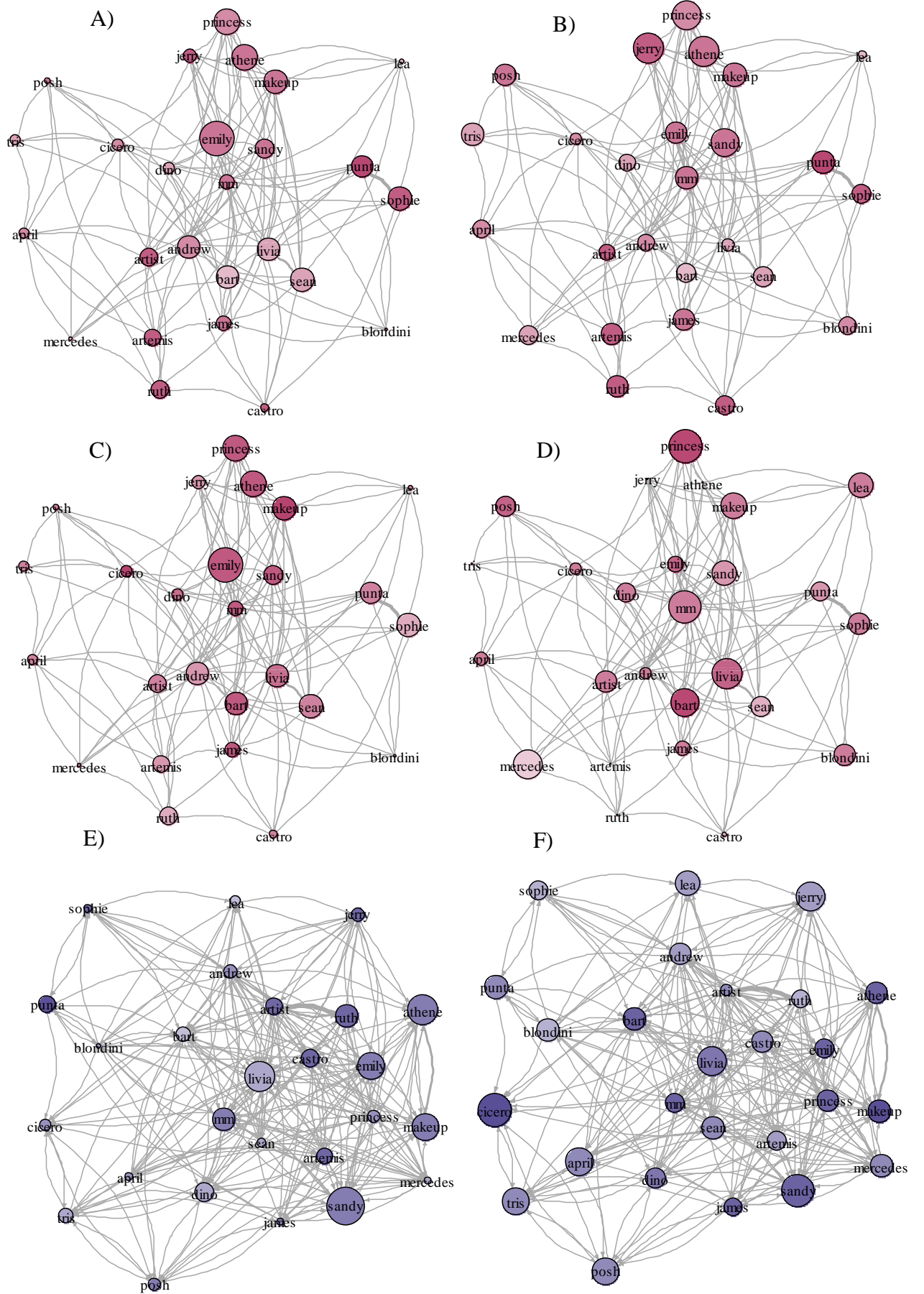
11.SUPPLEMENTARY MATERIALS:

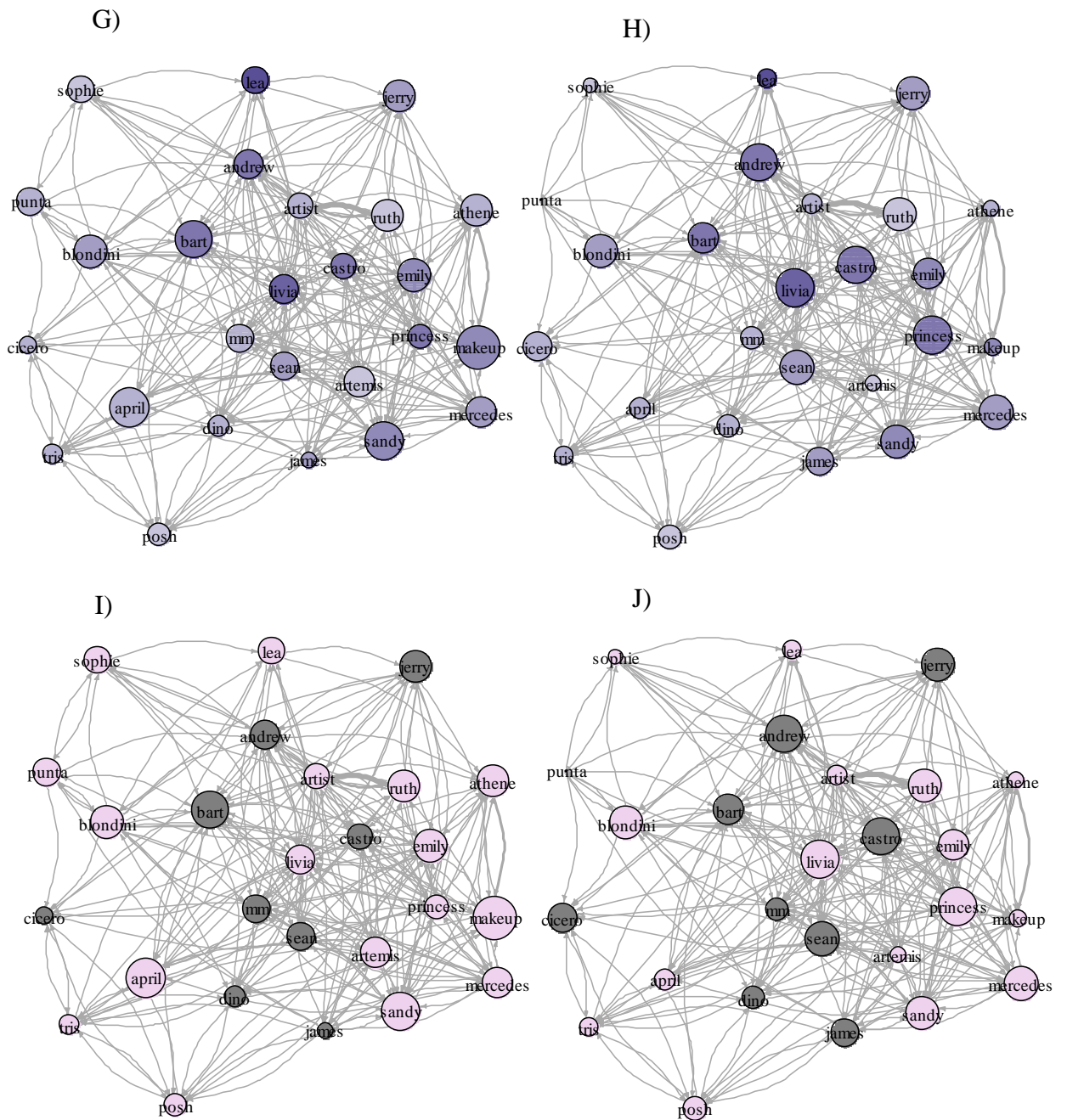
S1:



S1: Example of comparison of the observed estimate and the distribution of randomized estimates values. Observed value of the relationship between personality dimension Friendliness and strength in in the grooming network compared against the randomised distribution of 100 permutation tests. Observed value is the blue line. For each of the seven linear models, 100 randomized networks were created. Then the linear models were run again. Subsequently, a distribution of estimates values from randomized models was generated and the relationship between this distribution and the estimate calculated from the observed data was investigated. One tailed p-values were then calculated by comparing the number of estimates from randomized models that were higher than the observed estimate (Wooddell, 2019).

S2:





S2: Networks presenting the relationships between phenotypic traits and social network characteristics. A – D: represent the contact networks; E – J: represent the grooming networks; A – J: the size of the node represents the network characteristic value (the bigger = the higher the rating). A – H: the shadows of the colour represent the personality dimension value (the darker = the higher the rating). I- J: the colour of the node represent sex of the individual (female = pink, male = gray). A: network represents relationship between Friendliness and strength; B: network represents relationship between Friendliness and node transitivity; C: network represents relationship between Confidence and strength; D: network represents relationship between Activity/Excitability and betweenness; E: network

represents relationship between Friendliness and strength in; F: network represents relationship between Confidence and strength out; F: network represents relationship between Confidence and strength out; G: network represents relationship between Opportunism and transitivity; H: network represents relationship between Opportunism and betweenness; I: network represents relationship between sex and transitivity; J: network represents relationship between sex and betweenness