Communication and cultural transmission in populations of semi free-ranging Barbary macaques (Macaca sylvanus).

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Abstract

Communication and cultural transmission in populations of semi free-ranging Barbary macaques (*Macaca sylvanus*)

Ivan Garcia-Nisa

Social learning refers to the spread of novel behaviours between individuals and is important to survival. Visual attention is generally biased towards dominant individuals and/or affiliates in social animals. Therefore, social dynamics may represent patterns of social diffusion. Communication interactions, often depicting affiliative relations, may also represent social learning opportunities. This thesis aims to explore the role of communication networks in social learning in a nonhuman primate society. Specifically, the thesis answers three questions: (1) can communication acts predict affiliative relations, (2) can social learning be identified in Barbary macaques and (3) can communication interactions represent paths of social information diffusion. To address the first question I describe a series of networks based on affiliative behaviours (grooming, huddling, proximity) and communication interactions (aid-recruitment calls and vocal comments in affiliative and agonistic contexts) in a group of Barbary macaques housed in Blair Drummond Safari Park (BDG). All affiliative behaviours, except huddling, predicted the aid-recruitment network. Vocal comments in affiliative contexts were predicted by grooming and huddling. In agonistic contexts, vocal comments occurred when the aggressor was an ally and the victim was not an affiliate. For the second and third question, extractive foraging tasks were presented to two groups of Barbary macaques independently. Three tasks of increasing difficulty were presented to a group in Trentham Monkey Forest (TG) to investigate social learning. Evidence of social transmission was found only for the most difficult tasks. For BDG and TG, communication and/or affiliative networks were compared to observation networks during task introductions. Affiliative and observation networks predicted social learning. Communication networks predicted affiliative interactions. Only vocal comments in affiliative contexts predicted observation networks. Results suggest that communication networks, which mirror social bonds, may represent social learning opportunities. Integration of communication networks into studies of social learning is a fruitful avenue for further research.

Communication and cultural transmission in populations of semi free-ranging Barbary macaques (*Macaca sylvanus*)

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List of abbreviations

BDG	Blair Drummond Group
TG	Trentham Group
MHG	Middle Hill Group
SNA	Social Network Analysis
SRI	Simple Ratio Index
CSI	Composite Sociality Index
NBDA	Network-based Diffusion Analysis
OADA	Order of Acquisition Diffusion Analysis
TADA	Time of Acquisition Diffusion Analysis
PERC	Percolation-Conductance method
ADAGIO	Approach for Dominance Assessment in Gregarious species
CI	Confidence Interval
SE	Standard Error
RK	Rachel Kendal
CE	Cara Evans
MO	Mallory Owens
EM	Erin Morton
JK	Jeremy Kendal

Declaration

I confirm that no part of the material presented in this thesis has previously been submitted for a degree in this or any other institution. If material has been generated through joint work, this has been indicated where appropriate. All other sources have been referenced, and quotations suitably indicated.

Statement of copyright

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Dedication

I dedicate this thesis to my grandmother, Salud, who passed away two years ago. A terrible mental disease started to take you away ten years ago, when I was in my second year of college. It makes me sad to realize that you never got the chance to see the person I have become. Unlike most people, you always supported my decisions and loved me unconditionally. Your smile filled the room every time we were together. I am sorry I was not able to see how lonely you were and how unfair life was being with you before you got sick. I miss you.

Chapter 1

General Introduction

This thesis aims to incorporate the study of communication, social dynamics and social learning into one system to further understanding of the information transmission within primate societies.

Social learning is key to survival (Kendal, 2008) since it allows the transmission of behaviours or traditions (e.g. extractive foraging techniques, Marshall-Pescini & Whiten, 2008; Coelho et al., 2015) that increase individuals' fitness and help maintain group cohesion (Coussi-Korbel & Fragaszy, 1995; Perry & Smolla, 2020). For social learning to occur, the information must be transmitted from one individual to another (Hoppitt & Laland, 2008). Accordingly, the different types of social relations that individuals establish with each other may influence social learning (Franz & Nunn, 2009; Lonsdorf & Bonnie, 2010). Therefore, a holistic approach to the complexity of social relationships is important to understand how information relevant to survival is transmitted within a group of animals.

Social dynamics is the study of social relations (Durlauf & Young, 2004). Many factors (e.g. sex, age, social rank, kinship) and social behaviours (e.g. grooming, proximity) have been studied to investigate their role in shaping social relationships (i.e. social dynamics, McFarland & Majolo, 2011; Clay & de Waal, 2013; Molesti & Majolo, 2016, 2017; Berthier & Semple, 2018). Yet, although communication is a social behaviour (Liebal et al., 2013), little attention has been paid to its role in social dynamics (Kulahci et al., 2015; Roberts & Roberts, 2019a,b). In addition, those individuals with stronger bonds or that spend more time together are more likely to extract information (i.e. learn) from each other (Coussi-Korbel & Fragaszy, 1995; Hoppitt & Laland, 2013). If communication interactions influence the relationships among individuals in a social group, communication might also affect who learns from whom.

In their influential paper, Coussi-Korbel & Fragaszy (1995) already suggested that social dynamics and communication influence social learning in animal societies. Since then, many studies have used different types of social relations to predict social learning, especially in non-human primates (affiliative interactions, Schnoell & Fitchell, 2012; proximity, Claidière et al., 2013; dominance relations, Kendal et al., 2010a; group membership, van Leeuwen et al., 2020; who observes whom in novel foraging contexts, Hobaiter et al., 2014; Canteloup et al., 2020). However, the inclusion of communication interactions in the study of social learning in non-human animals has mostly been neglected (Snijders & Naguib, 2017). Communication may have a direct influence on social learning when communicative signals or cues are emitted during the social learning process. In this case, individuals may directly learn from active communicative signals or inadvertent information extracted from cues provided by a conspecific during a social learning context (Leadbeater & Chittka, 2007; Schaefer & Ruxton, 2012). Alternatively, communication interactions outside social learning contexts may represent individual preferences for particular conspecifics (Micheletta, 2012; Arlet et al., 2015; Kulahci et al., 2015), indirectly influencing who is likely to learn from whom.

Communication interactions outside social learning contexts might represent social learning opportunities for two main reasons. First, the study of deceptive communication has suggested that individuals might be able to distinguish who in their group is more reliable in terms of conveying information relevant to survival (Silk et al., 2000; Searcy & Nowicki, 2005; Wheeler et al., 2011). Accordingly, individuals will most likely pay attention to and, thus, learn from, reliable conspecifics. Second, communication interactions may represent social learning opportunities when they mirror social bonds. For instance, black crested macaques, ring-tailed lemurs and chimpanzees respond more often to communication signals of strongly-bonded partners than of those who they share weak or no bonds with (Micheletta, 2012; Kulahci et al., 2015; Roberts & Roberts, 2019a,b, respectively). Consequently, individuals of these primate species are more likely to learn from their affiliates.

Within this framework, I aim to determine how communication interactions influence social dynamics, both within and outside of a social learning context, in order to investigate the role of communication in the diffusion of social information.

1.1. Communication

1.1.1. Debates and controversies

Studies of communication in non-human primates have been relevant to understanding how human language evolved (Liebal et al., 2013). However, many debates have arisen around this topic. Some researchers argue against a continuity in the evolution of communication across humans and non-human primates (Reboul, 2015; Scott-Phillips, 2015), while others rely on comparative approaches among primates to explain the origins of human language (Fedurek & Slocombe, 2011; Liebal et al., 2013; Moore, 2016). Bickerton (1992) highlighted that studies of language evolution were traditionally dominated by non-linguistics, leading to an underestimation of language complexity. Since then, many scientists have suggested that cognitive mechanisms underlying communication are different between humans and non-human primates, arguing that language emerged for different purposes and was exapted for communication (Bickerton, 1992; Reboul, 2015; Scott-Phillips, 2015). However, many studies have provided evidence of shared features between human and non-human primate communication (Arbib et al., 2008; Wheeler et al., 2011; Liebal et al., 2013). In addition, some authors highlight that apparent discontinuities found across communication systems in primates can be overcome by using more realistic approaches such as communication networks and a multimodal perspective (McGregor & Peake, 2000; Slocombe et al., 2011; Krause et al., 2014).

One of the main debates in animal communication research is over how to conceptualize communication itself, which starts by defining the concept of a 'signal' (Krause et al., 2014). As mentioned previously, many scientists maintain that the concept of animal communication has been heavily shaped by linguistic metaphors (Rendall et al., 2009). Thus terms such as 'information' and 'meaning' may lead researchers to unconsciously rely on Shannon's Theory of Information, which assumes that both signaller and receiver have the same mental representation of the signal. However, nonhuman animal communication is believed to lack the same mental representational parity between signallers and receivers that is observed in human language (Rendall et al., 2009).

Those that criticize the 'information' theory (Rendall et al., 2009; Scott-Phillips, 2015) suggest a framework where communication is seen as 'influencing' or 'manipulating' others. However, this framework only accounts for the signaller's perspective, assuming that receivers are automata playing no role in the evolution of communication (Seyfarth et al., 2010). Against this view, many studies have demonstrated that receivers assess the environment and other contextual factors before responding to a signal (Wheeler et al., 2011; Liebal et al., 2013). Furthermore, some have highlighted the role of 'information' in communication by providing new definitions avoiding previous criticism. For instance, Seyfarth et al. (2010) understand 'information' as a reduction of uncertainty in receivers, allowing them to predict current or future events. Thus, 'information' can be understood as a property of the receiver, not inherent to the signal, so that receivers' responses may shape the evolution of communication and can be produced irrespective of signaller's intentions (Seyfarth et al., 2010; Schaefer & Ruxton, 2012).

Many authors argue that signallers may actively provide information through specific signals – suggesting intentionality in influencing receiver's behaviours – but some behaviours can also be perceived as inadvertent social information (Leadbeater & Chittka, 2007; Schaefer & Ruxton, 2012). Accordingly, some have attempted to unify the concepts of 'information' and 'influence'. Font & Carazo (2010) understand communication as acts 'where signallers influence receivers' behaviour in ways that increase their fitness and receivers eavesdrop, extracting information from signals that the signaller may not intend to have provided them with' (in Liebal et al., 2013, p. 4). Within this controversy, we must acknowledge that these definitions come from multiple disciplines, each studying communication from a different angle according to the particular research field. Moreover, interest in unravelling the origins of human language has driven the study of primate communication in a different direction (towards cognition) to studies of other taxa (Liebal et al., 2013).

In conclusion, communication can be understood at different levels depending on researchers' interests, discipline or standpoint. Accordingly, the different theories and frameworks, aforementioned, on how to define communication focus on different aspects of communication and may be seen as complementary rather than alternatives. Therefore, I propose a broad definition of communication based on that of Font & Carazo (2010) in order to overcome classical debates and fit with the aims of my project:

'*Acts or traits of a sender that may influence receivers' behaviour and reduce their uncertainty about changes in the environment, in the social structure or in the physiological or emotional states of the signaller, including eavesdropping, whereby information is extracted from signals or cues that the signaller may not have intend to provide*'.

1.1.2. Communication networks: a more realistic approach

My proposed definition of communication focuses on the receivers' perspective and highlights their active role in a communication interaction. Moreover, this definition brings out the concept of eavesdropping – extracting information by intercepting others' interactions (McGregor, 2005; Clay & Zuberbühler, 2011). As McGregor & Peake (2000) discussed, information is not only exchanged in signaller-receiver dyads, but communication often occurs within a social environment comprised of a network of several signallers and receivers. For example, aggressive interactions may provide opportunities for eavesdroppers to obtain information about the fighting abilities of potential opponents (McGregor & Dabelsteen, 1996). In primates, for instance, eavesdroppers may obtain social information by monitoring male-male fights, as seen in chacma baboons (*Papio hamadryas ursinus*; Kitchen et al., 2005) and geladas (*Theropithecus gelada*; Gustison et al., 2012). Research on animal communication networks has also shown that vocal signals produced in close-range aggressive encounters tend to be loud because they are directed towards bystanders (Zahavi, 1979; McGregor, 2005). Moreover, in non-aggressive contexts, knowledge of third party relationships has been demonstrated in primates using vocalizations (reviewed in McGregor, 2005). For instance, researchers have demonstrated that mother-infant relationships can be discriminated in vervet monkeys (Cheney & Seyfarth, 1980), free-ranging baboons (Cheney & Seyfarth, 1999) and long-tailed macaques (Dasser, 1988) using playback calls of pair-related individuals and looking at the reaction of unrelated conspecifics.

The cases illustrated above highlight the relevance of eavesdropping in the social life of primates and how information gained from signalling may evoke responses in bystanders. However, few studies have investigated how communication signals might shape the nature, quality and patterning of social relationships in an environment of several potential receivers (Kulahci et al., 2015; Roberts & Roberts, 2019a,b). These studies have used social network analysis (henceforth SNA) to determine how affiliative relations and communication interactions in nonhuman primates predict each other. SNA offers a framework by creating a fine-grained picture of group social structure for a better understanding of the role of communication in primate social lives (Kasper & Voelkl, 2009; Sueur et al., 2011).

Hinde (1983, p. 6) described the social structure of a group ‘in terms of the properties of the constituent relationships and how those relationships are patterned’. Social network theory allowed the implementation of Hinde’s definition into the study of animal societies (Croft et al., 2008; Kasper & Voelkl, 2009). A social network is normally depicted as a sociogram (i.e. visual graph) of pairwise relations between individuals. In these sociograms, individuals are represented as points (also called nodes or vertices) connected with each other by lines (also known as edges or ties) that represent social relations or interactions. Social network theory uses a series of mathematical tools, metrics and models that allow the study of complex social interactions by considering the inter-individual dependencies within a group of animals (Croft et al., 2008). Moreover, the analysis also includes the social structure of the group as an explanatory variable that may be crucial to understand any social behaviour (Kasper & Voelkl, 2009).

To my knowledge, few papers have relied on SNA metrics and graphs to study communication networks in primates. One example is Flack & Krakauer’s (2006) study of pig-tailed macaques (*Macaca nemestrina*), where power dynamics were decoded from the network of silent bared-teeth display signalling interactions to determine the group consensus regarding an individual’s capacity to use force. Kulahci et al. (2015) found that communication networks of ring-tailed lemurs based on contact calls were predicted by grooming networks, so that lemurs communicated with those they most frequently groomed. Finally, in a recent example, Roberts & Roberts (2019b) found that communication networks based on multimodal signals (pant-hoots combined with visual gestures) predicted networks based on time spent in proximity in chimpanzees. These examples highlight the utility of SNA for the extraction of detailed and realistic information regarding the role of communication at the group-level in a primate society. Moreover, consideration of communication networks also provides a better understanding of signal evolution and information transfer than dyadic interactions (McGregor & Peake, 2000). Therefore, failure to consider the social environment in which communication occurs might mask some homologous features between human and non-human primate communication systems, hindering the quest for evidences of a continuity with human language.

1.1.3. Unimodal versus multimodal communication

Primate communication research has provided thorough support for the evolutionary continuity between human language and communication systems of non-human primates (Arbib et al., 2008;

Slocombe et al., 2011; Liebal et al., 2013). As a result, two main theories emerged to explain the evolution of language: the vocal and the gestural theories (Wheeler et al., 2011; Liebal et al., 2013; Scott-Phillips, 2015). The vocal theory is largely based on studies of vocal communication in monkeys (Arbib et al., 2008). Homologous features have been found between human language and non-human primate vocalizations. First, vocalizations and human speech share the same sensory modality (Zuberbühler, 2005). Supporters of the vocal theory also argue that primate calls can refer to external objects and events – a precursor of the referential abilities of human language (Seyfarth et al., 1980a,b). Moreover, vocalizations in primate species can be combined in context-specific sequences (Ouattara et al., 2009a,b) and can be flexibly used and perceived, as in human verbal communication (Fischer, 1998; Egnor & Hauser, 2004; Fischer, 2011; Seyfarth & Cheney, 2010; Wheeler et al., 2011). In contrast, gestures are rarely used referentially, and their meaning or communicative function normally depends on the context, even when they are combined in sequences (Liebal et al., 2013).

Support for the gestural origin of language has mainly been provided by studies on great apes (Arbib et al., 2008; Wheeler et al., 2011). Those who defend the gestural theory emphasize the link between manual gestures and homologous areas of language production in the brain, something that has been reinforced by the discovery of the mirror neuron system in non-human primates (Rizzolatti & Arbib, 1998; Liebal et al., 2013). Interestingly, the mirror neuron system can be activated in response to a sound associated to a given action such as hand or mouth actions (e.g. southern pig-tailed macaques, *Macaca nemestrina*, Kohler et al., 2002; Ferrari et al., 2003), but not in response to non-action-related sounds (Kohler et al., 2002). The mirror neuron system involved in the production and perception of visuo-gestural and oro-facial communicative actions is located in a brain area homologous to the language production area of humans (Kohler et al., 2002; Ferrari et al., 2003). Moreover, it has been demonstrated that apes can learn human American Sign Language (Gardner & Gardner, 1969; Patterson, 1978) and that children use gestures for communication before the acquisition of speech (Liebal et al., 2013). In addition, gestures in great apes are voluntarily produced and flexibly used across contexts, can be adjusted according to the recipient's behaviour and can be learnt and innovated, as in human language (Call & Tomasello, 2007; Arbib et al., 2008; Tomasello, 2010).

In the last decade, more evidence has been provided in favour of the two classical theories of human language evolution. Homologies between human language and primate vocalizations include similarities in articulation and acoustics (e.g. use of proto-vowels and proto-consonants in great apes; Lameira, 2018), conversational rules (e.g. turn-taking and overlap avoidance in bonobos, *Pan paniscus*; Levréro et al., 2019), vocal convergence within groups (among individuals of the same age or rank class) and vocal divergence between neighbouring competitive groups (Prieur et al., 2020), intentionality (Clay & Zuberbühler, 2012; Clay et al., 2015), vocal learning (Nowicki & Searcy, 2014;

Watson et al., 2015) and the use of linguistic laws (e.g. Zipf's law of abbreviation and Menzerath's law which predicts that longer sequences are formed of shorter elements; Semple et al., 2010; Fedurek et al., 2017). Characteristics such as referentiality, intentionality and similarities in conversational rules and linguistic laws have also been found in the gestural communication systems of non-human primates (Prieur et al., 2020). Moreover, the strong interrelationship between speech and non-verbal communication (e.g. gestures accompanying speech, sign language and pre-linguistic gestures by children such as pointing) supports the arguments in favour of the gestural theory (Prieur et al., 2020).

Researchers highlight that some features of human language that are present in primate vocal communication, are not present in gestural communication, and vice versa (Slocombe et al., 2011). Accordingly, both theories based on unimodal approaches (vocal or gestural) have failed to find a continuity in the evolution of communication across humans and non-human primates. However, many authors have emphasized that communication is multimodal and those studies using multimodal approaches for the study of communication seem to have overcome this problem, indicating the evolutionary continuity of primate communication and human language (Partan & Marler, 1999, 2005; Slocombe et al., 2011; Semple & Higham, 2013; Waller et al., 2013). Multimodal communication can be defined as the simultaneous combination of signals from two or more different modalities (visual, auditory, olfactory) and/or any signals that require sensory integration by receivers (Liebal et al., 2013). In addition, different signals from the same modality can also be used simultaneously to form a combined signal (Partan, 2002; Micheletta et al., 2013), though this should be termed a 'multicomponent signal' (Rowe, 1999). For simplicity, I will use the term 'multimodal' from hereafter to encompass both multimodal and multicomponent concepts.

Multimodal communication has been demonstrated in many animal species, including human and non-human primates (Slocombe et al., 2011; Liebal et al., 2013; Genty et al., 2014). In both human and non-human primates, gestures can be associated with vocalizations (which necessarily imply oro-facial expressions), eye behaviours (e.g. eye gaze, eye blinking) and/or body/head posture/orientation (Partan, 2002; Arbib et al., 2008; Liebal et al., 2013; Frohlich et al., 2019; Prieur et al., 2020). For instance, the same rhythmic frequency range shared by lip-smacking (commonly used by non-human primates in face-to-face socio-positive interactions) and human speech led researchers to hypothesise that the visual and auditory speech rhythm of humans could have evolved from rhythmic oro-facial expressions in primate ancestors (MacNeilage, 2010). In addition, eye behaviours seem to be essential components of multimodal communication signals that convey valuable information about the status, spatial attention, emotional state or level of engagement of the signaller and receiver which help achieve, maintain and regulate social interactions in both human and non-human primates (Prieur et al., 2020). Furthermore, it has been highlighted that non-verbal communication such as pointing (observed in both humans and captive apes) facilitates gestural and vocal communication and may have been crucial in the origin of different levels of human language evolution, including verbal and non-verbal communication, social cognition and culture (Gontier, 2013). Accordingly, recent literature suggests that the coevolution of gestural, vocal, oro-facial and eye signalling in primate ancestors may have been responsible for the multimodal, rhythmic and social-interactive nature of human language (Prieur et al., 2020).

Multimodal communication has many benefits when considered within the social environment in which it occurs. For instance, multimodal signals are more accurate and less ambiguous than unimodal signals (Partan & Marler, 2005), which enhances the efficacy of information transmission (Partan & Marler, 1999) and the likelihood of detection (Chandrasekaran et al., 2011), eliciting stronger responses from receivers (Rowe, 1999; Liebal et al., 2013; Clay et al., 2016). Additionally, properties such as the flexible use and combination of components (Partan, 2002) and the evidence of multisensory integration of signals in primates (Ghazanfar & Schroeder, 2006) suggest that the way multimodal communication works is homologous between humans and non-human primates (Slocombe et al., 2011). Furthermore, both human language and primate communication systems are influenced by socioecological (e.g. sound propagation properties of habitats, ambient noise, range of vision, group size, social structure), genetic (e.g. innate signals of great apes, see Byrne et al., 2017), demographic (e.g. acquisition of signals influenced by sex, age, kinship), psychological (e.g. cognition, personality, empathy), physiological (e.g. hormones, cardiovascular reactivity), contextual (e.g. emotional valence of the context, audience composition, identity of the receiver) and communication-related (e.g. chimpanzees adjust the use of signal types according to social context and success of previous communication attempts, see Hobaiter et al., 2017) factors (reviewed in Prieur et al., 2020). Accordingly, the multicausal theory states that human language would have evolved from primate multimodal communication systems and its evolution was modulated by a cost-benefit trade-off with all the aforementioned factors and their mutual feedback (Prieur et al., 2020).

Human language can be seen as the result of a cognitive enrichment parallel to changes in primate ancestors' lifestyle at the ecological and social level. For example, ecological changes may have included moving from arboreal to terrestrial habitats or an increase of hunting due to increases in meat demands, whereas social changes refer to an evolution towards larger and more complex societies that resulted in an increase in cooperation, cultural innovation, social learning, cultural transmission and other sociocognitive abilities (Pinker, 2010; Whiten & Erdal, 2012; Prieur et al., 2020). This diverse, dynamic and increasingly complex environment may have been crucial for the development of the socio-cognitive abilities necessary for human language. In other words, this socio-cognitive niche allowed the co-evolution of cooperation, egalitarianism, theory of mind, language, social learning and culture (Pinker, 2010; Whiten & Erdal, 2012). All these elements nurture each other, indicating that there has been, and still is, a constant feedback in their co-evolution (Gontier, 2013). For instance, the acquisition of language occurs via social/cultural transmission and, at the same time, language allows the transmission of social information and culture in primates. Similarly, language/communication is required for cooperation (e.g. in humans and chimpanzees: social coordination in hunting) and the need to cooperate propelled the evolution of language (e.g. negotiation of alliances and coalitions; Pinker, 2010; Whiten & Erdal, 2012). Moreover, language lowers the costs of acquiring new skills and social information, while it multiplies the benefit by facilitating cooperation, mindreading, egalitarianism and culture (Pinker, 2010). Accordingly, language is not only multimodal, but also multicausal and evolved in a socio-cognitive niche in an intertwined feedback with other social and cognitive adaptations.

Although human language evolution should be studied from a multimodal-multicausal point of view in light of the multicausal theory and the socio-cognitive niche hypothesis, an integrated methodological and statistical approach is still required for that purpose (Pinker, 2010; Whiten & Erdal, 2012; Prieur et al., 2020). In recent years, studies on primate communication have mostly focused on the multimodal aspect of communication/language. To date, only a few studies have investigated the function of multimodal signals in non-human primates compared to their isolated components ('cue-isolation' experiments). For instance, Partan (1998) found that visual facial displays (i.e. lip-smacks) in rhesus macaques (*Macaca mulatta*) were followed by grooming sessions more often when they were accompanied by "girneys" (soft vocalizations) than when they were produced alone. In a more recent example, Micheletta et al. (2013) demonstrated that lip-smacking in crested macaques (*Macaca nigra*) was more likely to elicit affiliative responses when it was combined with grunts than when it was produced alone. Also, Micheletta et al. (2013) suggested that lip-smacking and bared-teeth displays combined might form a new signal. The integration of network analyses into the study of multimodal signalling has been scarce in animal research, despite the fact that use of networks have proved to be useful in disentangling the complexity of animal communication systems (Ay et al., 2007; Wilkins et al., 2015; Hebets et al., 2016).

Overall, it seems that network and multimodal approaches will benefit the study of human language evolution from a perspective of continuity with non-human primate communication. However, it has been suggested that multimodal communication in primates emerges first during ontogeny and it is later tuned to form effective unimodal signals (Liebal et al., 2013; Bard et al, 2014; Frohlich et al., 2016). Accordingly, adult primates will mainly rely on unimodal communication to effectively interact with each other. Moreover, some signals are naturally unimodal, such as those displaced in space or long-distance vocalizations in primates (Frohlich et al., 2019). For instance, calls elicited during conflicts are loud vocalizations that may signal submission and discourage the aggressor from continuing the assault (Fedurek et al., 2015), but that also convey information about the identity of the caller, the rank of the opponent, the nature of the conflict and/or the level of experienced aggression, helping recruit allies that may be at a distance and out of sight (Slocombe & Zuberbühler, 2007). Similarly, the so-called 'vocal comments' uttered after the observation of third-party interactions, are soft vocalizations not accompanied by any other behaviour or communication signal, and might reflect or influence social relations (Brumm et al., 2005; Whitham et al., 2007).

In conclusion, depending on the signals of interest, either multimodal or unimodal approaches (especially in the vocal domain) may be useful for studies of primate communication and human language evolution. Moreover, it seems that communication, whether or not perceived as multimodal, might have an effect in shaping social relationships (Slocombe & Zuberbühler, 2007; Whitham et al., 2007; Liebal et al., 2013; Micheletta et al., 2013). This links the field of communication with social dynamics.

1.2. Social dynamics and communication

Social dynamics are the group-level behaviour patterns that result from individual interactions and the relationships between both individual and group-level behaviour patterns (Durlauf & Young, 2004). In primatology, different aspects of primates' social lives have been investigated to understand how they shape the spatial and temporal patterns observed in the dynamics of social relationships, but little attention has been paid to the role of communication in social dynamics (Kulahci et al., 2015).

Communication is generally understood as a social behaviour that helps to maintain social systems (Liebal et al., 2013). Many have hypothesized that communication aids survival, reproduction and group living (Liebal et al., 2013). However, the most important correlation between communication and sociality is provided by the 'Social Complexity Hypothesis' which specifies a coevolution of social and communication complexity (Freeberg et al., 2012). Accordingly, it has been demonstrated that facial and vocal communication repertoires increase with group size across primate species (McComb & Semple, 2005; Gustison et al., 2012). Also, species with a rigid dominance structure show less diversity and complexity of communication repertoires and less flexibility in signal production than more egalitarian species and multi-level societies (Freeberg et al., 2012; Liebal et al., 2013). Moreover, the dynamics of social groups also influences communication interactions and, as the social system becomes more complex, sensitivity to vocal signals increases (Freeberg et al., 2012).

In line with the statements aforementioned, Dunbar's 'Gossip Hypothesis' highlights a relationship between communication and social bonds (Dunbar, 2004). Dunbar suggests that grooming evolved to buffer the indirect costs of living in social groups, but as group sizes increased, another mechanism was required to maintain social bonds and group cohesion. He proposed communication as a groom-at-distance behaviour. However, efforts to support this theory have been scarce to date. A few papers have shown a positive relationship between communication interactions and social bonds in primates (Schel et al., 2013a,b; Kulahci et al., 2015; Roberts & Roberts, 2019a,b). For instance, crested macaques give stronger responses to friends' (than non-friends') alarm calls (Micheletta, 2012), and a positive correlation has been found between time spent grooming and frequency of contact calls exchanged in female Japanese macaques (*Macaca fuscata*; Arlet et al., 2015). As social network analysis (SNA) allows a more detailed characterization of social relationships than conventional methods (Wey et al., 2008), and favours the study of different types of interactions within the same conceptual framework (Krause et al., 2014), it is the most appropriate approach for me to add to this literature. Moreover, SNA is also useful for identifying social transmission of information (Franz & Nunn, 2009; Sueur et al., 2011; Filvà et al., 2014; Coelho, 2015), making it the most fitting analytical tool to link the three areas of interest of this thesis: communication, social dynamics and social learning.

1.3. Social learning, communication and social dynamics

1.3.1. Social learning: introduction, strategies and processes

Social learning is defined as 'learning influenced by the observation of, or interaction with, a conspecific, or its products' (Heyes, 1994; Hoppitt & Laland, 2008). Such may shape the diffusion of social information through a population and is required for animal traditions, or culture, which are important to survival (Kendal, 2008). Social learning, therefore, allows naïve individuals to acquire information relevant to many life skills or adaptive behaviours invented by knowledgeable conspecifics (Kendal, 2008; Kendal et al., 2009a). For instance, the transmission of foraging techniques (e.g. nut-cracking, termite-fishing) that help chimpanzees and other primate species (e.g. capuchins) to make use of a wide diversity of food resources is known to happen through social learning (Marshall-Pescini & Whiten, 2008; Coelho et al., 2015). Also, the spread of ritualised behaviours that aid complex primate societies to maintain group cohesion, form alliances or test social bonds may also occur via social learning (Coussi-Korbel & Fragaszy, 1995; Perry & Smolla, 2020).

The acquisition of knowledge from others (i.e. social learning) may benefit individuals' fitness because it allows animals to acquire adaptive information without facing the costs (e.g. time and energy invested in searching for new food sources, predation risk) of learning by themselves (i.e. asocial learning; Kendal, 2008; Kendal et al., 2009b). However, the information obtained by knowledgeable individuals may be maladaptive (Boyd and Richerson 1985; Giraldeau et al., 2002; Laland, 2004). For instance, guppies and humans prefer to follow conspecifics through energetically costly long routes even when a shorter route is known and within reach (Laland & Williams, 1998; Reader et al., 2008). It seems that some behaviours like migratory patterns or mating sites are maintained by traditions, despite more optimal options being naturally available (Hoppitt & Laland, 2013). Accordingly, individuals face the trade-offs between costly but accurate and reliable information obtained by trial-and-error (asocial learning) and potentially unreliable but safe and easy-to-obtain social information (Boyd and Richerson 1985; Kendal et al., 2005).

Theoretical models of the evolution of social learning suggest that individuals must face the costs of gathering asocial information from the environment to some extent (Laland, 2004). If all individuals exclusively relied on social learning, no individuals would be directly sampling the environment to provide accurate and reliable information to others. Therefore, the value of copying others declines as the number of social learners increases. In line with this, each individual experience with the environment will generate different social information for potential learners to copy. Theoretical models indicate that copying others indiscriminately does not increase the mean fitness of the population (Boyd and Richerson 1985; Giraldeau et al., 2002). For social learning to be adaptive, therefore, individuals must engage in asocial sampling of the environment some of the time and follow copying strategies to obtain social information selectively (Galef, 1995).

Individuals may adopt a wide diversity of selective social learning strategies (also termed “transmission biases”, Kendal et al., 2018). ‘When’ strategies describe instances in which individuals copy others depending on their own mental, physical or physiological state such as copying when asocial learning is costly, when uncertain about the environment or when learners belong to specific classes (e.g. age, rank, reproductive state; Kendal, 2008; Kendal et al., 2009a, 2018). Frequency-dependent strategies refer to cases when individuals copy traits or behaviours depending on how often they have been observed in others (e.g. demonstrators) such as copying the majority (Rendell et al., 2011; Kendal et al., 2018). ‘What’ strategies are based on a direct assessment of the relative or perceived value of the trait observed, such as biases towards the most attractive/highest payoff variant of the trait (Vale et al. 2017) or against variants that trigger a negative emotional reaction (e.g. disgust, Rendell et al., 2011; Kendal et al., 2018). Finally, individuals adopting ‘who’ strategies will copy others depending on particular characteristics of the demonstrators such as copying the most successful, prestigious or dominant individual (Kendal, 2008; Kendal et al., 2009a, 2018; Rendell et al, 2011).

‘What’ strategies are also termed ‘direct biases’ because individuals directly assess the value or payoffs of the trait itself (Laland, 2004). In contrast, ‘who’ strategies are deemed as ‘indirect biases’ because individuals will adopt the trait of successful or high-status individuals, irrespective of the value or payoffs of the trait (Kendal et al., 2009a, 2018). Unbiased or random copying strategies must be distinguished from ‘indirect bias’. Transmission is considered unbiased when learners copy a convenient demonstrator (e.g. kin, friend) irrespective of the characteristics of the individual and the apparent utility of the trait they display (Kendal et al., 2009a). Nonetheless, it cannot be assumed that individuals consciously choose which social learning strategy to adopt and the underlying cognitive processes of social learning cannot be directly associated with particular transmission biases (Kendal et al., 2018). Actually, there is still a heated debate regarding whether social and asocial learning rely on the same underlying neural mechanisms (Leadbeater, 2015; Leadbeater & Dawnson, 2017; Heyes, 2018; Kendal, 2018).

Hoppitt & Laland (2008) developed a well-established classification of social learning processes based on empirical evidence in human and non-human animals. Social learning processes may result directly or indirectly in learning. Indirect social learning processes include *social* and *response facilitation*, and *local* and *stimulus enhancement*. *Social facilitation* occurs when the 'mere presence of a demonstrator affects the observer's behaviour' (Zajonc, 1965; Hoppitt & Laland, 2008), for instance, by increasing exploratory behaviours in a novel context. In *response facilitation*, the presence of a demonstrator performing a rewarded action increases the probability of the observer performing the same action (Byrne, 1994). Compared with *social facilitation*, *response facilitation* affects specific individual actions instead of a class of motivational behaviour (Hoppitt & Laland, 2008). Finally, when the observer's attention is attracted to a particular location or stimulus by a demonstrator, *local* or *stimulus enhancement* occurs and the individual then goes on to learn asocially. Some authors suggest that *stimulus* and *local enhancement* are two distinct processes and that the former can directly result in learning (Hoppitt & Laland, 2008; Arbilly & Laland, 2013; Webster & Laland, 2013).

Several social learning processes result in direct learning (Hoppitt & Laland, 2008). *Social enhancement of food preferences* results from the exposure to a demonstrator carrying cues associated with a food item that increases the likelihood of the observer to consume the same food (Galef, 1996). It has been suggested that the presence of a demonstrator (not only the cue or stimulus) is required for *social enhancement of food preferences*, so this learning process cannot be considered a case of *stimulus enhancement* (Galef & Wigmore, 1983; Hoppitt & Laland, 2008). In *observational conditioning*, an observer's response to a stimulus is conditioned by a demonstrator's response to it (Heyes, 1994; Hoppitt & Laland, 2008). For *observational response-stimulus learning* it is the exposure to a response-stimulus relationship through social observation of a demonstrator at time 1 that effects a change in the observer in any behaviour at time 2 (Heyes, 1994; Hoppitt & Laland, 2008).

Imitation and *emulation* are amongst the most contentious social learning processes that result in direct learning. Their meaning or definition has changed several times since they were first introduced to animal learning (Hoppitt & Laland, 2013). *Imitation* could be considered when an observer copies an action, sequence or combination of actions by observing a demonstrator performing the same action, sequence or combination of actions (Byrne, 2002; Hoppitt & Laland, 2008). Some authors maintain that only novel actions can be imitated or can be used to test for imitation (Hoppitt & Laland, 2013). Others (Byrne, 2002; Hopitt & Laland, 2008, 2013) define two types of imitation: contextual imitation (i.e. when the action is already in the observer's repertoire but it learns to perform it in the same specific context as the demonstrator) and production imitation (i.e. when the form of a novel action is learned through observation). Also, it has been suggested that an observer that learns the goal of a demonstrator's behaviour through observation is imitating by *goal emulation* (Horner & Whiten, 2005). *Emulation*, however, occurs when an observer is more likely to perform any actions that bring about a similar effect on objects in the environment than those observed in a demonstrator interacting with those objects (Tomasello, 1990; Custance et al, 1999; Hoppitt & Laland, 2008). In contrast to *goal emulation*, in *emulation* individuals learn from affordances of the environment, not from the actions or the demonstrator itself. The distinction between copying actions (imitation) and copying results (emulation) in experimental studies is key to distinguish the influence of demonstrator's actions and the results produced by those actions on observers during problem-solving contexts (Tennie et al., 2006). This has proven to be crucial to understand cultural evolution and the underlying cognitive processes of cultural transmission in human and nonhuman primates (Tennie et al., 2009).

Other forms of social learning processes include (i) opportunity providing (i.e. the products of the demonstrator's behaviour provide the observer with an opportunity to engage in operant learning, unlikely to occur otherwise) and (ii) inadvertent coaching (i.e. demonstrator's responses to observer's behaviour encourage or discourage that behaviour inadvertently) (Hopitt & Laland, 2013). Finally, the social learning processes here described relate to psychological mechanisms in the observer, whereas teaching processes (i.e. a tutor modifies its behaviour in the presence of a naïve observer, at a cost or no immediate benefit to the tutor, enhancing the learning rate of the observer) relate to activities of the demonstrator or tutor. Therefore, teaching may occur through inadvertent social learning processes such as local enhancement, observational conditioning, imitation, opportunity providing or coaching from the observers' perspective, with the difference that in teaching, the demonstrator's behaviour actively functioned to transmit the information to the observer (Caro & Hauser, 1992; Hopitt & Laland, 2013).

1.3.2. Social learning: studies in captivity vs in the wild and evolution of social learning methods

The study of social learning in non-human primates has, until relatively recently, mainly focused on the processes underlying the transmission of behavioural traditions (Dindo et al., 2008; Dindo, 2009).

Historically, studies on social learning have used controlled experiments in laboratory conditions, usually between dyads in isolated cubicles (Fragaszy & Visalberghi, 2004; Dindo, 2009; Kendal et al., 2010b). However, these studies provided weak evidences of social learning in primates, especially monkeys, which was in conflict with the inference of field observations that group behaviours are culturally transmitted (Dindo et al., 2008; Reader & Biro, 2010). Recently, modification of the methods used for social learning research have generated more conclusive results in both wild and captive primate populations (Dindo, 2009).

The first main advance in animal social learning studies was the introduction of novel foraging tasks to track the diffusion of novel behaviours (reviewed in Hoppitt & Laland, 2013). In these tasks, individuals must learn how to solve a puzzle-box (i.e. foraging task) to gain access to a reward. The novel trait that is transmitted is generally the action or sequence of actions necessary to solve the task. The animal literature suggests that individuals rely on social learning only when asocial learning of the task is challenging (Byrne & Russon, 1998; Kendal et al., 2009b). Therefore, tasks need to be difficult enough to require social learning, as has been demonstrated in primate species (Kendal et al., 2009b, 2010a). The second improvement was the inclusion of the two-action paradigm in which a task with two possible actions is tested (Dawson & Foss, 1965). Generally, each action is seeded in a different group by training a demonstrator in each group. If social learning occurs, it is expected that observers perform the action that has been seeded in their group (Dindo, 2009; Reader & Biro, 2010; Hoppitt & Laland, 2013). This allows researchers to control for asocial learning and indirect social learning processes (see ***section 1.3.1***, Hoppitt & Laland, 2008). Furthermore, social learning experiments have been traditionally tested in dyads of individuals. Coussi-Korbel & Fragaszy (1995) were the first to emphasize the need to move away from dyadic studies into a more realistic approach that considers the social context in which animals live (i.e. structured, complex and dynamic networks of relations). The introduction of 'open diffusion experiments' provided the third main improvement since it allowed an understanding of how novel behaviours are spread within a social group beyond the artificial dyadic context (Dindo, 2009; Hoppitt & Laland, 2013).

Dindo et al. (2009) were the first to conduct a social learning experiment training and seeding groups of captive primates and using the two-action paradigm in an open diffusion setting. In their experiment, Dindo et al. (2009) trained the alpha males of two groups in isolation, and then introduced the task for five days, only allowing the alpha males to interact with it to demonstrate the trained option in front of their social group. The task was removed from the experimental area if an individual other than the alpha male approached it. After five days of demonstrations, observers were allowed to interact with the task to investigate if they learned the option seeded in their group. In these captive studies, therefore, researchers can manipulate the actions seeded in the group and choose the subjects that have access to the task.

Captive studies present several advantages. First, tests can be run on consecutive days, controlling for different factors (such as scrounging strategies) that may slow down the diffusion of the novel trait (Reader & Biro, 2010; Hoppitt et al., 2010, 2011). Second, captive enclosures, compared to wild contexts, more readily allow researchers to record all observations and interactions with the task (i.e. who observed what), facilitating the collection of accurate and reliable data on social learning (Coelho, 2015). Despite advantages, captive studies cannot capture the complexity of the ecological and social context in which social learning actually occurs (Reader & Biro, 2010). In addition, captive studies are limited particularly when studying large or endangered species (Kendal et al., 2010b). The study of wild populations allows considering the structured social context and patterns of relations that influence individuals' opportunities for social learning (Coussi-Korbel & Fragaszy, 1995). The implementation of 'open diffusion experiments' plus the two-action paradigm in foraging tasks has been used to test for social learning in wild primates (Kendal et al., 2010a; van de Waal, 2010, 2013; Hobaiter et al., 2014; Coelho, 2015; Kendal et al., 2015). This study design allows testing for the spread of novel behaviours in a more ecologically valid context than captivity (Kendal et al., 2010b; Reader & Biro, 2010). Moreover, this approach is ideal to investigate the role of social relationships in the transmission of social information (Dindo, 2009). As McGregor & Peake (2000) discussed, information is not only exchanged in signaller-receiver dyads, but communication often occurs within a social environment comprised of a network of several signallers and receivers. Consequently, this experimental design is also appropriate to investigate whether communication networks may also reflect social learning opportunities in a nonhuman primate society. To my knowledge, no studies have explored to what extent communication networks may represent the potential paths of social diffusion of information within a group of primates in a foraging-task context.

Network-based diffusion analysis (henceforth, NBDA) was developed for assessing whether social learning was responsible for the spread of novel traits within a group of animals (Franz & Nunn, 2009). The analysis takes into account that individuals may not interact randomly in a social learning context but their interest in the novel behaviour can be biased by the identity of the individual performing the new trait. Accordingly, NBDA controls for the influence that individual attributes (e.g. sex, age, social rank, kinship) or the strength of the social relations established between individuals may have in the spread of novel information within a group (Franz & Nunn, 2009; Hoppitt & Laland, 2013). Therefore, NBDA considers the social structure of a network of social relations to determine whether the paths of social diffusion of the novel trait follow the patterns of relations of that network (Hoppitt & Laland, 2011). If they do, social learning is assumed to have influenced the spread of information in the group.

Moreover, use of networks based on who observes whom during task introductions at different distances can provide information relevant to social learning processes if they explain social transmission in NBDA: close observation networks would be more indicative of social learning processes that require transmission of detailed information of the trait (e.g. direct social learning processes, response facilitation) and distant observation networks of indirect social learning processes such as stimululs/local enhancement for which detailed information of the trait is not relevant for social learning to occur (further details regarding use of different NBDA modelling approaches to distinguish social learning processes is given in ***Chapter 5***).

The social structure of a group of animals is relevant to understand any kind of social behaviour, including social learning (Kasper & Voelkl, 2009). This relationship between social structure and social learning was already hinted by Coussi-Korbel & Fragaszy (1995) when they suggested that the directionality and the level of homogeneity of relationships in a group of animals would predict different patterns of social diffusion of information. Primate societies are difficult to characterize, but the application of sociometric tools, like SNA, in the study of animal sociality has allowed researchers to describe the complex organization of many primate populations in intricate detail (Croft et al., 2008; Kasper & Voelkl, 2009). SNA provides a series of metrics that can help researchers describe how social interactions or associations connect individuals within a group and, therefore, enable predictions regarding how these patterns of relations represent a social context in which individuals can learn from each other (Coussi-Korbel & Fragaszy, 1995; Kasper & Voelkl, 2009). Accordingly, SNA is useful to (i) describe the social learning opportunities within a group of primates based on their social interactions and (ii) test the occurrence of social learning by modelling the patterns of social diffusion of information using NBDA.

1.3.3. The links between social learning, communication and social dynamics

Coussi-Korbel & Fragaszy (1995) first pointed out the relationship between social learning, communication and social dynamics when they suggested that affiliative displays and food-related vocalizations may function as a form of stimuli available for social learning. Later, Heyes & Galef (1996) illustrated this relationship when they highlighted that interspecific differences in psychology, social dynamics and emotional expressiveness might be involved in the different degrees of reliance on social learning observed in different species (Heyes & Galef, 1996).

Regarding social dynamics, Coussi-Korbel & Fragaszy (1995) predicted that social relationships may influence social learning. Social relations are influenced by the levels of social tolerance (i.e. tolerance towards others in proximity) displayed by the group, being low in despotic societies and high in egalitarian societies. According to this framework, different levels of social tolerance may lead to the observation of different patterns of social diffusion of information, known as either directed- or non-specific social learning (Coussi-Korbel & Fragaszy, 1995). Directed social learning, which is influenced by the demonstrator's identity, will occur in despotic societies and species in the intermediate egalitarian-despotic spectrum due to the asymmetry of social relationships (Coussi-Korbel & Fragaszy, 1995). In egalitarian species where social relations are expected to be symmetric, Coussi-Korbel & Fragaszy (1995) predicted that information diffusion would likely occur via non-specific social learning as individuals have the opportunity to learn from any member of their group. Based on these predictions, research has demonstrated that social learning is affected by social dynamics (Lonsdorf & Bonnie, 2010). In addition, new methods, such as NBDA, have used social networks based on affiliation and other types of social interactions to test for social learning (Franz & Nunn, 2009; Hoppitt et al., 2010; Schnoell & Fitchell, 2012; Hobaiter et al., 2014; Claidière et al., 2013; van Leeuwen et al., 2020; Canteloup et al., 2020). For instance, the correlation between social relationships and social learning has been demonstrated in wild bearded capuchins (*Sapajus libidinosus*), where there is a significant influence of grooming interactions and co-feeding associations in the transmission of social information (Coelho, 2015).

Regarding communication and social learning, there has been a historical distinction between both fields, probably due to the controversy on how to conceptualise communication. According to my definition (***section 1.1.1. Debates and controversies***), communication can be understood as a wide field in which social learning is embedded. Social learning studies, unless focused on 'teaching', assume that observers may extract information from signals or cues that demonstrators may have not intended to provide (Font & Carazo, 2010; Leadbeater, 2015). Schaefer & Ruxton (2012) argued that learning acquired from cues (a form of by-product information) shapes the evolution of communication. The observation of a demonstrator's behaviour (or its products) may expose the observer to a stimulus from which the observer may extract inadvertent information (i.e. cues) about changes in the environment or its social context, causing a change in the observer's behaviour. In communication, behavioural cues emitted by a signaller may evolve into a stimulus (or signal) that takes advantage of observers' responses and is modified by natural selection to enhance its effectiveness and acquire a communicative function (Schaefer & Ruxton, 2012). Similarly, Hoppitt et al. (2008) argued that many cases of animal teaching evolved from inadvertent forms of social learning through the selection of cues/signals that increased the likelihood or efficiency of observers' learning. These studies, therefore, suggest a co-evolution of animal communication and social learning.

It has been demonstrated that social learning is crucial for the production, use and comprehension of vocal signals in several primate species (Snowdon, 2009; Watson et al., 2015; Lameira, 2017; Cheney & Seyfarth, 2018; Seyfarth & Cheney, 2018; Fischer et al., 2020). Also, Snowdon & Boe (2003) demonstrated that cotton-top tamarins (*Saguinus oedipus*) rely on facial expressions and vocalizations of conspecifics to learn about food palatability. In these examples, communicative signals (e.g., vocalizations such as food calls) or inadvertent cues (e.g., facial expressions of disgust) are directly influencing social learning during the learning process. Generally, signals are considered behavioural patterns or physiological traits that have been shaped by natural selection for their communicative function. In contrast to signals, cues are informative stimuli that did not evolve for communication purposes (Leadbeater & Chittka, 2007; Schaefer & Ruxton, 2012). Even though communication signals provide context-specific information for receivers to learn, they may also influence social learning of traits unrelated to the coded information in the signal, for instance, by drawing the attention of others to a particular location or social situation from which observers may extract social information unrelated to the signal. In this scenario, communication signals will enhance social learning via inadvertent cues. Moreover, conspecifics' behaviours can be considered social cues if receivers extract information from them via observation. Accordingly, observation networks during social learning contexts could be deemed as cue networks (i.e. communication networks based on social cues).

In the relationship between communication and social learning, communication may not always be at the core of the information that is directly being transmitted. That is, individuals may use social diffusion to learn about things other than those coded in or extracted from communication signals, but still, communication interactions may indirectly represent the pathways through which information is spread. On one hand, individuals' responses to communication attempts might indicate which conspecifics are perceived as reliable informers (Silk et al., 2000; Searcy & Nowicki, 2005; Wheeler et al., 2011). Accordingly, individuals are expected to bias observation preferences towards reliable partners in a social learning context. On the other hand, it has been demonstrated that communication networks may predict affiliative relations. For instance, ring-tailed lemurs mainly respond to the contact calls of strong grooming partners (Kulahci et al., 2015) and black crested macaques attend more to the alarm calls of friends compared to non-friends (Micheletta, 2012). Considering that affiliative networks may represent social learning opportunities (Coussi-Korbel & Fragaszy, 1995), communication interactions that mirror affiliative relations may also predict who is more likely to learn from whom.

1.4. Study species

Barbary macaques (*Macaca sylvanus*) are diurnal primates with a semi-terrestrial, semi-arboreal lifestyle. Although mostly herbivorous, Barbary macaques are opportunistic omnivores that eat roots, seeds and fruit, as well as insects, caterpillars, frogs and tadpoles when available (Mittermeier et al., 2013). As highly adaptable primates, Barbary macaques can be found in different environments and temperatures, from fir and mixed oak forests to sheer cliffs, from hot-summer Mediterranean areas at sea level to cold, snowy mountain regions. The distribution of wild populations covers the north of the Sahara desert in Morocco and Algeria (Alami et al., 2012; Mittermeier et al., 2013; Wallis et al., 2020). There is also an introduced population of over 200 individuals in Gibraltar (Mittermeier et al., 2013).

Barbary macaques live in multi-male, multi-female societies of 25 - 62 individuals on average (mean group size varies among regions, Ménard, 2002; Majolo et al., 2013; Waters et al., 2015). Females are the philopatric sex and have a separate linear hierarchy and a different dominant style than males. Male social rank is based on the outcomes of continuous competition and they normally outrank females, who have a strictly matrilineal hierarchy where daughters inherit the highest position under her mother (Prud'homme & Chapais, 1993a,b; Maestripieri, 1997; Kuester et al., 1998; Bayne, 2005). Both communication and affiliative interactions in Barbary macaques are asymmetrical and, therefore, influenced by individual-level attributes such as sex, age, kinship and social rank (Widdig et al., 2000; Brumm et al., 2005; McFarland & Majolo, 2011; Young et al., 2014; Roubová et al., 2015; Molesti & Majolo, 2017). Despite this, Barbary macaques are characterized as having high levels of social tolerance within macaques (Thierry, 2000, 2007).

It is known that Barbary macaques display high rates of tension-reducing contacts and some behaviours are used flexibly to express both formal submission (i.e. acknowledged lower status relative to higher-ranking conspecifics) and affiliation (Thierry, 2007). In addition, Barbary macaques form coalitions, reciprocate grooming or exchange it for benefits (e.g. access to resources, support in conflicts), tolerate others in proximity during foraging or feeding, and display affiliative behaviours with individuals of different age and sex (Widdig et al., 2000; Berghänel et al. 2011; Carne et al., 2011). Moreover, experimental studies have highlighted that they will cooperate to succeed in foraging tasks (Berghänel et al. 2011; Molesti & Majolo, 2016). These characteristics are typical of tolerant egalitarian species (Thierry, 2000, 2007; Molesti & Majolo, 2016). However, Barbary macaques also show some features typical of despotic societies such as low levels of counter-aggression (Balasubramaniam et al., 2012), and a steep dominance hierarchy (Kaburu et al., 2012). Accordingly, Barbary macaques are considered a relatively tolerant species, classified as intermediate on the egalitarian-despotic spectrum (Thierry, 2007).

Scientific literature suggests that social learning abilities are present in macaque species. In fact, the innovation and spread of a novel foraging behaviour (i.e. sweet potato-washing) observed in a group of Japanese macaques in the early 1950's (Kawai, 1965) prompted the use of the term 'animal culture' for the first time and raised questions about the social transmission of behavioural traditions in non-human animals (Huffman et al., 2010). Since then, many studies of culture or social learning have been conducted in macaques. There is still no clear consensus in the literature about the social learning abilities of macaques (Drapier & Thierry, 2002; Ducoing & Thierry, 2004; Ferrari et al., 2006; Huffman et al., 2010; Leca et al., 2010; Macellini et al., 2012; Redshaw, 2019). However, many studies have provided evidence of social transmission and maintenance of novel behaviours in macaque species. For instance, social learning has been reported for the diffusion of feeding techniques in Tonkean macaques (Drapier & Thierry, 2002), abnormal behaviours of captive rhesus macaques (Hook et al., 2002) and tool-use in long-tailed (Watanabe et al., 2007; Gumert et al., 2009; Tan et al., 2018; but see Bandini & Tennie, 2018) and Japanese macaques (Leca et al., 2007; Huffman et al., 2010).

Custance et al. (2006) found weak and transitory evidence of emulation in pig-tailed macaques. Studies of the mirror neuron system of macaques (a group of neurons that respond to both observed and self-produced actions) indicate that rhesus macaques can emulate (i.e. copy the product of observed actions), but they cannot imitate (Hecht et al., 2013). However, some authors have shown that rhesus macaques are capable of some forms of imitation where an individual copies an expert's use of a rule instead of the specific actions observed (i.e. cognitive imitation, Subiaul et al., 2004). In addition, Macellini et al. (2012) suggested that social facilitation may be relevant in macaques for tool-use learning. Furthermore, different types of 'who' (model-based) strategies have been reported in macaque species (Hikami et al., 1990; Deaner et al., 2005; Gariépy et al., 2014). For instance, individuals of different macaque species have been observed copying the behaviour of kin-related conspecifics (Japanese macaques, Tanaka 1995, 1998; long-tailed macaques, Tan et al., 2018), of strong affiliates or of the most productive and proficient partners in tool-use (long-tailed macaques Tan et al., 2018). In addition, cases of Japanese macaques copying the local behaviour (i.e. behavioural variant of the most geographically closer group) are reported in the literature (Leca et al., 2007; Whiten & van de Waal, 2018).

Little is known about the social learning abilities of Barbary macaques. Recent research has shown that Barbary macaques are capable of innovation (a pre-requisite for behavioural traditions) and cooperation (requiring high levels of social tolerance, important for social diffusion of information) in novel foraging and problem-solving contexts (Molesti & Majolo, 2016; Amici et al., 2020). However the main evidence of social learning in Barbary macaques comes from studies on vocal development and communication. Fischer (2004) suggests that despite the production of vocalizations in Barbary macaques likely being unlearned, call comprehension may be based on learning influenced by exposure to others' vocalizations. Moreover, the gradual development observed in the emergence of individual vocal recognition among Barbary macaques also suggests a social influence in the acquisition of call comprehension abilities (Seyfarth & Cheney, 2010).

The information-sharing hypothesis states that vocal learning evolved to expand vocal repertoires (Nowicki & Searcy, 2014). Literature suggests that both communication complexity and social learning co-evolved with sociality to help non-human primates navigate the complexities of social life (McComb & Semple, 2005; Freeberg et al., 2012; Street et al., 2017). Therefore, use and comprehension learning of communication signals (Egnor & Hauser, 2004) is expected to be relevant in species with a highly diverse repertoire of signals that can be used flexibly in different contexts (i.e. communication complexity). Among macaques, socially tolerant species like Barbary macaques (Thierry, 2007) display higher levels of vocal diversity and flexibility than despotic or less tolerant species in both agonistic and affiliative contexts (Rebout et al., 2017). This indicates that the uncertainty about all the possible social interactions and their consequences (i.e. social complexity) requires a flexible and diverse use and comprehension of the vocal repertoires (Rebout et al., 2017).

Although the production of communication signals is constrained in non-human primates (Seyfarth & Cheney, 2010), macaque species are capable of combining signals of different modalities (e.g. visual, vocal) flexibly in different contexts to produce a highly diverse catalogue of options (Partan, 2002). Barbary macaques display a wide array of vocal and gestural signals (Fischer & Hammerschmidt, 2002; Call & Tomasello, 2007). Even though Barbary macaques can use the same communication signal in different situations for, apparently, different purposes (Hammerschmidt & Fischer, 1998; Call & Tomasello, 2007), most of them can be easily distinguished by the context and the responses they elicit. For instance, aid-recruitment calls are long and high-pitched screams that occur during conflicts, accompanied by searching behaviours (standing up, stretching neck up, turning head towards particular subjects and/or looking around) that can trigger responses of support against an aggressor from eavesdroppers (Goodall, 1968; Fischer & Hammerschmidt, 2002). Similarly, vocal comments are defined as soft vocalizations that occur during the observation of a third-party interaction (either affiliative or agonistic) where the caller does not get involved and does not show any other reaction during or after vocalizing (Fischer & Hammerschmidt, 2002; Brumm et al., 2005).

As discussed earlier, tolerance between individuals is necessary for social diffusion of information, and the social bonds that individuals share with each other represent social learning opportunities (Coussi-Korbel & Fragaszy, 1995). Accordingly, the high levels of affiliative displays and social tolerance that characterize Barbary macaques makes them a good candidate species to investigate the relationship between social dynamics and social learning. In addition, Barbary macaques have a diverse and flexible vocal repertoire, typical of egalitarian and complex societies (Freeberg et al., 2012; Liebal et al., 2013). Considering that reliance on culture (or social learning) is positively correlated with social complexity (Street et al., 2017), Barbary macaques also make good candidates to investigate the relationship between communication, social dynamics and the diffusion of social information. Moreover, to my knowledge, no studies have yet demonstrated social learning in Barbary macaques.

1.5. Aims, research questions and hypotheses

In this thesis, I investigate the relationship between affiliative relations, social learning and communication networks based on unimodal signals (aid-recruitment calls and vocal comments) in free-ranging populations of Barbary macaques.

I here aim to answer three main questions regarding the role of communication and social learning in the social lives of Barbary macaques.

1.5.1. Aim 1

An investigation of the extent to which communication acts are shaped by social interactions and vice versa. Here I am interested in whether (i) networks based on affiliative relations (grooming, huddling and proximity) predict communication interactions (or vice versa), (ii) whether the nature of the communication network (aid-recruitment calls or vocal comments) influences these predictions, and (iii) which individual factors (sex, age, social rank and kinship) influence both social bonding and communication networks.

Since the relationship between communication and social bonds has been demonstrated in other macaque species (*crested macaques*, Micheletta, 2012; *Japanese macaques*; Arlet et al., 2015), I hypothesize that affiliative networks will predict communication networks in Barbary macaques. Moreover, aid-recruitment calls are for the recruitment of allies during agonistic encounters while vocal comments are triggered by the mere observation of other individuals interacting (Fischer & Hammerschmidt, 2002; Brumm et al., 2005). Therefore, I expect that affiliative interactions specifically predict communication networks (i) based on the responses to aid-recruitment calls (i.e. the relationship between helper and individual being helped) and (ii) based on the production of vocal comments (i.e. relationship between callers and individuals observed in the third-party interaction). Finally, given findings reported in ***section 1.4. Study species*** (Widdig et al., 2000; Brumm et al., 2005; McFarland & Majolo, 2011; Young et al., 2014; Roubová et al., 2015; Molesti & Majolo, 2017), I also expect that individual factors such as sex, age, social rank and kinship influence social bonding networks and communication networks in Barbary macaques.

1.5.2. Aim 2

I am interested in whether (i) novel information regarding foraging tasks is socially transmitted within a group of Barbary macaques, and (ii) social bonding networks predict who observes whom during task introduction times.

I expect to find evidence of social transmission in Barbary macaques as it is observed in other macaque species and considering that Barbary macaques display many characteristics that are useful for social learning, including the ability to innovate (Amici et al., 2020), high levels of social tolerance and sociality (Thierry, 2007; Rebout et al., 2017), and problem-solving skills (Molesti & Majolo, 2016). Based on previous studies, it is likely that Barbary macaques use non-imitative social learning processes, such as stimulus enhancement, social facilitation or emulation, to learn about the tasks (Subiaul et al., 2004; Custance et al., 2006; Macellini et al., 2012; Hecth et al., 2013) plus model-based social learning strategies to copy others according to their relationship with them (e.g. strength of social bonds) or the task payoffs observed (Tan et al., 2018). Also, since Barbary macaques are classified as intermediate in the despotic-egalitarian spectrum (Thierry, 2007; Rebout et al., 2017), I expect to find evidence of both directed and non-specific social learning, as predicted by Coussi-Korbel & Fragaszy (1995) and observed in other primate societies with similar levels of social tolerance (Coelho, 2015). Finally, since affiliative relations are said to represent social learning opportunities (Coussi-Korbel & Fragaszy, 1995), I expect that social bonding networks predict observation networks during task introductions.

1.5.3. Aim 3

I aim to explore the relative role of communication in the transmission of social information. Here I am interested in whether I can predict the spread of novel information throughout the group from communication networks outside of task introduction times equally well as networks based on who observed whom interacting with the task.

I hypothesize that communication networks will predict who observes whom in a social learning context. Since social learning involves the extraction of information by the observation of others' behaviours, I suggest that Barbary macaques will tend to observe those whom they share strong communication bonds with, who in turn I expect to be those whom they spend more time engaged in affiliative interactions with (Micheletta, 2012; Arlet et al., 2015). Accordingly, I expect that communications networks will help to predict the patterns of social information diffusion. This would indicate that (the hitherto neglected) knowledge of communication interactions in a group, may be useful in fully representing social learning opportunities.

1.6. Thesis outline

This thesis is comprised of six chapters. Chapter 2 presents a detailed description of the study sites and Barbary macaque groups, and contains an overview of the general sampling and statistical methods used in the subsequent chapters. In Chapter 3, I compare different types of affiliative relations between members of two groups of free-ranging Barbary macaques to describe the social context in which these monkeys may learn from each other. In Chapter 4, I explore the function and dynamics of communication networks based on two different vocalizations (aid-recruitment calls and vocal comments) and investigate the relationship between communication interactions and social bonds in Barbary macaques. In Chapter 5, I empirically test for social learning during open-diffusion experiments with novel foraging tasks and investigate how social bonds and communication interactions outside of task introduction periods, and observation networks during task introductions, predict the patterns of social diffusion of information. Chapter 6 is the General Discussion in which I integrate the findings of chapters 3, 4 and 5 to highlight the role of communication in social dynamics and social learning, as well as study limitations and considerations for future research. I conclude by discussing the implications of my findings beyond the social learning/communication fields, including conservation and human language evolution.

Chapter 2

General Methods

This research was originally planned to take place in Serra da Capivara National Park (Piauí, Northeast Brazil) with populations of wild-bearded capuchins (*Sapajus libidinosus*). However, fieldwork had to be cancelled due to problems derived from the coup d'état of May 2016 (when I moved to Brazil to start the study) that caused changes in the management of the park. The project was suspended for 6 months, during which, the situation in Brazil remained the same, and the decision was made to change the location of the study.

In April 2017, I went to Gibraltar to work with Barbary macaques in the Upper Rock Nature Reserve, but the study subjects disappeared from the study area after 1 month. After 6 months of trying to establish study of a new group with the Reserve management, I left Gibraltar and the project was suspended again for 3 months.

In February 2018, I began working with a group of Barbary macaques in Blair Drummond Safari Park, Scotland. Unfortunately, after 5 months collecting behavioural data and carrying out experiments, the park management terminated employment of the keepers and Director of the Macaque Reserve and I was not allowed to continue my research. The decision was made to continue with the dataset I had already collected and combine it with a non-coded/analysed dataset from a similar project that my supervisor had with a group of Barbary macaques in Trentham Monkey Forest, UK.

The group in Trentham Monkey Forest (TG) was studied by Cara Evans (henceforth CE) and her research assistant between the 4th of May and the 5th of September of 2011. Observations and experiments in the Blair Drummond Group (BDG) were carried out by me and my research assistant between the 2nd of February and the 20th of August of 2018. Both studies included data collection on social relationships and social learning experiments. Pilot tests of the tasks used to test for social learning in both groups were carried out in other groups of Barbary macaques. Communication interactions were not contemplated in the study with TG, so data on communication networks were only collected for BDG.

This chapter contains details of the study species and sites, the behavioural sampling methods used, a brief description of the tasks and the experimental procedures, and an overview of the statistical analyses implemented in this thesis. Further details of the methods and analyses, which pertain to specific research questions, can be found in the subsequent chapters of results.

2.1 Study sites and focal subjects

The studied groups, although captive, lived in large free-ranging habitats in troops of multiple males and females with linear hierarchies (see ***Appendix A***), and resemble natural groups of Barbary macaques in terms of size and sex ratio (1:1.5 for BDG, 1:1 for TG; 1:1 in wild populations, Mittermeier et al., 2013). Both sites (Trentham Monkey Forest and Blair Drummond Safari Park) have transferred and exchanged males with other European parks to emulate the natural male migration of this species, which is known to be lower than in other macaque species (Mittermeier et al., 2013). The exchange of individuals is a common procedure to emulate the natural migration of wild adult males and maintain a high genetic diversity in captive populations of Barbary macaques.

2.1.1. Blair Drummond Safari Park

Blair Drummond Safari Park is located 9 kilometres (coordinates: 56º 9’ 54’’ N, 4º 2’ 17’’ W) outside Stirling, in Scotland. It is home to over 350 animals and features reserve areas that visitors drive through in their cars or as passengers on the park’s safari bus to observe freely roaming animals in large enclosures. The park opens to visitors from mid-March until the end of October, 7 days per week, from 10:00 a.m. to 5:30 p.m. During the study period, researchers were permitted in the park from 9 a.m. until closing time.

In 2014, a group of 30 Barbary macaques was transferred to the park from Gibraltar to reduce the disruption they were beginning to cause with the local residents of the peninsula (and to prevent having to cull them as had been carried out previously). The Macaque Reserve in Blair Drummond Safari Park opened to the public in 2015 and it housed a group of 28 Barbary macaques at the beginning of this study. It comprised an inside enclosure of 166.7 m^2 and an outdoor area of 3.5 acres. The inside enclosure was used as the monkeys’ sleeping site and was left open during the day to allow macaques to shelter from the weather. The outdoor area was open and flat, containing three trees, a small mound, a pond and a group of five long low ridges at the periphery (see ***Figure 2.6***).

The macaques were provisioned with fresh vegetables and fruit twice per day (morning and afternoon) in the inside enclosure. During winter months, a mix of different seeds was scattered in the outside area 5 times per day (at 2 hour intervals). In summer months (June to September), scatter feeds were reduced to twice per day due to the abundance of plants, flowers, insects and other food resources that were naturally available in the enclosure.

2.1.2. Trentham Monkey Forest

Trentham Monkey Forest is a monkey park located in an ancient Staffordshire forest (52º 57’ 00’’ N, 2º 11’ 50’’ W), on the outskirts of Stoke-on-Trent, in England. It is home to 140 free-ranging Barbary macaques that live in a 60-acre forest that can be visited walking along a ¾ of a mile pathway (***Figure 2.5***). Trentham Monkey Forest belongs to a network of three other parks that house groups of free-ranging Barbary macaques around Europe: two parks in France (*La Montagne des Singes* in Kintzheim and *La Forêt des Singes* in Rocamadour) and one in Germany (*Affenberg Salem* in Salem). The parks in France and Germany were founded in the early-mid 1970’s. In 2004, two groups of Barbary macaques from the existing parks were transferred to Trentham, and the park opened its gates to the public in July 2005. Together, the four parks house ~700 Barbary macaques.

Trentham Monkey Forest is closed to the public from November to end of January. The forest opens to the public 7 days per week between 10:00 a.m. to 5:00 p.m. (and 6 p.m. in the school holiday period). At the time of the study, the park opened for full-time research at the beginning of April and closed in mid-October, and researchers were allowed between 9 a.m. and closing time. The monkeys were fed large amounts of fruit, vegetables and nuts between 9 a.m. and 10 a.m., before public entry was permitted. Scatter feeding occurred every hour to encourage the monkeys into the public-view areas and consisted of a mix of wheat and sunflower seeds (and sometimes fruit in the afternoon). Public feeding talks (15mins) took place every day at two hourly intervals (11:15-17:15).

There were two separate groups of Barbary macaques: the German group and the French group. Each group had separate and, generally, non-overlapping home ranges and contained free-ranging individuals of 8-10 matrilines (matrilineal relatedness for both groups was provided by the park staff). Pilot studies were conducted with the French group (N = 75). Observational and experimental data collection was carried out with the German group (N = 61).

2.1.3. Study groups

In both groups, age categories were assigned following Kuester & Paul (1997)’s classification for Barbary macaques:

- Infants: < 1 year old
- Juveniles: 1 – 3 years old
- Subadults: 4 years old for females, 4-6 years old for males
- Adults: > 5 years old for females, > 7 years old for males.

Blair Drummond Group (BDG)

At the beginning of the study, BDG comprised 28 individuals: 6 adult males, 13 adult females, 4 sub-adult males, 2 sub-adult females and 3 infants (***Table 2.1***). Two infants were born during the study period but one died within four days. The other infant survived, making a total of 29 Barbary macaques in the group at the end of the study.

The park staff provided a catalogue for monkey identification with pictures and descriptions of the macaques in BDG. During the first 6 weeks, I collected preliminary data while learning how to identify each individual in the group (including the infants) via observations in the field, photos and recorded videos. Every day I was tested by one of the keepers to assess my ability to identify the individuals at different distances (up to 30 m).

Table 2.1. Composition of Blair Drummond Group.

Name	Code	Birth date	Age	Age category	Sex	Mother
CHE	CH	1997	21	Adult	Male	-
JORDAN	JO	2010	8	Adult	Male	-
OLIVER	OL	2010	8	Adult	Male	-
PHIL	PH	2010	8	Adult	Male	-
TORY	TO	2010	8	Adult	Male	-
GHILLIE	GH	2011	7	Adult	Male	-
SHAW	SH	2012	6	Sub-adult	Male	-
SIR SCOFFALOT	SC	2013	5	Sub-adult	Male	-
HOLMES	HO	2014	4	Sub-adult	Male	-
ARRAN	AR	14/07/2015	3	Juvenile	Male	Liberty
SADIE	SA	1996	22	Adult	Female	-
JULIA	JU	2000	18	Adult	Female	-
CATS	CA	2000	18	Adult	Female	-
REBECCA	RE	2001	17	Adult	Female	-
VELVET	VE	2002	16	Adult	Female	-
CORAL	CO	2003	15	Adult	Female	-
WUWU	WU	2009	9	Adult	Female	-
LIBERTY	LI	2009	9	Adult	Female	-
MISS BRODIE	MB	2011	7	Adult	Female	-
ORCUS	OR	2012	6	Adult	Female	-
ZINC	ZI	2012	6	Adult	Female	-
FEENEY	FE	2012	6	Adult	Female	-

MARIE-THERESA	MT	2012	6	Adult	Female	-
ANNALEE	AN	2014	4	Sub-adult	Female	-
LAGUEA	LA	2014	4	Sub-adult	Female	Cats
BUTE	BU	19/06/2017	1	Infant	Female	Miss Brodie
BRESSAY	BR	02/07/2017	1	Infant	Female	Liberty
BARRA	BA	10/05/2017	1	Infant	Male	Cats
CALVAY	CV	23/04/2018	0	Infant	Male	Marie-Theresa

Only mother relatedness and the exact date of birth are known for those individuals that were born in Blair Drummond Safari Park.

Trentham Group (TG)

TG consisted of 61 individuals at the time of the study: 22 adult males, 27 adult females, 5 sub-adult males, 2 sub-adult females and 5 infants (***Table 2.2***). During the study, one adult male died and 7 infants were born, with 4 surviving.

Monkey ID keys were not available at Trentham at the time of study and the individual tattoos that the monkeys were given on their inner thighs were rarely visible. After a period of learning individual identities, it was determined that the identity of monkeys aged 3 years or less could not be reliably determined. Accordingly, only subjects older than 3 years were included in the study.

Table 2.2. Composition of Trentham Group.

Name	Code	Birth date	Age	Age category	Sex	Matriline	Mother
OLIVER[1]	OI	1990	21	Adult	Male	-	Unknown
SQUIRTER	SQ	1986	25	Adult	Male	4	Deceased
TWITCH	TW	1987	24	Adult	Male	1	Deceased
EDDIE	ED	1990	21	Adult	Male	2	Deceased
RUPERT	RU	1991	20	Adult	Male	8	Deceased
COCO	CC	1997	14	Adult	Male	1	Big Bertha
NORMAN	NO	1997	14	Adult	Male	1	Deceased
ANDY	AD	2001	10	Adult	Male	3	Andy's Mum
LAUREL	LE	1987	24	Adult	Male	-	Unknown
JIMMY	JI	1987	24	Adult	Male	-	Unknown
DEMON BOY	DB	2005	6	Sub-adult	Male	5	Deceased
DUNCAN	DU	1999	12	Adult	Male	-	Unknown
PJ	PJ	2000	11	Adult	Male	-	Unknown
BARNEY	BY	2001	10	Adult	Male	-	Unknown
J2	JT	1992	19	Adult	Male	5	Strange Face Sis

DENNIS	DE	1996	15	Adult	Male	2	Deceased
LITTLE FRED	LF	2007	4	Sub-adult	Male	2	Sarah
ZACK	ZA	2002	9	Adult	Male	2	Pinky
JACK	JA	2006	5	Sub-adult	Male	2	Little Sue
TIMMY	TI	2005	6	Sub-adult	Male	3	Andy's Mum
WALTER	WA	2006	5	Sub-adult	Male	3	Split Nose
ARNIE	AE	1995	16	Adult	Male	2	Deceased
FREAKY FRED	FF	1988	23	Adult	Male	7	Deceased
WAYNE	WY	2004	7	Adult	Male	2	Pinky
BOB	BO	1981	30	Adult	Male	2	Deceased
ET	ET	1987	24	Adult	Male	6	Deceased
PADDY	PA	1991	20	Adult	Male	-	Unknown
SPLIT NOSE	SN	2000	11	Adult	Female	3	Deceased
STRANGE FACE	SF	1986	25	Adult	Female	5	Deceased
ANDY’S MUM	AM	1997	14	Adult	Female	3	Deceased
SNOW WHITE	SW	1990	21	Adult	Female	10	Deceased
SARAH	SR	1997	14	Adult	Female	2	Deceased
BLANCHE	BL	1982	29	Adult	Female	7	Deceased
J-LO*	JL	1990	21	Adult	Female	1	Deceased
BIG BERTHA	BB	1990	21	Adult	Female	1	Deceased
FLOSSY	FL	2002	9	Adult	Female	1	Deceased
RIGHT SCAR	RS	2003	8	Adult	Female	2	Pinky
LITTLE SUE	LS	2001	10	Adult	Female	2	Sarah
BAM BAM	BM	2004	7	Adult	Female	1	Deceased
SMILEY	SM	1997	14	Adult	Female	2	Deceased
QUIFF	QU	2004	7	Adult	Female	2	Smiley
ROSIE**	RO	2006	5	Adult	Female	3	Big Sue
POSIE**	PO	2006	5	Adult	Female	2	Smiley
ANDY'S SIS*	AS	2006	5	Adult	Female	3	Andy's Mum
EYELINER CHICK*	EC	2007	4	Sub-adult	Female	2	Right Scar
GINGER	GI	1989	22	Adult	Female	2	Deceased
B92	BN	1984	27	Adult	Female	9	Deceased
BIG SUE	BS	1999	12	Adult	Female	3	Deceased
CANDY**	CY	2006	5	Adult	Female	1	Flossy
SPLIT NOSE'S DAUGHTER*	SD	2005	6	Adult	Female	3	Split Nose
BRAZEN	BZ	1988	23	Adult	Female	8	Deceased
STRANGE FACE SIS	SS	1988	23	Adult	Female	5	Deceased
PINKY	PI	1992	19	Adult	Female	2	Deceased

L35	LT	2007	4	Sub-adult	Female	4	Deceased
E50	EF	1987	24	Adult	Female	7	Blanche
F51	FO	1988	23	Adult	Female	1	Deceased
N55	NF	2009	2	Juvenile	Female	NA	NA
O64	OS	2010	1	Juvenile	Female	NA	NA
N50	NV	2009	2	Juvenile	Female	NA	NA
O66	OX	2010	1	Juvenile	Female	NA	NA
O65	OF	2010	1	Juvenile	Female	NA	NA

[1] Died during study. * Had offspring that survived during study. ** Had offspring that died during study. NA: Data Not Available. Those individuals without matriline are males that were transferred from another place to emulate male migration.

Groups for pilot tests

All experimental apparatuses tested in TG were previously piloted in the French group (N = 75), that had a similar composition than the German group, in which all sexes and age categories were represented.

Pilot tests of the task used in BDG were performed in a group of 25 wild Barbary macaques (named Middle Hill Group, MHG) that live in the Gibraltar Upper Rock Nature Reserve. The group consisted of one adult male, 8 adult females, 6 juvenile males, 6 juvenile females, 2 infant males and 2 infant females. Gibraltar Upper Rock Nature Reserve is home to 300 free-ranging Barbary macaques that form stable groups of different sizes around the reserve. The Middle Hill Group is one of the few groups that live in a fenced military area, outside touristic zones, only accessible to staff and researchers. This group was formed after the previous group in Middle Hill was transferred to Blair Drummond Safari Park.

2.2. Task experiments

2.2.1. Pilot tests

All tasks were piloted with another group of Barbary macaques in order to: a) test the suitability and feasibility of the tasks with this species, b) test the resistance and sturdiness of the materials used to build the tasks, c) test the level of monopolisation of the task by certain individuals (e.g. high-ranking subjects), d) test the level of motivation of macaques to interact with the tasks (i.e. whether tasks were easy or difficult and what type of rewards were more enticing).

Based on the performance of Barbary macaques during the pilot tests, the tasks were modified to make them more feasible, attractive and sturdy. The final versions of the tasks (described below) were resistant to the manipulation of Barbary macaques and feasible for all the individuals tested during the pilot experiments. Moreover, individuals maintained interest in interacting with the tasks for the duration of the sessions. The level of monopolisation of the tasks during the pilot tests was low. In all cases, dominant individuals allowed lower-ranking subjects to approach and interact with the tasks. Even though there was a constant flow of individuals being displaced by higher-ranking conspecifics, all subjects were seen solving or attempting to solve the task. All tasks were properly disinfected after the pilot tests, before introducing them into the study groups, to avoid cross contamination between groups.

2.2.2. Description of the tasks

Three extractive foraging tasks of increasing difficulty (with raisins used as rewards) were presented to TG. An open diffusion experiment was carried out with BDG using a different foraging task, but it could not be finished (for further details refer to ***5.2.2. Description of the tasks*** in ***Chapter 5***).

Task 1: Blue/yellow task

The blue/yellow task consisted of a rectangular wooden box 28 (w) x 16 (h) x 16 (d) cm with two option holes in the top (6 x 6 cm), one framed in yellow and another framed in blue (***Figures 2.1*** & ***5.1***) inspired by a task used by Kendal et al. (2005) with callitrichid monkeys. A mechanism inside the task prevented both holes from being used simultaneously to retrieve rewards. The task was fixed to the ground using long U-shaped metal anchor stakes.

Figure 2.1. Blue/yellow task set up at task area 2 (Car Park) in Trentham Monkey Forest. A mid-ranking adult female (FO) retrieving rewards from the blue hole (left) and a low-ranking adult female (EF) exploring the yellow hole (right).

Task 2: Push/lift-up task

The push/lift-up task was also inspired by a task used by Kendal et al. (2005) and consisted of a wooden square-box 21 (w) x 21 (h) x 21 (d) cm with a swing door at the front (and a 3-cm gap at the bottom) that could be pushed inward or lifted up outward (***Figures 2.2*** & ***5.2***). The task was attached to a metal cylinder that was already fixed to the ground in the enclosure.

Figure 2.2. Push/lift-up task set up at task area 2 (Car Park) in Trentham Monkey Forest. A high-ranking adult male (WY) using the lift-up option (left) and a low-ranking adult female (EF) reaching out for raisins using the push option (right).

Task 3: Rotating-door task

The rotating-door task was inspired by a task used with wild lemurs (Kendal et al., 2010a), and consisted of a squared-wooden box 23 (w) x 23 (h) x 23 (d) cm with a circular retrieval hole (8 cm in diameter) that was covered by a circular door (9.5 cm in diameter) that could be rotated clockwise or counter-clockwise (***Figures 2.3*** & ***5.3***). The task was fixed to the ground using long U-shaped metal anchor stakes.

Figure 2.3. Rotating-door task set up at task area 3 (Valley) in Trentham Monkey Forest. A high-ranking adult male (ZA) rotating the door counter-clockwise (left) and another high-ranking adult male (CC) reaching out for raisins after rotating the door clockwise (right).

Using prior knowledge of these tasks, RK and CE designed the tasks such that the actions required for solution were expected to increase in difficulty from the blue/yellow task, to the push/lift-up task, to the rotating-door task. Pilot tests with Barbary macaques indicated that this was the case.

BDG task: Twin-door task

The task presented to BDG consisted of a wooden box 90 (w) x 30 (h) x 30 (d) cm with two identical interactive modules (similar to the rotating-door task used in TG) separated by a non-interactive module (***Figures 2.4*** & ***5.4***). One interactive module contained highly desirable rewards (rich module) while the other contained less desirable rewards (poor module). This twin-door task was introduced for different purposes other than testing for social learning (see ***5.2.2. Description of the tasks*** in ***Chapter 5***). Unfortunately, experiments were not completed due to changes in the park management, but data on who observed whom during task introductions in BDG were used in this thesis (see ***section 5.2.5*** in ***Chapter 5***).

Figure 2.4. Twin-door task set up at task area 1 (Near inside enclosure) in Blair Drummond Safari Park. Top photo (close-up camera): A high-ranking adult male (OL) solving the task through the mesh by rotating the door of the interactive module containing desirable rewards while a mid-ranking sub-adult male (HO) is watching him from 3m. Bottom photo (wide-range camera): The same scene observed in the top photo with a camera capturing those individuals within 10m from the task (OL at the task and HO at 3m on the left).

2.2.3. Open diffusion experiments

In TG, all foraging tasks were placed inside the enclosure and fixed to the ground. Three areas for task introductions were designated by the park staff (***Figure 2.5***). These areas were (i) frequently visited by the monkeys, (ii) located far from the public paths to avoid disruption of the experiments by visitors and (iii) optimal to secure the tasks to the ground. Moreover, each of the three areas were in a clearing in the forest ensuring that monkeys within 10m of the task (i) had good visibility of the individual manipulating the task and (ii) could easily be identified by researchers. These areas were also feeding sites where keepers scattered fruits and vegetables on a daily basis, so the macaques were accustomed to human presence and to spending time on the ground looking for food in these locations.

In BDG, task locations were also designated by the park staff. In this case, the task was presented behind the metallic mesh fence of the Macaque Reserve. The task and the actions were modified to ease their manipulation through the holes in the mesh. The foraging task was introduced in two locations, separated 30 m from each other (***Figure 2.6***). The first location was near the inside enclosure: it was an open area with high visibility, frequented by the Barbary macaques and the furthest point from the road (car visitors' path) in the whole exterior area. This location was chosen because its good visibility and its distance from the visitors' path drew the attention of the subjects to the task and allowed accurate data collection within 10m distance from the task with minimum disruption by the public. The second location was near the car entrance to the enclosure, behind a low hump, not visible to the public. This second area was less frequented by monkeys and it was chosen to overcome problems of monopolisation of the task. Between both locations, there was a patch of tall vegetation that prevented individuals in the first location from seeing the second one. This allowed me to obscure the task from those that tended to monopolise it and, therefore, provide opportunities to other individuals to learn how to manipulate the task.

Figure 2.5. Map of Trentham Monkey Forest with the locations where the experiments were conducted. Area 1: Hill. Area 2: Car Park. Area 3: Valley.

Figure 2.6. Map of the Macaque Reserve in Blair Drummond Safari Park with the locations where the experiments were conducted. Area 1: Near inside enclosure. Area 2: Behind a hump, near the Car Entrance.

For further methodological information on how the open diffusion experiments were conducted and on how data was recorded and coded from video, refer to section ***5.2. Methods*** in ***Chapter 5***.

2.3. Data collection

2.3.1. Behavioural sampling

In order to understand the links between social dynamics, communication and social learning in Barbary macaques, three groups of networks were built. First, networks based on socio-positive relations to describe the social dynamics of the group and the social context in which Barbary macaques can learn. Second, networks based on communication interactions to describe the patterns of relations during communication interplays and understand whether these interactions follow the same patterns observed in the socio-positive networks. Third, networks based on who observes whom in a social learning context (i.e. task introductions) to further describe learning opportunities, test for social learning and understand whether observation networks during task introductions can be predicted by affiliative and communication networks.

Behavioural observations were carried out to collect the data necessary to build affiliative, communication and observation networks. Social behaviours represent < 5-10% of the daily activity budget of both semi-provisioned and wild-feeding Barbary macaques (Ménard & Vallet, 1997; Alami et al., 2012). The provision of food decreases the time individuals spent foraging and increases the occurrence of contest competition, but does not seem to increase the time spent in other social activities (Alami et al., 2012). Accordingly, a combination of different sampling methods and rules were used to increase the amount of data collected for infrequent social behaviours (Martin & Bateson, 2007). ***Table 2.3*** contains a description of all the social behaviours collected in this thesis.

Social behaviours like grooming, proximity and huddling were collected using focal, scan and behaviour (i.e. all occurrences, Martin & Bateson, 2007) sampling. Focal follows and scan samples were used to collect data on: (i) the identity and the activity of the focal individual, (ii) the identity of the individuals within 10m of the focal subject and their distance to the focal, (iii) any social interaction between the focal and conspecifics (both affiliative and agonistic). All occurrence sampling was used to collect additional data on relatively rare socio-positive behaviours and agonistic/dominance-submissive interactions between any individuals within view. Focal, scan and all-occurrence sampling was carried out simultaneously in sessions of 5 minutes of duration. For further details on the specific sampling rules and criteria used for data collection in each group, see section ***3.2*** in ***Chapter 3***.

Table 2.3. Ethogram of socio-positive and agonistic behaviours.

Social behaviours		**Description**
Affiliative interactions	Grooming	When individuals manipulate another's fur using hands or mouth. Coded during Focal follows and All Occurrences sampling. A new grooming bout was recorded whenever there was a pause of at least 5 minutes following the preceding grooming behaviour. A new bout was also considered when groomer and groomee exchanged roles (Coelho, 2015). The individuals involved and the direction/reciprocity of the behaviour was noted.
	Huddling	Two or more individuals are resting (i.e. to be still, sitting or lying, asleep or awake, with the eyes closed and/or facing down) with bodies in direct contact, lateral or ventral. Arms may be wrapped around one another.
Associations	Proximity	Proximity can be defined in many different ways depending on the criterion distance between subjects we use, which can be influenced by: a) the species itself, b) the size, design and complexity of the enclosure and, c) the group composition, among other factors. Proximity, as well, can be considered a measure of both association and social tolerance depending on the activity in which individuals are involved. Here, I define proximity as a measure of association. Proximity was recorded when two or more stationary individuals are found within 1m and between 1-5m. Proximity as a measure of association may provide information on the strength of social bonds and/or group membership (Whitehead, 2008). As moving individuals may have little control over whom they are close to, these events were not considered as proximity. The context in which individuals were found in proximity (e.g. feeding, foraging, resting, observing task manipulations) was also noted to determine whether it was a measure of association or social tolerance. Events in which the individuals within one meter of each other are eating (i.e. co-feeding events, task introductions with rewards available) were considered a measure of social tolerance.
Agonistic displays	Threaten	Rounded mouth or open mouth bared-teeth display with eyelids raised. May include vocalisations (pants, barks, noisy and complex screams) and a tense body posture (front body lowered) and/or a small movement (lunge) toward the monkey being threatened (sometimes hitting the ground with the hand).
	Re-directing aggression	When subjects threaten third-parties while being threatened by other individuals.

	Chase	When an individual runs towards another, who is moving rapidly away, displaying threatening behaviours. Involves quick movements with full body.
	Physical assault	Physical contact, in which a monkey pushes with hands, hits or bites a conspecific. It also includes rough and tumble fights. The types of aggression (e.g. push, bite, hit) as well as injuries incurred were noted.
Submissive behaviours	Move away	When threatened and/or chased, the target of the agonistic interaction moves away from the aggressor. It also includes events when an individual moves away from a place, a food patch or a partner that is being approached (within 1m) by another conspecific.
	Submissive grin	Facial expression with retracted lips usually produced in response to a threat, normally accompanied by teeth-chattering and presentation of the rear to the aggressor.
	Scream or cry	High-pitched vocalization usually issued in response to a threat and that may, or may not, elicit response from coalition partners.
Absence	Not present	When the subject leaves the outside enclosure and enters the inside enclosure (BDG only)
	Not visible	When the subject, without leaving the outside enclosure, goes out of sight of the researcher (e.g. behind an obstacle) (BDG and TG)

For observation networks, data on who observes whom during task introductions were collected for each group. Every time a monkey approached (within 0.5m) and started manipulating the task, the following data were recorded: a) the identity of the individual interacting with the task, the action used in each manipulation and whether it was successful or not in retrieving a reward, b) the identity of the individuals within 10m of the task, their distance from the task and whether they were attending (head oriented towards the individual manipulating the task) or not. Further details on how data for observation networks were collected are described in section ***5.2. Methods*** in ***Chapter 5***.

2.3.2. Vocal sampling

The vocal repertoire of Barbary macaques is a highly graded signalling system (Hammerschmidt & Fischer, 1998), meaning that there is a continuous variation within and between call types. Accordingly, the same vocal signal can be uttered in different contexts, triggering context-specific responses from receivers or eavesdroppers (Hammerschmidt & Fischer, 1998). With that in mind, Fischer & Hammerschmidt (2002) described the vocal repertoire of Barbary macaques, providing a general description of the contexts in which call types are uttered. Overall, Barbary macaques mainly produce screams, shrill barks, geckers and low-frequency pants, with occasional tonal contact (i.e. ‘coo’ like) calls and girneys (Fischer & Hammerschmidt, 2002, see ***Table 2.4*** for a full description of Barbary macaques' vocal repertoire).

Table 2.4. Vocal repertoire of Barbary macaques as described by Fischer & Hammerschmidt (2002).

General context	Call type	Specific contexts
Highly charged agonistic contexts	Noisy and complex screams	Uttered during agonistic contexts where individuals are being chased or physically assaulted by individuals of different age and/or sex. Also, during male-male fights.
	Noisy arched screams	Uttered during agonistic contexts where individuals are being threatened.
	Complex screams	Uttered during agonistic contexts where an individual is harassed by several individuals and during aid-recruitment contexts.
Aversive situations	Modulated tonal screams, undulated screams and squeaks	Uttered by yearlings and infants that are prevented (by mother or other individual) from establishing physical contact with their mother. Also, infants produce squeaks in their first attempts to climb a branch.
	Tonal screams and complex screams	Uttered by adult females when threatened or displaced by other group members.
	Threat pants (staccato-grunt structure)	Uttered by adult females when threatening another individual. Mild threats consist of a stare with the eyebrows slightly raised. Intense threats involve protruding the lips with an open-rounded mouth, often, but not always accompanied by threat pants.
Disturbances in the surroundings (alarm calls)	Shrill barks	Uttered when individuals are disturbed by a dog in the vicinity or in their sleeping strees after dusk (e.g., by a human approaching at night).
	Rasping calls	Uttered by monkeys in response to a flying vulture.
	Clucking barks	Uttered by monkeys in response to a snake nearby.
Mating (oestrus calls)	Rhythmic pant-grunts	Uttered by females during copulation or while in oestrus. During copulation, females utter a rhythmic series of low-frequenty grunts. Males typically remain silent. While in oestrus, females also utter rhythmic pant-grunts even though they are not engaged in any mating activity. Calls uttered during copulation or while in oestrus are structurally different and show temporal and spectral differences depending on the phase of the

		oestrus. Playback experiments showed that males can perceive this variation.
Social play (play calls)	Pants	Uttered by monkeys during rough-and-tumble play with the accompanying relaxed open-mouth play face.
Contact-related situations	Clear calls	Uttered by mothers in search of their infants
	Geckers	Uttered by monkeys when trying to establish contact with other individuals huddling.
	Girneys	Uttered by adults during triadic interactions ('agonistic buffering') or when the group travels to another area.
Observation of third-party interactions (vocal comments)	Rasping calls	Uttered when observing a third-party agonistic interaction. Fischer & Hammerschmidt (2002) indicate that in some cases, it appears that callers are supporting one of the parties. These calls may be given from more than 50m away from the interaction observed.
	Low-frequency soft pants and pant barks	Uttered when observing a third-party interaction involving infant-handling. Note that infant-handling plays an important social role in Barbary macaque societies. Adults of both sexes frequently engage in affiliative interactions involving infants to maintain group stability, buffer agonism and form coalitions (Deag, 1980; Small, 1990; Paul et al, 1996). Therefore, these calls are uttered during affiliative contexts.

No food-associated calls were observed in Barbary macaques.

Noisy screams are given by members of all age and sex classes (see ***Table 2.4***). The same is true for shrill barks, except that infants do not utter these calls (Fischer & Hammerschmidt, 2002). Undulated screams, play calls and geckers are most frequently given by infants and juveniles (Hammerschmidt & Fischer, 1998; Fischer & Hammerschmidt, 2002). However, sub-adults also use a fair amount of play calls and geckers. Mating calls, girneys, and calls associated with aversive situations and highly charged agonistic contexts are mainly uttered by adults and sub-adults, with the exception that juvenile males also have a preference for the latter two categories (Hammerschmidt & Fischer, 1998; Fischer & Hammerschmidt, 2002). Clear calls are mainly produced by adult females with infants.

Overall, there are no significant differences in call usage across general contexts between sexes, except for the aforementioned cases that include clear calls and oestrus calls which are characteristic of adult females (Hammerschmidt & Fischer, 1998; Fischer & Hammerschmidt, 2002). Regarding age-related differences, it seems that infants and juveniles most often use high-frequency screams, whereas older individuals more frequently use lower-frequency grunt-like calls. However, all age-classes are capable of producing the whole array of call types of the vocal repertoire (Hammerschmidt & Fischer, 1998), even though there is a decline in the peak frequency and maximum frequency range with increasing age (Hammerschmidt et al., 1994).

As illustrated in ***Table 2.4***, some call types are produced in different situations. For instance, tonal calls are uttered by females that are threatened as well as by females in search of their infant. Likewise, pants are given as vocal threats during agonistic encounters, but also during social play and when individuals observe infant-handling interactions, both affiliative situations. Therefore, in the study of Barbary macaques' vocalizations is important to consider the context in which these calls are produced and other accompanying behaviours, cues or communicative signals that help assign the call to a specific situation. Bearing that in mind, the selection of vocalizations used in this thesis was based on operational definitions of calls that may indirectly represent social learning opportunities by mirroring social affiliative bonds, in order to test for the role of communication interactions in social learning. Accordingly, I first used complex screams (***Table 2.4***) accompanied by searching behaviours (aid-recruitment calls, see below for further details) which may represent alliances established via social bonds between callers and recipients providing aid to them. I also used vocal comments (***Table 2.4***) defined as vocalizations not accompanied by any other behaviour when observing third-party interactions which may also mirror strong social bonds between callers and individuals observed (Whitham et al., 2007; see ***Part B*** in ***Chapter 4*** for further details).

Data on communication interactions were collected opportunistically during and between behavioural observations. During behavioural sampling sessions, each vocal behaviour was noted in the all-occurrence sampling sheet. Between behavioural observations, audio recording sessions of 5 minutes in duration were carried out to increase the likelihood of capturing vocal behaviours. For each communication event, I collected data on: (i) the identity of the caller or callers, (ii) the context in which the event occurred (i.e. agonistic or affiliative interaction, who initiated the interaction, and what happened), (iii) the identity of all individuals involved in the interaction, (iv) who responded to the vocalization and how, (v) the distance between the callers and the other individuals involved and (vi) the location in the enclosure where the event took place. More details on the data collection methods used for communication networks are found in section ***4.2. Methods*** in ***Chapter 4***.

2.3.3. Social networks

Values of the strength of connections for weighted networks (see below) were calculated in R and coded into adjacency matrices. These matrices were used to visualize the networks using the software NetDraw.

Association networks

During scan samples, data on proximity between individuals was collected and used to build two association networks: *proximity between individuals within a 1m radius* and *proximity between individuals within a 5m radius*. These two measures of social proximity were chosen to represent two different social contexts in which social information can be transmitted. The level of social tolerance required when proximity is restricted to 1m is expected to be higher than when associations up to 5m are considered and may represent contexts of directed and non-specific social learning (Coussi-Korbel & Fragaszy, 1995). Even though data on proximity up to 10m was collected in BDG, the dense vegetation in Trentham Forest limited visibility to 5m. Therefore, in order to compare both groups, 5m was chosen as the maximum distance to calculate association networks.

Both networks were undirected which means that proximity relations were considered to be symmetric: when individual A was in proximity (at distance X) of individual B, individual B was also in proximity (also at distance X) of individual A. Also, both networks were weighted, meaning that the strength of the social relation (a.k.a. the edge weight of the network) was calculated and represented in the network. Edge weights were calculated using the Simple Ratio Index (SRI):

$$SRI = \frac{x}{x + yAB + yA + yB}$$

where x is the number of sampling periods with A and B observed associated, yAB is the number of sampling periods with A and B identified but not associated, yA is the number of sampling periods with only A identified and yB is the number of sampling periods with only B identified (Whitehead, 2008). Each 5-minute recording session was considered a sampling period. The SRI estimates the proportion of sessions that two individuals (a dyad) have been seen in proximity, and it is weighted by the total number of sessions both individuals have been observed (together or not). Therefore, SRI measures the extent to which each dyad deviates from other dyads in terms of sessions spent in proximity, and it varies between 0 (the dyad has never been observed associated) and 1 (the dyad has always been observed associated).

Interaction networks

Grooming and huddling interactions collected during focal and all-occurrence samplings were used to build interaction networks. SRI was used to calculate edge weights in both networks. Huddling networks were considered symmetric: when two or more individuals gather and enter in physical contact to form a huddle (see ***Table 2.3***), all the individuals in the huddle are huddling with the each other. Grooming, however, is a behaviour that is directed from one individual to another: A grooming B does not always imply that B is grooming A. Two individuals can be grooming each other at the same time, but that is not frequent. Generally, one individual acts as the groomer (the individual that performs the act of grooming) and the other individual acts as the groomee (the individual that receives the act of grooming). Thus, grooming networks were constructed to represent the directionality of the social behaviour (i.e. who grooms whom).

Communication networks

Two types of vocalizations collected during behavioural samplings and audio recording sessions were used to build a total of seven networks. All networks were weighted and directed. SRI was used in all cases to calculate edge weights.

The first type of vocalization used was the so-called aid-recruitment call. These calls are produced in agonistic contexts and it is thought that they function to recruit allies that provide support during a conflict (Goodall, 1968; Fischer & Hammerschmidt, 2002). Three networks were built using data from aid-recruitment events to understand what and who triggers these calls, who the calls are directed to and what influences the response that other individuals provide to these calls:

- A network based on the relation between the caller (often, but not always the victim) and its opponent (often, but not always the aggressor). This network represents who calls after threats by whom.

- A network based on the relation between the caller and the individuals that provided support in the conflict (who provides coalitionary support to whom).

- A network based on the relation between those that provide support and the opponents (often, but not always aggressors) of those they provide support to (who provides coalitionary support against whom).

The second type of vocalization used was a group of calls that are referred to in the literature as vocal comments (Brumm et al., 2005). These calls are produced in both affiliative and agonistic contexts and occur when the caller is observing a third-party interaction in which he or she does not participate (Fischer & Hammerschmidt, 2002; Brumm et al., 2005). The function of these calls and who they are directed to are still not clear (Brumm et al., 2005, Whitham et al., 2007). Accordingly, four networks were built based on these vocalizations to depict all the possible relations that Barbary macaques can establish via these communication interactions:

- Two networks based on vocal comments produced during the observation of affiliative interactions (i.e. infant-handling events):
    - A network based on the relation between the caller and the adults involved in the third-party interaction.
    - A network based on the relation between the caller and the mother of the infant involved in the third-party interaction (mothers are not always involved in the event).
- Two networks based on vocal comments produced during the observation of agonistic encounters:
    - A network based on the relation between the caller and the aggressor in the conflict.
    - A network based on the relation between the caller and the victim in the conflict.

By analyzing these seven networks I can (i) have a better understanding of the nature of the communication interaction in each case, and (ii) better define between which individuals the communication interaction is relevant in order to investigate the type of relationship that dyads establish through communication interplays and how these relations may contribute to describe opportunities for social learning. For further details on the usefulness of these networks for the scope of this thesis, refer to ***Chapter 4***.

Aid-recruitment calls and vocal comments are assumed to be relatively common in macaques since they allow the collection of a few hundred of observations in short-term studies (i.e., less than 6 months of data collection; Silk, 1999; Brumm et al., 2005). Also, both vocalizations are reported in both sexes and in individuals of different age classes in macaque species (Gouzoles & Gouzoles, 1990, 1995; Silk, 1999; Brumm et al., 2005). However, detailed information on the frequency of these behaviours or class-related preferences (in terms of age, sex or other individual attributes) are not available in macaque literature (but see ***Chapter 4*** for detailed information on these measures in Barbary macaques, using the data collected in this thesis).

Observation networks

Data on who observes whom during successful task manipulations were used to build two observation networks for each task: a network based on *observation events within 1m distance from the task* and a network based on *observation events within 5m distance from the task*. As with association networks, these two measures of distance in the observation networks were chosen to represent different contexts, each requiring a different level of social tolerance between dyads that may result in different patterns of social information transmission.

Observation networks were all directed because knowing who observed whom manipulating the task is important in determining who is likely to learn from whom. Even though data on who observes whom during each task manipulation was collected in BDG, this level of accuracy was not achieved for the experimental sessions in TG, where data were only reliable at the bout level (a bout started when an individual entered the task area and ended when the same individual left the task area, see ***Appendix G*** for further details). The number of bouts was not sufficient to obtain accurate measures of the strength of relations of observation networks in TG, so edge weights were not calculated for the observation networks in this group. Instead, the connections between individuals in the observation networks of TG represent that, at least, one observation event was recorded for that dyad (i.e. unweighted network). In the adjacency matrix used to build these networks, therefore, values could only be 0 or 1, where 0 indicated that the individual in the row never observed the individual in the column solving the task and 1 indicated that the individual in the row observed one or more successful manipulations from the individual in the column. For BDG, weighted and unweighted observation networks were calculated.

Node attributes

Nodes in the networks represent individuals. Node (individual) attributes are relevant in Social Network Analysis (SNA) to describe the social structure or patterns of relations observed in the networks (Croft et al., 2008). Also, node attributes are useful to control for individual-level biases in social learning (Coussi-Korbel & Fragaszy, 1995; Franz & Nunn, 2009).

In the present study, I used sex, age, social rank and kinship as individual attributes in all networks. The sex and age of each individual was provided by the park staff in Trentham Monkey Forest and Blair

Drummond Safari Park. Data on kinship were only available for TG. Social ranks were determined using data on agonistic and submissive interactions using hierarchic and network-based ranking methods (see ***section 2.4.1.*** and ***Appendix A***).

2.4. Statistical analyses

Here, I give a brief presentation of all the statistical analyses conducted in the thesis. Further details can be found in the relevant chapter (***Chapters 3 – 5***). In all cases, only data on adults, sub-adults and juveniles were considered. Individuals < 3 years old were excluded from all the analyses due to the impossibility of identify them in TG.

Calculations of all measures and all statistical analyses were performed in R, unless indicated otherwise. All p-values obtained in multiple-comparison analyses were adjusted using Benjamini-Hochberg correction with a False Discovery Rate (FDR) = 5%. All p-values were considered significant when $p < 0.05$.

2.4.1. Social rank analysis

Social or dominance ranks were based on data collected during two types of agonistic encounters: agonistic competitions and instances of formal dominance. In agonistic competitions, an individual directs an agonistic behaviour towards a conspecific who responds with agonism (see ***Table 2.3***), and the conflict is resolved with one of the participants (the loser) showing submission towards the other (the winner). In formal dominance, the individual that receives the agonistic behaviour avoids confrontation with the aggressor and immediately responds with submission (see ***Appendix A*** for further details). For both BDG and TG, data on agonistic encounters were collected during and outside task introductions.

Social ranks were calculated following the guidelines provided by Funkhauser et al. (2018). Accordingly, five different methods were used to calculate and compare dominance ranks: three methods assuming a linear hierarchy structure (I&SI method, David's scores and Elo-ratings) and two network-based methods that analyse dominance without underlying structural assumptions (ADAGIO and PERC). The **I&SI method** is based in the re-organization of individuals by minimizing the number of inconsistencies (I) and the total strength of inconsistencies (SI) in a matrix of dominance relations (de Vries, 1995, 1998; Schmid & de Vries, 2013). For my analyses, I used the improved I&SI method (Schmid & de Vries, 2013) and the improved Landau h' test of linearity (de Vries, 1995) (see ***Table A.1.*** for further information). **David's scores** derives a dominance index based on the overall success of each individual and the relative strenght of its opponents by calculating the proportion of wins over losses in a matrix of agonsitic encounters relative to the total number of observed interactions and corrected for chance occurrences of observed outcomes (David, 1987; Gammell et al., 2013).

Elo-ratings is a non-matrix based technique to determine dominance ranks that also assumes a linear structure of the dominance hierarchy (Albers & de Vries, 2000). The Elo-rating method provides sequential estimations of individual dominance strengths based on the actual sequence of dominance interactions and it is based on the assumption that the chance of individual A winning B is a function of the difference in current ratings of the two contestants. Therefore, the Elo-rating method updates the rating of each individual after each contest based on the probability of winning that contest (i.e. current rating) and the actual outcome (Albers & de Vries, 2000; de Vries, 2009).

ADAGIO uses dyadic dominance relationships to extract a dominance hierarchy in the form of a directed acyclic graph (DAG) for a given dominance network. A DAG is a network free of cycles meaning that there is no path (connection) from one node (individual) back again to the same node (Douglas et al., 2017). **PERC** infers dominance potential probabilities (rank potentials) for all individuals using pairwise interactions drawned from dominance networks, and assigns social ranks by minimizing inconsistencies in rank potentials and computing confidence bounds for ratings represented via heat maps (Fushing et al., 2011). Further information on calculations of the methods can be found in ***Appendix A***.

Social ranks were derived from each of the five ranking methods. Spearman rank correlations with Benjamini-Hochberg corrections were used to determine the reliability across rankings provided by the different methods (Funkhauser et al., 2018). Funkhauser et al. (2018) suggested that this comparative approach across different ranking procedures is preferred over investigations where only one or few metrics and statistical analyses are considered because it accounts for variability and inconsistencies between behavioural measures and ranking methods. In addition, Funkhauser et al. (2018) stated that the calculation of median ranks across the different ranking methods when reliability across ranking procedures has been confirmed, minimizes errors in the ranking order and allows conservative interpretations with minimal data. Accordingly, social ranks of both groups were established using median ranks across the outcomes of different methods (reliability across procedures was confirmed, see ***Appendix A*** for results and further details).

For BDG, rankings were obtained using data on agonistic encounters outside task introduction times. However, the big size of TG (N = 56) and the characteristics of the environment that hindered field observations of dyadic interactions returned an incomplete and insufficient dataset on dominance relations outside task contexts. Therefore, data on dominance relations for the calculation of social ranks in TG was completed with observations of agonistic displays collected during task introductions. However, data collected on different agonistic contexts (outside versus during task introductions) may lead to biased dominance ranks (Funkhause et al., 2018). To ensure this was not the case, I repeated all the hierarchy analyses in BDG using agonistic data collected only in task introductions contexts and compared the resulting ranks across both contexts (outside and during task) in this group (for further details see ***Appendix A***).

Social ranks were used in the thesis in the form of ordinal social ranks or categorical social ranks. Ordinal social ranks are directly the median ranks across ranking methods, as stated above. Categorical social ranks were based on ordinal social ranks and calculated using Jenks Natural Breaks Classification. Jenks Natural Breaks Classification is an optimization method designed to determine the best arrangement of a set of values into different classes or categories (Jenks, 1967). In this case, the method uses social ranks established via hierarchical analyses and finds the best arrangement to split the ranks into a pre-defined number of classes (i.e., high, middle and low ranking classes). This is done by minimizing the average deviation from the class mean (i.e., reducing the variance within classes) while maximizing the deviation from the means of the other classes (i.e., maximizing the variance between classes). The method is commonly used in studies of animal dominance ranks (Foerster et al., 2016; Bray & Gilby, 2020; Bray, 2021).and already implemented in R packages for hierarchical analysis (Feldblum et al., 2021).

2.4.2. Inter-observer reliability

Cohen's Kappa was used to measure inter-observer reliability for: a) data on social behaviours collected during observational sessions, b) data on task manipulations and who observes whom collected during experimental sessions.

Fleiss et al. (2003) stated that:

- Values of Cohen's Kappa > 0.75 represent excellent agreement beyond chance.
- Values of Cohen's Kappa < 0.40 represent poor agreement beyond chance.
- Values of Cohen's Kappa between 0.40 and 0.75 represent fair to good agreement beyond chance.

Another logical interpretation of Cohen's Kappa was suggested by McHugh (2012) and can be found in ***Table 2.5.*** Both interpretations (Fleiss et al., 2003; McHugh, 2012) were considered to assess the levels of inter-observer reliability.

Table 2.5. Cohen's Kappa interpretation of levels of agreement proposed by McHugh (2012).

Value of Cohen's Kappa	Level of agreement	% of data that are reliable
0 – 0.20	None	0 – 4%
0.21 – 0.39	Minimal	4 – 15%
0.40 – 0.59	Weak	15 – 35%
0.60 – 0.79	Moderate	35 – 63%
0.80 – 0.90	Strong	64 – 81%
> 0.90	Almost Perfect	82 – 100%

The column "% of data that are reliable" corresponds to the squared value of Cohen's Kappa, an equivalent of the squared correlation coefficient, which is directly interpretable.

2.4.3. Adequacy of data

Whitehead (2008) recommends that once social network data has been collected, datasets for each social network should be described in terms of a series of attributes (see ***Table 2.6***). These attributes help allocate datasets into general types to explore whether they are sufficient to analyse the social structure of the studied population (Whitehead, 2008).

Table 2.6. Dataset attributes suggested by Whitehead (2008) analysed in this study.

Attribute	Description
Size of study population	Small, < 20 individuals; Intermediate, 21 – 100 individuals; Large, > 100 individuals
Rate of identification	Sparse, < 10% of study population; Intermediate, 10 – 80% of study population; Complete, > 80% of study population
Number of sampling periods during which a dyad is observed associated	Few, < 1 mean observed association/dyad; Some, 1 – 10 mean associations/dyad; Many, > 10 mean associations/dyad
Associations per individual	Few, < 10 mean associations/individual; Some, 10 – 100 mean associations/individual; Many, > 100 mean associations/individual
Length of dataset	Short, < 20 sampling periods; Medium, 20 – 100 sampling periods; Long, > 100 sampling periods.

The results and a more detailed description of this preliminary inspection for each of the datasets can be found in ***Appendix C***. Datasets with few observations per dyad were considered sparse. Sparse datasets are common in animal networks (Croft et al., 2008; Whitehead, 2008), but caution must be taken since they may lead to uncertainty in the strength and the existence of dyadic relations and, therefore, they may not be representative of the underlying social structure of the population (Farine & Strandburg-Peshkin, 2015).

Following the guidelines proposed by Farine & Strandburg-Peshkin (2015), bootstrap and Bayesian methods were used to assess the levels of uncertainty in estimating the strength of network connections (i.e. edge weights) between dyads for each data set. The non-parametric bootstrap re-samples the sampling periods of the original raw data to generate new datasets for which edge weights are calculated. By generating 1000 bootstrapped datasets, we obtain a distribution of the possible values of the edge weights of each dyad. Then, the observed edge weight values are compared with the bootstrapped values to calculate a series of measures of precision and accuracy. However, bootstrapping methods may underestimate uncertainty and lead to biased estimates when the sample size is very small, as is common in the case of animal social networks (Farine & Strandburg-Peshkin, 2015). For instance, if two individuals have only been observed interacting or associated once, the edge weight value in the bootstrap sample will be either 0 or 1 and the method will conclude that the uncertainty around this estimate is 0. The Bayesian approach has proven to be useful in addressing this problem (Farine & Strandburg-Peshkin, 2015). As in the bootstrap method, a distribution of edge weight values is generated from the observed data. The inferred distribution of edge weight values was obtained using the maximum-likelihood estimation, as done in Farine & Strandburg-Peshkin (2015). This distribution captures the most likely value of the edge weight and the uncertainty around it. For both bootstrap and Bayesian methods, 95% confidence intervals were estimated. A third approach to calculate 95% confidence intervals, the Clopper-Pearson method, was also used (Farine & Strandburg-Peshkin, 2015).

The approach suggested by Farine & Strandburg-Peshkin (2015) calculates edge weights using the simple ratio index (SRI). In order to evaluate the level of uncertainty of each dataset, three measures of precision and accuracy were calculated for each method: a) the absolute error (absolute difference between the mean of inferred edge weights and the mean of observed edge weights), b) a measure of relative accuracy (mantel rank correlations between inferred edge weights and observed edge weights) and c) the precision of uncertainty estimates: the rate of underestimated values (where observed values lie below the estimated 95% interval of the inferred networks) and the rate of overestimated values (where observed values lie above the estimated 95% interval of inferred networks). Bootstrap and Bayesian analyses were adapted from the R codes provided by Farine & Strandburg-Peshkin (2015) and used to calculate uncertainty of the weighted networks (grooming, huddling and proximity in both groups, and communication and observation networks in BDG).

An extra measure was calculated for association networks: social differentiation. When two or more individuals are found in proximity of each other, we assume that they are in a situation in which interactions usually take place (Whitehead & Dufault, 1999). However, this does not mean that the subjects will ever interact or that the association we observe is a real indication of a social bond between the two individuals (Whitehead, 2008). Therefore, association data differs from interaction data in that associations can occur by chance and, consequently, the estimated relationship measures will likely have errors. Whitehead (2008) developed a measure called social differentiation that indicates how homogenous the relationships in the population are. Social differentiation is the coefficient of variation of the true association indices calculated using a maximum-likelihood approach and it was calculated for all association networks using the software SOCPROG. Whitehead (2008) also estimated the quantity of data required (in terms of mean number of observed associations per dyad) for different levels of social differentiation (see ***Appendix C***). Based on these calculations, I can determine if the association network is a good representation of the social structure of the population or I need more observations to overcome the biases associated with this type of data (Whitehead, 2008).

Finally, before interpreting if a network is more conducive to non-specific, or directed, social learning, it is necessary to rule out the possibility that the social structure or patterns of relations observed are the result of random interactions or associations (Whitehead, 2008). Bejder's permutation tests were used to determine whether individuals had preferred or avoided companions or, conversely, social relations were randomly established (Whitehead, 2008). The Bejder's or MBFB permutation test uses the original data to create a series of randomized networks that preserve the number of identifications in each sampling period and the number of identifications of each individual (Bejder et al., 1998). Given that the method keeps constant these constraints, the data structure is not altered during the permutation procedure (Whitehead, 2008). By comparing the same statistic between the observed and the randomized networks, the test provides a measure of significance of the difference between both datasets. The statistic I used was the coefficient of variance of the association indices since it is easier to interpret and has the advantage of presenting a measure of effect size (Farine & Whitehead, 2015). A total of 10,000 permutations were carried out in each test.

2.4.4. Social Network Analysis

It is important to decide which social network measures are relevant to the research questions. In this case, I am interested in describing how the patterns of relations between individuals established through the social behaviours studied represent different patterns through which social information can be transmitted (Coussi-Korbel & Fragaszy, 1995). If individuals within a group are loosely connected with each other, the group is clustered or fragmented and/or social relations are asymmetric or heterogenous in terms of occurrence or strength, individuals are likely to learn via directed social learning (Coussi-Korbel & Fragaszy, 1995). If group cohesion is high, all individuals are connected with each other or form one single component and/or social relations are symmetric or homogeneous, social information will be likely acquired via non-specific social learning (Coussi-Korbel & Fragaszy, 1995). Within this framework, I chose a series of SNA metrics that would help me describe the social organization of the groups of Barbary macaques in terms of (i) group cohesion, (ii) level and patterns of connectivity between individuals and (iii) homogeneity or symmetry of social relations.

A description of all the SNA metrics used in this thesis can be found in ***Table 2.7.*** Eight group-level SNA metrics (i.e. measures calculated for the whole network) were chosen: density, component ratio, average degree, clustering coefficient, flow betweenness network centralization index (NCI), skewness, disparity and assortative mixing (***Table 2.7***). Three individual-level metrics (i.e. measures calculated for each individual) were also used: degree centrality, eigenvector centrality and flow betweenness. For further details on how these metrics were used to respond to specific research questions, refer to ***Chapters 3 – 5***.

Table 2.7. SNA measures based on definitions by Croft et al. (2008), Whitehead (2008) and Kasper & Voelkl (2009).

Parameter	Description	Network attribute
Density (U)	The number of connections (edges) present in our network divided by the total number of possible connections. All possible edges = N(N-1) for directed networks and ½ N(N-1) for undirected networks (N = group size). Values closer to 1 indicate that all the individuals are fully and directly connected to others. Lower values indicate that the network is sparse (i.e. not all the possible connections occur).	Group cohesion
Component ratio (U)	Measures whether the network consists of a single component or it is fragmented into smaller components or isolated nodes. Two individuals belong to the same component when there is a path connecting them directly or indirectly (via another node).	Group fragmentation
Average degree (U & W)	Average unweighted degree calculates the average number of connections of the nodes (i.e. with how many individuals each node is connected to on average). Average weighted degree is the average strength of the nodes' connections in the network.	Degree of connectivity
Node strength & skewness (W)	Node strength for each node is the sum of the products of the number of connections and the corresponding edge weight of all dyadic connections this node has been involved with. Skewness is a measure of the distribution of node strength. A positively skewed distribution indicates that only a small number of individuals have many and strong interactions. A negatively skewed distribution	Heterogeneity of the group

	suggests that a relatively high number of individuals have many and strong connections with others.	
Edge weight distribution & disparity (W)	Measures the level of heterogeneity of the strength of social relations. The shape of the edge weight distribution indicates whether all interactions in a group are equally strong or there are pronounced differences. If skewed, most of the interactions are strong (negatively skewed) or weak (positively skewed). Disparity (Y) is a measure of the skewness of this distribution. If all the weights are of the same order, Y ~ 1/(N-1), the edge weight distribution is homogenous; otherwise, it is heterogeneous and some social relations dominate over others. The inverse of disparity is a measure of the number of important edges with high weights.	Heterogeneity in the strength of interactions
Clustering coefficient (U & W)	Clustering coefficient evaluates the extent to which nodes adjacent to other nodes in the network are also adjacent to each other. For each node, it measures the density of its open neighbourhood (i.e. a subset of the network that consists of all the nodes connected to the node of interest), so it is a measure of local cliquishness (i.e. if some nodes are more strongly connected to their neighbours than others). For a weighted network, it calculates the weighted overall clustering coefficient (mean of clustering coefficients of nodes each one weighted by the node's degree). Clustering coefficient gives a measure of the extent to which there are areas of high and low density of connections within the network. The higher the average clustering coefficient, the quicker the transmission of information through the network (Croft et al., 2008). Average clustering coefficients of 1 indicate tight, closed and homogenous social units (all individuals connected in one cluster) while values near 0 occur in strict territorial societies where individuals only associate with their neighbours who may not associate with each other (Whitehead, 2008).	Local cliquishness
Flow betweenness (U)	A measure of the role or contribution of a node to all information flows possible. High flow betweenness indicate nodes that have a central position in the flow of information within the network and are important brokers in group-wide information transmission. Flow betweenness Network Centralization Index (NCI) is a measure of connectivity for the entire group (Borgatti et al., 2013) and can be	Contribution to and speed of information flow

	compared between groups and across different social networks. It is a measure of how fast information can flow throughout the network, so that high values of NCI would indicate that information is unevenly distributed, more centralized (coming from a few specific individuals) and, therefore, the flow of information will be slower (Cepik & Möller, 2017). High flow betweenness also indicates that more individuals have to be removed to disconnect the nodes, so network flow is also a measure of the resilience of network connectivity (Kasper & Voelkl, 2009).	
Centrality Degree (U & W)	This is a measure of the level of centrality of each node in the network. For unweighted networks, it measures the number of nodes connected to each node. For weighted networks, it is the sum of the strength of the ties connected to that node. If networks are directed, it measures in-degree (ties received) and out-degree (ties initiated) for each node. High values of centrality degree indicate that the node is central in the network. Depending on the behaviour, in- and out-degree centrality might indicate privileged roles in the network.	Centrality of nodes Privileged roles
Eigenvector centrality (U & W)	A measure of how well connected an individual is based on both (i) the number of nodes connected to that individual and (ii) the centrality degree of the nodes connected to that individual.	Centrality of nodes
Assortative mixing	This measures whether nodes of a certain class (age, sex, social rank or kinship) are more connected to individuals of the same class (homophily) or individuals of a different class (heterophily). It is calculated using the E-I index (see ***section 2.4.7***), which is the number of ties external to the class minus the number of ties internal to the class divided by the total number of ties. Values close to 0 indicate that the number of connections is similar within and between classes. Values between 0 and -1 indicate homophily (strongest connections between members of the same class; within class assortative mixing). Values between 0 and 1 indicate heterophily (strongest connections between members of different classes; between class assortative mixing). However, a value of 0 does not represent random interactions or the absence of preferred partners, since the occurrence of assortative mixing depends on the network density and the ratios of classes. Therefore, to detect assortative mixing and obtain p-values it is necessary to run	Heterophily of relations by class

	randomization tests to compare the observed results with what would be expected by random mixing (Scott & Carrington, 2011). The E-I index can also be calculated for weighted networks (Danchev & Porter, 2018).

U = unweighted. W = weighted.

2.4.5. Network-based diffusion analysis (NBDA)

This analysis was used to determine if individuals socially learned how to solve the tasks described in ***section 2.2.2.*** NBDA requires three main types of data: a) the order or time of acquisition of the novel trait, b) a social network that describes the association or interaction patterns of individuals and, therefore, represents the opportunities that they have to learn from each other (Coussi-Korbel & Fragaszy, 1995), and c) a series of individual-level attributes that can control for learning biases (e.g. sex, age, social rank, kinship, level of neophobia or monopolisation of the task, etc.; see ***Chapter 5***). Using these data, NBDA generates and compares two agent-based models. One model assumes that the order/time in which individuals learned the new trait was irrespective of the strength of their connections to others, and controls for the individual-level attributes provided (the ***purely asocial learning model***). A second model assumes that the strength of connections between individuals (provided by the social network used to inform the analysis) influenced the diffusion of the novel trait, so that social and asocial learning processes are taking place at the same time (***asocial + social learning model***).

Before an individual acquires the new trait, the analysis considers this agent (individual) as naïve. Once the individual has acquired the trait, the agent is considered skilled or knowledgeable. If social learning is playing a role in the diffusion of the novel trait, then the stronger the connection between the naïve and the knowledgeable individual, the more likely the information is to spread between them. NBDA fits both agent-based models (***purely asocial*** and ***asocial + social***) to the observed data and uses maximum-likelihood approaches to determine which of the two models better explains the observed diffusion of the novel trait. The asocial model sets the social parameter (*s*) – a parameter that determines the strength of the social transmission – to zero. In the asocial + social learning model the *s* parameter is a function of the individual-level factors included and the strength of connections of the social network used to inform the analysis. Evidence for social transmission occurs when the model that includes the *s* parameter has a better fit. The Akaike Information Criterion (AICc) is used to determine which model provides a better fit. Enough evidence of social transmission is said to have occurred when the asocial + social learning model has an AICc at least, 2 units lower than the purely asocial learning model.

The order or time of acquisition of the trait is used to quantify the rate of diffusion of the trait. When order of acquisition is used, the NBDA analysis is named *order of acquisition diffusion analysis* (OADA), and when time of acquisition is used, it is referred to as *time of acquisition diffusion analysis* (TADA). Both analyses have pros and cons. TADA is sensitive to the asocial rate of acquisition but it is more powerful than OADA, so TADA is preferred when the baseline rate function can be easily modelled. In contrast, OADA does not make assumptions about the baseline (asocial) rate of acquisition of the trait so this analysis is preferred when the baseline rate function is difficult to model (e.g. it fluctuates according to unmeasured environmental conditions, Hoppitt & Laland, 2011). When there are "fluctuating variables influencing the rate of acquisition that affects all individuals equally" or when it is believed the diffusion of the trait will have a curved shape that is difficult to model (such as a stepped curve), then OADA is preferable to TADA (Hoppitt et al., 2010, p. 548). This might occur when knowledgeable individuals block naïve individuals' access to the task, for instance, by monopolising or depleting the resource, or when individuals adopt scrounging strategies instead of attempting to solve the task. I observed some instances where individuals monopolised the task even when they were not interacting with it, or left the task area when they emptied the task, causing other individuals to attempt to solve the task unsuccessfully before it was refilled. Accordingly, I opted to run both TADA and OADA. For further detailed discussion of the NBDA analysis see ***Chapter 5***.

2.4.6. Permutation-based mixed models

To understand the links between social dynamics, communication and social learning, I investigated how the patterns of social relations established through affiliative and communication events and the patterns of social diffusion of information observed during task introductions predict each other. I ran permutation-based mixed models, where a pair of networks was compared: one of the networks was entered as a dependent matrix and the other one as the independent matrix. For instance, to understand if affiliative relations predict communication interactions, data used to build the affiliative network were entered as the independent matrix and data for the communication network were entered as the dependent matrix. If the dependent network was weighted (i.e. values were continuous because they represent the strength of relations between pairs of individuals), I used linear regression models. If the dependent network was unweighted (i.e. values were categorical because they represent the existence, "1", or absence, "0", of relations between pairs of individuals), I used logistic regression models.

Each model was informed with other independent variables or fixed effects (i.e. individual attributes such as sex, age, social rank and kinship) and random effects (i.e. individual identity was used to control for the number of observations, a confounding factor that may bias effect sizes and hinder the interpretation of results, Hardy & Briffa, 2013; Franks et al., 2021). Different models (different combinations of fixed and random effects) were tested for the same pair-wise matrix comparison and the Akaike Information Criterion (AIC) was used to determine which model better explained the data. Variance Inflation Factor (VIF) was used to determine the collinearity of the variables before each regression. A VIF measure of >4.0 indicated that variables were highly correlated and, therefore, explained the same variance (Hair et al., 2010).

The best model was used for regressions with the observed networks and each permutation of the dependent matrix. A total of 10,000 permutations were run for each pair-wise network comparison. Results of the regressions with the permuted matrices were used to build random distributions of the regression coefficients of each variable that were compared with the regression coefficients obtained with the original dependent matrix in order to calculate p-values. P-values represented the probability that the regression coefficients (for the independent variables) obtained with the permutations of the networks were greater than the observed regression coefficients obtained with the original networks. Regressions were run to test whether (i) affiliative networks predict each other (see ***Chapter 3***), (ii) affiliative networks predict communication networks (see ***Chapter 4***) and (iii) affiliative and communication networks predict observation networks during task introductions (see ***Chapter 5***).

2.4.7. Other inferential statistics

The social structure or patterns of relations observed in each network were compared between networks and macaque groups using the SNA metrics described in ***Table 2.7.*** For some of these comparisons, the differences found in the SNA measures between networks were tested for significance. For individual-level SNA metrics, Spearman's rank correlations were used. For SNA metrics calculated at the group-level, a bootstrap procedure, analogous to the classical paired-sample t-test was used to obtain p-values of the differences in the SNA measures between networks (Snijders & Borgatti, 1999). The procedure calculates a bootstrap sample of each network of a pair and estimates the difference for each SNA metric of the re-sampled networks. This is repeated 5,000 times to obtain a bootstrapped distribution of estimates. Since the bootstrap distribution is based on the observed networks, it is centred on the observed difference rather than the theoretical expected value (usually, zero). Therefore, the mean of the bootstrap distribution from each bootstrap difference score is subtracted. Finally, the procedure counts the proportion of mean-centred bootstrap samples that yield an absolute difference as large as the absolute difference observed (p-value). Further details of when and why these tests were used can be found in ***Chapters 3 – 5***.

Assortative mixing was measured using the E-I index (see ***Table 2.7***):

$$E - I\ index = \frac{E - I}{E + I}$$

where *E* is the number or the strength of external connections and *I* is the number or strength of internal connections. If E-I index is calculated for unweighted networks, we use the number of external and internal connections. If E-I index is calculated for weighted networks, we use the strength of external and internal connections. External and internal connections are defined by the specific variable for which we want to measure assortative mixing (i.e. preferred partners). For instance, if we want to measure assortative mixing for sex, external connections will refer to relations with those of a different class (i.e. different sex) while internal connections will refer to relations with those of the same class (i.e. same sex).

E-I index for sex, age and social rank was measured for each network as a whole and for class subsets of the networks. For instance, E-I index for sex was measured considering all the external and internal connections for both classes (males and females) simultaneously (whole network) and for each of these classes (e.g. for females, male-male interactions were removed to calculate the E-I index and only female-female and male-female dyads were considered). Kinship was only measured for the whole network and not for each of the several matrilines.

E-I index was calculated for both weighted (W) and unweighted (U) versions of the networks (Danchev & Porter, 2018). Since E-I index may vary depending on group size, network densities and class ratios (Krackhardt & Stern, 1988; Borgatti et al., 2013), it is not possible to establish a general threshold to assess the level of significance of the measure. A randomization procedure was used to calculate a random distribution of E-I index values from the observed data. A total of 5,000 random measures were obtained and compared with the observed result to calculate p-values. If the probability (p) to obtain the observed result by chance was <0.05, I considered the observed measure as significant. The randomization procedure was used to determine if the results of assortative mixing (***Table 2.7***) were significantly different from what would be obtained if interactions or associations were arbitrary, as well as to discuss whether individuals showed the same patterns of preferred companions in all networks.

A chi-square goodness-of-fit analysis was conducted to test whether individuals in the group showed a preference for one of the two available options to solve each of the tasks (see ***Chapter 5*** for further details). Finally, Kruskal-Wallis rank sum tests and post-hoc Dunn tests were used to compare different measures between groups or contexts (more details can be found in ***Chapters 4 – 5***).

Chapter 3

The social learning context: social dynamics of affiliative and agonistic relations

Abstract

In this chapter, I aim to describe the patterns of social learning that can be predicted from social contexts in two groups of Barbary macaques. A species with intermediate-to-high levels of social tolerance like Barbary macaques is expected to display both symmetric and asymmetric relations, each resulting in different patterns of social information diffusion (i.e. directed through particular partners or non-specific). Here, I use social network analysis within a theoretical framework presented by Coussi-Korbel & Fragaszy (1995) to: a) describe and compare a series of socio-positive networks, b) make predictions about the social learning opportunities that may arise from these networks, c) determine what individual attributes may influence the transmission of information in a social learning context. Confirming predictions, networks based on grooming, huddling and proximity within 1m were similar in their social structure and depicted asymmetric social relations, with individuals showing partner preferences influenced by sex, age, social rank and kinship. As predicted, results indicate that relations based on grooming, huddling and proximity within 1m depict opportunities to learn from particular conspecifics (i.e. directed social learning). Networks based on proximity within 5m significantly differed from the other networks and resulted in more symmetric relations, confirming the expectation that where less tolerance of proximity is required, transmission of information will be less influenced by the identity of individuals (i.e. non-specific social learning). A network combining different affiliative behaviours may be more representative of socio-positive relations and, therefore, more informative of social learning opportunities than networks based on single affiliative behaviours.

Cara Evans (CE) and Mallory Owen (MO) collected social network data on one of the groups: TG.

3.1. Introduction

Primate societies can be classified along an axis usually described as running from egalitarian to despotic based upon the dynamics of social interactions (van Schaik, 1989). Despotic societies are characterised by strict hierarchies, well-defined unilateral dominant-subordinate relations and few but violent aggressive interactions (Matsumura, 1999; Lehmann & Bryson, 2008). Compared to despotic societies, egalitarian species present less well-defined hierarchies, frequent but less violent agonistic encounters, a greater symmetry in contests (i.e. more counter attacks) and higher rates of affiliation and post-conflict tension-reducing contacts (Matsumura, 1999; Lehman & Bryson, 2008). Egalitarian societies are, therefore, characterised by higher levels of social tolerance than despotic species (Coussi-Korbel & Fragaszy, 1995; Matsumura, 1999; Thierry, 2004; Lehman et al., 2005).

Coussi-Korbel & Fragaszy (1995) presented a theoretical framework that links social dynamics and social tolerance with the diffusion of information within animal societies. According to this theory, behavioural coordination in space (for which individuals must tolerate others in proximity) and/or time between individuals increases their opportunities to learn from one another. Visual attention is required for behavioural coordination and any bias in individuals' attention towards particular conspecifics increases the likelihood of acquiring information from those particular individuals (Coussi-Korbel & Fragaszy, 1995). Moreover, social bonds, sex, age, kinship and/or social rank influence attention biases in animals, including macaques (Coussi- Korbel & Fragaszy, 1995; Micheletta, 2012). Consequently, individual attributes and the dynamics of affiliative social behaviours may also affect the likelihood of acquiring social information in a learning context (Coussi-Korbel & Fragaszy, 1995). In this case, any apparent learning biases could be a by-product of social dynamics and not representative of a social learning strategy, such as "copy dominant individuals" (Kendal et al. 2015).

Coussi-Korbel & Fragaszy's (1995) model allows researchers to make predictions about the patterns of social learning observed based on the levels of social tolerance displayed by a group of animals. The authors defined two main patterns of social diffusion of information: directed and non-specific social learning. Directed social learning occurs when individual identity influences the social transmission of information. In contrast, in non-specific social learning, individuals may learn from any partner, irrespective of their individual attributes. In egalitarian societies, affiliative and aggressive interactions are evenly distributed between dyads and these high levels of symmetric relations within the group would result in the predominance of non-specific social learning (Coussi-Korbel & Fragaszy, 1995).

In despotic societies, the asymmetry of relations would be conducive to directed social learning, whereby information spreads through specific pathways in groups since social tolerance (enabling proximity for learning) is restricted to particular individuals with particular attributes (i.e. social tolerance is more likely to depend on individual factors such as sex, age, kinship or social rank). For species classified as intermediate in the despotic-egalitarian spectrum, such as Barbary macaques (Thierry, 2000, 2007; Rebout et al., 2017; Rosati & Santos, 2017) both directed and non-specific social learning may be found depending on the type of information that is being transmitted (Coussi-Korbel & Fragaszy, 1995). Those skills that require more behavioural coordination in space and time are more likely to be passed through directed social learning, while those that do not require a high degree of behavioural coordination may spread irrespective of individual identity.

By describing the complexity of the social structure and the factors that influence the patterns of social relations in the study population, we can outline the social context in which individuals can learn from each other (Coussi-Korbel & Fragaszy, 1995). Describing the social learning context is important to understand how information relevant to survival spreads within a group of animals (see ***Chapter 1***). Social network analysis (SNA) provides a set of analytic tools that permit the quantification of social relations and the description of a social structure (Croft et al., 2008). This analysis allows the study of the degree of symmetry of social relations that are conducive to either directed or non-specific social learning plus which individual attributes are influential regarding who may have the opportunity to learn from whom.

SNA offers a series of robust measures (see ***2.4.4. Social Network Analysis***) that help characterize the overall structure of a network of social relations and the specific pathways through which information may spread within a group of individuals (Croft et al., 2008; Whitehead, 2008; Kasper & Voelkl, 2009). Since affiliative relations are said to influence the social diffusion of novel information (Coussi-Korbel & Fragaszy, 1995), the use of social networks based on socio-positive behaviours (e.g. grooming) has been generalized in studies of social diffusion of information (Franz & Nunn, 2009; Kendal et al., 2010a; Hoppitt & Laland, 2013; Hobaiter et al., 2014). Affiliative networks are thought to represent opportunities for social learning (Coussi-Korbel & Fragaszy, 1995) and are, therefore, used to inform analyses that model the spread of novel behaviours in order to test for the occurrence of social learning, such as the Nework-based diffusion analysis (NBDA, Franz & Nunn, 2009; Hopitt & Laland, 2013, see ***2.4.5. Network-based diffusion analysis***). Moreover, SNA metrics can help us understand which individuals in the network are more relevant or contribute more to the diffusion of social information (Croft et al., 2008; Kasper & Voelkl, 2009).

Affiliative social networks can be based on either associations (e.g. proximity) or interactions (e.g. grooming, huddling) between individuals (Croft et al., 2008; Whitehead, 2008). Many authors argue that associations can be used as a proxy of interactions in the study of animal social networks (Croft et al., 2008; Whitehead, 2008; Farine, 2015). However, the assumption that proximity in space gives rise to an interaction has been rejected by some researchers who point out that individuals may associate in space for reasons other than to establish a social bond (Barton & Whiten, 1993; Flack et al., 2006; Pinter-Wollman et al., 2014; Castles et al., 2014; but see Feczko et al., 2015). In addition, individuals may interact via signals that do not require proximity or occur at distances beyond the range used in social network studies (Carter et al., 2015). Furthermore, the levels of social tolerance displayed in associations may vary with the proximity range considered.

Social tolerance is generally described as the probability that individuals can stay in close proximity during a competitive situation with little or no aggression (Schnöll, 2014). As we increase the distance range at which we measure associations, the probability of finding more association partners increases since resources would be more scattered and, consequently, the levels of competition to gain access to them are expected to be lower than when we consider a shorter range. Consequently, we might expect to find differences in the structure and the patterns of relations between networks based on affiliative interactions requiring close proximity (e.g. grooming, huddling) and those of proximity measured at a long range. The greater the distance considered between individuals, the higher the symmetry of relations and the less likely directed social learning would be (Coussi-Korbel & Fragaszy, 1995).

Barbary macaques are classified as intermediate (grade 3) in the 4-grade despotic-egalitarian spectrum for macaque species, in which social tolerance increases with grade (Thierry, 2007; Carne et al., 2011; Roubová et al., 2015; Rosati & Santos, 2017). Despite being a tolerant species, Barbary macaques show clear partner preferences in social relations. McFarland & Majolo (2011) found that close associations and social interactions (e.g. grooming) in Barbary macaques were asymmetric and particularly frequent in female-female dyads, with age similarity playing a significant role in close proximity associations. Roubová et al. (2015) found that grooming in Barbary macaques was positively correlated with measures of close proximity, with individuals preferentially grooming their kin and those of a higher social rank (in exchange for commodities such as tolerance or access to resources), except between females for which it was reciprocal between those of the same rank.

Other studies have also described high levels of asymmetry in the social relations of Barbary macaques. Molesti & Majolo (2017) termed the distribution of grooming relations as partner-specific in Barbary macaques. Campbell et al. (2018) found that the formation of huddles in Barbary macaques was not influenced by sex or social rank, but it was predicted by strong grooming interactions. Since huddling is a thermoregulation strategy in Barbary macaques, it is likely that grooming is exchanged for huddling (understood as a commodity), as has been suggested for other macaque species (Ueno & Nakamichi, 2018). The asymmetry of relations found for grooming, huddling and close proximity in Barbary macaques suggests that individual identity would be relevant in determining who learns from whom in this species (Coussi-Korbel & Fragaszy, 1995).

In this chapter I integrate Coussi-Korbel & Fragaszy's (1995) theoretical framework with Social Network Analysis (SNA) to describe the opportunities for social learning in two groups of free-ranging Barbary macaques. I focus on three types of socio-positive behaviours to describe the social learning context: grooming, huddling and proximity (measured at 1 and 5m), and include sex, age, kinship and social rank to control for individual-level biases influencing patterns of social information diffusion.

I hypothesise (Hypothesis 1) that the social structure (or patterns of relations) of proximity within 1m will be more similar to those of grooming and huddling than to those of networks based on proximity within 5m, each network suggesting different patterns of social diffusion of information (i.e. directed or non-specific social learning). I predict that networks based on grooming, huddling and proximity within 1m will result in asymmetric relations conducive to directed social learning (prediction a). In contrast, I expect that associations within 5m will depict symmetric relations conducive to non-specific social learning (prediction b).

Regarding what may impact visual attention in a social learning context, I investigate which social behaviours and individual attributes influence the relational patterns observed in each of the socio-positive networks. I hypothesise (Hypothesis 2) that networks based on close proximity, grooming and huddling will be highly correlated with each other, and that sex, age, social rank and kinship will be the main factors influencing the social structure of these networks. I predict that proximity within 1m will predict grooming interactions and that the strength of grooming relations will predict huddling networks (prediction a). I also predict that grooming interactions and proximity within 1m will mainly occur between related individuals and individuals of the same sex (females), same age (adults) and different social rank (prediction b). I do not expect that individuals show a preference for huddling partners in terms of individual attributes other than the social bonds they have established with their conspecifics via grooming interactions (prediction c).

3.2. Methods

3.2.1. Behavioural data sampling

Data were collected for two groups of Barbary macaques: one in Trentham Monkey Forest (TG, N = 56) and one in Blair Drummond Safari Park (BDG, N = 25). Behavioural data on TG were collected from June to September 2011 for a total of 76 days that resulted in 532 hours of fieldwork (time spent in data collection: range = 115 – 175 minutes per subject; median = 145 min per subject). TG consisted of 61 individuals: 22 adult males, 27 adult females, 5 sub-adult males, 2 sub-adult females and 5 infants. Data collection for BDG was carried out between March and August 2018 on a total of 46 days, involving 299 hours of fieldwork (time spent in data collection: range = 195 – 215 minutes per subject; median = 205 minutes per subject). During the study period, BDG included 29 individuals: 6 adult males, 13 adult females, 4 sub-adult males, 2 sub-adult females and 4 infants.

Data on three socio-positive behaviours were collected for both groups: grooming, huddling and proximity. Proximity was collected within 1 and 5m in both groups to represent different levels of social tolerance. Additionally, data on agonistic encounters were also collected for both groups to construct a dominance hierarchy and determine the social dominance rank of each individual (see ***Appendix A*** for further details). For definitions of the behaviours collected see ***Table 2.3.***

Sampling and recording rules for data collection slightly varied between TG and BDG due to differences in group size and environmental constraints. The high density of vegetation, the wide roaming area and the large group size of TG hindered the observation of non-focal individuals and limited the distance at which subjects were visible to the observers. In contrast, all individuals of BDG were generally in sight of the researcher most of the time. For TG, 5-minute focal follows were used to collect data on any instance of grooming and huddling involving the focal subject. Individuals within 5m of the focal individual were recorded using scan samples at 0 and 4 minutes, respectively. Group size made it impossible to collect all instances of proximity in a shorter time window (e.g. every minute). In BDG, focal continuous sampling was used to record instances of grooming and huddling, and proximity to the focal individual at 1m and 5m was recorded every minute using scan sampling. Agonistic interactions and submissive interactions between any subjects in the groups were collected on an all-occurrence basis. The three types of sampling methods were used simultaneously during the 5-minute focal follows. Proximity within 5m was chosen as the cut-off distance for associations in both groups due to the difficulty in locating and identifying individuals beyond this distance in TG.

In BDG a randomisation list with a sampling window of 5 individuals was used to randomly choose the focal subject on each session. Focal sampling started with the first subject encountered of the first window of five. For the following session, the sampling window would move down and the first individual found amongst the next five individuals listed was sampled, and so on. This procedure was repeated until all subjects were sampled. Completely randomised focal samplings were not possible for TG due to group size and the wide home range. Instead, focal follows were pseudo-randomised and balanced across individuals in TG for time of day. For both groups, the observer stood 5-10m away from the focal subject to avoid interruption or biasing of monkeys' behaviours. All the observations were made in the outdoor enclosures as the size of the indoor enclosures meant observation may not have been ecologically valid: proximity distances would be constrained, as well as the occurrence of target behaviours due to dominant individuals or competitors in the vicinity of the focal individual. Observational data were not collected during feeding times, weekends or holidays because the natural behaviour of the subjects was interrupted by the presence of a high number of public visitors.

3.2.2. Social networks

I used three measures of affiliation to portray relationships conducive to social learning: grooming, huddling and proximity. Simple Ratio Index (SRI; Whitehead, 2008, see ***section 2.3.2. Social networks*** in ***Chapter 2***) was used to calculate the strength (weight) of relations between pairs of individuals for all the four types of networks produced (two interaction networks for each group: grooming and huddling; two association networks for each group: proximity within 1m and proximity within 5m).

To aid comparisons among behaviours, all SNA metrics were calculated for undirected versions of the networks. Therefore, the directionality of grooming was not considered to calculate the SNA measures, only whether the two individuals were connected or not via grooming. Weighted (accounting for the strength of relations) and unweighted (considering occurrence of the relation only) versions of each network were generated for the calculation of different network measures using R and coded into adjacency matrices. These matrices were used to visualize the network using the software NetDraw (see ***2.3.2. Social networks*** in ***Chapter 2***). SRI's for weighted networks were calculated in R.

3.2.3. Social network metrics and statistical analyses

Only data of adults and sub-adults were included in the analyses due to the difficulty of identifying the infants in TG. BDG included one juvenile (HO) whom was considered as a sub-adult for the analyses.

To describe and compare the social structure or patterns of relations of the networks and determine whether they were more conducive to non-specific or directed social learning, seven group-level SNA metrics were used (see ***Table 2.7*** for a detailed description):

1) *Density* as a measure of group cohesion.
2) *Component ratio* to assess network fragmentation.
3) *Average degree* to describe the extent of node connectivity or partner selectivity (i.e. partner selection may explain a pattern whereby individuals in a network show a relatively low average number of connected partners).
4) *Average clustering coefficient* to indicate whether there are areas in the network that information may potentially be transmitted faster (cliques).
5) *Flow betweenness network centralization index* (NCI) as a measure of potential speed of information flow within the network.

6) *Disparity* (a measure of the edge weight distribution) to describe the homogeneity or heterogeneity of the strength of relations in the network (i.e. whether the network is dominated by weak or strong connections between individuals or all edges have the same strength).
7) *Assortative mixing* for sex, age and social rank (and kinship, for TG) to study the degree of homophily or heterophily of social relations (i.e. whether individuals prefer to interact with those of the same or a different class, respectively).

SNA metrics were compared among networks for each group of Barbary macaques. A bootstrap procedure, analogous to the classical paired-sample t-test (Snijders & Borgatti, 1999), was used to test whether differences of each group-level SNA metric between pairs of networks within groups were significantly different than chance. Assortative mixing was calculated using the E-I index. See ***section 2.4. Statistical analyses*** in ***Chapter 2*** for a complete description of how all SNA metrics were calculated.

Three individual-level SNA measures of centrality were used to determine which individuals contribute more to the diffusion of information (see ***Table 2.7***):

i) *Degree centrality* as a measure of the number of connections per node (individual).
ii) *Eigenvector centrality* as a measure of how well-connected each node is with other nodes and with other well-connected individuals.
iii) *Flow betweenness* to determine who has the potential to contribute more to the flow of information within each network. Scores were normalized using the normalization method suggested by Koschutzki et al. (2005).

In many cases, these three centrality measures explain the same biological processes and, consequently, are positively correlated with each other (Valente et al., 2008). However, the structure of a network may impact the correlation of individual-level centrality measures in some cases, changing the interpretation of each metric and, thus, the relative importance of the nodes in the network (Farine & Whitehead, 2015). Spearman's rank correlations were used to determine the relationship between the three centrality measures in each network so as to enable accurate interpretation of the relative importance of the nodes in the networks for the social learning context.

Flow betweenness is the most informative centrality measure for social learning as it depicts the importance of a node in terms of the strength of connections and the speed of potential information diffusion (Borgatti et al., 2013). Spearman's rank correlations were used to (i) determine the relationship between individual-level measures of flow betweenness among all affiliative networks and (ii) describe the roles that individuals may have in each of these networks in terms of their contribution to the transmission of information within the group. Shapiro-Wilk normality tests were performed for node strength and all group and individual-level SNA metrics aforementioned, calculated for all datasets (Rimbach et al., 2015). In most cases, data were not normally distributed (see ***Appendix E***), so non-parametric tests were used for further analyses.

To test whether affiliative networks predicted each other, permutation-based linear mixed models were used (see section ***2.4.6. Permutation-based mixed models*** in ***Chapter 2***). All the statistical analyses were performed in R. Group and individual-level SNA metrics were also calculated using R software [using the package *sna*]. All the p-values obtained in network comparisons were adjusted using a Benjamini-Hochberg correction (Benjamini & Hochberg, 1995) with a False Discovery Rate (FDR) of 5%. The adjusted p-values only were reported.

3.2.4. Node attributes

Sex, age, social rank and kinship were used as individual attributes to calculate assortative mixing and as fixed effects in linear mixed models. Sex (male, female) and age categories (adult, sub-adult) were assigned to each individual to calculate assortative mixing. Sex and age similarity matrices based on the aforementioned categories were built to inform the regression models.

Kinship was only available for TG. The group was composed of 10 well-defined matrilines and seven males that came from other parks in Europe (migrants). For assortative mixing, individuals were assigned a numeric code corresponding to their matriline. For linear mixed models, an adjacency matrix was built based on the coefficient of maternal relatedness of each dyad.

Agonistic encounters were used to calculate social rank. A similarity matrix based on the social rank categories was built for the linear mixed model regressions. Three social rank categories (high, middle and low), determined by the Jenks Natural Breaks Classification (see ***section 2.4.1*** and ***Appendix A***), were assigned to each individual for assortative mixing analyses.

3.3. Results

To ease the description and the discussion of results of association networks, proximity within 1m is referred to as close proximity and proximity within 5m as long-range proximity. Only corrected p-values are reported.

3.3.1. Adequacy of data

First inspection of the data indicated that complete datasets were collected but, in the case of grooming, huddling and proximity within 1m, they were sparse (see ***Appendix C***) as only a few observations per dyad were available. Precision and accuracy measures indicated that the levels of uncertainty of the datasets were low and that the sampling effort was high enough to generate reliable measures of edge weights in all cases (see ***Appendix C*** for a full description of the methods and results).

Measures of accuracy for association networks (social differentiation and the correlation coefficient between true and estimated association indices, see ***Appendix C***) proposed by Whitehead (2008) confirmed that datasets were "somewhat" ($r \sim 0.4$) to "good" representations ($r \sim 0.8$) of the social structure for proximity networks, except in the case of proximity within 1m in TG ($S = 0.545$, $r = 0.181$). This result indicated that the mean number of associations collected per individual and/or per dyad in TG may be insufficient to represent the social structure of associations within 1m in this group. However, the relative accuracy measure – which is more meaningful in animal networks than absolute values (Farine & Strandburg-Peshkin, 2015) – indicated that, in terms of ranks, true and estimated association indices were highly correlated for proximity within 1m in TG. Thus, proximity within 1m in TG was included in further analyses, and caution in the interpretation of results was reported according to the relative or absolute nature of the tests.

Bejder's permutation tests suggested that the patterns of the relationships captured in the datasets were not the result of arbitrary interactions or associations in any case (see ***Appendix C***).

3.3.2. Description and graphical representation of networks

Statistical analysis will follow this descriptive presentation section.

Grooming networks

A total of 608 instances of grooming were recorded in BDG when focal and behavioural sampling data were combined. In TG, 352 events were observed during focal follows.

Density, average degree, clustering coefficient and mean edge weight were 1.8 – 5.4x higher in BDG than in TG for undirected versions of the networks (see ***Table 3.1***). Density values of directed versions of these networks indicated that many interactions were not reciprocal ($\text{Density}_{BDG} = 0.340$, $\text{Density}_{TG} = 0.076$) and only a proportion of all the possible dyadic exchanges of grooming occurred (59.96% in BDG and 62.29% in TG). In BDG all individuals were fully connected, forming one single component (***Figure 3.1***). In TG, all individuals except PJ constituted one network component (***Figure 3.2***). PJ was fully disconnected from the big component in both interaction networks (grooming and huddling), most likely because he was a recent migrant not fully integrated in the group at the time of the study. Disparity, a measure of the edge weight distribution, was 1.3x higher in TG than in BDG (***Table 3.1***), suggesting that the strength of grooming exchanges was more evenly distributed in BDG than in TG.

BDG (N=25)

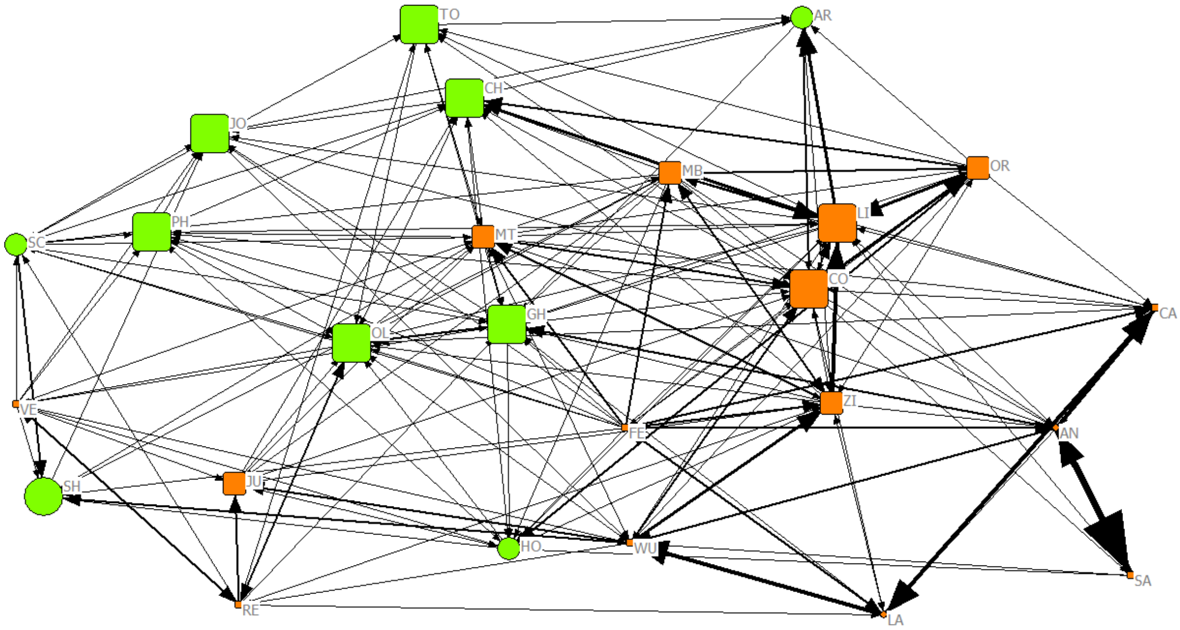


Figure 3.1. Graph representation of the grooming network of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads) and arrows point from groomer to gromee.

TG (N=56)

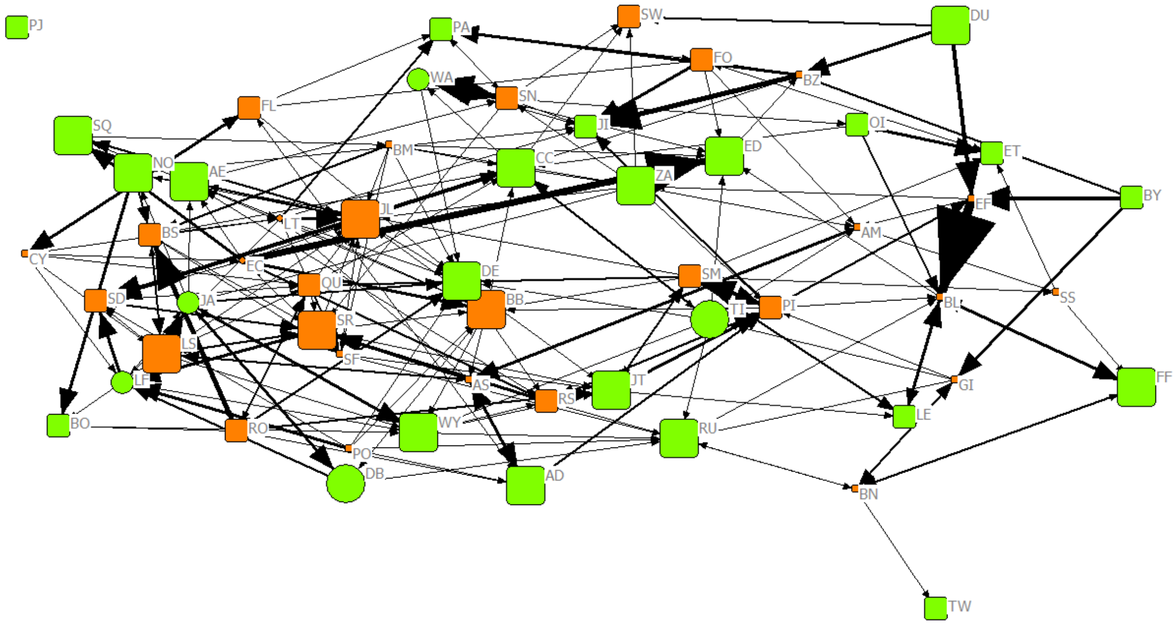


Figure 3.2. Graph representation of the grooming network of TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads) and arrows point from groomer to groome.

Huddling networks

A total of 411 and 420 huddling events were recorded for BDG and TG, respectively. Density, mean edge weight, clustering coefficient and disparity were 1.3 – 3.2x higher in BDG than in TG (***Table 3.1***). The huddling network was twice more densely saturated and twice less clustered in BDG than in TG (***Table 3.1***). Again, BDG formed one single component (***Figure 3.3***), but in TG, the network was fragmented with PJ forming a single component on his own (***Figure 3.4***). In both groups, individuals were connected to a similar number of partners on average (see ***Table 3.1***), despite TG being twice the size of BDG. NCI measures indicated that huddling networks were three times more centralized in BDG than in TG (***Table 3.1***).

BDG (N=25)

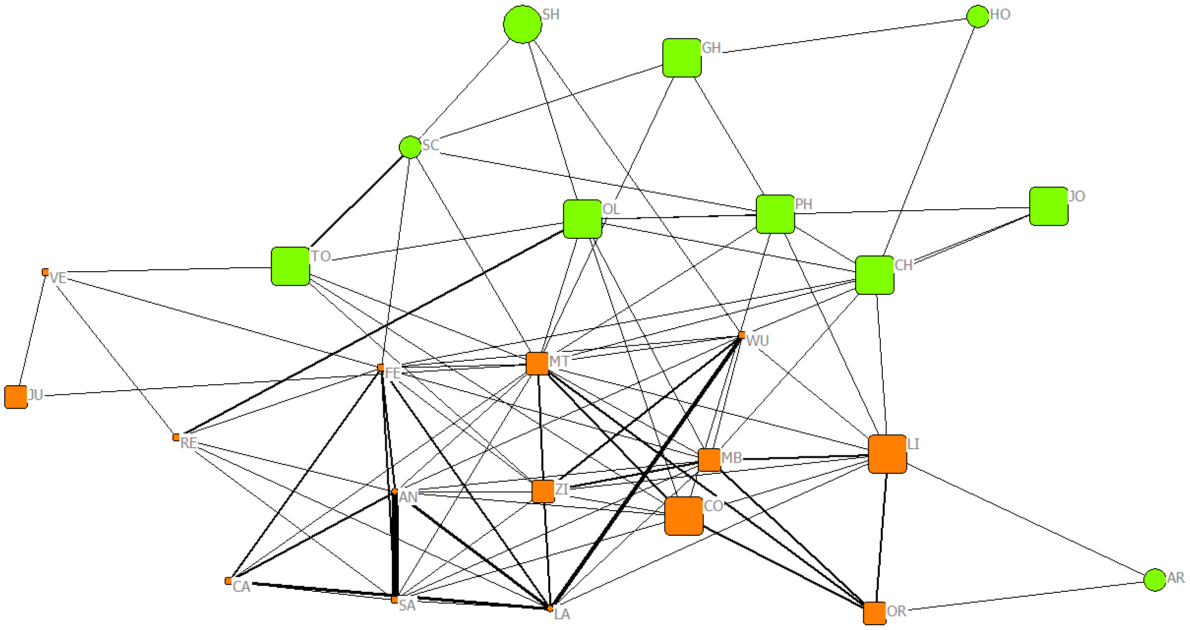


Figure 3.3. Graph representation of the huddling network of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads).

TG (N=56)

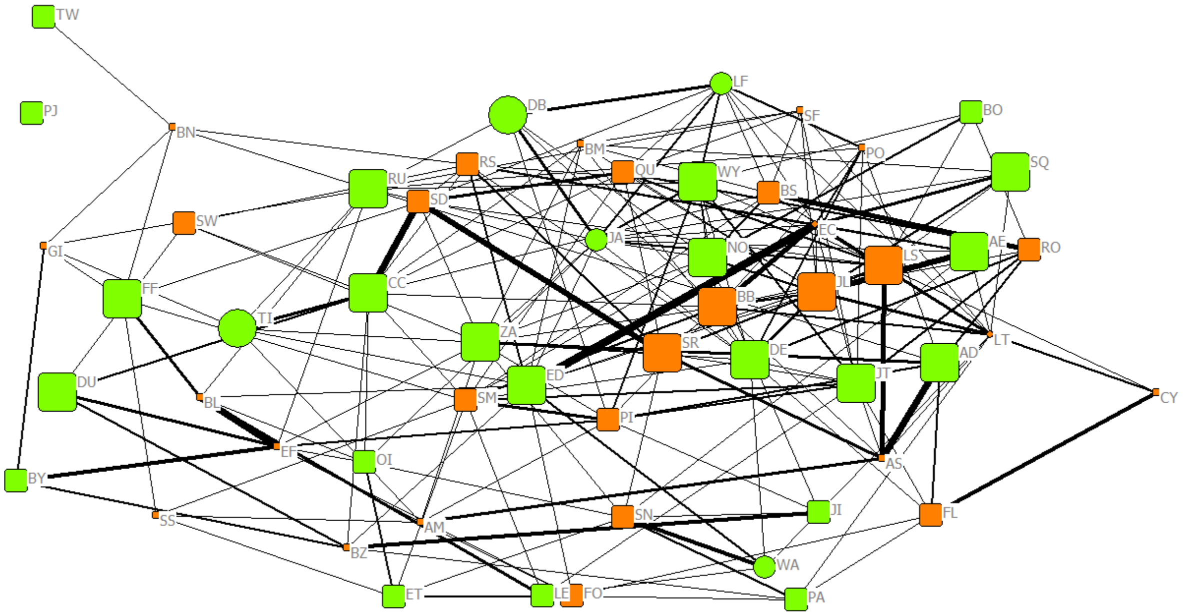


Figure 3.4. Graph representation of the huddling network of TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads).

Proximity networks

For BDG, the total of dyadic associations observed was 228 for proximity within 1m and 1,678 for proximity within 5m. For TG, 352 instances of associations were collected for proximity within 1m and 3,989 for proximity within 5m. In both groups, density values increased with increasing distances between dyads and were 1.2 – 2.2x higher in BDG than in TG (***Table 3.1***). In BDG, >90% of all possible dyadic associations occurred within 5m, while 80% was not even reached in TG for the same measure of proximity. Average degree showed that individuals in both groups associated with a similar number of partners (~8) within 1m. The number of average partners increased for each group when proximity within 5m was considered (***Table 3.1***) with the value in TG being twice the value of BDG (where group size was half the size of TG).

All proximity networks were formed by one single component (***Figures 3.5 – 3.8***). Note that in TG, the last two individuals to be introduced in the group (PJ and BY) were the two least connected nodes in the close (1m) proximity network and the most peripheral subjects in proximity within 5m. Mean edge weight and disparity measures (see ***Table 3.1***) indicate that associations in BDG, on average, were 1.2 – 2.2x stronger and more heterogeneous than those of TG. The clustering coefficient was 1.1 – 2.1x higher in BDG than in TG (***Table 3.1***), suggesting that individuals in Blair Drummond formed a more compact social unit than individuals in Trentham where nodes were more cliqued. Finally, NCI indicates that BDG proximity networks were 1.1 – 1.8x more centralized than TG proximity networks. In both groups, proximity networks within 5m were 4.8 – 7.8x less centralized than proximity networks within 1m (***Table 3.1***).

BDG (N=25)

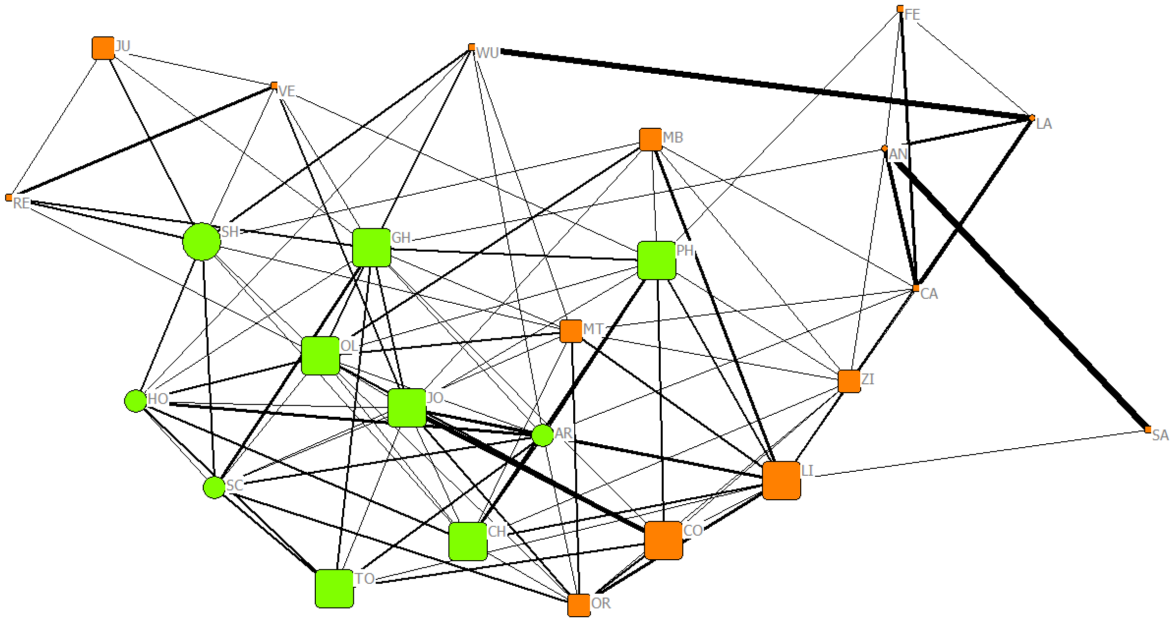


Figure 3.5. Graph representation of the network for proximity within 1m of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads).

TG (N=56)

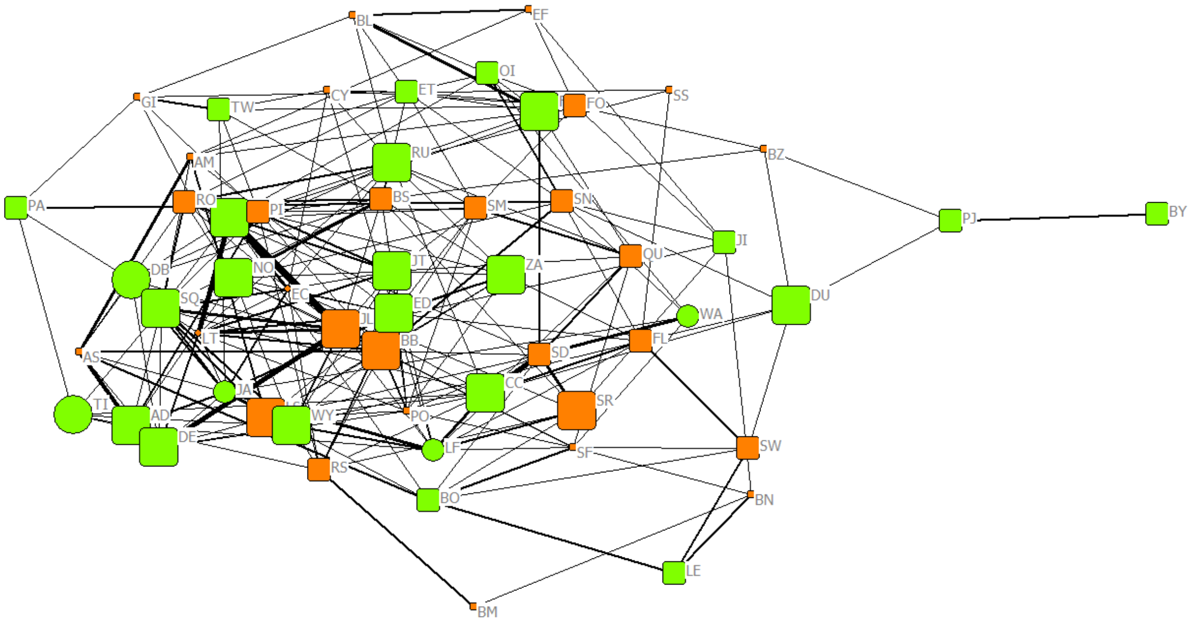


Figure 3.6. Graph representation of the network for proximity within 1m of TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads).

BDG (N=25)

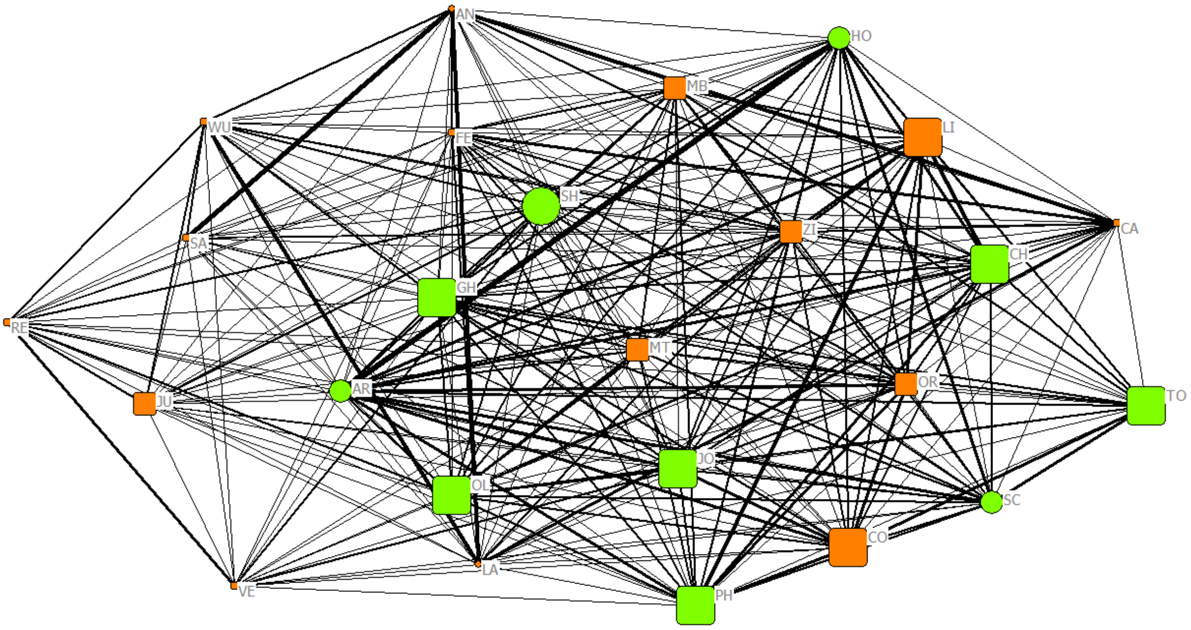


Figure 3.7. Graph representation of the network for proximity within 5m of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads).

TG (N=56)

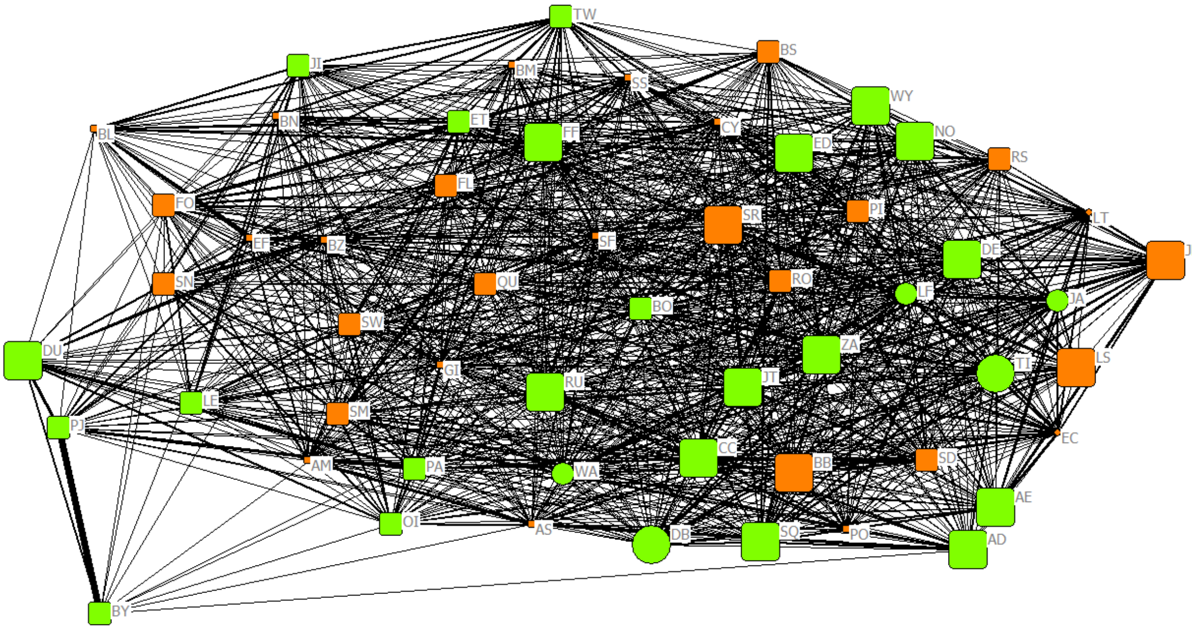


Figure 3.8. Graph representation of the network for proximity within 5m of TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads).

Table 3.1. Results of the group-level SNA metrics for both groups and unweighted versions of the interaction and association networks.

Network	Density	Degree	CR	Components	MEW	Disparity	CC	NCI (%)
Grooming BDG	0.517	12.4 (0.517)	0	1	0.005955	0.192281	0.615	4.105
Grooming TG	0.122	6.71 (0.119)	0.018	2	0.001114	0.24615	0.142	3.912
Huddling BDG	0.297	7.12 (0.297)	0	1	0.004115	0.297212	0.449	9.666
Huddling TG	0.141	7.75 (0.138)	0.018	2	0.001289	0.231666	0.196	3.011
Proximity 1m BDG	0.347	8.32 (0.347)	0	1	0.002279	0.222111	0.481	5.435
Proximity 1m TG	0.156	8.57 (0.153)	0	1	0.001054	0.183524	0.230	3.054
Proximity 5m BDG	0.910	21.84 (0.910)	0	1	0.015983	0.081737	0.918	0.701
Proximity 5m TG	0.761	41.86 (0.747)	0	1	0.01239	0.046101	0.803	0.635

BDG: Blair Drummond Group. TG: Trentham Group. Degree: Average Degree (Proportion). CR: Component ratio. MEW: Mean edges weight. CC: Clustering Coefficient. NCI: Network Centralization Index.

3.3.3. Comparison of group-level SNA metrics within groups

Results of the bootstrap procedure analogous to the paired-sample t-test are reported for density, component ratio, node strength, average degree, clustering coefficient, disparity and flow betweenness centralization index (NCI). The statistic reported is the observed difference (Diff) of the SNA metric between pairs of networks. Comparisons were made within groups for the following networks: grooming, huddling, proximity within 1m and proximity within 5m. P-values represent the probability that the absolute difference in the SNA metric between the bootstrapped (random) networks is greater than the observed absolute difference between the original (observed) networks. Thus if the p-value is <0.05, the observed difference between SNA metrics can be considered significantly greater than chance.

Density

In both groups, all networks significantly differed in density from each other (***Tables 3.2*** & ***3.3***). Networks based on proximity within 5m were significantly more saturated than the other networks in both groups. In BDG, the second most densely connected network was grooming (see ***Table 3.1***). The network based on proximity within 1m was more saturated than the huddling network in both groups. The least saturated network in TG was grooming (***Figure 3.9***).

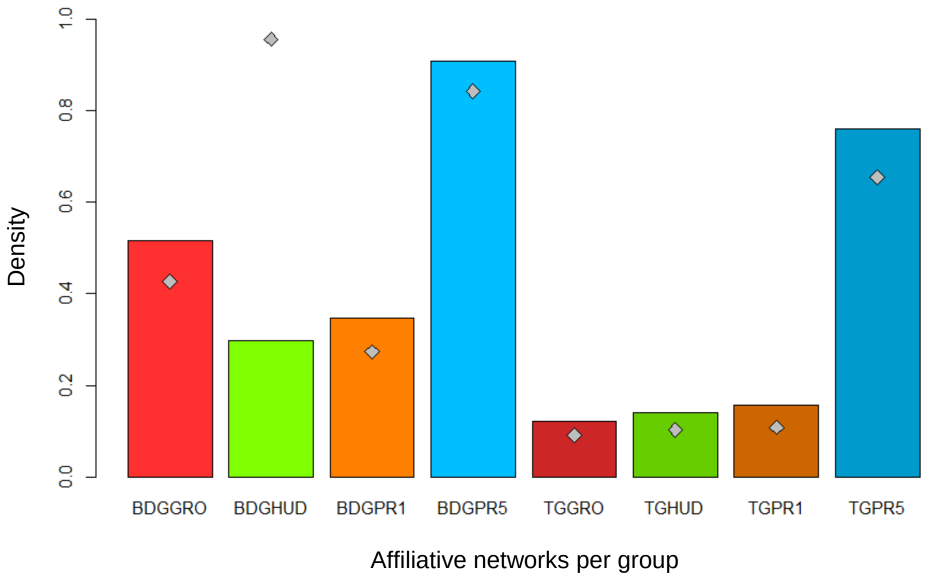


Figure 3.9. Barplot of density for all affiliative networks. Grey diamonds indicate the median average density of the bootstrapped distribution of each network. BDG: Blair Drummond Group. TG. Trentham Group. GRO: Grooming. HUD: Huddling. PR1 Proximity within 1m. PR5: Proximity within 5m. All networks significantly differed in density from each other (see ***Tables 3.2*** & ***3.3***).

Component ratio

In both groups, component ratios did not significantly differ among networks (***Tables 3.2*** & ***3.3***). All networks in BDG and both proximity networks in TG formed one single component (component ratio = 0). In TG, grooming and huddling networks had two components: one with only PJ and another with the rest of the group (***Figures 3.2*** & ***3.4***).

Node strength

Average node strength was significantly different in all the pair-wise network comparisons in both groups (***Tables 3.2*** & ***3.3***). Grooming interactions were significantly stronger than huddling relations and proximity within 1m, and huddling bonds were significantly stronger than close proximity associations in BDG (***Table 3.1***). In TG, huddling relations were significantly stronger than grooming interactions and close proximity associations, and grooming relations were stronger than close proximity. Node strength for proximity within 5m was significantly higher than for the other networks in both groups (***Figure 3.10***).

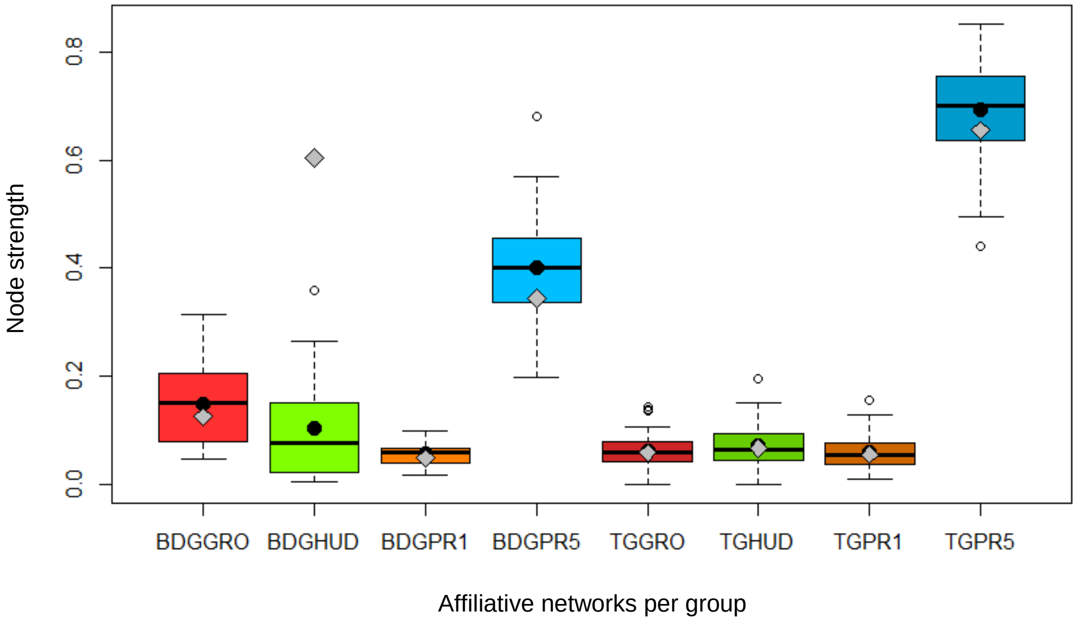


Figure 3.10. Box-plot of node strength for all affiliative networks. Black spots represent the average node strength. Grey diamonds indicate the median average node strength of the bootstrapped distribution of each network. BDG: Blair Drummond Group. TG. Trentham Group. GRO: Grooming. HUD: Huddling. PR1 Proximity within 1m. PR5: Proximity within 5m. All networks significantly differed in node strength from each other (see ***Tables 3.2*** & ***3.3***).

Table 3.2. Results of the bootstrap procedure for BDG comparing group-level metrics between networks.

	D	**CR**	**NS**	**AD**	**CC**	**Y**	**NCI**
GRO-HUD	**Diff = 0.220** **p<0.001**	Diff = 0 p = 1	**Diff = 0.046** **p<0.001**	**Diff = 5.28** **p<0.001**	**Diff = 0.166** **p<0.001**	**Diff = -0.105** **p<0.001**	**Diff = -5.560** **p<0.001**
GRO-PR1	**Diff = 0.170** **p<0.001**	Diff = 0 p = 0.993	**Diff = 0.092** **p<0.001**	**Diff = 4.08** **p<0.001**	**Diff = 0.134** **p = 0.006**	Diff = -0.029 p = 0.143	Diff = -1.329 p = 0.543
GRO-PR5	**Diff = -0.393** **p<0.001**	Diff = 0 p = 1	**Diff = -0.251** **p<0.001**	**Diff = -9.44** **p<0.001**	**Diff = -0.303** **p<0.001**	**Diff = 0.111** **p<0.001**	**Diff = 3.404** **p = 0.008**
HUD-PR1	**Diff = -0.050** **p<0.001**	Diff = 0 p = 0.993	**Diff = 0.046** **p<0.001**	**Diff = -1.20** **p<0.001**	Diff = -0.032 p = 0.429	**Diff = 0.075** **p<0.001**	**Diff = 4.231** **p = 0.046**
HUD-PR5	**Diff = -0.613** **p<0.001**	Diff = 0 p = 1	**Diff = -0.297** **p<0.001**	**Diff = -14.72** **p<0.001**	**Diff = -0.469** **p<0.001**	**Diff = 0.215** **p<0.001**	**Diff = 8.965** **p<0.001**
PR1-PR5	**Diff = -0.563** **p<0.001**	Diff = 0 p = 1	**Diff = -0.343** **p<0.001**	**Diff = -13.52** **p<0.001**	**Diff = -0.437** **p<0.001**	**Diff = 0.140** **p<0.001**	**Diff = 4.734** **p = 0.041**

GRO: Grooming. HUD: Huddling. PR1: Proximity within 1m. PR5: Proximity within 5m. D: Density. AD: Average Degree (Proportion). CR: Component ratio. NC: Number of components. MEW: Mean edges weight. Y: Disparity. CC: Clustering Coefficient. NCI: Network Centralization Index. Diff: Difference between values of the SNA metric of the observed networks. Significant p-values in bold.

Table 3.3. Results of the bootstrap procedure for TG comparing group-level metrics between networks.

	D	**CR**	**NS**	**AD**	**CC**	**Y**	**NCI**
GRO-HUD	**Diff = -0.018** **p<0.001**	Diff = 0 p = 0.752	**Diff = -0.009** **p<0.001**	**Diff = -1.04** **p<0.001**	**Diff = -0.054** **p = 0.031**	Diff = 0.014 p = 0.285	Diff = 0.902 p = 0.429
GRO-PR1	**Diff = -0.034** **p<0.001**	Diff = 0.019 p = 0.298	**(Diff = 0.003** **p = 0.007**	**Diff = -1.86** **p<0.001**	**Diff = -0.088** **p=0.002**	**Diff = 0.056** **p = 0.021**	Diff = 0.858 p = 0.450
GRO-PR5	**Diff = -0.639** **p<0.001**	Diff = 0.019 p = 0.070	**Diff = -0.631** **p<0.001**	**Diff = -35.14** **p<0.001**	**Diff = -0.661** **p<0.001**	**Diff = 0.197** **p<0.001**	Diff = 3.278 p = 0.131
HUD-PR1	**Diff = -0.015** **p=0.002**	Diff = 0.019 p = 0.298	**Diff = 0.013** **p<0.001**	**Diff = -0.82** **p = 0.002**	Diff = -0.033 p = 0.276	Diff = 0.042 p = 0.074	Diff = -0.043 p = 0.450
HUD-PR5	**Diff = -0.620** **p<0.001**	Diff = 0.019 p = 0.070	**Diff = -0.635** **p<0.001**	**Diff = -34.11** **p<0.001**	**Diff = -0.607** **p<0.001**	**Diff = 0.182** **p<0.001**	Diff = 2.376 p = 0.233
PR1-PR5	**Diff = -0.605** **p<0.001**	Diff = 0 p = 0.544	**Diff = -0.635** **p<0.001**	**Diff = -33.29** **p<0.001**	**Diff = -0.574** **p<0.001**	**Diff = 0.140** **p<0.001**	Diff = 2.419 p = 0.296

GRO: Grooming. HUD: Huddling. PR1: Proximity within 1m. PR5: Proximity within 5m. D: Density. AD: Average Degree (Proportion). CR: Component ratio. NC: Number of components. MEW: Mean edges weight. Y: Disparity. CC: Clustering Coefficient. NCI: Network Centralization Index. Diff: Difference between values of the SNA metric of the original networks. Significant p-values in bold.

Average degree

All networks differed in average degree for both groups (***Tables 3.2*** & ***3.3***). Grooming in BDG showed a significantly higher average degree than huddling and proximity within 1m. In contrast, grooming in TG had a significantly lower average degree than huddling and close proximity (***Table 3.1***). Huddling had a significantly lower average degree than close proximity in both groups (***Tables 3.2*** & ***3.3***). In all comparisons, average degree was significantly higher in proximity within 5m than in the other networks (***Figure 3.11***).

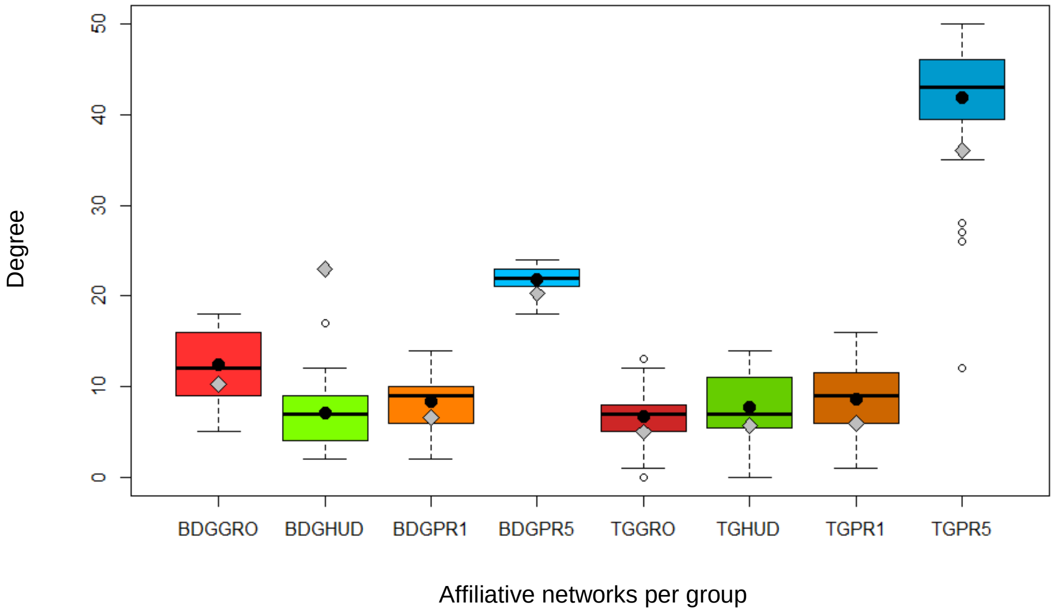


Figure 3.11. Box-plot of degree for all affiliative networks. Black spots represent the average degree. Grey diamonds indicate the median average degree of the bootstrapped distribution of each network. BDG: Blair Drummond Group. TG. Trentham Group. GRO: Grooming. HUD: Huddling. PR1 Proximity within 1m. PR5: Proximity within 5m. All networks significantly differed in average degree from each other (***Tables 3.2*** & ***3.3***).

Clustering coefficient

Clustering coefficient for grooming was significantly higher in BDG (but significantly lower in TG) than huddling and close proximity (***Tables 3.1 – 3.3***). In both groups, no significant differences were found between huddling and close proximity (***Tables 3.2*** & ***3.3***). Clustering coefficient was significantly higher in proximity within 5m than in the other networks in both groups (***Figure 3.12***).

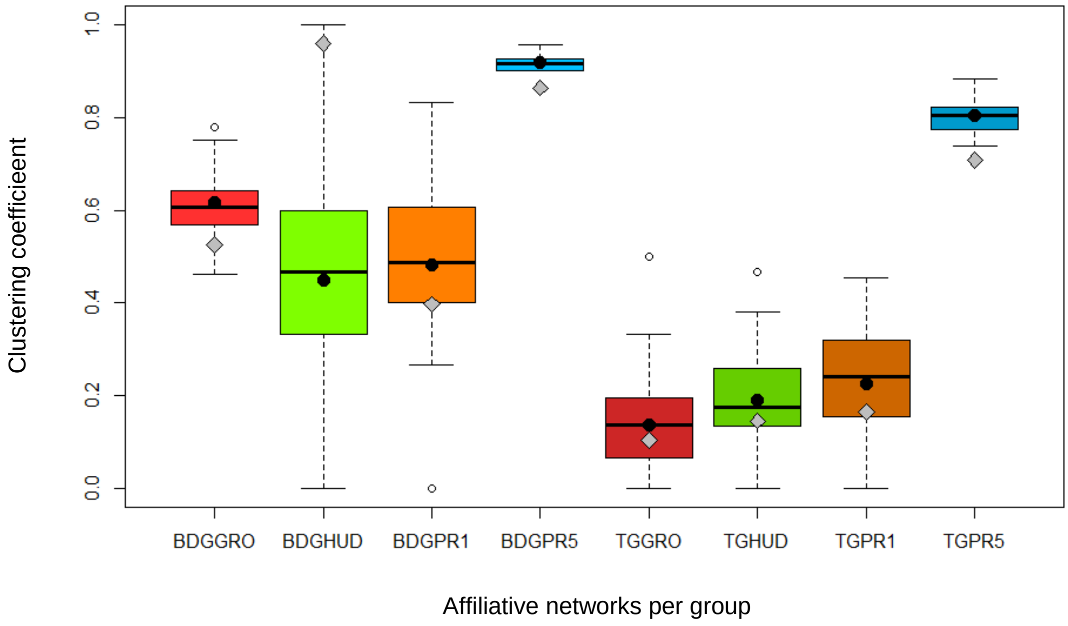


Figure 3.12. Box-plot of clustering coefficient for all affiliative networks. Black spots represent the average clustering coefficient. Grey diamonds indicate the median clustering coefficient of the bootstrapped distribution of each network. BDG: Blair Drummond Group. TG. Trentham Group. GRO: Grooming. HUD: Huddling. PR1 Proximity within 1m. PR5: Proximity within 5m. All networks significantly differed in clustering coefficient from each other except huddling and proximity within 1m (see ***Tables 3.2*** & ***3.3***).

Disparity

Significant differences between grooming and proximity within 1m were only found in TG (***Tables 3.2*** & ***3.3***). Huddling disparity was significantly higher than that of grooming and close proximity in BDG (***Table 3.1***). However, huddling did not differ in disparity from grooming and close proximity in TG (***Table 3.3***). Proximity within 5m showed significant lower levels of disparity than the other networks in both groups (***Figure 3.13***).

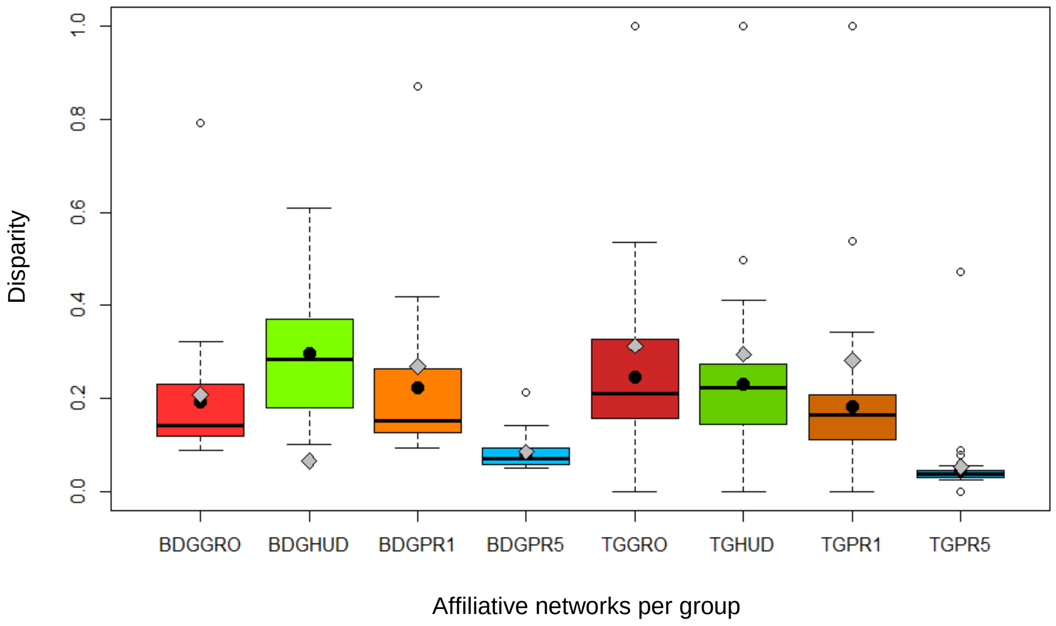


Figure 3.13. Box-plot of disparity for all affiliative networks. Black spots represent the average disparity. Grey diamonds indicate the median average disparity of the bootstrapped distribution of each network. BDG: Blair Drummond Group. TG. Trentham Group. GRO: Grooming. HUD: Huddling. PR1 Proximity within 1m. PR5: Proximity within 5m. All networks significantly differed in disparity except grooming and 1m proximity in BDG, and grooming and huddling and huddling and 1m proximity in TG (see ***Tables 3.2*** & ***3.3***).

Flow betweenness network centralization index (NCI)

In BDG, the huddling network was significantly more centralized than the grooming network and the close proximity network (***Tables 3.1*** – ***3.3***). No significant differences were found between the close proximity network and the grooming network in BDG (***Table 3.2***). Networks based on proximity within 5m were significantly less centralized than the other networks in BDG (***Figure 3.14***). No significant differences were found for network comparison in TG (***Table 3.3***).

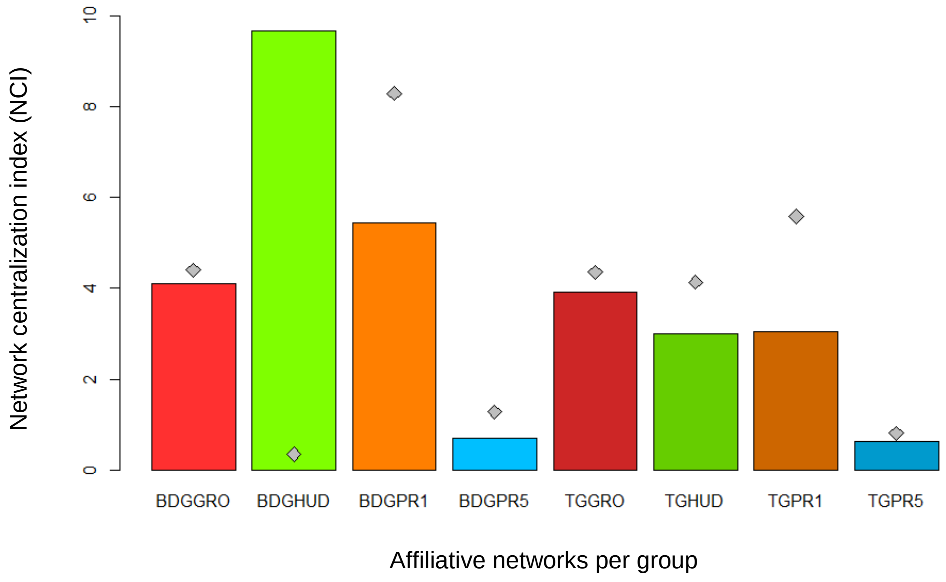


Figure 3.14. Barplot of NCI for all affiliative networks. Grey diamonds indicate the median average NCI of the bootstrapped networks. BDG: Blair Drummond Group. TG. Trentham Group. GRO: Grooming. HUD: Huddling. PR1 Proximity within 1m. PR5: Proximity within 5m. All networks significantly differed in NCI in BDG except grooming and proximity within 1m, and they did not differ in any case in TG (see ***Tables 3.2*** & ***3.3***).

Assortative mixing

All measures and results for assortative mixing (calculated using the E-I index, see ***section 2.4.7***) can be found in ***Tables D.1*** & ***D.2*** in ***Appendix D***. For significant results we must consider that: (i) if the E-I index is greater than chance, whether positive or negative, this indicates a preference for external connections (heterophily), (ii) if the E-I index is lower than chance, whether positive or negative, this indicates a preference for internal connections (homophily). See ***section 2.4.7*** for more details on the interpretation of the E-I index.

Networks based on grooming and huddling showed homophily for sex in BDG (***Figure 3.15***). For both grooming and huddling networks females in BDG significantly preferred to interact with other females. In contrast, females showed a preference for males in huddling and in both proximity networks in TG and also in proximity within 5m in BDG. Males preferred to groom with females in both groups. Males also showed a preference for females in huddling and both proximity networks in TG and in proximity within 5m in BDG (see ***Tables D.1*** & ***D.2*** and ***Figure 3.15***).

Sub-adults showed a preference for adults in grooming, huddling and proximity within 5m in BDG networks and in both association networks in TG. Adults only showed a preference for sub-adults in proximity within 5m in BDG (***Figure 3.16***).

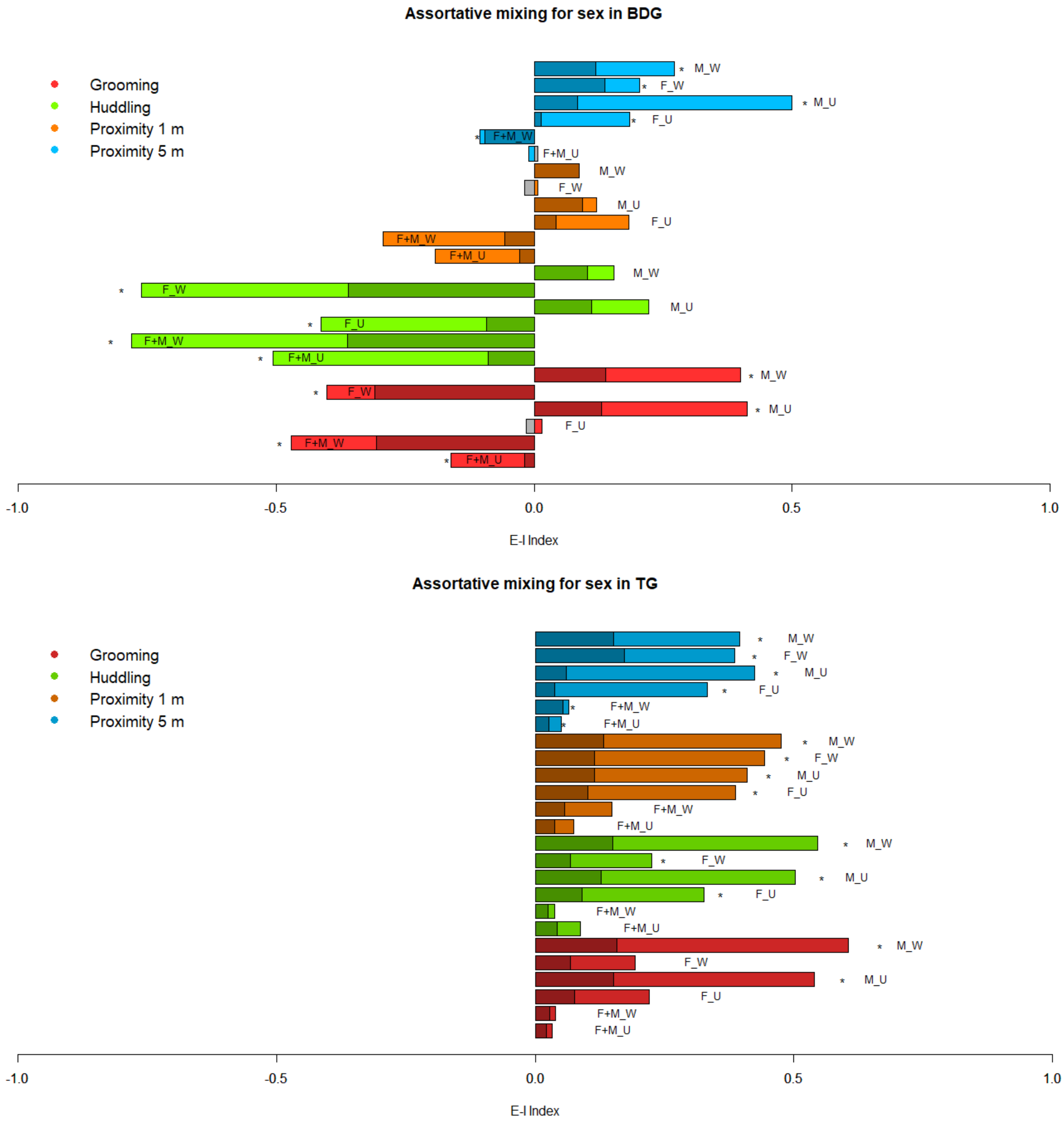
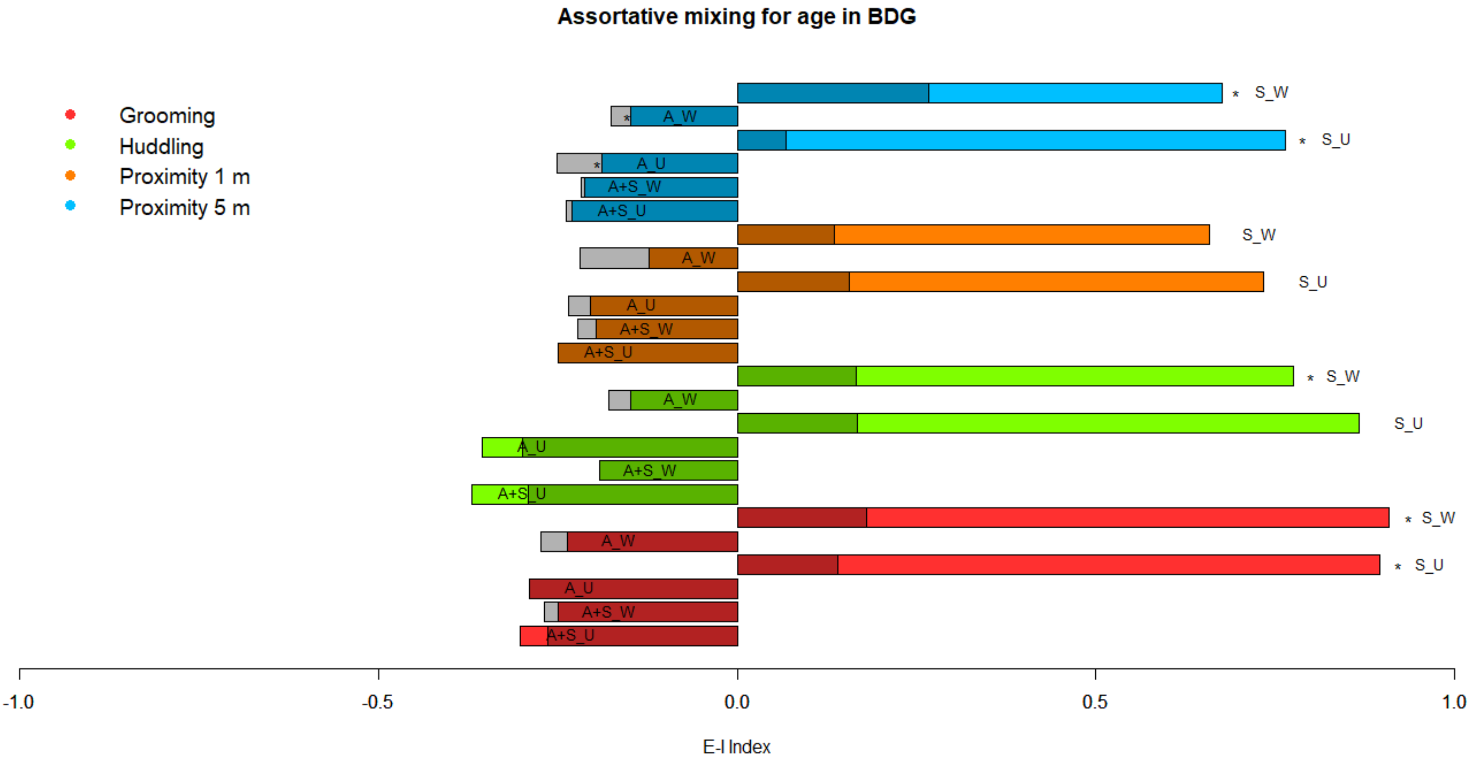


Figure 3.15. Assortative mixing for sex (affiliative networks). U: Unweighted network. W: Weighted network. F+M: E-I index measures of all possible interactions among males and females. F: E-I index measures of interactions involving females (i.e. excluding M-M interactions). M: E-I index measures of interactions involving males (i.e. excluding F-F interactions). The grey bars (darker shades when overlapped with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates

that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

In both groups, a general preference for individuals of the same rank was found for networks based on proximity within 5m as a whole. However, each social rank class separately preferred to associate within 5m with individuals of a different rank class (***Figure 3.17***). The huddling network in BDG showed homophily for social rank with lower-ranking individuals showing stronger relations with those of the same rank (***Tables D.1*** & ***D.2***).

Finally, despite individuals appearing to have fewer relations with those of a different kin than would be expect by chance, this difference was only significant for the association network within 5m in TG (***Figure 3.18***).



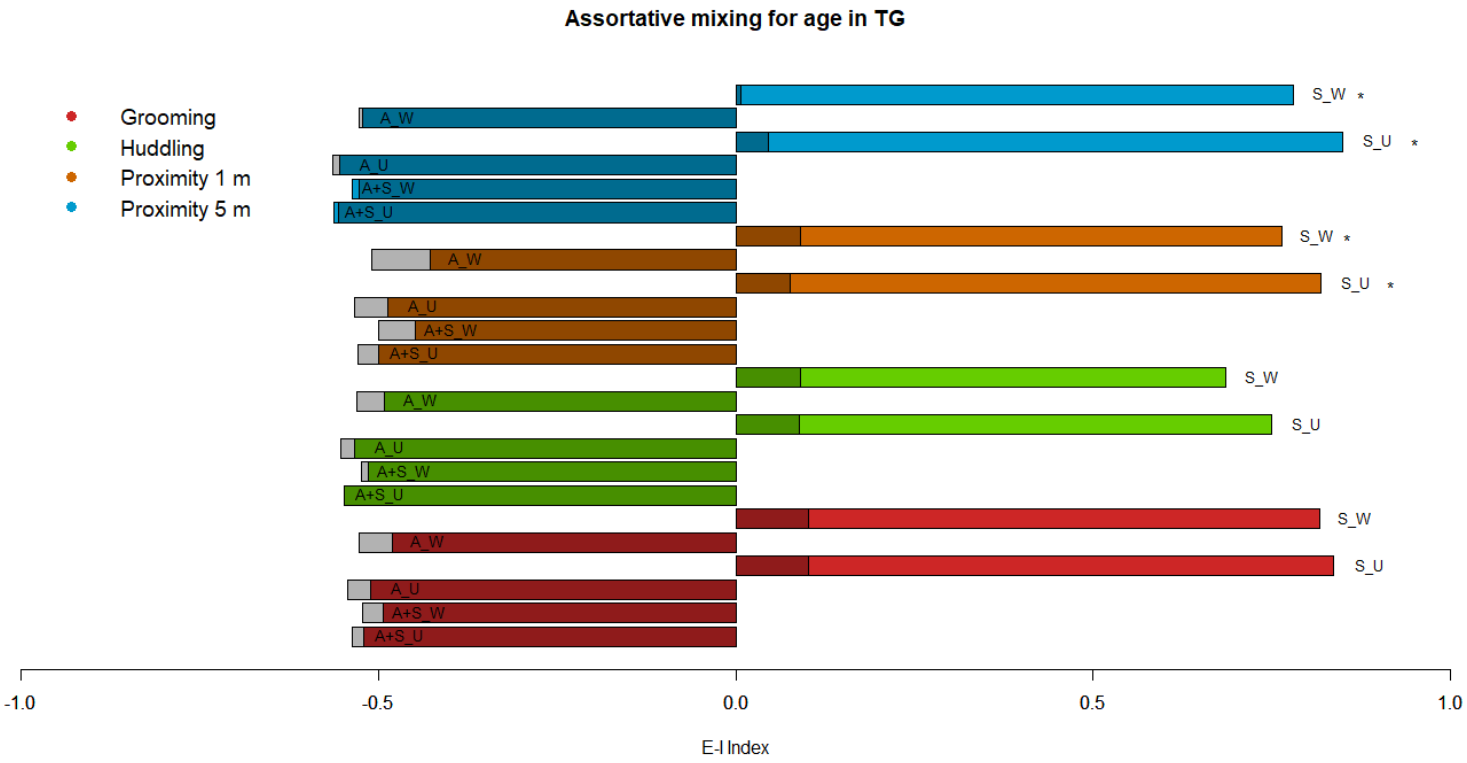


Figure 3.16. Assortative mixing for age (affiliative networks). U: Unweighted network. W: Weighted network. A+S: E-I index measures of all possible interactions among adults and sub-adults. A: E-I index measures of interactions involving adults (i.e. excluding S-S interactions). S: E-I index measures of interactions involving sub-adults (i.e. excluding A-A interactions). The grey bars (darker shades when overlapped with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

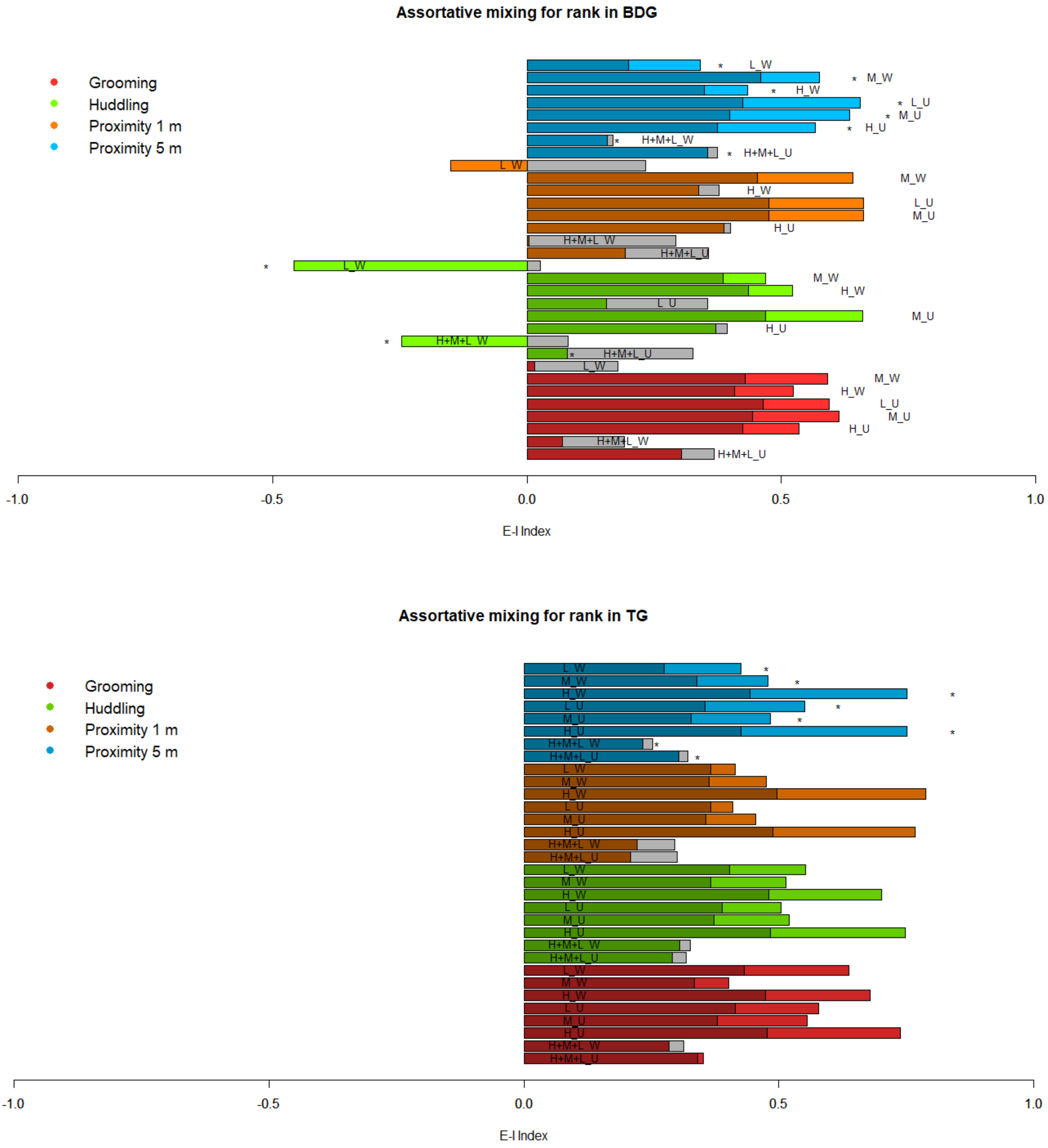


Figure 3.17. Assortative mixing for social rank (affiliative networks). U: Unweighted network. W: Weighted network. H+M+L: E-I index measures of all possible interactions among high, mid and low-ranking individuals. H: E-I index measures of interactions involving high-ranking individuals. M: E-I index measures of interactions

involving middle-ranking individuals. L: E-I index measures of interactions involving low-ranking individuals. The grey bars (darker shades when overlapped with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

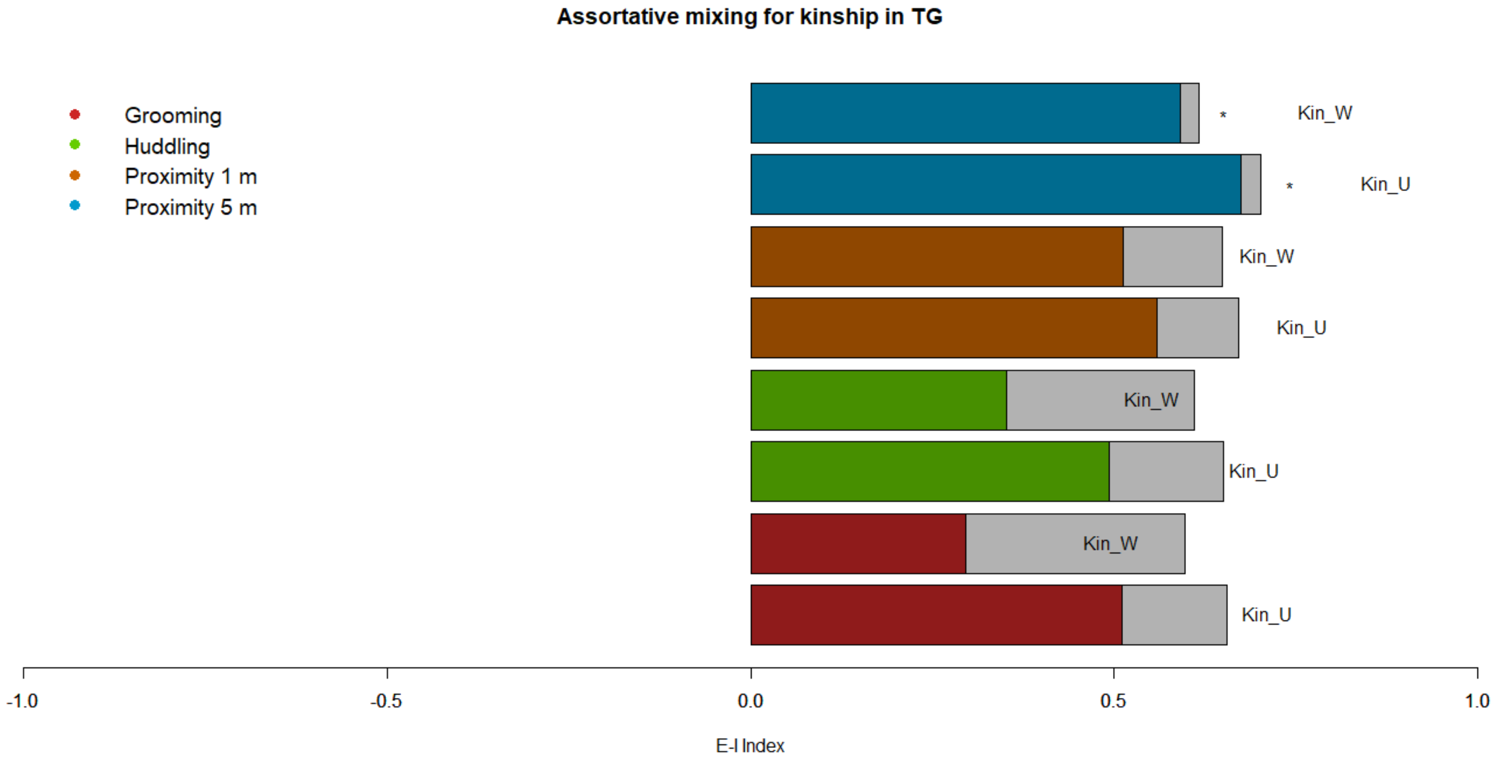


Figure 3.18. Assortative mixing for kinship (only TG, affiliative networks). For each network, two bars are represented and depict the observed E-I index measures for the whole network for both unweighted (U) and weighted measures (W). The grey bars (darker shades when overlap with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

3.3.4. Network regressions

Network regressions were conducted to determine whether affiliative relations based on different social behaviours predict each other. Across all regression models no variables showed multicollinearity, and in all analyses, the independent network significantly predicted the dependent network (***Tables 3.4*** and ***3.5***).

Table 3.4. Results of the permutation-based linear mixed model regressions for BDG.

	VIF	AIC	r (p-value)
Grooming predicts Huddling	SRI$_{GRO}$ = 1.073, SS = 1.113, AS = 1.029, SR = 1.084, ID1 = 1.013, ID2 = 1.013	-4055.09 (-4042.97, -3993.01)	SRI$_{GRO}$ = 0.771 ($p < 0.001$)* SR = 0.003 ($p = 0.005$)*
Proximity 1m predicts Grooming	SRI$_{PR1}$ = 1.080, SS = 1.089, AS = 1.029, SR = 1.109, ID1 = 1.016, ID2 = 1.016	-3745.93 (-3742.63, -3707.55)	SRI$_{PR1}$ = 1.965 ($p < 0.001$)*
Proximity 1m predicts Huddling	SRI$_{PR1}$ = 1.080, SS = 1.089, AS = 1.029, SR = 1.109, ID1 = 1.016, ID2 = 1.016	-3821.65 (-3816.18, -3750.64)	SRI$_{PR1}$ = 1.955 ($p < 0.001$)* SR = 0.003 ($p = 0.007$)*
Proximity 5m predicts Grooming	SRI$_{PR5}$ = 1.127, SS = 1.081, AS = 1.028, SR = 1.143, ID1 = 1.028, ID2 = 1.028	-3656.93 (-3655.19, -3609.88)	SRI$_{PR5}$ = 0.564 ($p < 0.001$)* AS = -0.003 ($p = 0.036$)*
Proximity 5m predicts Huddling	SRI$_{PR5}$ = 1.127, SS = 1.081, AS = 1.028, SR = 1.143, ID1 = 1.028, ID2 = 1.028	-3656.16 (-3655.46, -3582.47)	SRI$_{PR5}$ = 0.501 ($p < 0.001$)* SR = 0.003 ($p = 0.006$)*

VIF: Variance Inflation Factor of each of the variables. SRI: Simple Ratio Index of the independent network. SS: Sex similarity. AS: Age similarity. SR: Social rank similarity. ID1: Identity of individual 1. ID2: Identity of individual 2. AIC: indicates the lowest AIC value of all the tested regression models and the range between the next lowest AIC value and the maximum AIC value of all the tested models. r: regression coefficients. p: p-values. Only regression coefficients and p-values of significant variables in the fitted model are reported. *: $p<0.05$

Table 3.5. Results of the permutation-based linear mixed model regressions for TG.

	VIF	AIC	r (p-value)
Grooming predicts Huddling	SRI$_{GRO}$ = 1.160, SS = 1.039, AS = 1.008, SR = 1.043, KI = 1.161, ID1 = 1.009, ID2 = 1.009	-27911.10 (-27896.00, -27747.40)	SRI$_{GRO}$ = 1.007 ($p < 0.001$)*
Proximity 1m predicts Grooming	SRI$_{PR1}$ = 1.029, SS = 1.042, AS = 1.009, SR = 1.046, KI = 1.025, ID1 = 1.008, ID2 = 1.008	-25862.80 (-25845.20, -25291.80)	SRI$_{PR1}$ = 0.438 ($p < 0.001$)* KI = 0.010 ($p = 0.014$)* SR*KI = 0.027 ($p = 0.003$)*
Proximity 1m predicts Huddling	SRI$_{PR1}$ = 1.029, SS = 1.042, AS = 1.009, SR = 1.046, KI = 1.025, ID1 = 1.008, ID2 = 1.008	-25120.10 (-25114.60, -24948.40)	SRI$_{PR1}$ = 0.728 ($p < 0.001$)* KI = 0.013 ($p = 0.002$)*
Proximity 5m predicts Grooming	SRI$_{PR5}$ = 1.038, SS = 1.041, AS = 1.009, SR = 1.053, ID1 = 1.007, ID2 = 1.007	-25758.00 (-25740.70, -25191.60)	SRI$_{PR5}$ = 0.082 ($p < 0.001$)* SR = -0.001 ($p = 0.023$)* KI = 0.009 ($p = 0.014$)* SR*KI = 0.027 ($p = 0.002$)*
Proximity 5m predicts Huddling	SRI$_{PR5}$ = 1.038, SS = 1.041, AS = 1.008, SR = 1.053, ID1 = 1.007, ID2 = 1.007	-24713.90 (-24699.00, -24544.70)	SRI$_{PR5}$ = 0.116 ($p < 0.001$)* SR = -0.001 ($p = 0.045$)* KI = 0.008 ($p = 0.045$)*

VIF: Variance Inflation Factor of each of the variables. SRI: Simple Ratio Index of the independent network. SS: Sex similarity. AS: Age similarity. SR: Social rank similarity. KI: Kinship similarity (maternal relatedness). ID1:

Identity of individual 1. ID2: Identity of individual 2. AIC: indicates the lowest AIC value of all the tested regression models and the range between the next lowest AIC value and the maximum AIC value of all the tested models. r: regression coefficients. p: p-values. Only regression coefficients and p-values of significant variables in the fitted model are reported. *: $p<0.05$

There was a significant regression between grooming and huddling relations in both groups (***Tables 3.4*** & ***3.5***). Therefore, dyads that were frequently seen engaged in grooming interactions were also frequently observed huddling together (see ***Figure 3.19***). The grooming-huddling regression in BDG was significantly influenced by social rank similarity such that frequent grooming partners more similar in rank were more frequently observed huddling than those more dissimilar in rank (***Table 3.4***). No individual attributes were significant in the grooming-huddling regression for TG (***Table 3.5***).

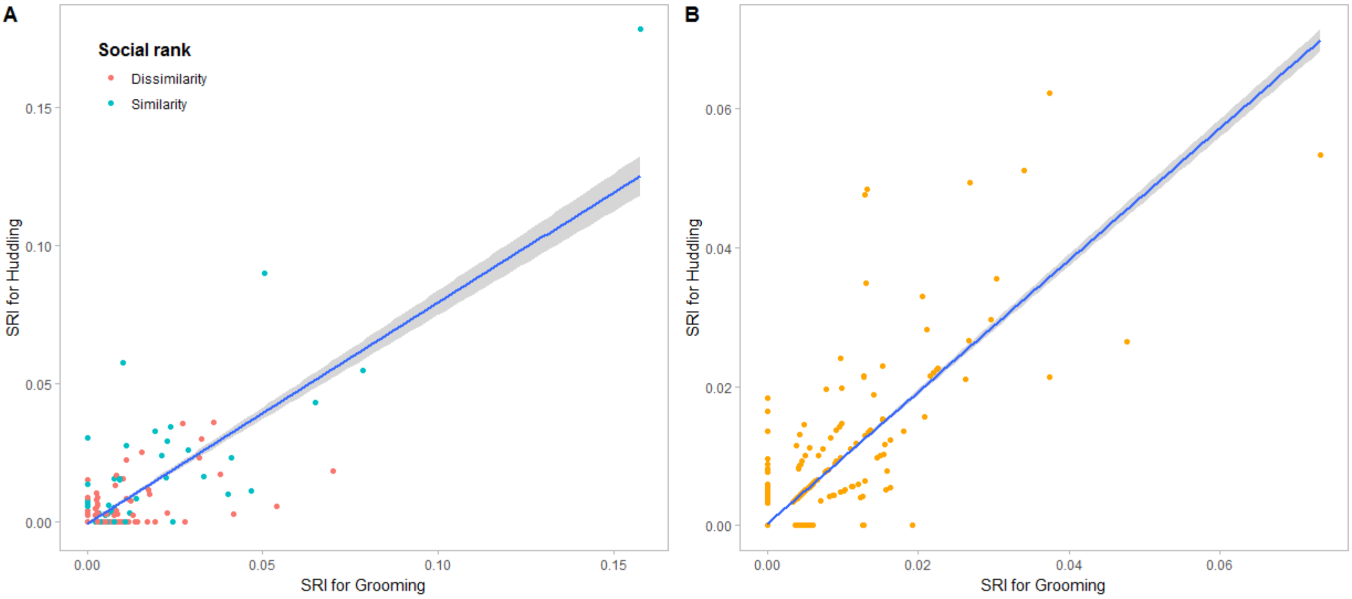


Figure 3.19. Regression between grooming and huddling Simple Ratio Indices (SRI) for BDG (**A**) and TG (**B**). Data points in **A** are coloured according to the variable that significantly influenced the regression (i.e. social rank). Note that the cliqued social structure of TG may be responsible for the scattered distribution observed in **B**, with some points aligned following regressions of different steepness**.** This indicates that the relationship between the strengths of grooming and huddling interactions apparently increases at different rates within each clique. Accordingly, affiliative relations were probably constrained to individuals within the same clique, generating less variability (i.e., more alignment) in the data points of the regression between individuals of the same clique than with those of different cliques. This configuration of the data points was not observed for BDG (**A**), which was less sub-structured in strongly-bonded cliques of individuals compared to TG.

Close proximity predicted grooming and huddling interactions in both groups (***Figures 3.20*** & ***3.21***). In BDG, the close proximity-huddling regression was positively influenced by social rank similarity, meaning that close associates of similar rank were more frequently observed huddling than those belonging to different rank classes (***Table 3.4*** & ***Figure 3.21A***). In TG, the strength of close proximity relations increased with grooming as a function of kinship and social rank similarity (***Figure 3.20B***). A positive influence of kinship was also found in the close proximity-huddling regression in TG such that kin-related associates at 1m engaged in huddling more frequently than non-kin (***Table 3.5*** and ***Figure 3.21B***).

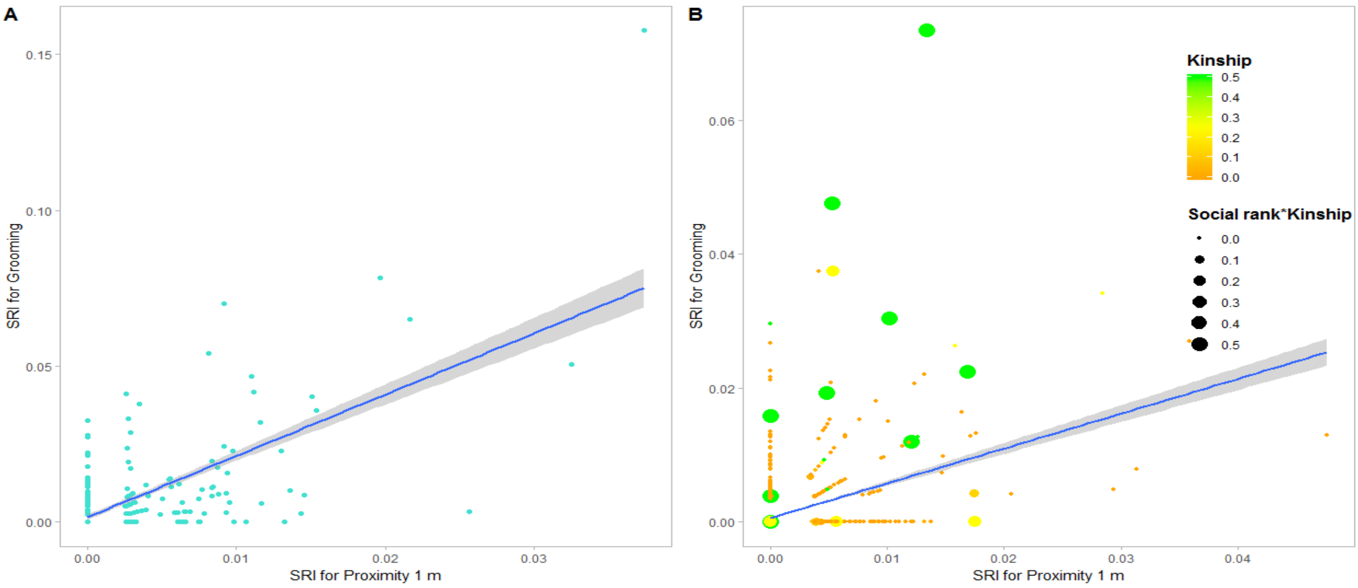


Figure 3.20. Regression between close proximity and grooming Simple Ratio Indices (SRI) in BDG (**A**) and TG (**B**). Data points in **B** are coloured and sized according to the fixed factors that significantly influenced the regression (kinship and social rank). Kinship values in the legend represent the coefficient of maternal relatedness (0 = unrelated, 0.5 = mother-offspring). Social rank*Kinship values represent the product of the coefficients of maternal relatedness and social rank similarity (0 = different social rank, 1 = same social rank). Note that the cliqued social structure of TG may be responsible for the scattered distribution observed in **B**, with some points aligned following regressions of different steepness**.** This indicates that the relationship between the strengths of associations (proximity) within 1m and grooming interactions apparently increases at different rates within each clique. Accordingly, affiliative relations were probably constrained to individuals within the same clique, generating less variability (i.e., more alignment) in the data points of the regression between individuals of the same clique than with those of different cliques. This configuration of the data points was not observed for BDG (**A**), which was less sub-structured in strongly-bonded cliques of individuals compared to TG.

In all cases, regressions with proximity within 5m as a predictor network had the lowest regression coefficients for the strength of network relations (SRI, see ***Tables 3.4*** & ***3.5***). In BDG, age dissimilarity positively influenced the regression between proximity within 5m and grooming while the regression between long-distance proximity and huddling was influenced by rank similarity (***Table 3.4***). This indicates that those in BDG observed associated within 5m where more frequently observed grooming or huddling together when belonged to different age or similar rank classes, respectively, than otherwise. Social rank and kinship influenced the regression between long-range proximity and interaction networks in TG (***Table 3.5***). Accordingly, associates at 5m in TG preferred to groom and huddle with those of the same kin. Regarding social rank, it seems that associates at 5m in TG preferred to groom those of a different rank, except when they were relatives. In this latter case, macaques preferred to groom those of the same rank.

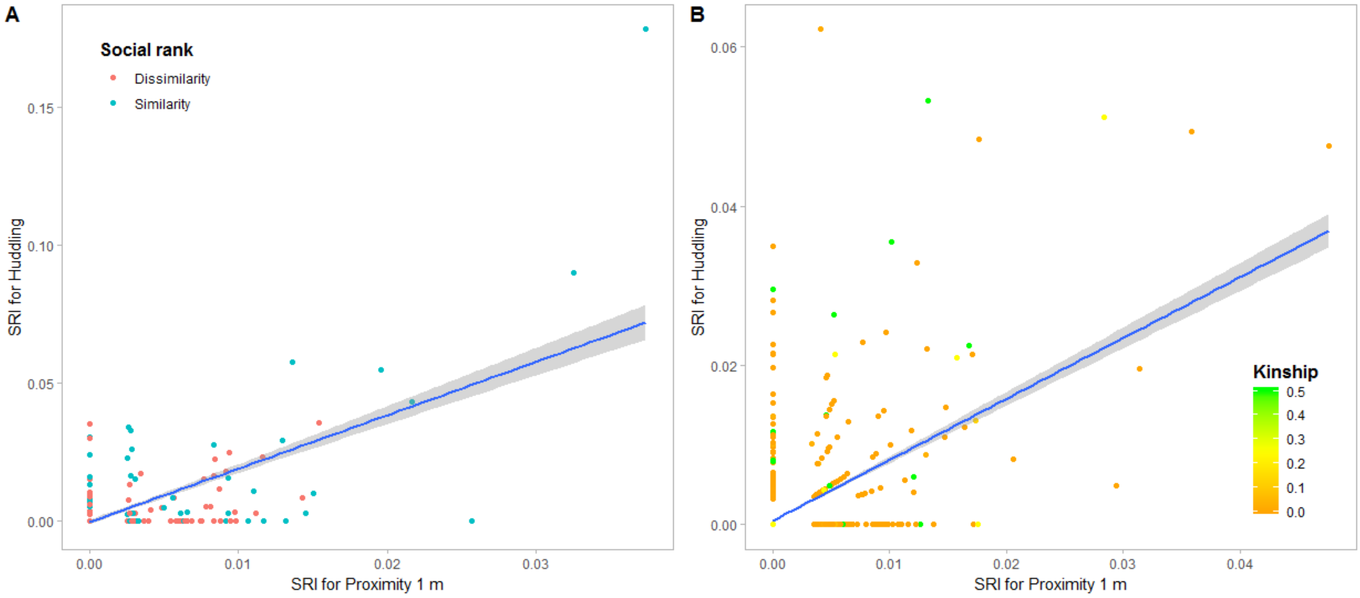


Figure 3.21. Regression between close proximity and huddling Simple Ratio Indeces (SRI) in BDG (**A**) and TG (**B**). Spots are coloured according to the individual factors that influenced the regressions (social rank in **A** and kinship in **B**). Kinship values in the legend represent the coefficient of maternal relatedness (0 = unrelated, 0.5 = mother-offspring). Note that the cliqued social structure of TG may be responsible for the scattered distribution observed in **B**, with some points aligned following regressions of different steepness**.** This indicates that the relationship between the strengths of associations (proximity) within 1m and huddling interactions apparently increases at different rates within each clique. Accordingly, affiliative relations were probably constrained to individuals within the same clique, generating less variability (i.e., more alignment) in the data points of the regression between individuals of the same clique than with those of different cliques. This configuration of the data points was not observed for BDG (**A**), which was less sub-structured in strongly-bonded cliques of individuals compared to TG.

3.3.5. Correlations of individual centrality measures and individual attributes

The correlation analysis was conducted only for centrality measures of the grooming, huddling and close proximity network because these behaviours represent instances of high social tolerance, a pre-requisite for social learning (Coussi-Korbel & Fragaszy, 1995). Since these three networks predicted each other, correlations of centrality measures were conducted to explore whether individuals that may contribute more to the flow of information have the same role (i.e. network positions) in all the affiliative networks (Valente et al., 2008; Borgatti et al., 2013). Degree centrality and eigenvector centrality were significantly correlated in the three networks in both groups (***Table 3.6***). Correlations with flow betweenness were only significant for degree centrality in grooming and huddling networks in both groups. In BDG, the correlation between eigenvector centrality and flow betweenness was significant only for grooming, while in TG, it was not significant for any network. No group showed a significant relationship between flow betweenness and the other centrality measures for proximity within 1m (***Table 3.6***).

Table 3.6. Spearman's rank correlation coefficients of the comparison between individual-level centrality measures.

	BDG	**TG**
Grooming	*D-E: 0.982 (p < 0.001)**	*D-E: 0.884 (p < 0.001)**
	*D-F: 0.906 (p < 0.001)**	*D-F: 0.501 (p < 0.001)**
	*E-F: 0.825 (p < 0.001)**	E-F: 0.115 (p = 0.399)
Huddling	*D-E: 0.975 (p < 0.001)**	*D-E: 0.938 (p < 0.001)**
	*D-F: 0.518 (p = 0.012)**	*D-F: 0.451 (p < 0.001)**
	E-F: 0.401 (p = 0.053)	E-F: 0.185 (p = 0.259)
Proximity 1m	*D-E: 0.951 (p < 0.001)**	*D-E: 0.944 (p < 0.001)**
	D-F: 0.403 (p = 0.053)	D-F: 0.119 (p = 0.399)
	E-F: 0.178 (p = 0.393)	E-F: -0.139 (p = 0.394)

D: Degree centrality. E: Eigenvector centrality. F: Flow betwenness. *: Indicates significant results.

Individual values of flow betweennes for grooming and huddling networks were significantly correlated in both groups (Spearman's rank; BDG: $r_{GRO\text{-}HUD} = 0.598$, p-value = 0.005; TG: $r_{GRO\text{-}HUD} = 0.824$, p-value < 0.001). Individual flow betweenness between close proximity and interaction networks were not significant in any case (BDG: $r_{PR1\text{-}GRO} = 0.046$, p-value = 0.844, $r_{PR1\text{-}HUD} = -0.042$, p-value = 0.844; TG: $r_{PR1\text{-}GRO} = 0.048$, p-value = 0.726, $r_{PR1\text{-}HUD} = 0.129$, p-value = 0.510).

Plots of the distribution of flow betweenness for individuals allow the description of how subjects vary in their contribution to the information flow within their group. Networks based on grooming, huddling and proximity within 1m showed a clearly skewed distribution of individual-level measures of flow betweenness in both groups (***Figures 3.22*** & ***3.23***), indicating that some individuals have the potential to contribute more to the transmission of information than others. In association networks within 5m, the distribution of individual flow betweenness in both groups was more uniform than in the other networks (***Figures 3.22*** & ***3.23***), indicating that group members did not vary much in their roles as connecting paths through which information can flow at this distance.

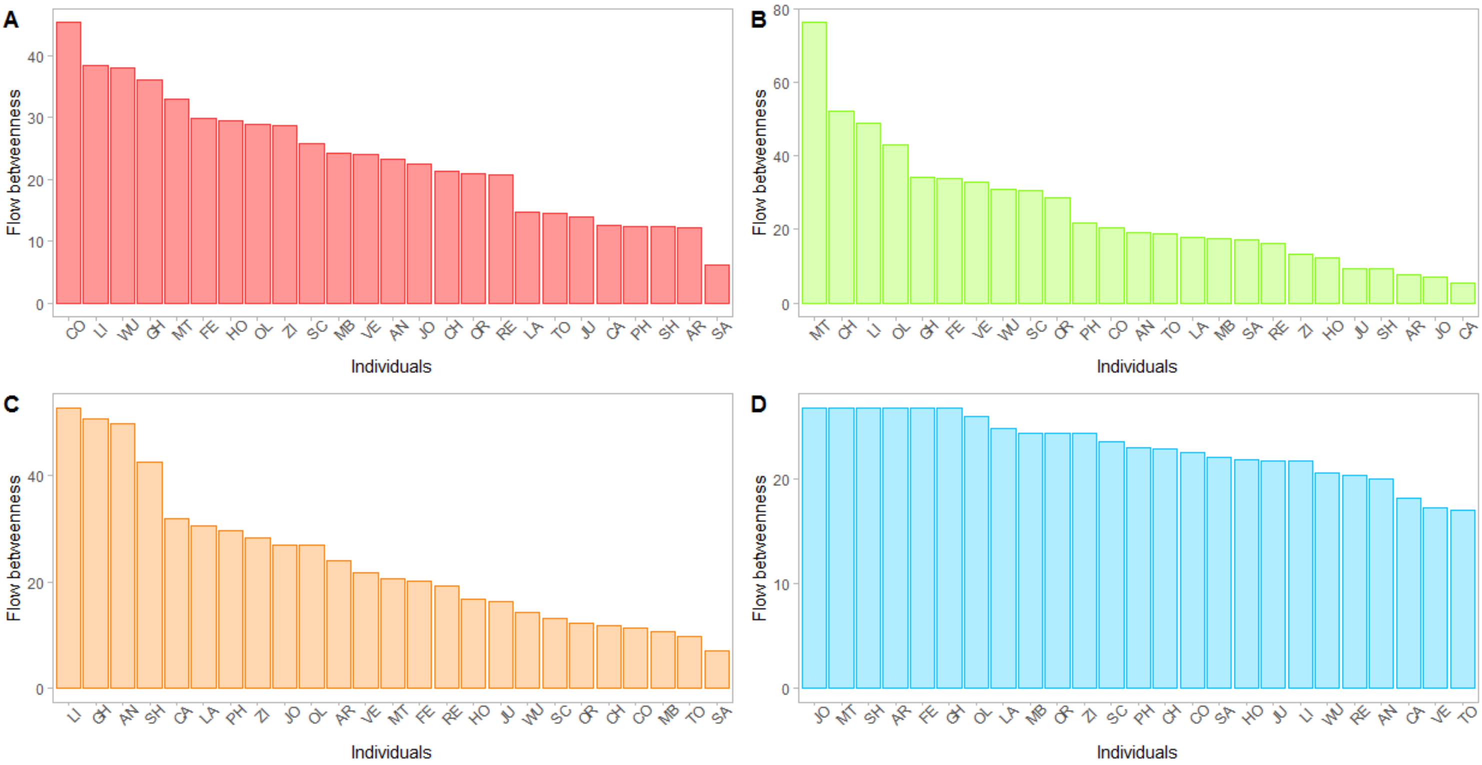


Figure 3.22. Bar-plots for individual-level measures of flow betweenness for interaction (**A:** grooming, **B:** huddling) and association (**C:** proximity 1m, **D:** proximity 5m) networks in BDG.

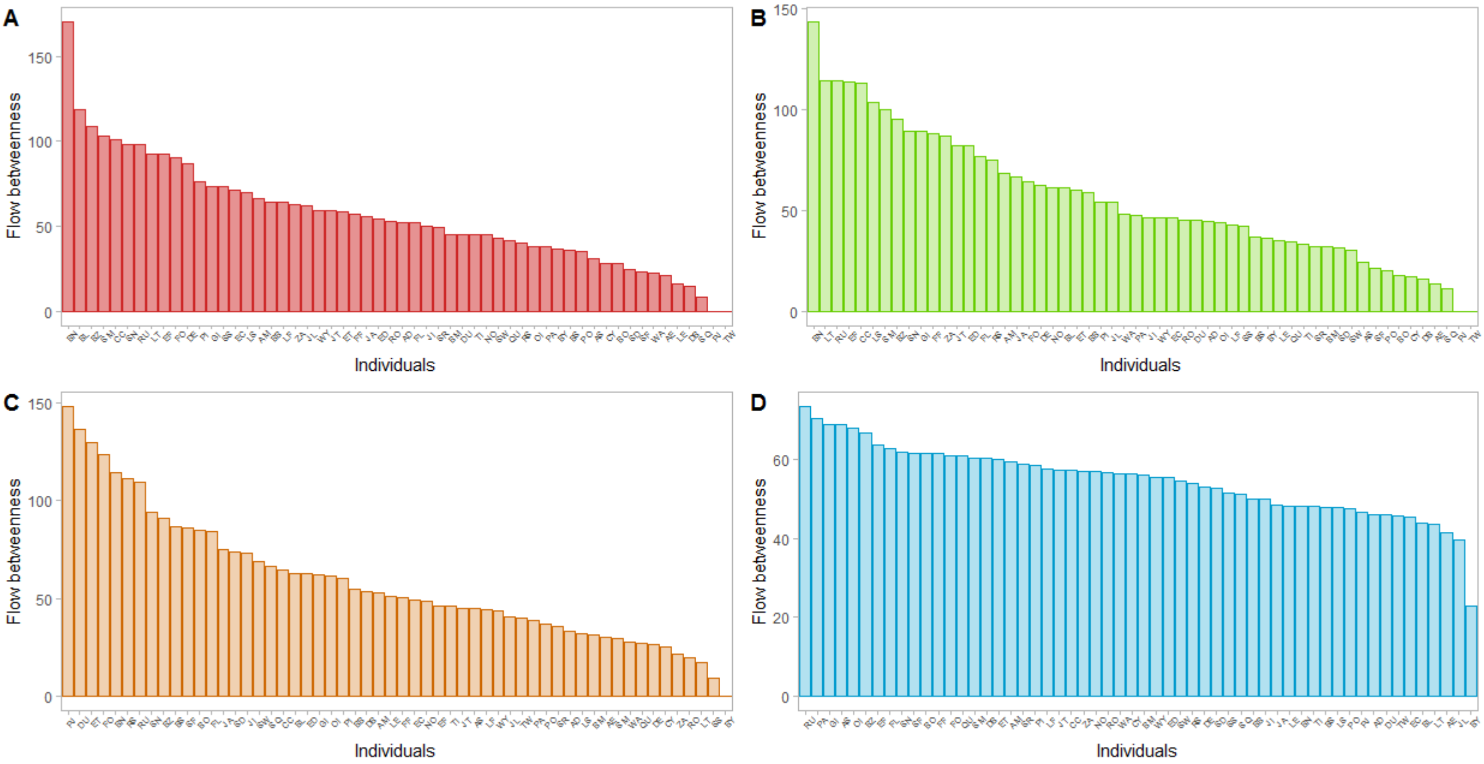


Figure 3.23. Bar-plots for individual-level measures of flow betweenness for interaction (**A:** grooming, **B:** huddling) and association (**C:** proximity 1m, **D:** proximity 5m) networks in TG.

Individuals did not occupy the same position in the plot distribution between networks (***Figures 3.22* & *3.23***), indicating that each affiliative behaviour might be representing a different aspect of the socio-positive relations. Therefore, the role that we assign to each individual in the transmission of information will depend on the measures of affiliation that we use (***Figure 3.24B* & *D***). An affiliative network that combines measures of grooming, huddling and close proximity (CSI, see ***Appendix F***) also showed a skewed distribution for individual-level measures of flow betweenness in both groups (***Figure 3.24A* & *C***).

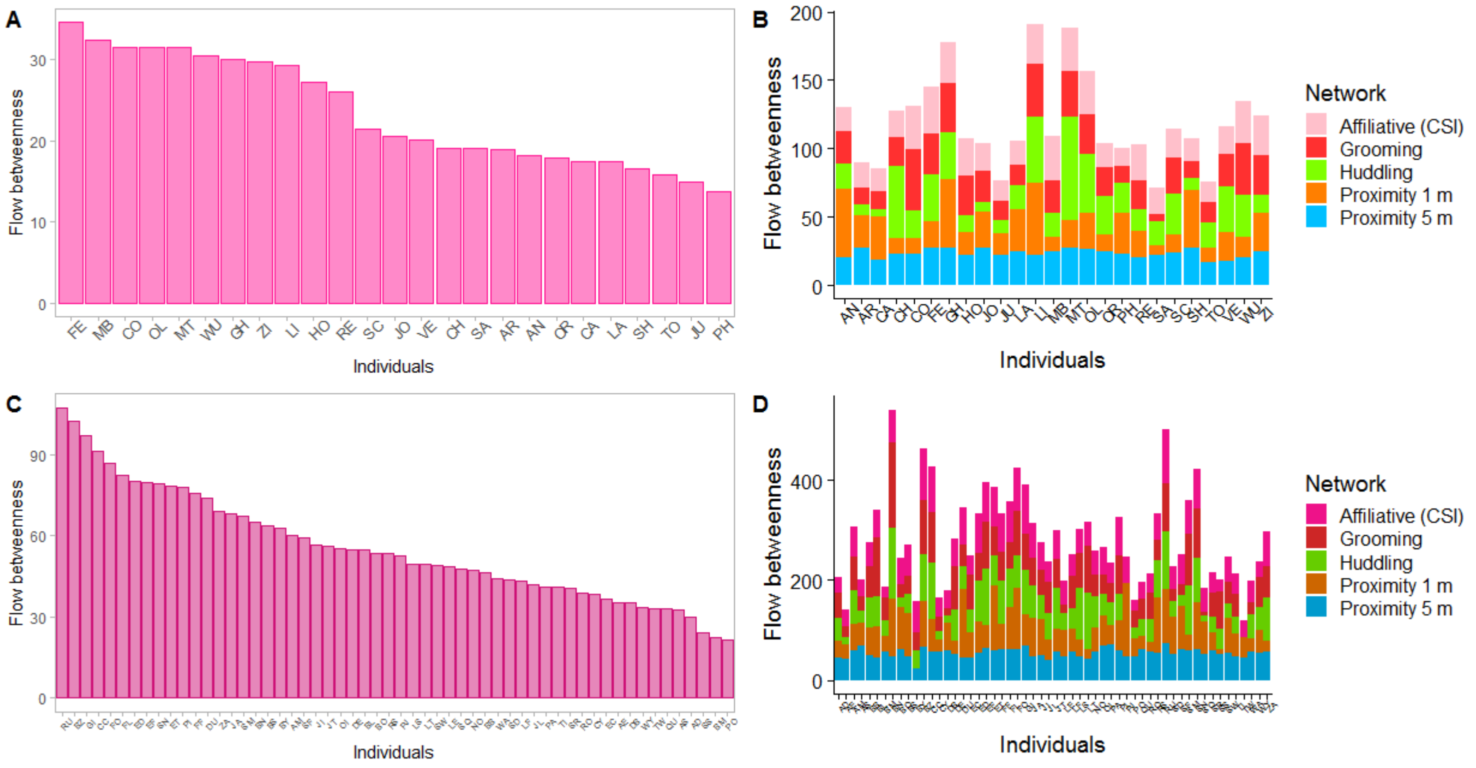


Figure 3.24. Bar-plots for individual-level measures of flow betweenness for both BDG (**A** & **B**) and TG (**C** & **D**). **A:** Bar-plot of individual flow betweenness for the affiliative network CSI of BDG. **B:** Stacked bar-plot of individual measures of flow betweenness for all the networks of BDG. **C:** Bar-plot of individual flow betweenness for the affiliative network CSI of TG. **D:** Stacked bar-plot of individual measures of flow betweenness for all the networks of TG. Affiliative (CSI): network combining grooming, huddling and proximity within 1m (see ***Appendix F***).

3.4. Discussion

In this chapter, I aimed to assess predictions regarding the opportunities for social learning that can be inferred from socio-positive networks in two groups of Barbary macaques. Results confirmed the hypothesis (Hypothesis 1) that grooming, huddling and close proximity networks will be similar in their social structure, depicting asymmetric relations and, therefore, in line with a prediction of, identity dependent, directed social learning (*sensu* Coussi-Korbel & Fragaszy 1995; prediction a). In addition, outcomes support the prediction (prediction b) that association networks within 5m would substantially differ from interaction and close proximity networks, and that social relations would become more symmetric as proximity distances increase. Therefore, results confirm prediction b that information transmission in long-range proximity networks would be less partner-specific (i.e. more conducive to, identity independent, non-specific social learning, *sensu* Coussi-Korbel & Fragaszy 1995) than the other networks, since partner selection and social tolerance becomes less relevant with distance between individuals.

Confirming Hypothesis 2, all networks predicted each other and were influenced by individual attributes (sex, age, social rank and kinship). Close proximity predicted grooming and grooming predicted huddling, as anticipated (prediction a). Although, sex, age and social rank influenced grooming and proximity networks, preferences for those of the same or different category depended on the macaque group and the other types of relations that individuals established with each other. Results, therefore, only partially supported prediction b that stated grooming interactions and close proximity will occur between individuals of the same sex, age and kinship and different social rank. Finally, huddling relations were influenced by the strength of grooming interactions, as anticipated (prediction c). However, grooming partner preferences were also reflected in huddling networks, suggesting that huddling may also be influenced by sex, age, social rank or kinship, contradicting prediction c.

3.4.1. Evidence for directed and non-specific social learning in affiliative networks

Differences in the group-level measures between BDG and TG may be explained by the fact that some dyadic encounters were probably less frequent or less likely in TG compared to BDG due to its larger group size and the more complex ecology of the enclosure. I discuss this in full detail in ***Chapter 6***.

Within each group, significant differences and similarities in the social structure or patterns of relations were found among interaction (grooming and huddling) and close proximity networks. The lowest level of cohesiveness and the greatest heterogeneity in the strength of relations of the huddling networks compared to the close proximity networks suggests that individuals of both groups probably were more selective in choosing their huddling partners than their close associates.

Comparisons with grooming networks led to different conclusions depending on the group considered. Overall, results of the SNA for grooming, huddling and close proximity suggest that (i) in terms of quantity of relations, individuals affiliate with more conspecifics via grooming in BDG, or close proximity in TG, than via other socio-positive behaviours, and (ii) in terms of quality of relations (i.e. strength of relations and distribution of weak and strong connections), grooming networks resembled those based on close proximity in BDG, or huddling in TG.

Despite group differences, values of the group-level measures for grooming, huddling and close proximity were much more similar among these networks within groups than when compared with long-range proximity networks. Long-range (5m) proximity networks displayed higher levels of group cohesion and connectivity, and more homogeneous (i.e. less disparity in the strength of connections) and symmetric relations (i.e. uniform distribution of flow betweenness) than interactions (grooming and huddling) and close proximity networks.

Overall, results suggest that long-range (5m) proximity networks would be more conducive to ‘non-specific social learning’ than grooming, huddling and close proximity, as information that could be readily acquired at a distance would spread rapidly and evenly through this network. Grooming, huddling and close proximity relations were more asymmetric than networks based on associations within 5m, indicating partner choice and selectivity in social tolerance towards specific individuals, implying the flow of information requiring closer proximity would be via ‘directed social learning’ and hence be restricted to certain portions of the group and slow to spread to the whole group (Coussi-Korbel & Fragaszy, 1995).

3.4.2. Affiliative networks predict each other

In both groups, individuals with strong grooming connections were more likely to huddle together, and frequent partners in grooming and huddling interactions were more likely to be found associated within 1m, confirming predictions. The positive relationship among these behaviours concurs with previous findings in Barbary macaques (McFarland & Majolo, 2011; Robouvá et al., 2015; Molesti & Majolo, 2017; Campbell et al., 2018; Ueno & Nakamichi, 2018).

Outcomes support the idea that proximity and affiliative interactions can be used as a proxy of each other (Farine, 2015). However, regression coefficients between long-range (5m) proximity and the other networks, despite being significant, were lower than those obtained in the other network pair-wise comparisons, especially in TG. This may suggest that the ability of proximity to predict interactions will depend on the distance considered (Carter et al., 2015). Moreover, large groups of primates (N > 40) like TG (N > 56) are said to be sub-structured into cliques of strongly bonded individuals (Kudo & Dunbar, 2001; Tokuda et al., 2012). Cliques may form when access to conspecifics is constrained by contextual or environmental factors (Barrett & Henzi, 2001; Henzi & Barrett, 2002), such as natural barriers. Therefore, social relations in TG were probably constrained by the characteristics of the enclosure (see ***Chapter 6***), as indicated by network visualizations and the low values of clustering coefficients that indicate the presence of cliques in this group. This might explain the low regression coefficients for long-range proximity networks and support the idea that the social dynamics of a group or animal taxa may also influence the appropriateness of proximity measures as predictors of interactions (Carter et al., 2015).

3.4.3. Influence of individual attributes in interaction and proximity networks

Grooming networks

Results for BDG seem to confirm previous studies indicating that female Barbary macaques establish stronger grooming relations with other females (McFarland & Majolo, 2011; Roubová et al., 2015). Males are the dispersing sex in Barbary macaques (Thierry et al., 2004), while females do not leave the natal group and have more opportunities to establish strong relations than males (McFarland & Majolo, 2011). Despite this, females tended to interact with males in TG. Kinship is an important factor in partner choice as shown by my results and previous findings (Carne et al., 2011; Roubová et al., 2011) and, at the time of study, 74% of males belonged to one of the 10 matrilines in the TG group. This might explain the bias (significant only for huddling, see below) of TG females for male partners. Kinship was not available for BDG, but one individual (HO) was adopted from another group and half of the males were older than the age at which they leave the natal group (Kuester & Paul, 1999), so they already came from other groups before transfer to Blair Drummond Safari Park. Therefore, only 40% of the males in BDG were likely to have female relatives in the group, suggesting that kinship probably did not have much influence on grooming interactions between sexes in this group.

Interestingly, males showed a preference for grooming with other females (the philopatric sex in Barbary macaques, Thierry et al., 2004; McFarland & Majolo, 2011) in both groups. This preference for the philopatric sex has also been observed in studies of social learning with non-human primates (van de Waal et al., 2010). van de Waal and colleagues (2010) found that vervet monkeys (*Chlorocebus pygerythrus*) significantly paid more attention to females (the philopatric sex) than males when observing the manipulation of a novel foraging task. Since affiliative relations are said to represent social learning opportunities (Coussi-Korbel & Fragaszy, 1995), selective attention towards the philopatric sex in learning contexts (directed social learning, van de Waal et al., 2010) may be mediated by the strength of social relationships between observers and those observed. Grooming relationships established among females (see above) and between males and females in Barbary macaques may indicate potential selective attention (for instance, in a social learning context) towards the philopatric sex in this species.

Results showed that sub-adults had stronger grooming bonds with adults than with other sub-adults. This seems to contradict the “similarity principle” which states that individuals of a similar age are more likely to share stronger bonds with each other (Waal & Luttrell, 1986; McFarland & Majolo, 2011). However, there is evidence, both in favour and against, of grooming preferences for same-age class individuals in Barbary macaques (Widdig et al. 2000; Berghänel et al. 2011; Carne et al. 2011, McFarland & Majolo, 2011). Moreover, age-graded dominance patterns are common in primates (Borgeaud et al., 2016) and have been found in both males and females in Barbary macaques (Paul & Kuester, 1987; Kuester & Paul, 1988). Therefore, the apparent preference of young Barbary macaques to establish socio-positive relations with other age classes may be mediated by the commodities that higher-ranking adult conspecifics may offer (Widdig et al., 2000), as has been observed in other primate species (O'Brien, 1993; Cords et al., 2010). In addition, Barbary macaques of different age classes are often seen engaged in alloparental and triadic interactions that may buffer agonistic tension and lead to other affiliative interactions (Deag & Crook, 1971; Taub, 1980; Small, 1990; Paul et al., 1996; Kümmerli & Martin, 2008; Barale et al., 2015).

In TG, outcomes showed that associates within 5m of an individual with different social rank were preferred as grooming partners except when they were kin; in this latter case, individuals of the same rank class were the preferred partner choice. This double influence of kinship and social rank in partner choice has been found in previous studies with primate species (Suchak et al., 2014; Roubová et al., 2015). Suchak et al. (2014) found that chimpanzees tended to approach (during cooperation tasks) individuals of similar rank to themselves unless the individual at the apparatus was their kin (only in this case, they approached higher ranking individuals). Roubová et al. (2015) found that grooming was more frequent among related than unrelated Barbary macaques and it was directed up the hierarchy. Similarly, my results indicate that individuals associated within 5m engaged in grooming interactions more frequently with those of different rather than same social rank, unless they were kin.

Proximity networks

Barbary macaques tended to associate with those of the opposite sex and age class at both close and long-range distances in TG and at long-range distances in BDG. Individuals in both groups associated within 5m with those of other rank classes. Close proximity networks showed no significant sex and age preferences in BDG and no significant rank preferences in any of the two groups, but a more pronounced general tendency than long-range associations towards same class individuals in some cases. As we increase the distance between individuals, social tolerance for those of other age, sex, or rank classes increases and, therefore, more individuals are expected to be found associated (Coussi-Korbel & Fragaszy, 1995; McFarland & Majolo, 2011; Schnöll, 2014). Accordingly, individuals will be less selective with their associates at 5m than at 1m.

On the other hand, habitat constraints and group size may influence gregariousness (Wrangham, 1980; Cibien et al., 1989; Kudo & Dunbar, 2001) and, consequently, the probability of finding potential partners. Therefore, the fact that sex and age preferences in TG were similar among all networks can be explained by the constraints of the enclosure and the formation of cliques that seem to have restricted both interactions and associations to particular individuals in this group (most likely, influenced by social rank and the degree of mother-relatedness, see below).

Huddling networks

Sex and age preferences in huddling networks converge with those of grooming networks in each group. Campbell et al. (2018) found that the selection of huddling partners in Barbary macaques was only determined by the strength of grooming relations, but not by individual attributes like sex or social rank. Since grooming predicted huddling networks in both study groups, it is likely that the significant results obtained for assortative mixing in huddling networks in this study are a reflection of the partner preferences obtained with grooming. However, outcomes may also be explained by differences in the methods used in this thesis and Campbell et al.'s (2018) study. Campbell et al. (2018) tested the influence of individual attributes in huddling networks using the Multiple Regression Quadratic Assignment Procedure (MRQAP), which generally applies matrix permutations on calculated edge weights (post-network permutation methods, Weiss et al., 2020). Animal network data generally contains greater uncertainty than human networks (Fisher et al., 2017). Accordingly, statistical tools that were developed for the study of human networks, like MRQAP (Krackhardt, 1988), may overlook issues caused by these greater levels of uncertainty in animal network analyses and increase the effect of sampling errors. Therefore, in animal networks, it is preferable to use node-label permutations which rearrange the original adjacency matrix before edge weight calculations (pre-network permutation methods, Weiss et al., 2020), as I did in this thesis.

Results indicate that the social rank of grooming partners and associates (within 1 and 5m) in BDG influenced Barbary macaques' decisions of whom to huddle with. Data showed that the strongest huddling interactions occurred among the lowest ranking females (SA, AN, LA, CA and WU, see ***Appendix A***) who also shared the strongest bonds in grooming and proximity networks (***Figures 3.1–3.7***). Dominant individuals can be a highly valuable resource due to the commodities they can provide in exchange for behaviours like grooming (Barrett et al., 1999; Henzi et al., 2003). Therefore, individuals that already benefit from these privileges may prevent lower-ranking individuals from gaining access to dominant partners (Seyfarth, 1977, 1980; Schino, 2001; Barrett & Henzi, 2001), limiting interactions to other low-ranking conspecifics.

In TG, however, social rank and kinship influenced the choice of huddling and grooming partners among associates. It seems cliques in TG were mainly defined by mother relatedness as 64% and 72% of huddling and close proximity events, respectively, involved, at least, one pair of kin-related individuals, and ~75% (71 out of 95) of all the kin-related pairs observed in huddling networks were also observed in close proximity networks. Kinship was not available for BDG. Considering the matrilineal rank acquisition that characterizes group hierarchy in Barbary macaques (Prud'homme & Chapais, 1993a,b; Maestripieri, 1997; Kuester et al., 1998; Bayne, 2005), I cannot rule out the possibility that the positive influence of social rank on huddling relations obtained in BDG was a spurious result caused by the absence of factors controlling for maternal relatedness in the regression model.

3.4.4. Node contribution to the transmission of information

The differences in the group-level SNA measures found among interaction (grooming and huddling) and close proximity networks indicate that, although they were correlated with each other, these networks might be explaining slightly different aspects of the socio-positive relations. Correlations of centrality measures among these networks provide additional support to this statement.

In grooming and huddling networks, individuals connected to more conspecifics (degree centrality) were those that contributed more to information diffusion (flow betweenness). Degree centrality was not important for information flow in close proximity networks. Network visualizations suggest that individuals that contribute more to the information flow in close proximity networks are those that connect highly dense areas of the network (i.e. bridging individuals connecting cliques or clusters within the network). This result suggests that close proximity captures aspects of affiliative social relations not represented in grooming or huddling networks. Individuals with many connections and strongly connected to highly connected partners (eigenvector centrality) in grooming networks contribute greatly to information flow in BDG, but not in TG. Those with the highest scores of flow betweenness in TG were those bridging highly dense areas of the network. This result may be explained by the presence of cliques that may have constrained the flow of information in TG. The absence of a significant correlation between eigenvector centrality and flow betweenness in huddling and close proximity networks indicates that these two networks, compared to grooming, may explain different biological processes (Farine & Whitehead, 2015; Valente et al., 2008). Based on my findings, I suggest that a network that combines the different measures of affiliation used in this thesis will better capture all the aspects of the socio-positive relations established between pairs of individuals than networks based on single measures of affiliation. Therefore, this combined network would be more representative of social bonds and, hence, more informative about the social learning context (i.e. social learning opportunities) than networks based on one single behaviour (e.g. grooming, huddling or close proximity).

Central individuals seem to have access to many social connections, allowing them access to diverse and less redundant social information than those with fewer connections (Baer et al., 2015). This will make central individuals more likely to acquire highly accurate social information than less central individuals, facilitate the spread of information to others, refine and improve innovations via peer feedback and succeed in novel problem-solving tasks (Fleming & Waguespack, 2007; Rawlings, 2018). Previous research has reported that central individuals (in terms of degree centrality, eigenvector centrality and flow betweenness) in human and nonhuman animal societies are more likely to acquire social information than less central individuals, and may facilitate social diffusion within the group (Mednick et al., 2010; Claidière et al., 2013; Kulahci et al., 2016; Carter et al., 2016; Rawlings, 2018). Moreover, highly innovative individuals are thought to score high in centrality measures such as flow betweenness or eigenvector centrality (Kratzer & Lettl 2008; Aplin et al., 2012; Wascher, 2015).

My results highlight that the ability of each centrality measure to determine how individual network positions influence the information flow will depend on the social behaviour and the group considered. Group size and the characteristics of the environment seem to have influenced social dynamics and structure (e.g. more cliqued in TG than in BDG) in the groups here studied (see ***Chapter 6. General discussion*** for further details). Accordingly, in networks with many areas of high and low density of connections (such as cliqued affiliative networks in TG or close proximity in BDG), individuals connecting these areas (i.e. bridging individuals connecting cliques or clusters) seem to be more important in social information diffusion than those central in terms of degree or number of highly connected partners (eigenvector centrality). In summary, social structure that depends on the nature of the interaction considered (e.g, grooming, proximity) and the number of available partners (group size and environmental constraints) will influence the contribution of each individual to the pattern of social diffusion of information (see ***Chapter 6***).

3.4.5. Conclusion

Grooming, huddling and close proximity networks were similar in their social structure and depicted asymmetric relations conducive to directed social learning. Long-range proximity networks were more conducive to non-specific social learning (i.e. they depicted more symmetric relations) than interaction (grooming and huddling) and close proximity networks. Moreover, all affiliative networks predicted each other.

Flow betweenness may predict which individuals contribute more to the spread of novel information within a group. However, other variables such as social tolerance near a highly valuable resource and the dynamics of who has priority access to resources (not considered in this analysis) may be relevant factors in shaping the order of acquisition of social information in a learning context.

Grooming, huddling and close proximity networks showed similarities in their social structure but they seemed to explain slightly different aspects of the social relations. These three networks can be informative for modelling social learning using NBDA, but a network combining grooming, huddling and close proximity may be more representative of affiliative relations to test for social learning.

Chapter 4

Communication networks: on the relationship between communication and social dynamics

Abstract

In this chapter, I aim to understand how social relations established via affiliative interactions (grooming, huddling) and associations (proximity) predict communication behaviours in Barbary macaques. I use Social Network Analysis (SNA) to: a) describe a series of communication networks reflecting affiliative and agonistic situations, b) make predictions about the relationship between communication and social dynamics in socio-positive contexts, c) provide a new layer of understanding regarding the function of some vocalizations, d) determine what individual attributes shape the exchange of information through the communication signals collected, and e) discuss the potential link between social bonds, communication and social learning.

Outcomes indicated that affiliative networks predicted communication networks. Females that uttered vocalizations in agonistic contexts to recruit coallitionary support (aid-recruitment calls) received support from closely bonded female and male partners, when opponents had a lower rank than the helper. The occurrence of vocalizations (known as 'vocal comments') uttered when observing infant-handling interactions (i) were predicted by huddling relations between callers and infant-handlers, and by grooming relations between callers and the mothers of the infants involved, and (ii) seemed to function to signal collective arousal or social tolerance near the infant involved in the infant-handling party. Results also indicated that vocalizations (also 'vocal comments') uttered when observing third-party agonistic encounters can be understood as vocal alliances since they mainly occurred when the aggressor was an ally and the victim was a relatively weakly-bonded conspecific. As affiliative relations (representing potential pathways of social information diffusion) predicted communication networks, the findings highlight that communication networks may well represent social learning opportunities.

This chapter begins with general introduction and methods sections before splitting into Part A, on aid-recruitment calls, and Part B, on vocal comments, each with their own results and mini discussion, before finishing with a general discussion.

I acknowledge the contribution of Dr. Julia Fischer, from the Cognitive Ethology Laboratory at the German Primate Center, who provided the audio files of Barbary macaques' vocalizations used in this thesis for sound quality analyses and comparisons with vocalizations recorded in this study.

4.1. General Introduction

Disagreements on how to conceptualize communication have been, and still are, a source of intense debates in the scientific literature (Rendall et al., 2009; Font & Carazo, 2010; Seyfarth et al., 2010; Wheeler et al., 2011; Schaefer & Ruxton, 2012; Liebal et al., 2013; Krause et al., 2014; Scott-Phillips, 2015). However, many theories and empirical studies have highlighted the importance of communication in the evolution of social complexity irrespective of the communication definition adopted (McComb & Semple, 2005; Freeberg et al., 2012; Sullivan, 2017). One of the first arguments in favour of the role of communication in the maintenance of social relationships was provided by Dunbar (2004) in order to explain how human language evolved. The 'Gossip Hypothesis' (Dunbar 2004) states that communication developed to help maintain social bonds and group cohesion in large primate societies.

Many authors have demonstrated the association between social and communication complexity in primate species (McComb & Semple, 2005; Freeberg et al., 2012; Sullivan, 2017). McComb & Semple (2005) showed that vocal repertoires in non-human primates increase with group size and the time spent in socio-positive interactions. A prior study by Maestripieri (2000) also suggested that gestural communication complexity coevolved with social organization in macaques. Later, Freeberg et al. (2012) reviewed all the evidence in support of the 'Social Complexity Hypothesis' which posits that species with complex social systems require more complex communication repertoires to manage social interactions and bonds among individuals. The authors discussed the role of social complexity as a driver of communication complexity, highlighting that those societies where individuals frequently and repeatedly interact with each other in different contexts need a larger number, and greater diversity, of communicative behaviours than other social groups (Freeberg et al., 2012).

In the last two decades, primatologists have been interested in exploring the relationship between communication and sociality, not only to unravel how human language evolved (Maestripieri, 2000; McComb & Semple, 2005; Pollick & de Waal, 2007; Arbib et al., 2008; Corballis, 2009; Dunbar, 2012; Freeberg et al., 2012), but also to understand how primates navigate the complexities of social life (Snijders & Naguib, 2017). Calls, gestures and facial expressions seem to have coevolved with sociality in primate species (Gustison et al., 2012; Liebal et al., 2013; Snijders & Naguib, 2017). For instance, Fedurek et al. (2013) found that male chimpanzees were more likely to join the pant-hoots of their long-term and short-term affiliates than those of other individuals, indicating that coordinated vocal displays may function as bonding signals in this species. More recently, Roberts & Roberts (2019b) determined that the rate of production of visual gestures in chimpanzees was positively correlated with time spent in close proximity only when they were accompanied by synchronized pant-hoot calls, highlighting the role of multi-modal communication in the establishment and maintenance of social relations.

Most of the above studies are based on signaller-receiver dyads in which it is assumed that responses to communication behaviours are only exchanged between the two individuals of a pair (McGregor, 2005; Snijders & Naguib, 2017). However, communication occurs within a social environment and may affect individuals that are not involved in the initial interaction (McGregor & Peake, 2000). Animal communication signals are key in cooperative and competitive relations, mate choice, foraging behaviours and anti-predator and resource-defence strategies, and provide information about the quality of individual features and individuals' motivations or intentions (Bradbury & Vehrencamp, 2011; Liebal et al., 2013; Snijders & Naguib, 2017). For instance, eavesdropping of friendly male grunts and female copulation calls allows male chacma baboons (*Papio ursinus*) to monitor consortships between high-ranking males and oestrus females to recognize unexpected mating opportunities (Crockford et al., 2007). Accordingly, eavesdropping effects should be considered when we aim to understand how communication is able to shape social relations (Snijders & Naguib, 2017).

To this date, only a few animal studies have included the social context in which signals occur to investigate the links between communication and social dynamics (Snijders & Naguib, 2017). The approach used by most of these studies is Social Network Analysis (SNA) whereby a network of dyadic interactions is built that connects several or all the individuals in a group (Kasper & Voelkl, 2009; Sueur et al., 2011). In primates, the use of SNA to integrate communication and social networks has been scarce. Grooming networks have been found to significantly predict a communication network based on contact calls in ring-tailed lemurs (Kulahci et al., 2015). In a more recent case, Roberts & Roberts (2019b) found a relationship between close proximity networks and communication networks based on multi-modal signals (a combination of gestures and vocalizations) in chimpanzees. The use of SNA tools to build communication networks provides a better approach to study the role of communication signals in primate social lives than methods based on independent dyadic relations (McGregor, 2005; Snijders & Naguib, 2017).

Many of the investigations that have integrated communication signals in the study of sociality have focused on how communication signals connect individuals or help to maintain social bonds (Waser & Wiley, 1979; Wiley, 1983; Whitehead, 1987; Gerhardt & Bee, 2006; Naguib et al., 2011; Maciej et al., 2013; Roberts & Roberts, 2019a,b). For instance, Whitehead (1987) showed how mantled howler monkeys (*Alouatta palliate palliata*) use vocalizations to adjust the spacing between groups, and Maciej et al. (2013) determined that Guinea baboons (*Papio papio*) use grunts to regulate close proximity interactions. However, the strength and the positive or negative nature of dyadic relations may also influence the way individuals communicate or respond to signals (Fayet et al., 2014; Kulahci, 2015). This approach, however, has been poorly explored in animal network studies (Snijders & Naguib, 2017). Accordingly, the study of vocalizations that represent the strength and nature of social relations might provide more insights on the role of communication interactions in animal social lives.

Calls elicited in conflicts to recruit coalitionary support are a good example of vocalizations that mirror the strength of socio-positive relations between individuals (Gouzoles et al., 1984; Slocombe & Zuberbühler, 2007; but see Fedurek et al., 2015). In many primate species, including Barbary macaques, individuals that provide agonistic support to one of the individuals involved in a conflict (the aggressor or the victim) are generally strong affiliates of the recipient of support (Widdig et al., 2000; Watts, 2002; Berghänel et al., 2011; Gilby et al., 2013; Young et al., 2014). Other vocalizations that may reflect the strength and nature of social relations are, so-called, 'vocal comments' (Brumm et al., 2005). These calls are elicited by individuals that observe a third-party interaction that can be affiliative or agonistic (Fisher & Hammerschmidt, 2002; Brumm et al., 2005) and might help to strengthen social bonds (Whitham et al., 2007). Accordingly, in this chapter, I aim to use SNA to investigate how socio-positive networks that represent social bonds (grooming, huddling and proximity) affect communication interactions, specifically aid-recruitment calls and vocal comments.

I hypothesized that affiliative networks would predict communication networks in Barbary macaques, as has been reported in other primate species (Kulahci et al. 2015; Roberts & Roberts, 2019a,b). Specifically, I predicted that grooming, huddling and close proximity networks (which predict each other, see ***Chapter 3***) would predict the patterns of relations of communication networks based on: a) who provides support to whom after aid-recruitment calls uttered in agonistic contexts, b) the relationship between individuals producing vocal comments and those involved in the third-party interaction observed. In other words, those individuals with strong connections in social networks representing grooming, huddling and close proximity are expected to have strong connections in networks representing helping responses to aid-recruitment calls and in networks representing the affiliative relations between vocal commenters and those involved in the commented-upon third party interaction.

4.2. General Methods

4.2.1. Data collection

Data on communication interactions was only collected in BDG (see ***Chapter 2***). Vocalizations were recorded opportunistically during the 1029 sessions of behavioural observations. Also, 263 audio recording sessions of 5 minutes of duration were carried out to increase the likelihood of capturing vocal behaviours. These recording sessions took place during feeding times and between behavioural sampling sessions. A total of 6460 minutes (an average of 258.4 minutes per subject) of observations and recordings (1292 sessions) during 54 days were devoted to collect aid-recruitment calls and vocal comments.

Aid-recruitment calls were defined as calls produced after agonistic displays (see ***Table 2.3*** in ***Chapter 2***) accompanied by searching behaviours (i.e. standing up and/or stretching up the neck to look around or to turn the head apparently towards a particular individual). The following data were collected during aid-recruitment vocal events: a) callers' ID, b) IDs of all subjects involved in the conflict and their apparent role (victim, aggressor, etc.), c) ID of all subjects that provided agonistic support to one of the parties (i.e. the individual supports the aggressor or the victim by directing agonistic displays to its opponent, see ***Table 2.3***), d) location in the enclosure where the event occurred, e) context (who started the conflict and what happened after), f) a sample of the vocalization (only during audio recording sessions).

Vocal comments were defined as vocalizations occurring within 2 seconds after a social interaction between other group members in view of the caller who does not participate in the interaction and does not show any other reactions within 5 seconds of vocalizing (Brumm et al., 2005). Only those calls that met this description and where callers were directing their gaze or face towards the third-party interaction (a deviation of about 30º to either side was tolerated) were considered vocal comments. The following data were gathered during vocal comments: a) callers' ID, b) ID of all the participants in the third party interaction, c) distance between caller and individuals involved in the third-party interaction, d) a sample of the vocalization (only during audio recording sessions) and e) context (if third party individuals were involved in agonistic or affiliative interactions, see ***Part B***).

All audio recordings were collected using a Seinheisser ME66 Condenser Microphone + K6 Power Module and a Marantz PMD661 Audio Recorder. Vocalizations were captured in Dual Mono, at a distance of 5 – 10m from the source, using a sampling rate of 48 kHz, stored at a bit depth of 16-bits and named following the recommendations by Fischer et al. (2013). Sound pressure was measured before the recordings to determine the background noise and ensure a good signal-to-noise ratio (McGregor, 2005). The use of headphones connected to the audio recorder allowed adjustment of the recording-level gear to avoid clipping of the sounds.

4.2.2. Qualitative analysis of sound recordings

Prior to data collection, I spent six weeks collecting audio recordings to become familiarized with the vocalizations and the contexts in which they were produced. The spectrograms and the sounds recorded were compared with audio files of Barbary macaque vocalizations provided by Julia Fischer (Fischer & Hammerschmidt, 2002) and the spectrograms presented in Brumm et al. (2005). Raven Pro

1.5 Interactive Sound Analysis Software was used to visualize and inspect the audio recordings to ensure that the vocalizations studied shared the same acoustic and temporal characteristics as those described in previous studies.

All spectrograms were initially visualized using a Hanning window type of size = 375 samples and a 3 dB Filter Bandwidth = 184 Hz, a frequency grid of 512 samples of DFT size and 93.8 Hz of grid spacing, a time grip overlap of 80% and a hop size of 75 samples (Charif et al., 2010). Window size was later set to 800 samples only for vocal comments. According to the quality of the recordings, some of these features were adjusted along with brightness and contrast to ease the visualization of the spectrograms and the comparison with those of previous studies (Fischer & Hammerschmidt, 2002; Brumm et al., 2005).

To identify the vocalizations in the 5-minute-long recordings, I used the Band Limited Energy Detector (BLED) tool incorporated in Raven Pro 1.5 Interactive Sound Analysis Software. This automatically detects the signals that meet a series of predefined acoustic and temporal parameters (signal-to-noise ratio, noise power, frequency and duration range, and bandwidth). Criteria were chosen according to acoustic and temporal features of the calls of interest described in previous research (Fischer & Hammerschmidt, 2002; Brumm et al., 2005) and the guidelines of sound quality provided by Fischer et al. (2013). An inspection of the selected signals removed those that met the criteria but were not the Barbary macaque calls under study, and included those of interest that were not selected by the BLED tool. After a visual and acoustic inspection of the calls selected, I classified the recordings into three quality categories: good, low and bad.

Bad quality recordings were those in which: a) the background noise was higher than a threshold value (i.e. low signal-to-noise ratio, generally due to visitors' car engines), b) the call was recorded from a long distance (i.e. signals were of low power), c) the recording contained overlapping screams of several subjects (this generally occurred during conflicts among adult males, making it impossible to isolate the calls of each subject). Low quality recordings were those where: a) some parts were of low power, b) there was some background noise overlapped with some signals, c) some calls were clipped in the waveform. Good quality recordings were those where all the recording or a great part of it (containing several calls) were clearly audible and did not include any distortion of their acoustic or temporal features. This first analysis allowed me to adjust the settings of the recording sessions and the equipment, as well as to improve my sound recording technique.

The calls extracted from the good recordings were visually inspected and, a series of acoustic and temporal parameters were measured to make comparisons with the available data in Fischer & Hammerschmidt (2002) and Brumm et al. (2005). The different calls and their contexts were classified and contrasted with those of the aforementioned studies to ensure that the call types recorded had already been described in the situations I aimed to study. This qualitative analysis was the final step to filter the events that were included in the construction of the communication networks (see ***Appendix I*** for a detailed description of the analyses and the vocalizations used in this thesis).

4.2.3. Social network metrics and statistical analyses

For the analyses, the only juvenile in the group (AR) was considered a sub-adult. Adequacy of datasets was tested following the recommendations of Whitehead (2008) and Farine & Strandburg-Peshkin (2015) (see ***Chapter 2*** for further details).

To describe and compare the social structure and patterns of relations of the communication networks with those of affiliative networks, I used the same group-level SNA metrics used in Chapter 3 (see ***Table 2.7***): Average node strength, Density, Component ratio, Average degree, Average clustering coefficient, Flow betweenness centralization index (NCI), Mean edge weight, Disparity and Assortative mixing (measured using the E-I index, see ***Chapter 2***) for sex, age and social rank (entered as categorical variables). A randomization procedure was used to determine if the results for assortative mixing in each network were significantly different from what could be obtained if interactions were arbitrary, as well as to investigate whether different networks displayed the same patterns of preferred relations (see ***Chapter 2*** for further details). Grooming, huddling, proximity within 1m (close proximity) and a combination of these three social behaviours using the Composite Sociality Index (CSI) were used as affiliative networks (see ***Appendix F***).

Permutation-based linear-mixed-model regressions were used to test whether socio-positive relations predict the communication interactions observed. In all linear regressions, communication networks were entered as the dependent matrix and socio-positive networks as the independent matrix. The grooming network was chosen as the socio-positive matrix in the first set of regression models. As the outcomes of the previous chapter indicate that huddling and close proximity may reflect aspects of the social relations that are not captured by grooming interactions, an affiliative network combining grooming, huddling and close proximity relations was built (see ***Appendix F***) to make a second set of regressions with communication networks. This enabled testing of whether extra information regarding social bonds provides better predictions of the interactions established through vocal behaviours. Akaike Information Criterion (AICc) was used to determine which model better explained the data.

Sex, age and social rank were entered as confounding factors in network regressions. Sex and age were entered as categorical variables in the form of similarity matrices. Triadic awareness in Barbary macaques (see ***Part A***) suggests that the relative differences in social rank amongst all the individuals involved in agonistic or infant-handling situations is relevant to understand the occurrence of aid-recruitment calls and vocal comments, and the response to these calls. Accordingly, social rank was entered as a matrix of the relative differences in the ordinal ranks obtained as the median rank of all the rank hierarchy calculation methods (see ***Appendix A***).

All networks were undirected for the calculation of SNA metrics to aid comparisons of these measures amongst behaviours. Weighted and unweighted versions of each network were generated for the calculation of different network measures (see ***Table 2.7***). The strength of relations was calculated in R for weighted networks using the Simple Ratio Index (SRI), and coded into adjacency matrices (see ***Chapter 2***). These matrices were used to visualize the network using the software NetDraw. Directed and weighted versions of the networks were used in regression analyses. Shapiro-Wilk normality tests were performed for all the SNA metrics. In most cases, data was not normally distributed, so non-parametric tests were used for further analyses (see ***Appendix E***).

All the statistical analyses were performed in R. SNA metrics were also calculated using R software. All the p-values obtained in network comparisons were adjusted using a Benjamini-Hochberg correction with a False Discovery Rate (FDR) = 5%.

4.3. PART A – AID-RECRUITMENT CALLS

4.3.1. Introduction

Aid-recruitment calls are high-pitched complex screams of long duration that occur during agonistic interactions (Fischer & Hammerschmidt, 2002). Callers normally stand up and/or stretch up their necks and turn their heads towards a particular subject or look around while producing these vocalizations (Fischer & Hammerschmidt, 2002). After these calls, individuals not involved in the conflict may hurry toward the caller and provide support by threatening or charging the aggressor (Goodall, 1968). It is known that aid-recruitment calls can be modified depending on the audience composition (Slocombe & Zuberbühler, 2007), making them more likely to occur (Caine et al., 1995; Brosnan & de Waal, 2000; Di Bitetti, 2005; Zuberbühler, 2017) or more salient (Pollick et al., 2005; Slocombe & Zuberbühler, 2007; Zuberbühler, 2017) to attract allies. However, these calls can also be seen as advertisement signals: vocal displays that (apart from attracting mates) may also have an effect on repelling rivals (Snijders et al., 2017).

It has been suggested that primates may use one of two main strategies when deciding whether to intervene in a third-party interaction, depending on their level of triadic awareness (Slocombe & Zuberbühler, 2007). Triadic awareness is defined as the cognitive ability to understand the social relations that other individuals establish and to picture the different triangular relationships that are formed within their social group (Slocombe & Zuberbühler, 2007). Some primates (e.g. sooty mangabeys) use egocentric heuristics, and base their decision on a set of simple rules rather than recognition of third-party relationships (Range & Noë, 2005). In contrast, other primate species (e.g. baboons, chimpanzees) have a sophisticated knowledge of triadic relationships that can be based on a complex hierarchical organization (e.g. relative individual social ranks and matrilines, Bergman et al., 2003) or on strategic changes in coalition partners (Slocombe & Zuberbühler, 2007).

Grooming is known to be exchanged in return for coalitionary support (Watts, 2002) and contributes to the development and maintenance of alliances that can influence social ranks (Mitani, 2009; Gilby et al., 2013; Langergraber et al., 2013). Therefore, social bonds established via grooming can be an important factor in deciding whether to respond to an individual's recruitment call. In addition, it is known that priority access to resources or commodities can be guaranteed through social bonds established via social behaviours other than grooming. For instance, coalition support has been labelled as a commodity that Barbary macaques obtain from their close associates as well as their grooming partners (Young et al., 2014).

Barbary macaques are known to provide coalitionary support to others based on their degree of relatedness, the social bonds that they share and the social rank of the individuals involved in the conflict (Widdig et al., 2000; Young et al., 2014). Widdig et al. (2000) found that male Barbary macaques intervened twice as often in conflicts when kin-related individuals were involved than in those involving non-kin (kin selection). Also, male Barbary macaques gave support to those from whom they received support in the past (reciprocal altruism) and when both individuals involved in the conflict were of lower rank than themselves (Widdig et al., 2000). In fact, Barbary macaques, like other animal species, seem to evaluate the risks of each situation and display coalition behaviours when the benefits of the intervention outweigh the costs (Snijders & Naguib, 2017). Young et al. (2014) confirmed that Barbary macaque males provide aid in conflicts when the recruiter and the supporter are strongly bonded via grooming or proximity. Moreover, recruiters do not simply ask to the closest individual for help but direct their recruitment requests to the highest ranking individual (Young et al., 2014). Consequently, it seems that Barbary macaques have a considerable amount of triadic awareness and use their social knowledge flexibly when recruiting allies during agonistic encounters.

According to the studies aforementioned, I hypothesized that communication networks based on aid-recruitment calls would be predicted by affiliative networks and influenced by individual attributes. Specifically I predict:

(i) Grooming networks will predict who responds to whose recruitment calls in BDG.

(ii) Considering that grooming also predicted huddling and proximity networks in the previous chapter and that affiliative behaviours other than grooming may also be exchanged for coalition support, I expect that huddling and proximity will also predict who backs up whom in aid-recruitment events.

(iii) The social rank of the individuals involved in the conflict will influence the decision to provide support, so that individuals will only respond to a recruitment call if the individuals involved in the agonistic interaction are of lower rank than themselves.

I will explore what characteristics of the aggressors may be relevant to trigger aid-recruitment calls and further investigate the potential role of these calls in dissuading an aggressor from directing agonistic displays (see ***Table 2.3***) towards the victim. Due to the lack of kinship data and the short study period, I will not test for kin selection or reciprocal altruism in aid-recruitment contexts.

4.3.2. Specific methods and analyses

Five roles were described for individuals involved in agonistic contexts in which aid-recruitment calls were produced: a) recruiter: individual that produces the aid-recruitment vocalization, b) aggressor: adversary of the recruiter in the conflict, c) helper: individual that provides support to either the recruiter or the aggressor, d) recipient: individual (it can be either the recruiter or the aggressor) that receives support from the helper, e) opponent: individual who the helper goes against. Based on these roles, I built three types of networks to investigate what triggers the occurrence of aid-recruitment calls and which factors are relevant to Barbary macaques when responding:

- **Recruiter-aggressor network:** to study what individual attributes may influence whether an individual calls for help.

- **Helper-recipient network:** who provides support to whom; to investigate how the strength of social bonds and the relative differences in terms of individual attributes (e.g. sex, age, rank) between individuals that receive support and helpers, influence conflict interventions.

- **Helper-opponent network:** who provides support against whom; to determine the relationship between the helper and the rival of the individual that receives support as well as their differences in terms of sex, age and social rank that may explain the pattern of helping behaviour.

Group-level SNA metrics were used to make network comparisons and discuss the dynamics of the occurrence of these calls and the responses they elicit.

Permutation-based linear-mixed-model regressions were used to test which individual factors (sex, age and social rank) influenced communication networks and whether they were predicted by affiliative relations. The three communication networks based on aid-recruitment calls were tested against grooming (understood as a coalitionary behaviour) in network regressions. In addition, since grooming, huddling and close proximity predict each other but reflect different aspects of social relations (see ***Chapter 3***), an affiliative network combining the three behaviours (CSI, see ***Appendix F***) was used to test whether these three aid-recruitment networks were predicted by social bonds in network regressions. Finally, the helper-recipient network was also tested against huddling and close proximity to explore which of the affiliative behaviours were more relevant in predicting who is backing up whom during agonistic encounters.

In communication networks, the direction of the behaviour is relevant to understand the dynamics of these interactions. Assortative mixing and linear regressions show whether communication interactions are established between individuals of the same or different sex, age or social rank, but do not tell us which of these attributes characterize the caller and which the receiver. Therefore, I tested whether the strength of connections of pairs of individuals of the same class was significantly higher or lower than the strength of connections of pairs of individuals of a different class for each attribute (sex, age, social rank). This involved Kruskal-Wallis rank sum tests followed by post-hoc Dunn tests adjusted for multiple comparisons using Benjamini-Hochberg corrections.

To further investigate what triggers aid-recruitment calls in Barbary macaques, Kruskal-Wallis and Dunn tests were also calculated for agonistic contexts where aid-recruitment calls were not produced (i.e. non-vocalized instances), and results were compared with those obtained for the recruiter-aggressor network. Similar results between vocalized (aid-recruitment calls) and non-vocalized instances might indicate that the greater occurrence of calls between particular dyads (e.g. female callers against male aggressors) may be a spurious result due to a greater number of agonistic encounters between these dyads. In order to identify spurious results, a chi-square analysis was carried out comparing those dyads that resulted in similar outcomes for both vocalized and non-vocalized instances. The chi-square analysis compared the proportion of cases per dyad obtained for non-vocalized versus vocalized instances.

4.3.3. Results

Adequacy of datasets

Results can be found in ***Appendix C***. This first inspection of the data indicated that long and complete datasets were collected, yet all communication networks could be deemed as sparse as few observations per dyad were available. Precision and accuracy measures showed that the levels of uncertainty of the communication networks were low and that the sampling effort was high enough to generate reliable measures of edge weights in all cases. The results suggest that the patterns of the relationships captured in the datasets were not the result of random interactions in communication networks of aid-recruitment calls.

Description and visualization of communication networks

Aid-recruitment calls were collected during 111 sessions of a total of 1292 sessions (8.59%). Aid was provided in response to aid-recruitment calls in 50 of 1292 sessions (3.87%). These measures indicate that occurrence of aid-recruitment calls and the responses they elicit are not frequently observed in Barbary macaques and a big sampling effort is required to obtain representative datasets. In total, 23 of 25 individuals (excluding infants) were observed producing aid-recruitment calls with an average of 6.92 (range: 1 – 28) calls observed per individual (see ***Table 4.1*** for detailed information per classes of individuals).

Table 4.1. Sampling effort and completeness of the datasets per classes of individuals (aid-recruitment calls).

	Females	**Males**	**Adults**	**Sub-adults**	**High-ranking**	**Middle-ranking**	**Low-ranking**
Sampling effort	104 (8.05%)	23 (1.78%)	100 (7.74%)	27 (2.09%)	22 (1.70%)	56 (4.33%)	49 (3.79%)
Total individuals per class	15/15	8/10	17/19	6/6	7/9	8/8	8/8
Average (range) of calls per individual	9.07 (1 – 28)	4.25 (1 – 7)	8.12 (1 – 28)	5.33 (2 – 9)	4.86 (1 – 7)	8.63 (2 – 17)	8.38 (1 – 28)
% of events observed per class	80%	20%	81.18%	18.82%	20%	40.59%	39.41%

Sampling effort: Total number of sessions where individuals of each class were observed producing aid-recruitment calls (percentage calculated dividing by total number of sessions collecting vocalizations = 1292 sessions). Total individuals per class: number of individuals of each class observed producing aid-recruitment calls/number of individuals of that class in the group. Only OL and PH (the two highest-ranking males at the end of the study) were not observed producing aid-recruitment calls. Note that in one session, more than one event may occur, and more than one individual may be calling in the same event.

During the study period, macaques were recorded producing aid-recruitment calls on 219 occasions. In 86 (39.27%) of these events other individuals intervened in the conflict to back up one of the parties. In 25 of the 86 events (29.07%), more than one ally provided support to one of the parties. Note that in non-vocalized contexts, aid to third-parties was only provided in 1.2% (10) of all agonistic encounters recorded (838 in total).

In 50% of the 86 events, callers were backed up by one or more allies while in the other 50% of the events it was the aggressors who received aid from allies. Only in 6 events, both callers and aggressors received support simultaneously.

Group-level SNA metrics

Density, node strength, average degree and mean edge weight measures were higher in the recruiter-aggressor network than in helper-recipient and helper-opponent networks (***Table 4.2***), indicating that not all the individuals that produced aid-recruitment calls received support from their peers.

Interestingly, both recruiter-aggressor and helper-recipient networks formed a single component connecting all the individuals in the group. In the helper-opponent network we find one isolated individual: AR (***Figures 4.1 – 4.3***). This macaque was the youngest male and the only juvenile in the group at the time of the study. AR produced recruitment calls on seven occasions and acted as an aggressor on one occasion. No individual in the group went against this juvenile when providing support to an ally, likely as he was a high-ranking juvenile.

Table 4.2. Results of the group-level SNA metrics for communication networks based on aid-recruitment calls.

Network	NS	Density	Degree	NC	CR	MEW	Disparity	CC	NCI (%)
Recruiter-aggressor	0.029	0.367	8.8	1	0	0.001159	0.181878	0.466	6.695
Helper-recipient	0.016	0.247	5.92	1	0	0.000654	0.292713	0.352	8.161
Helper-opponent	0.016	0.247	5.92	2	0.0435	0.000646	0.249196	0.385	8.370

NS: Node strength. Degree: Average Degree. NC: Number of components. CR: Component ratio. MEW: Mean edges weight. CC: Average Clustering Coefficient. NCI: Network Centralization Index.

Clustering coefficient was lower and disparity was higher in helper-recipient and helper-opponent networks than in the recruiter-aggressor network (***Table 4.2***). Also, NCI measures indicated that helper-recipient and helper-opponent networks were more centralized than the recruiter-aggressor network (***Figures 4.1 – 4.3***). Overall, these results indicate that aid was not evenly distributed within the group but generally provided towards and against specific individuals.

Recruiter-aggressor network

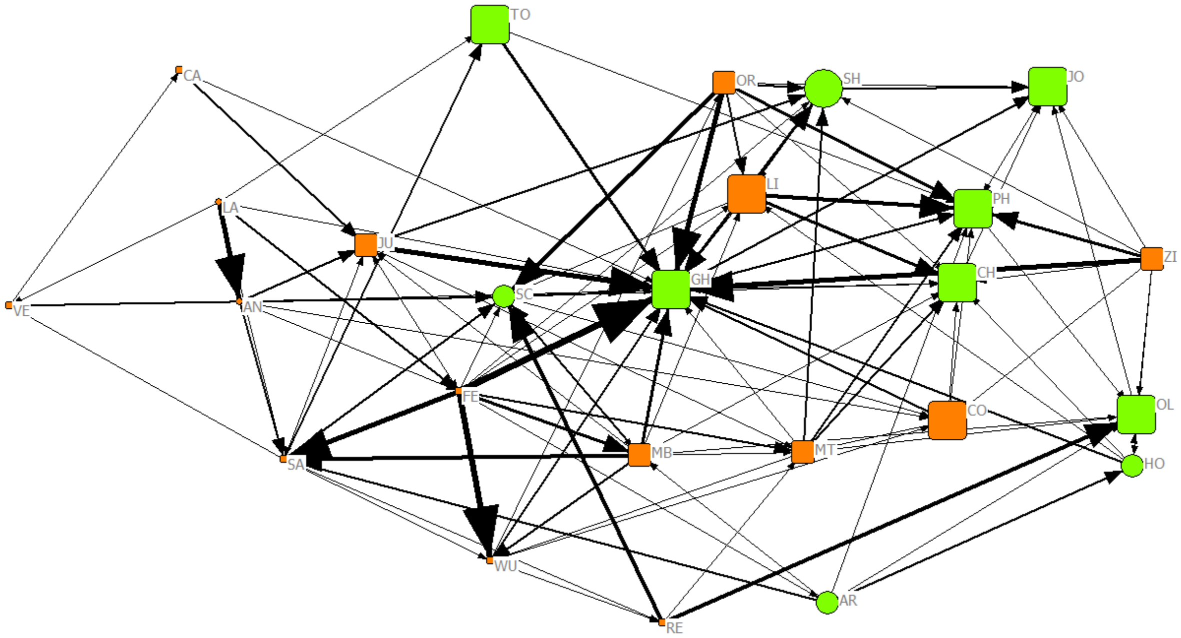


Figure 4.1. Graph representation of the recruiter-aggressor network of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads) and arrows point from the recruiter (caller) to the aggressor.

Helper-recipient network

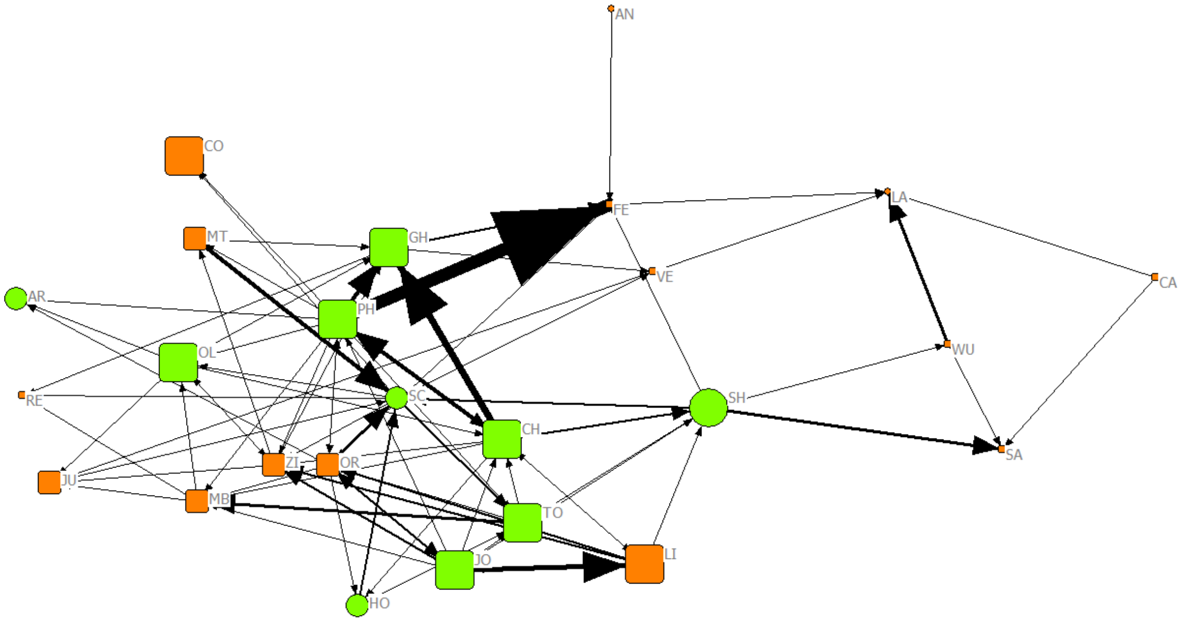


Figure 4.2. Graph representation of the helper-recipient network of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads) and arrows point from the helper to the recipient of agonistic support.

Helper-opponent network

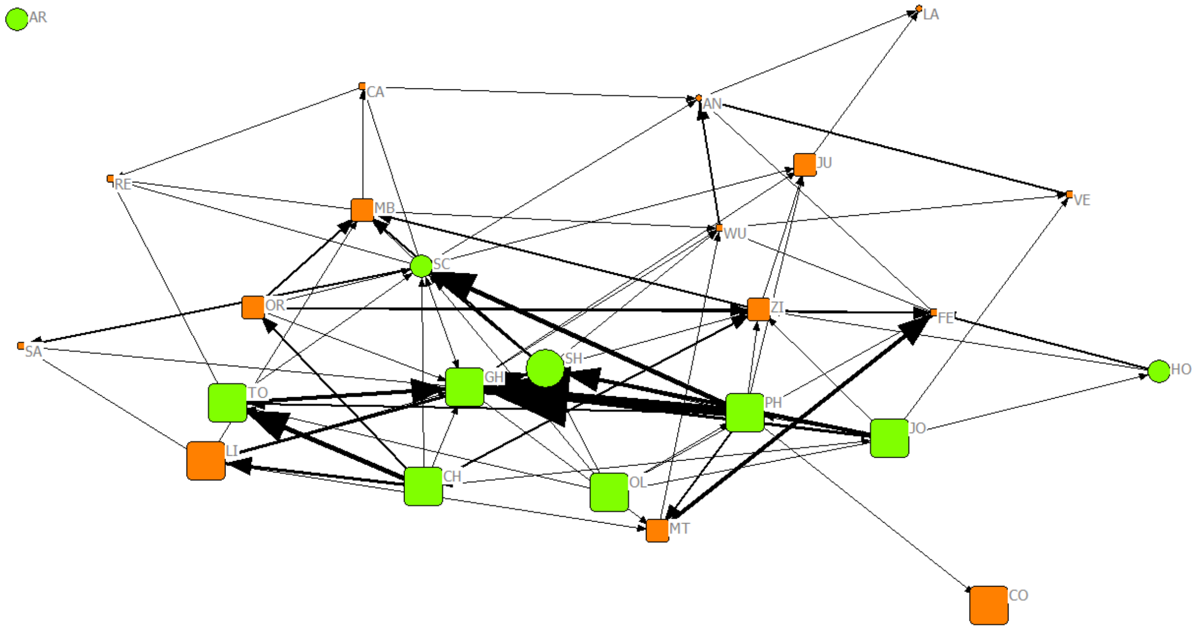


Figure 4.3. Graph representation of the helper-opponent network of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads) and arrows point from the helper to the opponent of the recipient of support.

Assortative mixing

All measures and results for assortative mixing (calculated using the E-I index, see ***section 2.4.7***) can be found in ***Table D.1*** in ***Appendix D***. For significant results we must consider that: (i) if the E-I index is greater than chance, whether positive or negative, this indicates a preference for external connections (heterophily), (ii) if the E-I index is lower than chance, whether positive or negative, this indicates a preference for internal connections (homophily). See ***section 2.4.7*** for more details on the interpretation of the E-I index.

Results indicate that interactions of both males and females generally occurred with individuals of the opposite sex in the recruiter-aggressor network. In contrast, heterophily (preference for the opposite sex) was only found for interactions involving females (i.e. excluding male-male dyads) in the helper-recipient network (***Figure 4.4***). A general tendency towards sex homophily was found in the helper-opponent network, indicating that individuals provided help against conspecifics of the same sex as them. In the three networks, we see that sub-adults had more and stronger connections with adults than with other sub-adults (***Figure 4.5***).

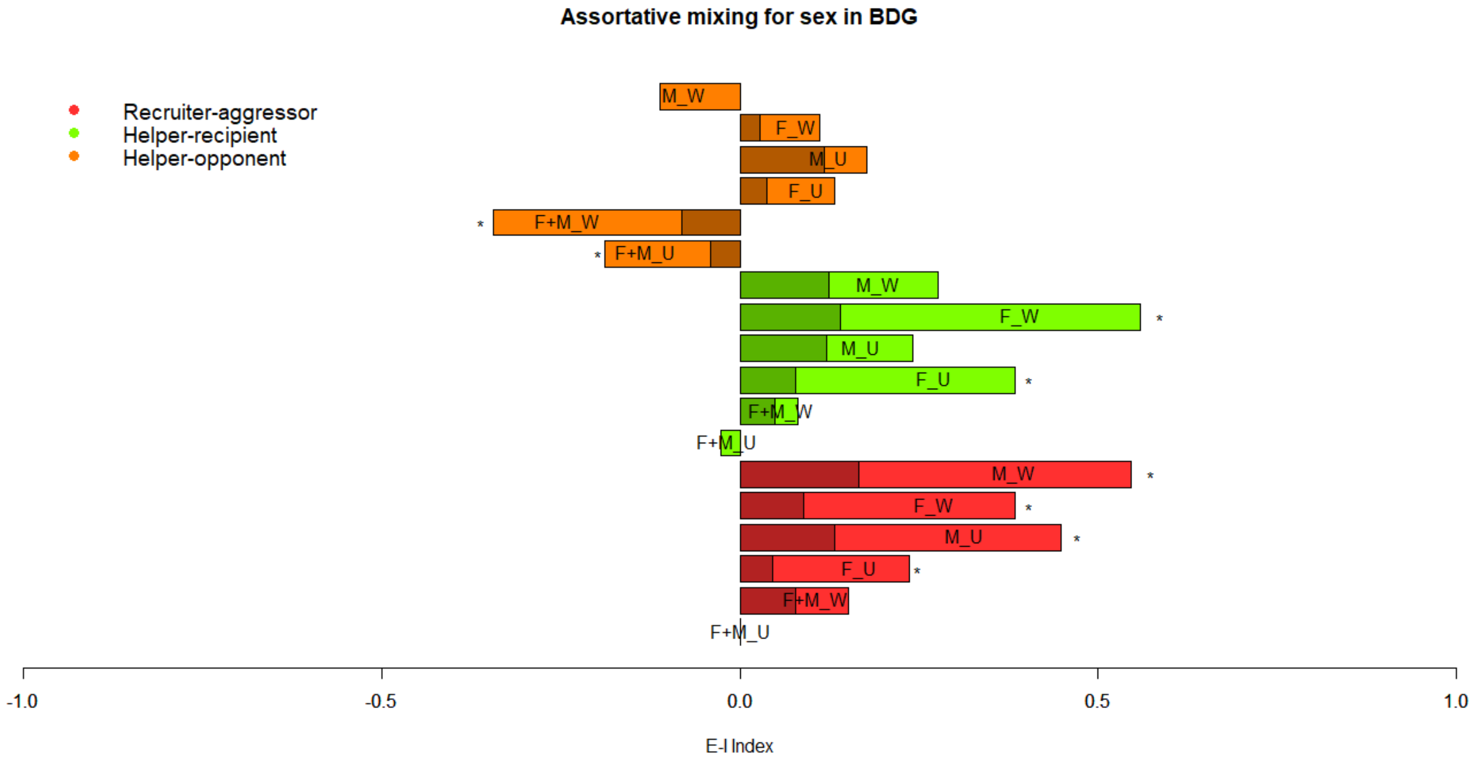


Figure 4.4. Assortative mixing for sex in aid-recruitment networks. U: Unweighted network. W: Weighted network. F+M: E-I index measures of all possible interactions among males and females. F: E-I index measures of interactions involving females (i.e. excluding M-M interactions). M: E-I index measures of interactions involving males (i.e. excluding F-F interactions). The grey bars (darker shades when overlapped with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

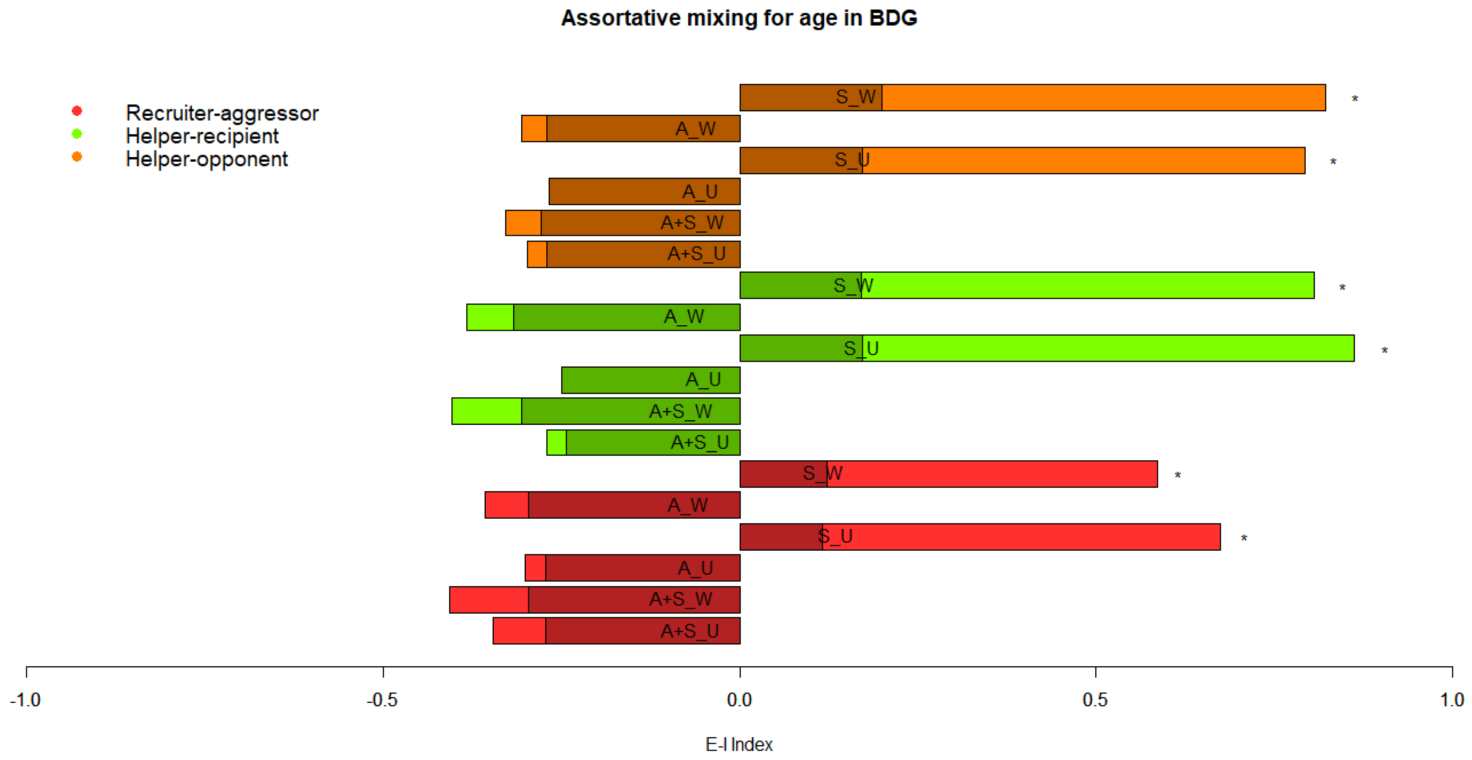


Figure 4.5. Assortative mixing for age in aid-recruitment networks. U: Unweighted network. W: Weighted network. A+S: E-I index measures of all possible interactions among adults and sub-adults. A: E-I index measures of interactions involving adults (i.e. excluding S-S interactions). S: E-I index measures of interactions involving sub-adults (i.e. excluding A-A interactions). The grey bars (darker shades when overlapped with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

Finally, interactions in helper-recipient and helper-opponent networks normally occurred within rank classes, meaning that individuals provided support to and against those of the same rank class as them. In the recruiter-aggressor network, communication interactions involving middle-ranking subjects were generally established with those of a different social rank (***Figure 4.6***). Directionality of these reported relationships is investigated further below (Kruskal-Wallis & Dunn tests).

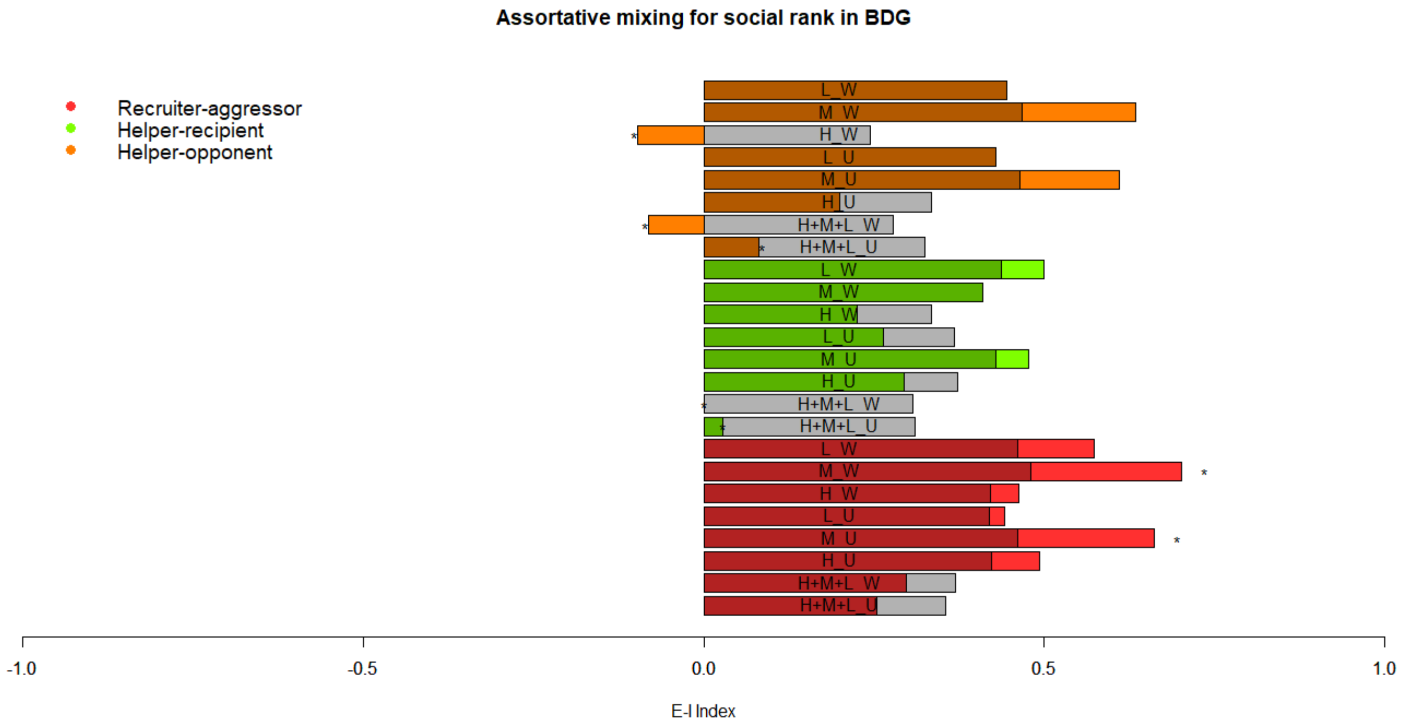


Figure 4.6. Assortative mixing for social rank in aid-recruitment networks. U: Unweighted network. W: Weighted network. H+M+L: E-I index measures of all possible interactions among high, mid and low-ranking individuals. H: E-I index measures of interactions involving high-ranking individuals. M: E-I index measures of interactions involving middle-ranking individuals. L: E-I index measures of interactions involving low-ranking individuals. The grey bars (darker shades when overlapped with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

Network regressions and influence of individual attributes

No variables showed multi-collinearity in any of the analyses (***Table 4.3***). Affiliative relations did not predict the recruiter-aggressor network, indicating that the strength of the social bonds (either weak or strong) between the individuals involved in a conflict did not predict the occurrence of aid-recruitment calls (***Table 4.3***). All affiliative networks, except huddling, predicted the helper-recipient network. Results suggest that help generally came from closely-bonded partners of the opposite sex (almost significant). Among grooming partners and, in general affiliates (CSI network), aid tended to occur between individuals of similar rank. Among individuals in close proximity, aid occurred between individuals of different social rank and same age class (***Table 4.3***). Finally, network regressions indicated neither grooming or affiliative interactions in general (CSI) predicted the helper-opponent network (***Table 4.3***).

Table 4.3. Results of the permutation-based linear mixed model regressions for aid-recruitment calls in BDG.

Affiliative network	Communication network	VIF	AIC	r (p-value)
Affiliative (CSI)	Recruiter-aggressor	CSI = 1.092, SS = 1.167, AS = 1.031, SR = 1.148, ID1 = 1.016, ID2 = 1.016	-5598.01 (-5611.18, -5529.62)	CSI = 3.08e-05 (p = 0.245) SS = -6.75e-04 (p = 0.027)* AS = 6.36e-04 (p = 0.037)* SR = -9.01e-05 (p = 0.003)*
	Helper-recipient	CSI = 1.092, SS = 1.167, AS = 1.031, SR = 1.148, ID1 = 1.016, ID2 = 1.016	-5898.11 (-5898.11, -5790.04)	CSI = 6.05e-05 (p = 0.012)* SS = -2.19e-04 (p = 0.052) SR = -4.96e-05 (p = 0.003)*
	Helper-opponent	CSI = 1.108, SS = 1.116, AS = 1.031, SR = 1.106, ID1 = 1.013, ID2 = 1.013	-6013.3 (-6015.73, -5936.68)	CSI = -1.12e-05 (p = 0.419) SS = 5.16e-04 (p = 0.018)* SR = 6.12e-04 (p = 0.007)*
Grooming	Recruiter-aggressor	SRI_{GRO} = 1.074, SS = 1.161, AS = 1.029, SR = 1.142, ID1 = 1.015, ID2 = 1.015	-5607.59 (-5621.47, -5538.45)	SRI_{GRO}= 0.001 (p = 0.392) SS = -6.60e-04 (p = 0.027)* AS = 6.31e-04 (p = 0.037)* SR = -9.27e-05 (p = 0.003)*
	Helper-recipient	SRI_{GRO}= 1.074, SS = 1.161, AS = 1.029, SR = 1.142, ID1 = 1.015, ID2 = 1.015	-5890.35 (-5906.27, -5798.30)	SRI_{GRO}= 0.006 (p = 0.047)* SS = -2.02e-04 (p = 0.064) SR = -5.24e-05 (p = 0.027)*
	Helper-opponent	SRI_{GRO}= 1.074, SS = 1.161, AS = 1.029, SR = 1.142, ID1 = 1.015, ID2 = 1.015	-6021.85 (-6028.65, -5930.93)	SRI_{GRO}= 0.001 (p = 0.282) AS = 4.39e-04 (p = 0.027)* SR = -5.71e-05 (p = 0.003)*
Huddling	Helper-recipient	SRI_{HUD}= 1.107, SS = 1.121, AS = 1.032, SR = 1.103, ID1 = 1.012, ID2 = 1.012	-5894.41 (-5911.23, -5817.62)	SRI_{HUD}= 0.003 (p = 0.174) SS = -1.48e-04 (p = 0.057) SR = 6.11e-04 (p = 0.007)*
1m Proximity	Helper-recipient	SRI_{PR1}= 1.080, SS = 1.089, AS = 1.029, SR = 1.109, ID1 = 1.016, ID2 = 1.016	-5912.38 (-5928.68, -5838.17)	SRI_{PR1} = 0.059 (p = 0.003)* AS = 2.06e-04 (p = 0.038)* SR = 5.11e-04 (p = 0.021)*

VIF: Variance Inflation Factor of each of the variables. SRI: Simple Ratio Index of the independent network. SS: Sex similarity. CSI: Composite sociality index combining grooming, huddling and proximity within 1m. GRO: Grooming. HUD: Huddling. PR1: Proximity 1m. AS: Age similarity. SR: Differences in ordinal ranks of dominance. ID1: Identity of individual 1. ID2: Identity of individual 2. AIC: indicates the AIC value of the chosen regression model and the range of the AIC values of all the models tested. r: regression coefficients. p: p-values. Only regression coefficients and p-values of significant variables in the fitted model are reported. *: $p<0.05$

Considering individual characteristics of those involved in coallitionary interactions, there were significant differences for sex, age and/or social rank, depending on the network (***Table 4.4***). For the recruiter-aggressor network, Dunn tests indicated that females produced aid-recruitment calls more often than males when confronting female aggressors (***Figure 4.7A***). Also, males were more likely to produce aid-recruitment calls when the aggressor was a male than when it was a female (***Table 4.6***). Adult aggressors triggered more aid-recruitment calls from individuals of both age classes than did sub-adult aggressors (***Figure 4.7B***). Finally, high-ranking individuals produced aid-recruitment calls more often when aggressors were also high-ranking than when they belonged to lower ranking categories (***Figure 4.7C***). Also, middle-ranking individuals were more likely to produce aid-recruitment calls when the aggressor was a high ranking individual than low or mid ranking. In contrast, the social rank of the aggressor did not seem to influence the frequency of aid-recruitment calls produced by low-ranking macaques (***Table 4.5***).

Table 4.4. Kruskal-Wallis test results for each network and individual attribute.

Attributes	Recruiter-aggressor	Helper-recipient	Helper-opponent
Sex	$\chi^2 = 18.510$ ($p < 0.001$)*	$\chi^2 = 12.421$ ($p = 0.006$)*	$\chi^2 = 17.329$ ($p < 0.001$)*
Age	$\chi^2 = 21.225$ ($p < 0.001$)*	$\chi^2 = 6.982$ ($p = 0.072$)	$\chi^2 = 5.854$ ($p = 0.119$)
High vs lower	$\chi^2 = 21.711$ ($p < 0.001$) *	$\chi^2 = 1.887$ ($p = 0.389$)	$\chi^2 = 4.364$ ($p = 0.113$)
Middle vs high	$\chi^2 = 10.464$ ($p = 0.005$)*	$\chi^2 = 5.655$ ($p = 0.059$)	$\chi^2 = 6.972$ ($p = 0.031$) *
Low vs higher	$\chi^2 = 0.694$ ($p = 0.707$)	$\chi^2 = 7.656$ ($p = 0.022$)*	$\chi^2 = 11.897$ ($p = 0.003$) *

Higher vs lower: Comparison of high ranking individuals directing behaviours to other high ranking individuals vs high ranking individuals directing behaviours to lower-ranking classes. Middle vs high: Comparison of middle ranking individuals directing behaviours to high ranking individuals vs middle ranking individuals directing behaviours to middle and low ranking partners. Low vs higher: Comparison of low ranking individuals directing behaviours to other low ranking individuals vs low ranking individuals directing behaviours to higher ranking partners. * indicates significant p-values.

Dunn-test results for non-vocalized instances were similar to those obtained for sex and age in the recruiter-aggressor network (see ***Appendix B***). A chi-square analysis comparing Female-Female and Female-Male dyads (caller-aggressor dyads) between vocalized and non-vocalized instances indicated that aid-recruitment calls were mainly produced by females (***Table 4.5***), who rarely remained silent (and called for support instead) when the aggressor was a male ($\chi^2 = 40.76$, df = 1, p-value < 0.001, see ***Table 4.5***). Males did not call more than remained silent against male aggressors ($\chi^2 = 0.02$, df = 1, p-value = 0.892). Moreover, the chi-square analysis suggested that adults vocalized (instead of remaining silent) when sub-adults acted as aggressors ($\chi^2 = 5.39$, df = 1, p-value = 0.020). In addition, the result that high-ranking individuals called more often when other high-ranking (rather than mid or low ranking) conspecifics were aggressors was probably due to lower ranking individuals rarely directing aggression towards higher ranking individuals (i.e. no significant differences in the frequency of dyads involving only high-ranking individuals between vocalized and non-vocalized contexts; $\chi^2 = 0.22$, df = 2, p-value = 0.641; see ***Appendix B*** & ***Table 4.5***). The absence of significant results of the Kruskal-Wallis test for middle-ranking individuals in non-vocalized instances (***Appendix B***) suggests that middle-ranking macaques did tend to produce aid-recruitment calls against high-ranking aggressors (***Tables 4.4*** & ***4.6***). Significant results of the Kruskal-Wallis test in non-vocalized (but not in vocalized) instances for low-ranking individuals (see ***Appendix B***) indicates that low-ranking macaques tended to respond to aggression with formal submission.

Table 4.5. Percentage of instances observed per combinations of sex, age and rank class dyads in vocalized and non-vocalized agonistic encounters.

	FF	FM	MF	MM
Vocalized	25.6	54.8	2.7	16.9
Non-vocalized	54.5	28.5	2.6	14.4
	AA	**AJ**	**JA**	**JJ**
Vocalized	62.6	15.9	13.7	7.8

Non-vocalized	61.0	8.23	22.7	8.0

	HH	HM	HL	MM	MH	ML	LL	LH	LM
Vocalized	17.8	0.9	0	8.7	31.9	0.5	8.7	15.5	15.9
Non-vocalized	11.7	0.4	0	14.8	19.7	0.2	14.6	11.5	20.1

F: Females. M: Males. A: Adults. J: Sub-adults/Juveniles. H: High-ranking individuals. M: Middle-ranking individuals. L: Low-ranking individuals. First and second letter of the dyad indicate the roles of the subjects in the recruiter-aggressor network. For instance, FM indicates that the recruiter is a female and the aggressor is a male.

Dunn tests also indicated that it was mainly males who provided support in conflicts to other conspecifics, irrespective of the sex, age or social rank of the recipient of support (except for low-ranking individuals, see ***Tables 4.4*** & ***4.6*** and ***Figure 4.8A***). Low-ranking macaques were significantly backed up more often by other low-ranking individuals than by high-ranking conspecifics (***Figure 4.8B***). Moreover, males supported others irrespective of the sex of the opponent, but females generally aided others when the opponent was another female (***Table 4.6*** and ***Figure 4.8C***). Finally, middle-ranking macaques rarely provided support against high-ranking opponents, and mainly provided support against low-ranking opponents. Low-ranking individuals were never seen providing support against higher-ranking conspecifics during aid-recruitment events (***Figure 4.8D***).

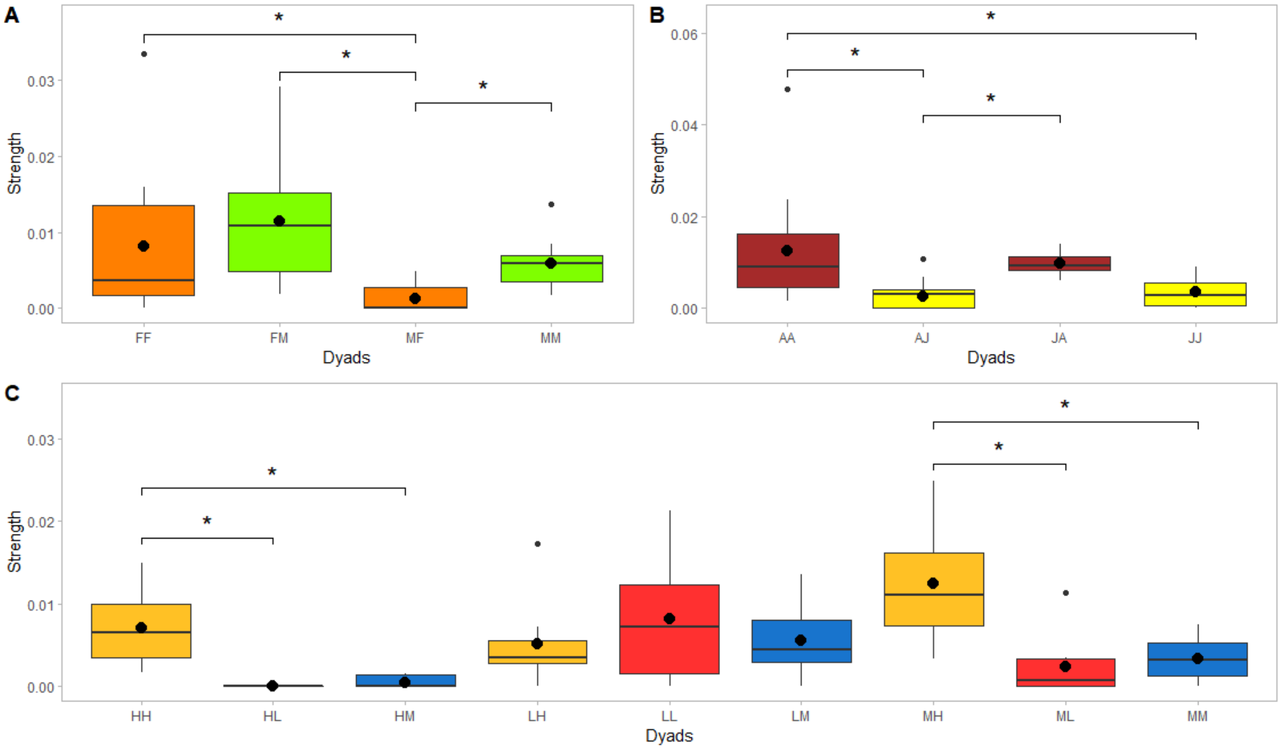


Figure 4.7. Box-plot of the strength of interactions in the recruitment-aggressor network for sex (**A**), age (**B**) and social rank (**C**) categories. F: Females. M: Males. A: Adults. J: Sub-adults/Juveniles. H: High-ranking individuals. M: Middle-ranking individuals. L: Low-ranking individuals. Dyads names describe who the recruiter (first letter) is and who the aggressor (second letter) is. For instance, FM indicates that females call after threats of males, AJ

indicates that adults call after threats of sub-adults and LH indicates that low-ranking individuals call after threats of high-ranking conspecifics.

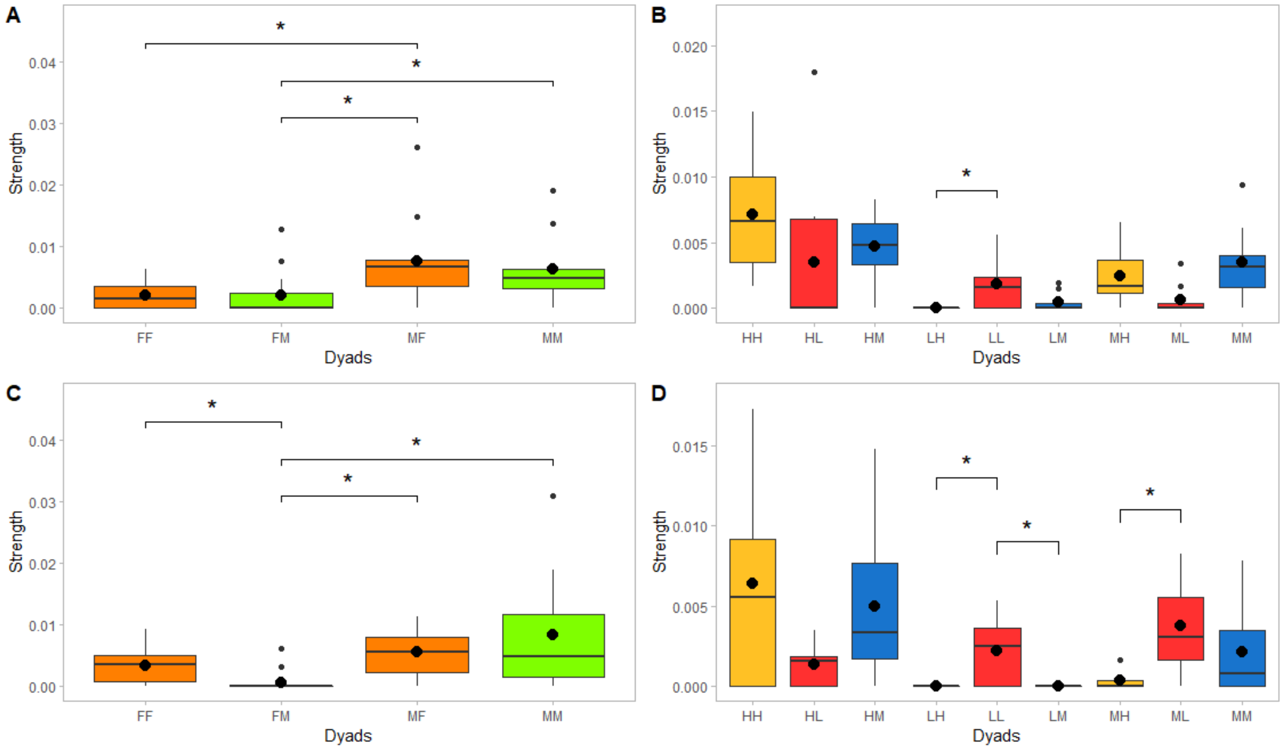


Figure 4.8. Box-plot of the strength of interactions in the helper-recipient network (**A** & **B**) and in the helper-opponent network (**C** & **D**) for sex (**A** & **C**) and social rank (**B** & **D**) categories. F: Females. M: Males. H: High-ranking individuals. M: Middle-ranking individuals. L: Low-ranking individuals. Dyads names in A & B describe who the helper (first letter) is and who the aided individual (second letter) is. For instance, MF indicates males providing support to females and HM indicates high-ranking individuals providing support to middle-ranking conspecifics. Dyad names in C & D describe who the helper (first letter) is and who the opponent they go against (second letter) is. For instance, MF indicates males going against females and ML indicates middle-ranking individuals going against low-ranking conspecifics.

Table 4.6. Dunn test results for each network and individual attribute.

Attributes	Recruiter-aggressor	Helper-recipient	Helper-opponent
Sex	FF-FM: 1.71 (0.132) FF-MF: -2.75 (p = 0.012)* FF-MM: 0.264 (p = 0.792) FM-MF: -4.27 (p<0.001)* FM-MM: -1.26 (p = 0.248) MF-MM = 2.75 (p = 0.012)*	FF-FM: -0.55 (0.703) FF-MF: 2.31 (p = 0.042)* FF-MM: 2.13 (p = 0.050) FM-MF: 2.79 (p = 0.027)* FM-MM: 2.61 (p = 0.027)* MF-MM = -0.17 (p = 0.869)	FF-FM: -2.72 (0.013)* FF-MF: 1.10 (p = 0.405) FF-MM: 0.90 (p = 0.440) FM-MF: 3.54 (p = 0.002)* FM-MM: 3.34 (p = 0.003)* MF-MM = -0.18 (p = 0.855)
Age	AA-AJ: -4.10 (p<0.001)* AA-JA: 0.22 (p = 0.828) AA-JJ: -2.28 (p = 0.045)* AJ-JA = 3.06 (p = 0.007)* AJ-JJ: 0.56 (p = 0.693) JA-JJ: -2.03 (p = 0.064)	NA	NA
Rank	HH-HM: -3.52 (p<0.001)* HH-HL: -4.40 (p<0.001)* HL-HM: 0.88 (p = 0.379) MH-ML: -3.09 (p = 0.010)*	LH-LL: 2.73 (p = 0.019)* LH-LM: 0.97 (p = 0.333) LL-LM: -1.76 (p = 0.117)	MH-ML: 2.64 (p = 0.025)* MH-MM: 1.26 (p = 0.206) ML-MM: -1.38 (p = 0.206) LH-LL: 2.99 (p = 0.004)*

MH-MM: -2.35 (p = 0.028)*	LH-LM: 0.00 (p = 1)
ML-MM: 0.75 (p = 0.454)	LL-LM: -2.99 (p = 0.004)*

NA: Not applicable. Dunn tests were only performed for significant Kruskal-Wallis analyses. F: Females. M: Males. A: Adults. J: Sub-adults/Juveniles. H: High-ranking individuals. M: Middle-ranking individuals. L: Low-ranking individuals. Pairs of dyads are compared, the first and second letter of the dyad indicating the roles of the subjects in that network. For instance, FM in the recruiter-aggressor network indicates that the recruiter is a female and the aggressor is a male. In FF-FM for the recruiter-aggressor network, the strength of connections between female callers and female aggressors is compared with the strength of connections between female callers and male aggressors. *: indicates significant results

4.3.4. Discussion

Results showed that Barbary macaques provided agonistic support to their affiliates. As anticipated, agonistic support was provided to grooming partners and close associates (proximity 1m), but not to huddling partners, contradicting predictions. Females supported other females but it was the males who mainly provided support to other conspecifics irrespective of their sex. Aid was mainly provided to individuals of the same rank when the opponent had a lower social rank than the helper, as predicted. Finally, exploration of the data showed that the occurrence of aid-recruitment calls was more likely when males threatened females and when middle-ranking individuals were attacked by higher-ranking conspecifics.

4.3.4.1. Factors influencing the provision of agonistic support

In BDG, Barbary macaques generally provided support to their affiliates, especially to their frequent grooming partners and close associates (proximity 1m). A previous study also found that recruitment of support in Barbary macaques was based on strong grooming and close proximity relations (Young et al., 2014). It was males who significantly provided frequent support to females and other males. Male Barbary macaques seem to intervene in male-male conflicts to stabilize their rank more often than to improve it (Widdig et al., 2000). Moreover, the interest of males in the formation of coalitions changes over time and is more dominance-oriented than among females (Hemelrijk & Ek, 1991; Widdig et al., 2000). The fact that males also support their female affiliates suggests that males may be contributing to the maintenance of group stability and their alliances at the same time as investing in their reproductive success (Aureli et al., 2000). The findings also seem to support a previous study that found that Barbary macaques were more likely to intervene in a conflict when the opponent had a lower rank than the helper (Widdig et al., 2000).

In this study, females did not provide support more often to other females than to males, and help provided to higher-ranking individuals was not significantly more frequent than help provided to same or lower rank individuals. This contrasts with findings in Cercopithecine species, where the advantages of high rank are marked and females are more prone than males to establish alliances with higher-ranking group-mates (Cords et al., 2010). Prud'Homme & Chapais (1993) found that middle-ranking females were more prompt to intervene in conflicts on behalf of higher ranking females than of lower ranking ones in Barbary macaques. It seems that female Barbary macaques would be interested in allying with higher ranking females to assert their dominance status or outrank a female competitor (Chapais, 1985; Datta, 1992; Prud'Homme & Chapais, 1993a,b). Moreover, young females seem to support high-ranking adults in conflicts against females they had targeted for rank reversal (Pereira, 1989; Prud'Homme & Chapais, 1993a,b). Therefore, during rank acquisition, young females may establish amicable relations with adult females that are considered valuable social partners (Cords et al., 2010), and may use these bonds to climb up in the hierarchy (Pereira, 1989; Prud'Homme & Chapais, 1993a,b; Cords et al., 2010). Individuals in BDG generally called for help when confronting aggressors with a higher rank than themselves. Accordingly, individuals providing support to a higher-ranking individual will have to confront a much higher ranking opponent than themselves. However, my results, in agreement with previous studies (Widdig et al., 2000), suggest that Barbary macaques rarely provided support against individuals with a higher rank than themselves. It is likely that the preference of females in BDG to provide support against other females, irrespective of the sex of the ally, reflects the competition among females to outrank or assert their dominance status against a competitor (Prud'Homme & Chapais, 1993a,b).

Although instances of aid provided to higher-ranking individuals were observed, in general, support was provided to individuals with the same or lower social rank than the helper. Also, Barbary macaques mainly intervened in conflicts when the opponent was of lower rank, as predicted. This is in line with previous studies in Barbary macaques that demonstrate that individuals rarely challenged higher ranking conspecifics to support a lower ranking ally because these situations are associated with a high risk of retaliation (Datta, 1983; Bernstein & Ehardt, 1985; Widdig et al., 2000; Young et al., 2014).

4.3.4.2. Factors influencing the production of aid-recruitment calls

Only 26% of all the agonistic encounters observed led to the production of aid-recruitment calls. In most agonistic encounters, one of the subjects responded by fleeing upon approach or with formal submission. This suggests that conflicts were generally resolved using non-agonistic assessments (i.e. recognition of dominance status or power over resources; Parker, 1974), and escalated fights did not take place (Drews, 1993). It is known that the subordinate will normally accept its inferior position based on the outcomes of previous encounters or the recognition of dominance features of the opponent (Vessey, 1981). Consequently, we may assume that, in the majority of the agonistic encounters, the dominance relationship was readily accepted instead of agonistically challenged.

Overall, these results suggest that aid-recruitment calls might be produced for two main, non-mutually exclusive, reasons. First, aid-recruitment calls may be used to avoid the consequences derived from high aggression. Barbary macaques present a linear hierarchy where males normally outrank females (Maestripieri, 1997; Bayne, 2005). Therefore, threats of males can be perceived by females as instances of high aggression, triggering the production of aid-recruitment calls. The ultimate goal of these calls is to get help from potential allies. Accordingly, we should expect that frequent vocalizations come from individuals with strong alliances. Barbary macaques are a matrilineal society (Preuschoft et al., 1998) and grooming, a coalition behaviour (Watts, 2002; Carne et al., 2011), seems to be more important among females than among males in this species (McFarland & Majolo, 2011; Robouvá et al., 2015). This might explain why females, who invest more time in the formation of coalitions with both sexes than males (see ***Chapter 3***), produced aid-recruitment calls more frequently than males.

As we go down in the hierarchy, it is less likely that individuals have strong higher-ranking allies. Low-ranking individuals would have more conspecifics higher in the hierarchy than them (than would mid or high ranking individuals) who would displace them during alliance maintenance behaviour, such as grooming (Tiddi et al., 2012), preventing them from forming coalitions with higher-ranking subjects. Results imply that the production of aid-recruitment calls in agonistic contexts can be counterproductive because it may draw the attention of allies of the aggressor via eavesdropping effects. Therefore, individuals with very few allies would be at a disadvantage when they attempt to recruit help because they may draw the attention of many rivals. Since triadic awareness is considered to be high in Barbary macaques (Young et al., 2014), it is likely that low-ranking individuals were aware of the risks of producing aid-recruitment calls and responded with formal submission.

The second reason for production of aid-recruitment calls would be to protect one's social status against potential competitors. Social rank in females is inherited from mothers to daughters and defended with aggression (Prud'Homme& Chapais, 1993a,b; Preuschoft et al., 1998), whereas male hierarchy is generally based on the outcomes of continuous competition (Preuschoft et al., 1998). Accordingly, the recruitment of allies during agonistic encounters involving female-female and male-male dyads of victim-aggressor may contribute to protect victims' social status. Even when females call for support when confronting males, the production of aid-recruitment calls may contribute to protect the social status when individuals involved in the conflict belong to different age and rank classes. For instance, in Barbary macaques where males generally outrank females (Kuester & Paul, 1988; Maestripieri, 1997), young males, by the age of 2 years, commonly challenge older (and higher ranking) females in order to scale up in the hierarchy (Kuester & Paul, 1988), likely triggering the production of aid-recruitment calls in these females to protect their rank.

In summary, my results suggest that threats from higher ranking individuals or potential competitors of the same or lower rank than the caller may cause arousal which triggers the production of aid-recruitment calls (proximate explanation) resulting in the recruitment of allies that help callers defend themselves from high aggression or protect their social status (ultimate explanation).

4.4. PART B – VOCAL COMMENTS

4.4.1. Introduction

Vocal comments are calls that occur within 2 seconds after a social interaction between third parties in view of the caller, who does not participate in the interaction and does not show any other reactions within 5 seconds of vocalizing (Brumm et al., 2005). Commenting behaviour seems to be widespread among primates since it has been documented in several species such as Barbary and Japanese macaques and cherry crested mangabeys (Brumm et al., 2005). Fisher & Hammerschmidt (2002) reported three types of vocalisations in Barbary macaques that match the description of commenting behaviour (i.e. vocal comments) and occurred in two different contexts: rasping calls (harsh vocalizations produced when observing an agonistic interaction), and soft pants and pant barks (soft calls produced when observing an interaction with an infant). Brumm et al. (2005) also found that 'vocal comments' in Barbary macaques were mainly produced in these contexts additionally reporting that callers and the third-parties tended to be the same sex. Although the acoustic and temporal features of the calls are known to differ between contexts (Brumm et al, 2005), the function of these calls remains unclear (Brumm et al., 2005; Whitham et al., 2007).

Other soft vocalizations (grunts and girneys) have been described in primate species during infant-handling events (Rowell & Hinde, 1962; Rowell et al., 1964; Bauers, 1993; Silk et al., 2000). Bauers (1993) reported that if adult stump-tailed macaques (*Macaca arctoides*) grunted when exhibiting interest in infants they were less likely to receive aggression from mothers than when grunts were not produced. In chacma baboons (*Papio ursinus*), females were more likely to engage in infant-handling if they emitted grunts when approaching mother-infant dyads than if they remained silent (Silk et al., 2003). Moreover, the production of grunts and/or girneys in female rhesus macaques (*Macaca mulatta*) was positively associated with gentle versus rough infant-handling and the initiation of grooming interactions, and reduced the likelihood of aggression and submissive behaviours (Silk et al., 2000). These calls, therefore, seem to signal benign intentions towards infants and are thought to facilitate positive interactions between adult females and mother-infant dyads in macaques and baboons (Whitham et al., 2007).

Some of the aforementioned examples do not fall into the definition of vocal comments because the calls were accompanied and/or followed by other behaviours (Rowell et al., 1964; Whitham et al., 2007). However, Rowell et al. (1964) interpreted as 'comments' grunts directed towards infants housed in a separate enclosure, uttered when physical contact with these infants was impossible. In addition, Whitham et al. (2007) reviewed most of the evidence on grunts and girneys and concluded that these soft calls were not followed by any social behaviour in most cases. This finding is consistent with the definition of 'vocal comments' and inconsistent with the benign intent hypothesis, since these vocalizations, apparently, did not convey precise information about the caller's intentions or subsequent behaviour (Whitham et al., 2007). This nonrepresentational interpretation of the calls would suggest that they may work as cues that express infant-related arousal in the caller (Owren et al., 2003; Rendall, 2003).

Some researchers have highlighted that individuals may have learned to associate such calls with low-risk behaviours and, consequently, respond with social tolerance towards the caller (Owren et al., 2003; Rendall, 2003). Whitham et al. (2007) found that grunts and girneys were generally produced when dominant subjects were involved in infant-handling situations. Therefore, it is likely that callers may be signalling for social tolerance when approaching dominant partners with infants. Brumm et al (2005), however, concluded that vocal comments in both agonistic and infant-handling contexts likely signal caller's awareness of the observed interaction (proximate explanation) and serve to attract the attention of others (ultimate explanation). In nonhuman animals, signals can carry information on whether to consider an interaction as affiliative or agonistic (Snijders & Naguib, 2017) and their meaning and interpretation may be context-specific (Whitham et al., 2007). It is likely that vocal comments produced when third-party infant-handling interactions are observed are triggered by infant-related arousal (proximate cause) and may ultimately serve to either capture the attention of the infants, elicit tolerance near the infant from the mothers, or draw the attention of others towards the situation (Owren et al., 2003; Rendall, 2003; Brumm et al., 2005; Whitham et al., 2007).

Regarding vocal comments produced in third-party agonistic contexts, it is likely that callers may be supporting one of the parties with their vocal behaviour (Fisher & Hammerschmidt, 2002) and/or these calls function as advertisement signals (i.e. to attract potential mates or repel potential rivals) towards one of the individuals involved (Snijders & Naguib, 2017). Moreover, vocalizations during third-party conflicts may provide intentional or inadvertent information to eavesdroppers about alliances between callers and the third parties and may modify their level of aggressiveness (Snijders & Naguib, 2017). It is known that Barbary macaques evaluate the risks when it comes to getting involved in a conflict (Widdig et al., 2000; Young et al., 2014). Accordingly, dominance relations among all participants are probably important for the occurrence of these calls, whatever is their function.

As aforementioned, vocal comments may signal high levels of social tolerance between caller and third-parties (Owren et al., 2003; Rendall, 2003), as is common among affiliates (Coussi-Korbel & Fragaszy, 1995). The calls may lead to initiation of grooming interactions (Silk et al., 2000), are produced in affiliative contexts (Fisher & Hammerschmidt, 2002; Brumm et al., 2005) and may serve to provide support to allies in conflicts (Fisher & Hammerschmidt, 2002). Furthermore, Whitham et al. (2007) suggested that these calls might help to strengthen social bonds. Therefore, it seems that social bonds between callers and individuals involved in the third-party interaction observed may be relevant to understand the function of these calls. Also, if vocal comments in infant-handling situations serve to improve access to infants, relations between callers and mothers of the infants, whom are often exchanged for privileges (e.g. grooming, Barrett et al., 1999; Henzi et al., 2003) may be important to understand the function of these calls.

I hypothesize that the strength of socio-positive relations and individual-level attributes would predict communication networks based on vocal comments. Specifically, given the literature reviewed, I predict that:

(i) Grooming, huddling and proximity networks will predict who emits vocal comments when particular others are involved in affiliative and agonistic contexts.

(ii) Individuals will produce vocal comments more often when participants in the interaction observed are the same, rather than different, sex as them.

(iii) Regarding affiliative infant-handling contexts, if vocal comments ultimately serve to gain access to infants, calls will be more frequently uttered when a) dominant, rather than low-ranking, individuals are involved in the third-party interaction, and b) callers and mothers of the infants share strong grooming relations (i.e. grooming used in exchange of commodities such as access to infants). Moreover, if vocal comments in infant-handling contexts are produced in situations where calls cannot be perceived by other conspecifics (i.e., these soft calls are uttered when callers are more than 10m away from any other group member), proximate causes like arousal-related epiphenomena may explain what triggers the production of these calls.

(iv) Regarding agonistic contexts, if vocal comments serve to provide support to one of the parties involved, I would expect that: a) callers and one of the parties share strong affiliative bonds, especially through coalition behaviours like grooming, b) the communication network based on vocal comments would predict the helper-recipient network based on aid-recruitment calls (see ***Part A,*** this chapter) and c) the other party involved is not a strong affiliate and has a lower rank than the caller (further explained below).

The first two predictions can be deemed as 'a priori' predictions (i.e. based on previous literature). The last two predictions can be deemed as 'a posteriori' predictions (i.e. based on the exploration of the data). Therefore, this study is exploratory for hypotheses and predictions related to the proximate and ultimate functions of vocal comments, for which data found in the literature is insufficient and unclear.

4.4.2. Specific methods and analyses

Two contexts were considered for vocal comments:

- **Agonistic:** The individuals observed are involved in agonistic displays (see ***Table 2.3***).

- **Infant-handling:** Two or more adults and/or sub-adults are involved in interactions with infants (i.e. individuals grooming, huddling or playing with the infant, triadic interactions – the infant is usually held between the two handlers, sometimes upside-down, and remains passive while the handlers often touch the infant's genitalia, showing facial expressions accompanied of lip-smacking[1] and teeth-chattering[1]).

I built two different networks for vocal comments in affiliative infant-handling interactions. Three roles were defined for the individuals involved: a) commenter: individual observing the interaction and producing the vocal comment, b) handlers: adults and/or sub-adults involved in handling the infant, c) infant: individual < 1 year-being 'handled'. The networks were:

- **Commenter-handler network:** A communication network that links callers with the adults and sub-adults involved in the third-party interaction to investigate whether these comments were directed towards strongly bonded partners or not.

- **Commenter-mother network:** A communication network that links callers with the mothers of the infants involved in the affiliative interaction (irrespective of whether these mothers were also taking part in the infant-handling interaction or not) to study whether Barbary macaques were most likely to 'comment on' situations that involve infants of mothers with whom they share strong social bonds.

For agonistic contexts, three roles were defined for the individuals involved: a) commenter: individual observing the interaction and producing the vocal comment, b) aggressor: individual that directs aggression towards another conspecific in the interaction observed, c) victim: receiver of the

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[1] A full description with images of these gestures and facial expressions can be found in Call & Tomasello (2007).

aggression in the third-party interaction. Two networks were built for vocal comments in agonistic contexts:

- **Commenter-aggressor network:** A communication network that links callers with the aggressors in the third-party conflict observed to investigate whether these calls may serve to provide support to allies or strong affiliates. If so, this network should resemble the helper-recipient network (see ***Part A*** above) with callers likely of lower social rank and/or having strong social bonds to the third-party aggressor.

- **Commenter-victim network:** A communication network that links callers with the victims of the conflict observed to investigate whether vocal comments in agonistic interactions serve to 'bully' a rival or a competitor who is the victim in the third party interaction. If so, this network should resemble the helper-opponent network (see ***Part A*** above) with commenters likely to be of higher rank and/or have weak social bonds to the third-party victim.

As in the case of aid-recruitment calls, group-level SNA metrics were used to describe the dynamics of the occurrence of these calls, and permutation-based linear-mixed-model regressions were used to test the influence of social bonds and individual factors (sex, age and social rank) in communication networks.

Grooming, huddling and close proximity predict each other but represent different aspects of socio-positive relations (see ***Chapter 3***). Therefore, grooming, huddling and close proximity networks plus the affiliative network that combines these three behaviours (CSI network) were used in network regressions to investigate whether social bonds in general, or specific affiliative relations, predict vocal comments in affiliative infant-handling contexts (e.g. strong grooming bonds between commenters and infant mother's). To test if social bonds and, specifically, coalition behaviours predict communication networks based on vocal comments in agonistic contexts, only CSI and grooming were used in network regressions. Furthermore, to determine if vocal comments during conflicts serve to provide support to aggressors or 'bully' the victims, the commenter-aggressor and the commenter-victim networks were tested in linear regressions against the helper-recipient and the helper-opponent networks, respectively.

Finally, Kruskal-Wallis rank sum tests followed by post-hoc Dunn tests (adjusted for multiple comparisons using Benjamini-Hochberg corrections) were used to test whether the relationship between the commenter and each of the individuals involved in the third-party interaction was determined by the specific sex, age or social rank class of the third parties.

4.4.3. Results

Adequacy of datasets

Results can be found in ***Appendix C***. This first inspection of the data indicated that long and complete datasets were collected, yet all communication networks could be deemed as sparse as few observations per dyad were available. Precision and accuracy measures showed that the levels of uncertainty of the communication networks were low and that the sampling effort was high enough to generate reliable measures of edge weights in all cases. The results suggest that the patterns of the relationships captured in the datasets were not the result of arbitrary interactions, except for the commenter-mother and the commenter-victim networks. Despite this, these two networks were included in subsequent analyses for the following reasons:

(i) The commenter-mother network represents the relationship between callers and mothers of the infants involved. However, as mothers may, or may not, have participated in the interaction observed relations in this network do not represent real interactions but virtual ones established to explore whether the relationship between callers and mothers explains the production of these calls.

(ii) The commenter-victim network may also represent virtual relations if the occurrence of vocal comments in agonistic contexts is mainly influenced by the identity of the aggressor and not the victim.

(iii) Although the adequacy data analysis suggests that relations in these two networks are arbitrary, and therefore not relevant for the production of these calls, the analysis is insufficient to rule them out (i.e. it does not control for other factors like social bonds).

Description and visualization of communication networks

Vocal comments were collected in 84 sessions of a total of 1292 sessions (6.50%) during affiliative contexts and in 65 of 1292 sessions (5.03%) during agonistic contexts. These measures indicate that occurrence of vocal comments are not frequently observed in Barbary macaques and a big sampling effort is required to obtain representative datasets. In total, 23 and 22 of 25 individuals (excluding infants) were observed producing vocal comments in affiliative (with an average of 17.43 and a range of 3 – 167 calls per individual) and agonistic contexts (with an average of 9.14 and a range of 2 – 18 calls per individual), respectively (see ***Table 4.7*** for detailed information per classes of individuals).

Table 4.7. Sampling effort and completeness of the datasets per classes of individuals (vocal comments).

Vocal comments in affiliative contexts

	Females	Males	Adults	Sub-adults	High-ranking	Middle-ranking	Low-ranking
Sampling effort	66 (5.12%)	23 (1.78%)	64 (4.95%)	22 (1.70%)	17 (1.32%)	30 (2.32%)	50 (3.87%)
Total individuals per class	15/15	8/10	17/19	6/6	7/9	8/8	8/8
Average (range) of calls per individual	22 (5 – 167)	8.88 (3 – 25)	19.47 (3 – 167)	11.67 (3 – 19)	8 (3 – 25)	13.38 (5 – 22)	29.75 (5 – 167)
% of events observed per class	82.29%	17.71%	82.54%	17.46%	13.97%	26.68%	59.35%

Vocal comments in agonistic contexts

	Females	Males	Adults	Sub-adults	High-ranking	Middle-ranking	Low-ranking
Sampling effort	52 (4.02%)	21 (1.63%)	57 (4.41%)	12 (0.93%)	23 (1.78%)	32 (2.48%)	21 (1.63%)
Total individuals per class	13/15	9/10	17/19	5/6	8/9	8/8	6/8
Average (range) of calls per individual	11.54 (2 – 18)	5.67 (2 – 11)	10.47 (2 – 22)	4.6 (2 – 7)	8.63 (3 – 22)	9.63 (2 – 18)	9.17 (2 – 18)
% of events observed per class	74.63%	25.37%	88.56%	11.44%	34.33%	38.31%	27.36%

Sampling effort: Total number of sessions where individuals of each class were observed producing vocal comments (percentage calculated dividing by total number of sessions collecting vocalizations = 1292 sessions). Total individuals per class: number of individuals of each class observed producing vocal comments/number of individuals of that class in the group. OL (the highest-ranking males at the end of the study) was not observed producing vocal comments in affiliative contexts.JO (the alpha male at the beginning of the study) and AN & SA (two of the three lowest ranking females) were not observed producing vocal comments in agonistic contexts. Note that in one session, more than one event may occur, and more than one individual may be calling in the same event.

During the study period, 1,622 affiliative events not involving infants, 955 socio-positive events involving infants and 838 agonistic encounters were observed. Vocal comments were produced in ~10% of the affiliative situations involving infants (94 events) and in ~8.0% of the agonistic encounters (65 events). On 3 occasions, vocal comments were produced in affiliative contexts when the youngest individual was not an infant but a juvenile male (AR) or one of the two youngest females (LA, AN). Therefore, vocal comments were produced almost exclusively during infant-handling situations (i.e., in 94 of 97 events in which vocal comments were produced during affiliative contexts). In ~63% of infant-handling interactions, mothers of the infants involved were also involved in the third-party.

The commenter-mother network is a network of virtual relations and some SNA metrics of this network will be biased by the fact that the females involved in the network are a sub-set (current mothers of infants) in the group. Therefore, measures of density, average degree, clustering coefficient, NCI and assortative mixing were not discussed for this network (see ***Table 2.7*** in ***Chapter 2*** for a full description of these measures).

Group-level SNA metrics

The commenter-handler network had the highest values for density, node strength, average degree and mean edge weights (***Table 4.8***). More vocal comments were observed during infant-handling than in agonistic situations, which may explain why the group-level metrics were lower in the commenter-aggressor and commenter-victim networks.

None of the networks formed a single component (***Figures 4.9 – 4.12***). Two high-ranking males (JO and OL) were found isolated in the networks based on infant-handling contexts (***Figures 4.9*** & ***4.10***). JO, the alpha male at the beginning of the study, was never seen producing or receiving vocal comments in infant-handling contexts. OL, the dominant male at the end of the study, never produced vocal comments while observing infant handling of third parties but was 'commented on' in this context.

Two of the lowest ranking females (SA and AN) were never seen producing comments during agonistic encounters and never triggered vocal comments when they acted as aggressors in a conflict, but did when they were victims. JO and TO (the former alpha male) never produced vocal comments during conflicts and never triggered comments when they were the victims of aggression but did when they were aggressors (***Figures 4.11*** & ***4.12***).

Disparity was higher in the commenter-mother network than in the other networks (***Table 4.8***). Therefore, vocal comments were produced more often when certain infants were involved in infant-handling interactions. Average clustering coefficient and NCI were higher in the commenter-handler network than in the networks based on agonistic encounters (***Table 4.8***). Accordingly, vocal comments during infant-handling interactions seem to connect more individuals of the group, and are more selectively directed towards specific individuals than those uttered in agonistic contexts.

Table 4.8. Results of the group-level SNA metrics for communication networks based on vocal comments.

Network	NS	Density	Degree	NC	CR	MEW	Disparity	CC	NCI (%)
Commenter-handler	0.023	0.287	6.88	2	0.0435	0.000926	0.241204	0.658	12.127
Commenter-mother	0.014	0.153	3.68	3	0.0909	0.000577	0.459528	0.729	33.558
Commenter-aggressor	0.012	0.200	4.80	3	0.0909	0.000464	0.291979	0.474	8.893
Commenter-victim	0.011	0.203	4.88	3	0.0909	0.000436	0.296810	0.436	9.803

NS: Node strength. Degree: Average Degree. NC: Number of components. MEW: Mean edges weight. CC: Average Clustering Coefficient. NCI: Network Centralization Index.

Commenter-handler network

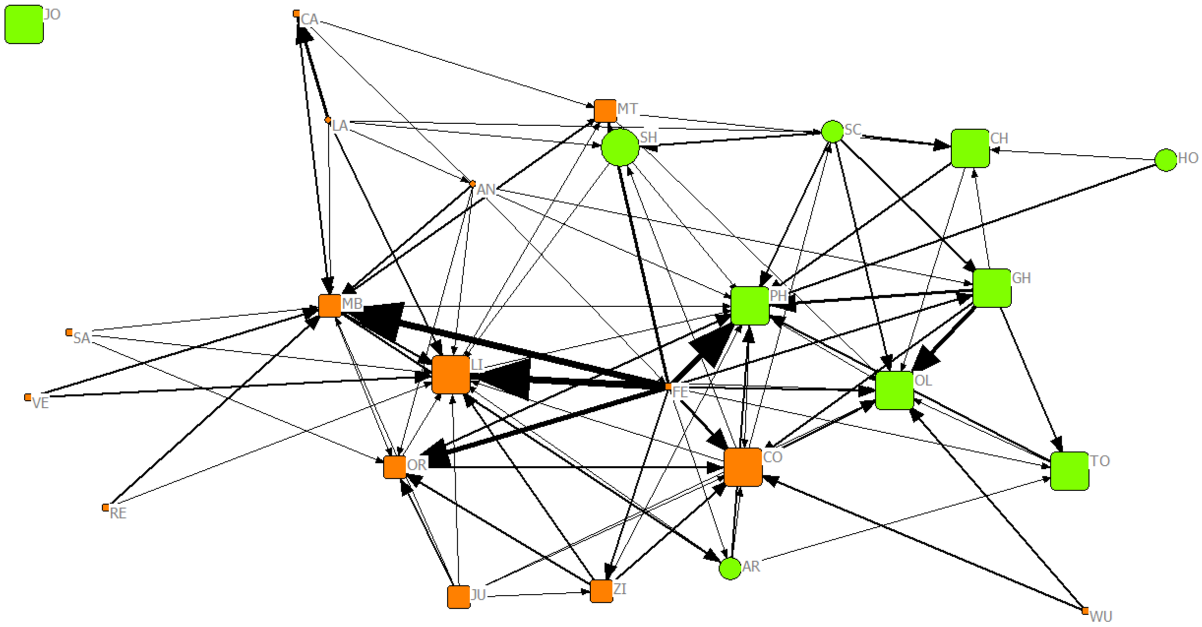


Figure 4.9. Graph representation of the commenter-handler network of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads) and arrows point from the commenter to the infant handler.

Commenter-mother network

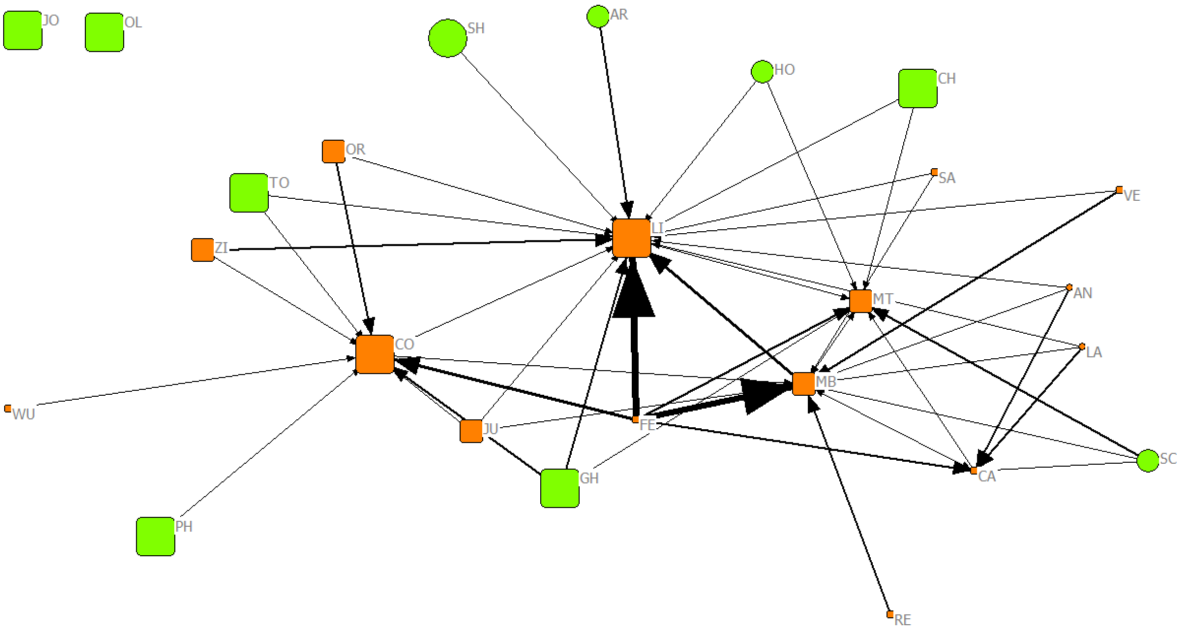


Figure 4.10. Graph representation of the commenter-mother network of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads) and arrows point from the commenter to the infant's mother.

Commenter-aggressor network

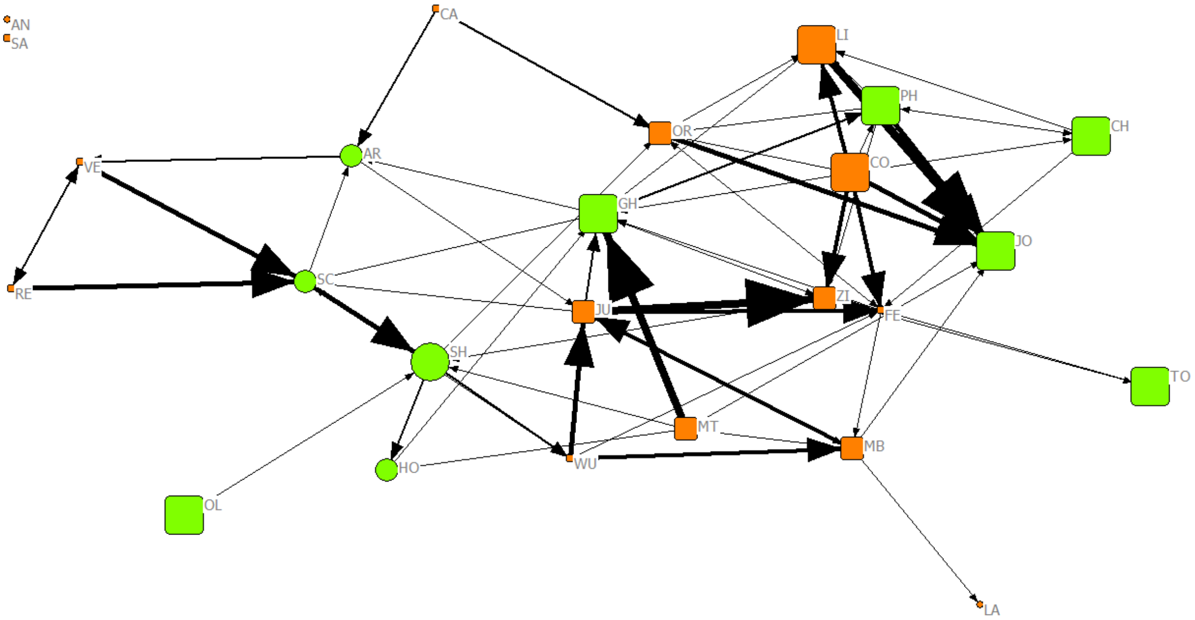


Figure 4.11. Graph representation of the commenter-aggressor network of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads) and arrows point from the commenter to the aggressor in the third-party interaction.

Commenter-victim network

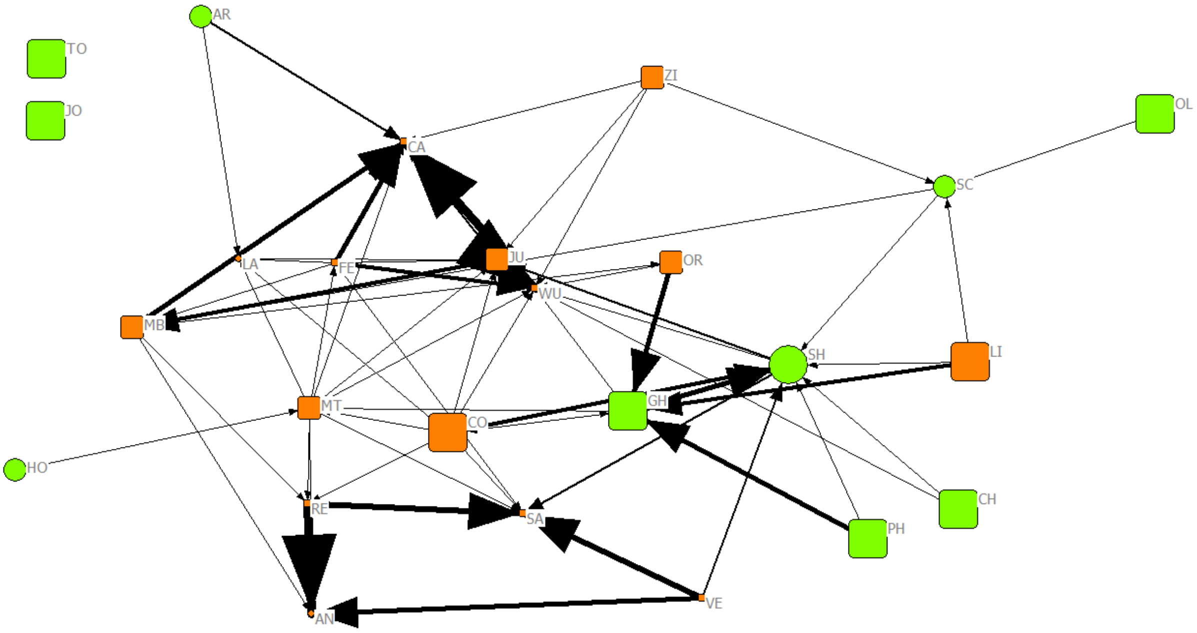


Figure 4.12. Graph representation of the commenter-victim network of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low

rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads) and arrows point from the commenter to the victim in the third-party interaction.

Assortative mixing

All measures and results for assortative mixing (calculated using the E-I index, see ***section 2.4.7***) can be found in ***Table D.1*** in ***Appendix D***. For significant results we must consider that: (i) if the E-I index is greater than chance, whether positive or negative, this indicates a preference for external connections (heterophily), (ii) if the E-I index is lower than chance, whether positive or negative, this indicates a preference for internal connections (homophily). See ***section 2.4.7*** for more details on the interpretation of the E-I index.

Vocal comments in affiliative infant-handling contexts were produced more frequently when callers and observed third parties belonged to the same sex class than when they had opposite sexes. It was mainly females who vocalized when other females were engaged in infant-handling behaviours (***Figure 4.13***). Also, more comments were produced when callers and infant-handlers belonged to the same age class than when they belonged to different age classes. However, comments were more frequent between sub-adults and adults than among sub-adults, during infant-handling contexts (***Figure 4.14***).

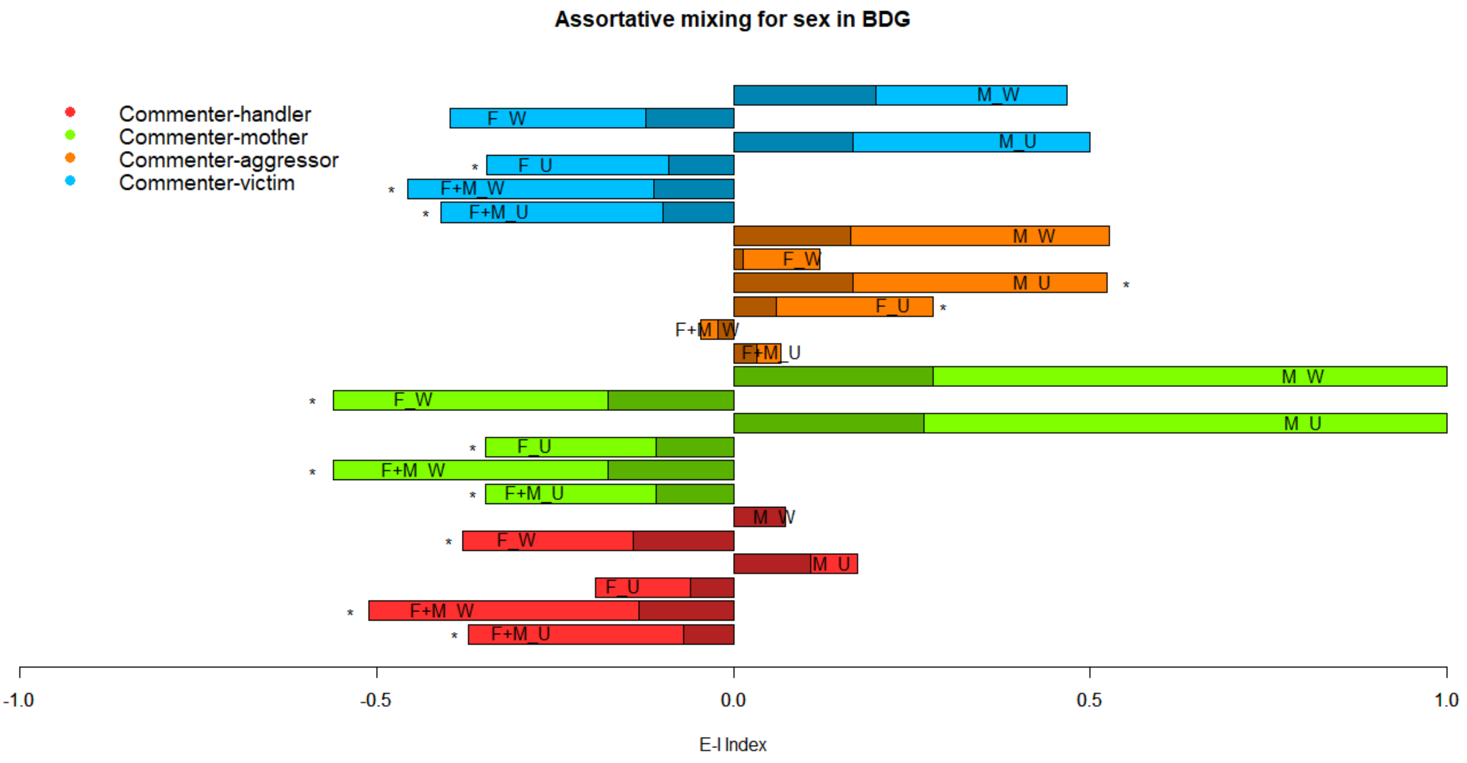


Figure 4.13. Assortative mixing for sex in vocal comments networks. U: Unweighted network. W: Weighted network. F+M: E-I index measures of all possible interactions among males and females. F: E-I index measures of interactions involving females (i.e. excluding M-M interactions). M: E-I index measures of interactions involving

males (i.e. excluding F-F interactions). The grey bars (darker shades when overlapped with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

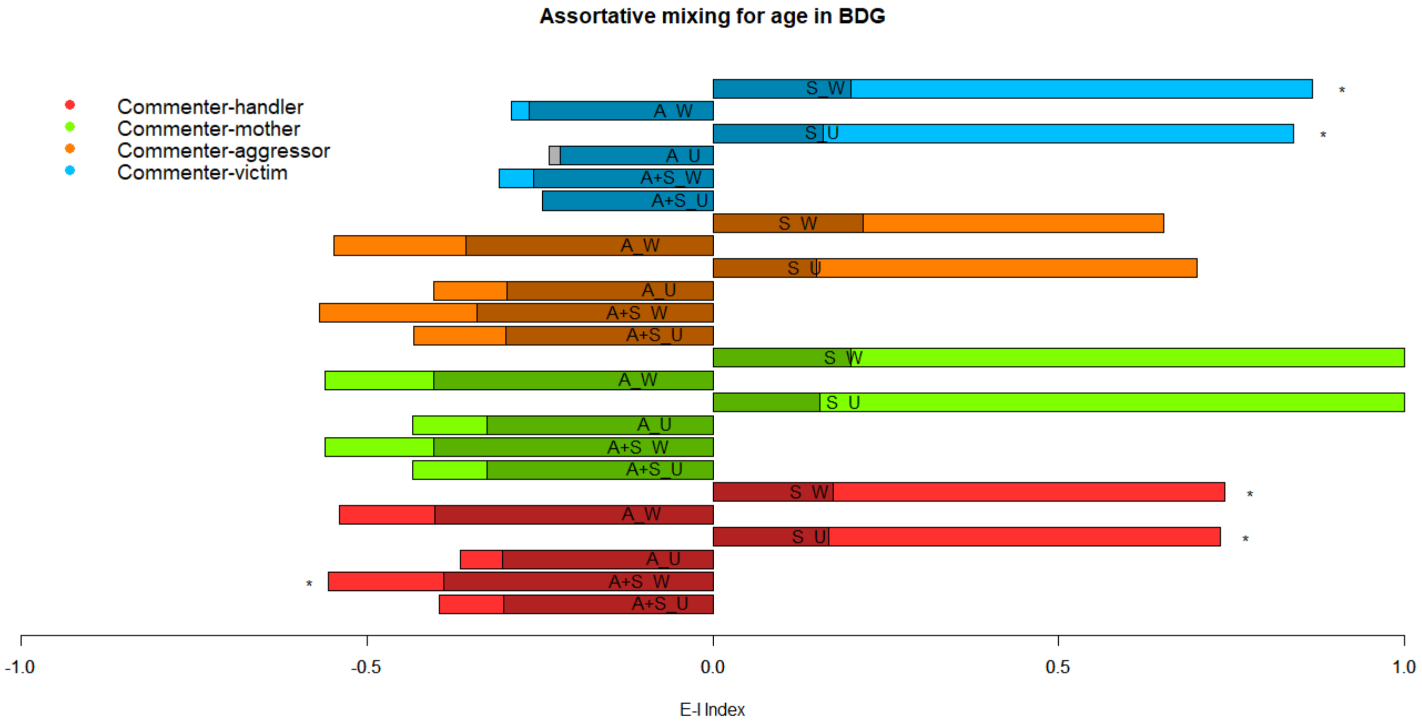


Figure 4.14. Assortative mixing for age in vocal comments networks. U: Unweighted network. W: Weighted network. A+S: E-I index measures of all possible interactions among adults and sub-adults. A: E-I index measures of interactions involving adults (i.e. excluding S-S interactions). S: E-I index measures of interactions involving sub-adults (i.e. excluding A-A interactions). The grey bars (darker shades when overlapped with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

Finally, middle- and low-ranking individuals showed significant levels of heterophily for both weighted and unweighted measures of the E-I index in the commenter-handler network. This indicates that vocal comments produced during infant-handling contexts preferably occurred when callers and infant-handlers belonged to a different (rather than the same) rank class if they were middle or low-ranking individuals (***Figure 4.15***).

Both females and males had more ties with individuals of the opposite sex in the commenter-aggressor network than with individuals of the same sex (***Figure 4.13***). In contrast, homophily for sex characterised the commenter-victim network, especially in the case of females who tended to comment when victims were other females (***Figure 4.13***). Sub-adults showed heterophily in the commenter-victim network, while age was not significant in the commenter-aggressor network (***Figure 4.14***). Finally, neither of the two networks based on vocal comments produced during third-party agonistic interactions returned significant results of the E-I index analysis for social rank (***Figure 4.15***).

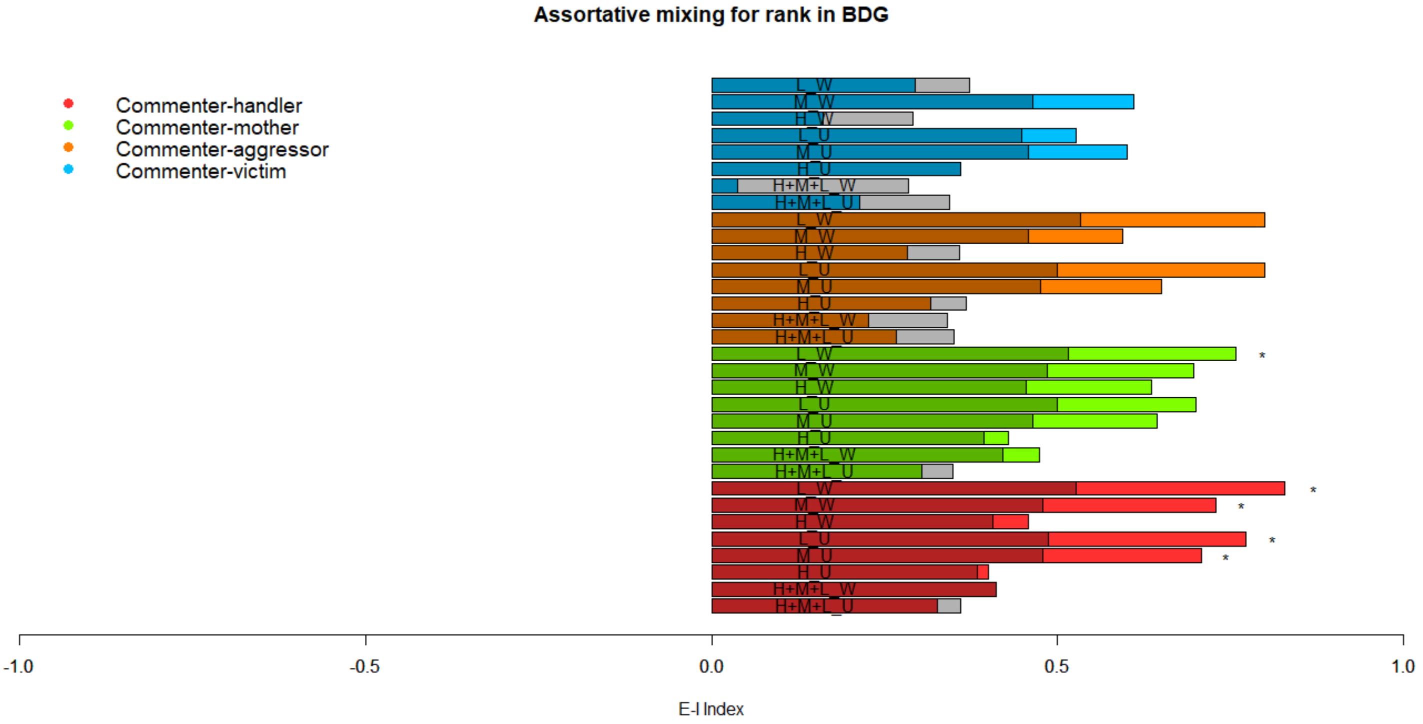


Figure 4.15. Assortative mixing for social rank in vocal comments networks. U: Unweighted network. W: Weighted network. H+M+L: E-I index measures of all possible interactions among high, mid and low-ranking individuals. H: E-I index measures of interactions involving high-ranking individuals. M: E-I index measures of interactions involving middle-ranking individuals. L: E-I index measures of interactions involving low-ranking individuals. The grey bars (darker shades when overlapped with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

Network regressions and influence of individual attributes

There was no multi-collinearity of variables in any of the linear regressions performed (***Table 4.9***). The occurrence of vocal comments in infant-handling contexts was predicted by: a) huddling relations between callers and infant-handlers, b) grooming interactions between callers and mothers of the infants involved in the third-party interaction (***Table 4.9***). No other socio-positive networks significantly predicted communication networks based on vocal comments in this context.

Table 4.9. Results of the network regressions for vocal comments in infant-handling contexts.

Affiliative network	Communication network	VIF	AIC	r (p-value)
Affiliative (CSI)	Commenter-handler	CSI = 1.092, SS = 1.167, AS = 1.031, SR = 1.148, ID1 = 1.016, ID2 = 1.016	-5680.68 (-5680.68, -5575.53)	CSI = 4.84e-05 (p = 0.259) SS = 9.28e-04 (p < 0.001)*
	Commenter-mother	CSI = 1.092, SS = 1.167, AS = 1.031, SR = 1.148, ID1 = 1.016, ID2 = 1.016	-5737.08 (-5737.08, -5623.69)	CSI = 7.10e-05 (p = 0.122) SS = 3.93e-04 (p = 0.997)
Grooming	Commenter-handler	SRI_{GRO} = 1.074, SS = 1.161, AS = 1.029, SR = 1.142, ID1 = 1.015, ID2 = 1.015	-5696.83 (-5696.83, -5592.82)	SRI_{GRO}= 0.016 (p = 0.081) SS = 8.94e-04 (p < 0.001)*
	Commenter-mother	SRI_{GRO}= 1.074, SS = 1.161, AS = 1.029, SR = 1.142, ID1 = 1.015, ID2 = 1.015	-5754.97 (-5754.97, -5642.46)	SRI_{GRO}= 0.019 (p = 0.018)* SS = 3.67e-04 (p = 0.997)
Huddling	Commenter-handler	SRI_{HUD}= 1.074, SS = 1.161, AS = 1.029, SR = 1.142, ID1 = 1.015, ID2 = 1.015	-5754.97 (-5754.97, -5642.46)	SRI_{HUD}= 0.019 (p = 0.018)* SS = 3.67e-04 (p = 0.997)
	Commenter-mother	SRI_{HUD}= 1.086, SS = 1.175, AS = 1.032, SR = 1.139, ID1 = 1.014, ID2 = 1.014	-5732.08 (-5743.39, -5629.45)	SRI_{HUD}= 0.006 (p = 0.913) SR = -1.61e-05 (p = 0.016)*
1m Proximity	Commenter-handler	SRI_{PR1}= 1.065, SS = 1.140, AS = 1.030, SR = 1.151, ID1 = 1.019, ID2 = 1.019	-5693.95 (-5693.95, -5589.30)	SRI_{PR1}= 0.029 (p = 0.196) SS = 9.24e-04 (p < 0.001)*
	Commenter-mother	SRI_{PR1}= 1.065, SS = 1.140, AS = 1.030, SR = 1.151, ID1 = 1.019, ID2 = 1.019	-5749.20 (-5749.20, -5635.48)	SRI_{PR1}= 0.034 (p = 0.122) SS = 4.01e-04 (p = 0.997)

CSI: Composite sociality index combining grooming, huddling and proximity within 1m. GRO: Grooming. HUD: Huddling. PR1: Proximity 1m. VIF: Variance Inflation Factor of each of the variables. SRI: Simple Ratio Index of the independent network. SS: Sex similarity. AS: Age similarity. SR: Differences in ordinal ranks of dominance. ID1: Identity of individual 1. ID2: Identity of individual 2. AIC: indicates the AIC value of the chosen regression model and the range of the AIC values of all the models tested. r: regression coefficients. p: p-values. Only regression coefficients and p-values of significant variables in the fitted model are reported. *: $p<0.05$

In agonistic contexts, macaques mainly produced vocal comments during third-party conflicts when the victim was not a frequent grooming partner nor a strong affiliate, and when callers and victims belonged to the same rank classes (***Table 4.10***). None of the affiliative networks predicted the commenter-aggressor network.

Table 4.10. Results of network regressions for vocal comments in agonistic contexts.

Affiliative network	Communication network	VIF	AIC	r (p-value)
Affiliative (CSI)	Commenter-aggressor	CSI = 1.092, SS = 1.167, AS = 1.031, SR = 1.148, ID1 = 1.016, ID2 = 1.016	-6414.69 (-6423.62, -6329.87)	CSI = 5.22e-06 (p = 0.458) AS = 3.11e-04 (p = 0.047)* SR = -4.056e-05 (p = 0.001)*
	Commenter-victim	CSI = 1.092, SS = 1.167, AS = 1.031, SR = 1.148, ID1 = 1.016, ID2 = 1.016	-6544.74 (-6553.8, -6447.94)	CSI = -6.12e-05 (p = 0.009)* SS = 2.66e-04 (p = 0.099) SR = -4.19e-05 (p < 0.001)*
Grooming	Commenter-aggressor	SRI_{GRO}= 1.074, SS = 1.161, AS = 1.029, SR = 1.142, ID1 = 1.015, ID2 = 1.015	-6425.15 (-6434.30, -6340.48)	SRI_{GRO}= 0.002 (p = 0.458) AS = 3.12e-04 (p = 0.052) SR = -4.02e-05 (p < 0.001)*
	Commenter-victim	SRI_{GRO}= 1.074, SS = 1.161, AS = 1.029, SR = 1.142, ID1 = 1.015, ID2 = 1.015	-6561.14 (-6561.14, -6454.17)	SRI_{GRO}= -0.008 (p = 0.030)* SR = -4.77-05 (p < 0.001)*

CSI: Composite sociality index combining grooming, huddling and proximity within 1m. GRO: Grooming. VIF: Variance Inflation Factor of each of the variables. SRI: Simple Ratio Index of the independent network. SS: Sex similarity. AS: Age similarity. SR: Differences in ordinal ranks of dominance. ID1: Identity of individual 1. ID2: Identity of individual 2. AIC: indicates the AIC value of the chosen regression model and the range of the AIC values of all the models tested. r: regression coefficients. p: p-values. Only regression coefficients and p-values of significant variables in the fitted model are reported. *: p<0.05

Kruskall-Wallis and Dunn tests confirmed that macaques frequently produced vocal comments when they and the individuals they observed in infant-handling interactions belonged to the same sex class (***Tables 4.11*** & ***4.12***). Females produced more frequent comments on other females than males on females interacting with infants. Also, males produced vocal comments more often when other males were handling infants than when females were (***Figure 4.16A***). Both adults and sub-adults commented more often on infant handling interactions that involved adults in comparison to those that involved sub-adults (***Figure 4.16B***). In addition, high- and middle-ranking individuals generally produced vocal comments when high-ranking partners were involved in infant-handling interactions (***Figure 4.16C***) whereas low-ranking individuals did not show a rank class preference (***Table 4.11)***.

Table 4.11. Kruskal-Wallis test results for each network and individual attribute's categories.

Attributes	Commenter-handler	Commenter-aggressor	Commenter-victim
Sex	χ^2 = 14.577 (p = 0.002)*	χ^2 = 2.315 (p = 0.509)	χ^2 = 10.006 (p = 0.019)*
Age	χ^2 = 31.497 (p < 0.001)*	χ^2 = 13.879 (p = 0.003)*	χ^2 = 10.086 (p = 0.018)*
Higher vs lower	χ^2 = 14.480 (p < 0.001) *	χ^2 = 3.512 (p = 0.173)	χ^2 = 0.762 (p = 0.683)
Middle vs higher	χ^2 = 15.354 (p < 0.001)*	χ^2 = 6.044 (p = 0.049)*	χ^2 = 6.246 (p = 0.044)*
Low vs higher	χ^2 = 3.761 (p = 0.153)	χ^2 = 5.046 (p = 0.080)	χ^2 = 4.053 (p = 0.132)

Higher vs lower: Comparison of higher ranking individuals directing behaviours to other higher ranking individuals vs higher ranking individuals directing behaviours to lower-ranking classes. Middle vs higher: Comparison of Middle ranking individuals directing behaviours to higher ranking individuals vs middle ranking individuals directing behaviours to middle and low ranking partners. Low vs higher: Comparison of low ranking individuals directing behaviours to other low ranking individuals vs low ranking individuals directing behaviours to higher ranking partners. *: indicates significant results.

Females produced more vocal comments when other females were the victims of aggression than when males were (***Figure 4.18A***). Also, vocal comments during agonistic encounters were more frequent when aggressors were adults than when they were sub-adults (***Table 4.12*** & ***Figure 4.17A***). Adults called more often when adult victims were involved in conflicts than sub-adults when sub-adult victims were observed (***Figure 4.18B***). Finally, middle-ranking macaques significantly called more often when (i) aggressors were high-ranking individuals than when aggressors were low-ranking conspecifics (***Figure 4.17B***), and (ii) when victims of the aggression were low-ranking than when victims were high-ranking (***Figure 4.18C***).

Table 4.12. Dunn test results for each network and individual attribute.

Attributes	Commenter-handler	Commenter-aggressor	Commenter-victim
Sex	FF-FM: -2.16 (0.062) FF-MF: -3.70 (p = 0.001)* FF-MM: -0.99 (p = 0.349) FM-MF: -1.77 (p = 0.077) FM-MM: 0.94 (p = 0.349) MF-MM = 2.47 (p = 0.040)*	NA	FF-FM: -3.01 (0.016)* FF-MF: -1.84 (p = 0.132) FF-MM: -2.18 (p = 0.089) FM-MF: 0.85 (p = 0.594) FM-MM: 0.51 (p = 0.730) MF-MM = -0.31 (p = 0.759)
Age	AA-AJ: -4.87 (p<0.001)* AA-JA: 0.69 (p = 0.492) AA-JJ: -2.46 (p = 0.021)* AJ-JA = 4.06 (p<0.001)* AJ-JJ: 0.92 (p = 0.432) JA-JJ: -2.55 (p = 0.021)*	AA-AJ: -3.32 (p = 0.005)* AA-JA: -2.10 (p = 0.072) AA-JJ: -2.54 (p = 0.033)* AJ-JA = 0.20 (p = 0.842) AJ-JJ: -0.24 (p = 0.842) JA-JJ: -0.36 (p = 0.842)	AA-AJ: -2.12 (p = 0.103) AA-JA: -1.68 (p = 0.184) AA-JJ: -2.85 (p = 0.026)* AJ-JA = -0.22 (p = 0.827) AJ-JJ: -1.39 (p = 0.249) JA-JJ: -0.95 (p = 0.413)
Rank	HH-HM: -2.88 (p = 0.006)* HH-HL: -3.59 (p<0.001)* HL-HM: 0.71 (p = 0.479) MH-ML: -3.89 (p<0.001)* MH-MM: -2.34 (p = 0.029)* ML-MM: 1.55 (p = 0.121)	MH-ML: -2.45 (p = 0.042)* MH-MM: -1.36 (p = 0.260) ML-MM: 1.09 (p = 0.275)	MH-ML: 2.50 (p = 0.38)* MH-MM: 1.14 (p = 0.255) ML-MM: -1.36 (p = 0.255)

NA: Not applicable. Dunn tests were only performed for significant Kruskal-Wallis analyses. F: Females. M: Males. A: Adults. J: Sub-adults/Juveniles. H: High-ranking individuals. M: Middle-ranking individuals. L: Low-ranking individuals. Pairs of dyads are compared, the first and second letter of the dyad indicating the roles of the subjects in that network. For instance, FM in the recruiter-aggressor network indicates that the recruiter is a female and the aggressor is a male. In FF-FM for the recruiter-aggressor network, the strength of connections between female callers and female aggressors is compared with the strength of connections between female callers and male aggressors. *: indicates significant results.

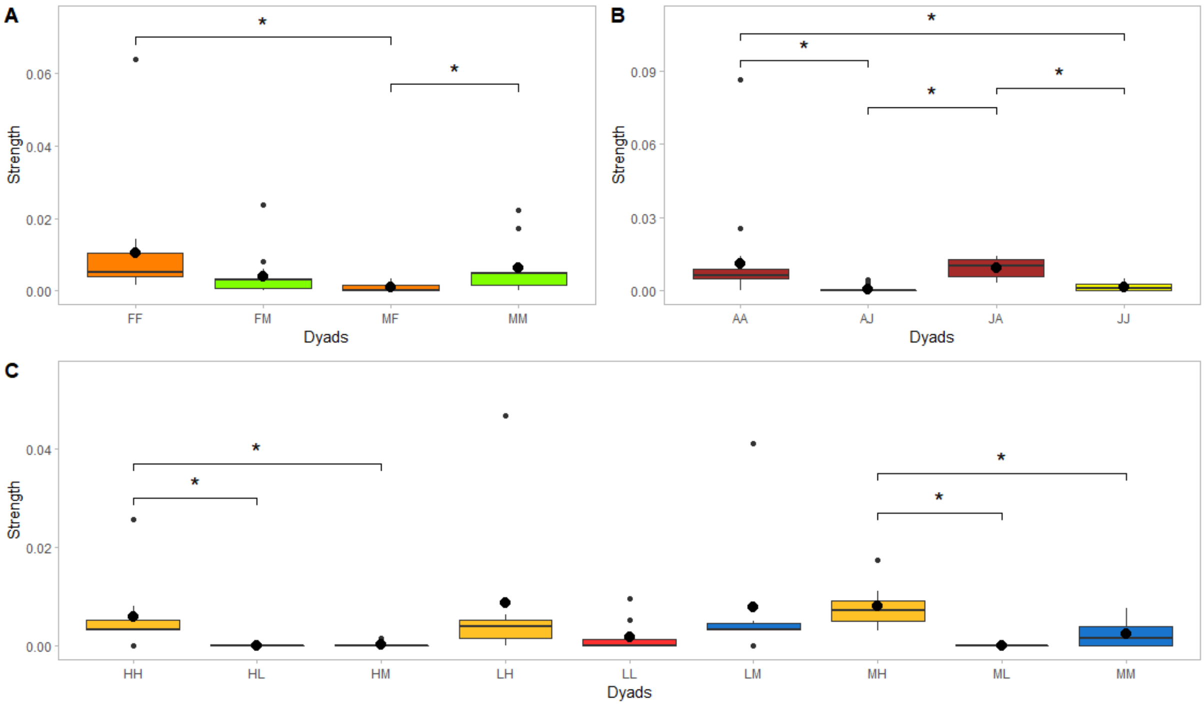


Figure 4.16. Box-plot of the strength of interactions in the commenter-handler network for sex (**A**), age (**B**) and social rank (**C**) categories. F: Females. M: Males. A: Adults. J: Sub-adults/Juveniles. H: High-ranking individuals. M: Middle-ranking individuals. L: Low-ranking individuals. Dyads names describe who the commenter (first letter) is and who the handler (second letter) is. For instance, FM indicates that females call when males were observed handling infants, AJ indicates that adults call when sub-adults were observed handling infants and LH indicates that low-ranking individuals call when high-ranking conspecifics were observed handling infants.

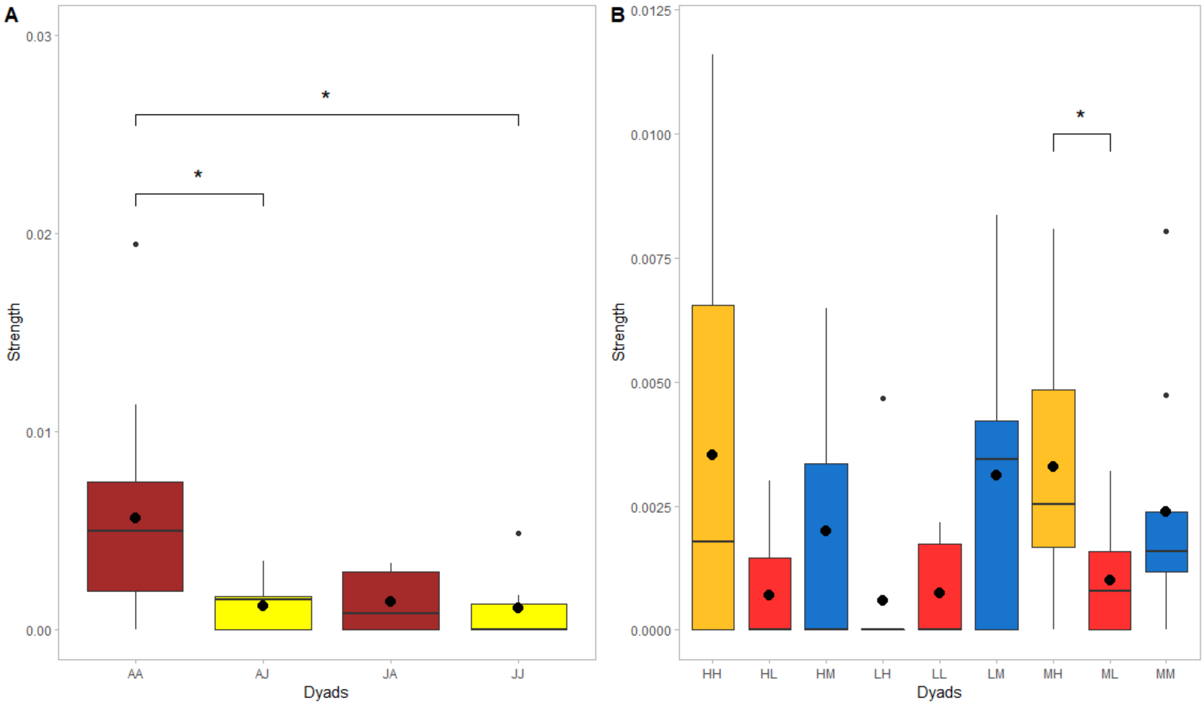


Figure 4.17. Box-plot of the strength of interactions in the commenter-aggressor network for age (**A**) and social rank (**B**) categories. A: Adults. J: Sub-adults/Juveniles. H: High-ranking individuals. M: Middle-ranking individuals.

L: Low-ranking individuals. Dyads names describe who the commenter (first letter) is and who the aggressor (second letter) is. For instance, AJ indicates that adults call when sub-adults were the aggressors in the conflict observed and MH indicates that middle-ranking individuals call when high-ranking conspecifics were the aggressors in the conflict observed.

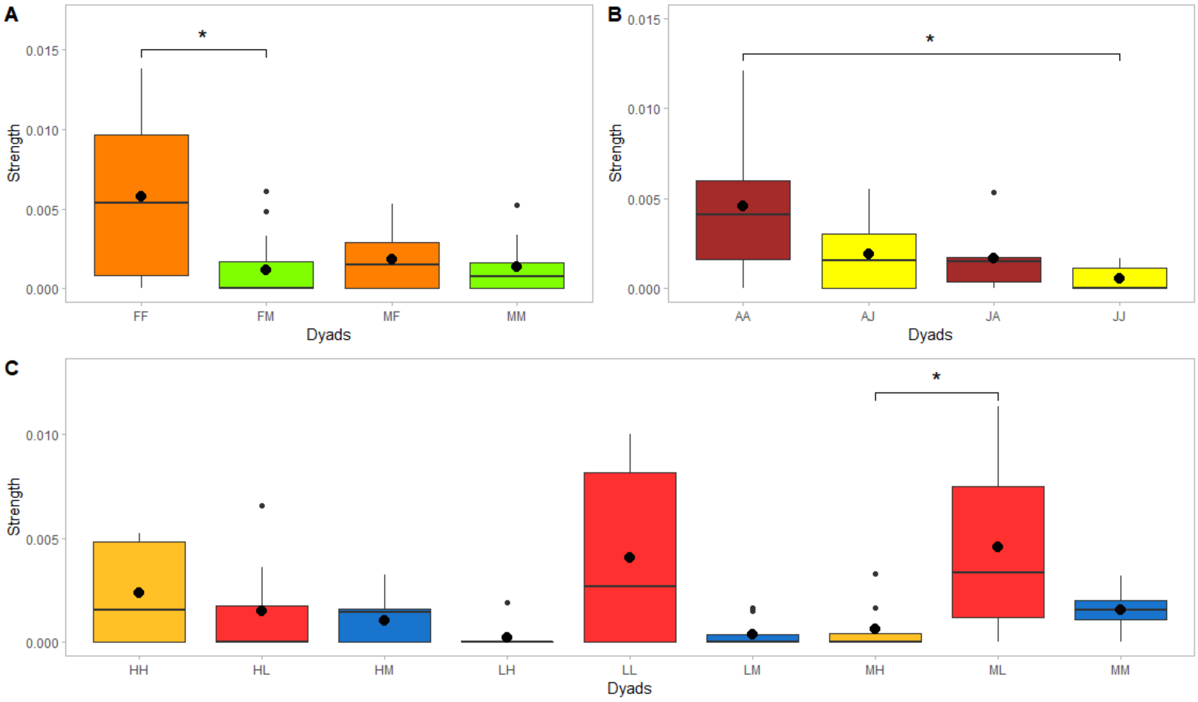


Figure 4.18. Box-plot of the strength of interactions in the commenter-victim network for sex (**A**), age (**B**) and social rank (**C**) categories. F: Females. M: Males. A: Adults. J: Sub-adults/Juveniles. H: High-ranking individuals. M: Middle-ranking individuals. L: Low-ranking individuals. Dyads names describe who the commenter (first letter) is and who the victim (second letter) is. For instance, FM indicates that females call when males were the victims in the conflict observed, AJ indicates that adults call when sub-adults were the victims in the agonistic encounter observed and ML indicates that middle-ranking individuals call when low-ranking conspecifics were the victims in the conflict observed.

Comparison between communication networks

Regressions between networks based on aid-recruitment calls and on vocal comments indicated the helper-recipient network predicted the commenter-aggressor network (r = 0.208, p = 0.029, ***Figure 4.19A***), but the helper-opponent network did not predict the commenter-victim network (r = 0.111, p = 0.196, ***Figure 4.19B***).

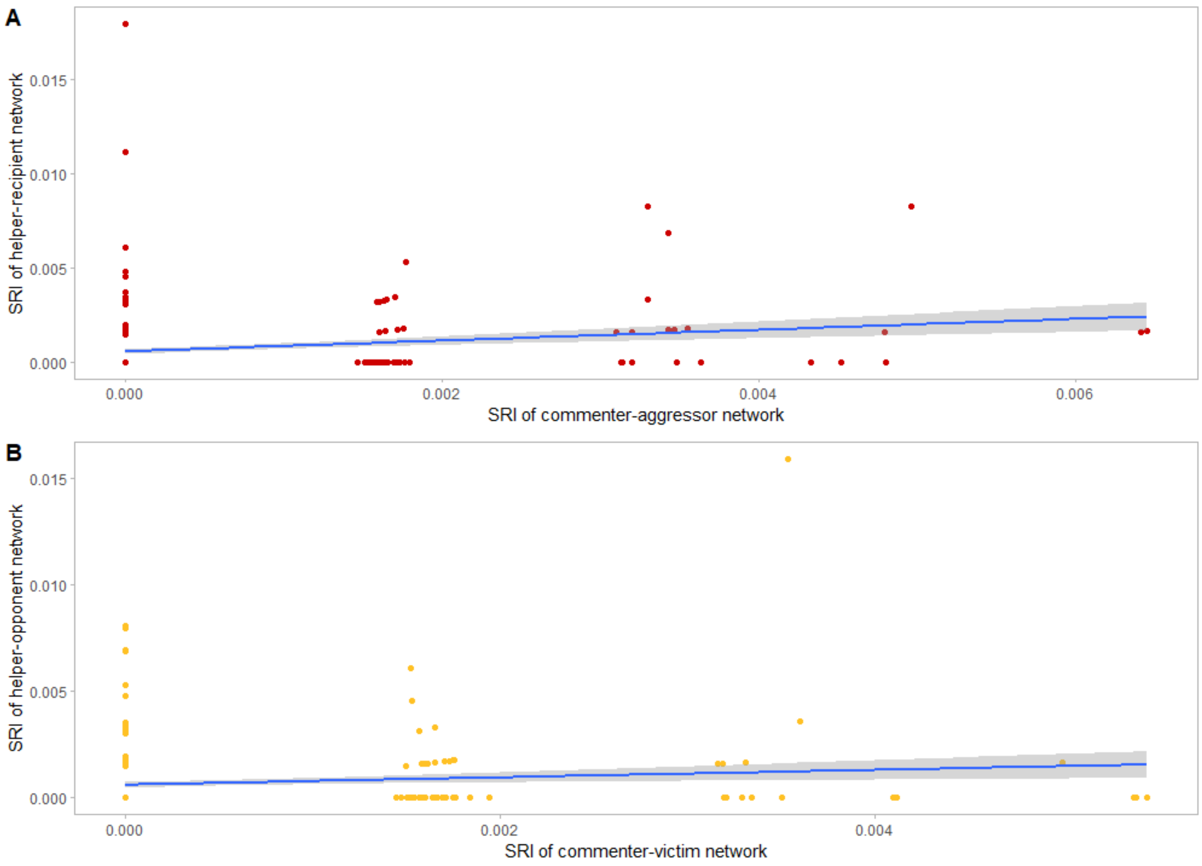


Figure 4.19. Scatter-plot of the regression between commenter-aggressor and helper-recipient networks (**A**) and between commenter-victim and helper-opponent networks (**B**). Dots represent values of the strength of connections measured using the Simple Ratio Index (SRI).

4.4.4. Discussion

Confirming 'a priori' predictions, communication networks based on vocal comments were predicted by affiliative networks in both infant-handling and agonistic contexts. Specifically, the occurrence of vocal comments in infant-handling contexts were predicted by the huddling bonds between callers and the third parties, and by the grooming ties established between commenters and the mothers of the infants involved in the third-party interaction, as predicted 'a posteriori'. In agonistic contexts, alliances between callers and aggressors observed during aid-recruitment contexts, and weak social bonds between callers and victims of the third-party interaction predicted the occurrence of vocal comments, following 'a posteriori' predictions.

Following 'a priori' predictions, vocal comments were more frequent when callers and third parties belonged to the same (rather than different) sex. Specifically, females commented more frequently when other females were observed handling infants, and when other females were the victims of aggression, than when males were infant-handlers or victims. Also males commented to male handlers more often than to female handlers. Moreover, individuals mainly commented when higher-ranking conspecifics were observed handling infants (following ‘a posteriori’ predictions) and when victims of the third-party aggression had the same or lower rank than the caller.

4.4.4.1. Vocal comments during infant-handling contexts

Vocal comments in socio-positive contexts were mainly triggered by the observation of infants engaged in close and affiliative interactions with adults.

Grooming bonds between commenters and mothers of the infants involved in the infant-handling interaction predicted the occurrence of vocal comments. Grooming is known to be exchanged for commodities (e.g. social tolerance) or access to resources (Barrett et al., 1999; Henzi et al., 2003). In Barbary macaques, infants are attractive to both males and females, and play an important role in maintaining group stability, buffering agonism or forming coalitions (Deag, 1980; Small, 1990; Paul et al, 1996). Therefore, infants seem to be a valuable resource in Barbary macaques. Grooming bonds with mothers of infants may provide privilege access to infants. It is likely that Barbary macaques uttered vocal comments to gain access to infants (who were being handled by a party that may have involved the mother) when access to them was more likely (i.e. when infants belonged to mothers who they shared strong bonds with). As suggested by previous studies, it is possible that vocal comments may intentionally or inadvertently signal for social tolerance when approaching an infant (Owren et al., 2003; Rendall, 2003; Whitham et al., 2007)

Interestingly, huddling relations between callers and the individuals involved in infant handling also predicted the occurrence of vocal comments. All infant-handling situations involved close and static interactions between infants and adults and/or sub-adults (e.g. grooming, huddling, triadic interactions). Thus, infant handling can be understood as individuals gathering in small huddles where affiliative interactions are exchanged. Accordingly, as individuals utter vocal comments when frequent huddling partners are observed handling infants, it is likely that the ultimate function of these calls is to signal the intention of joining the party. In the huddling network, it was females who frequently huddled with other females (see ***Chapter 3***). Similarly, it was females who mainly uttered vocal comments during third-party infant-handling contexts when other females were involved. Therefore, it is likely that vocal comments emitted during infant-handling interactions were directed towards the individuals handling the infant rather than other group members (as suggested by Brumm et al., 2005). In addition, these vocalizations were more frequently uttered when individuals involved in the third-party interaction had a higher, versus lower, rank than commenters, suggesting that vocal comments, in this infant-handling contexts, may serve to elicit social tolerance near the infants, as suggested in predictions.

Overall, these findings suggest that Barbary macaques display high levels of triadic awareness and assess the type of relations they have with the different agents involved in a third-party interaction to evaluate the risks and opportunities of producing certain behaviours. Specifically, Barbary macaques seem to produce vocal comments when the chances of joining the social interaction are high, so it is likely that they use these vocalizations to request or inform about their intention to participate. However, the operational definition of 'vocal comments' states that individuals do not get involve in the third-party interaction after vocalizing, although it is unknown how these vocalizations might increase the likelihood of participation of the caller, at the long-term, in future infant-handling interactions (Brumm et al., 2005). Moreover, these vocal comments are sometimes produced at long distances, where no individual can hear them, suggesting that they might not be directed at the third parties (Brumm et al., 2005). Therefore, I cannot rule out the hypothesis that these calls do not convey information about Barbary macaques' intentions (Whitham et al., 2007). Emotional contagion may explain the production of vocal comments at long distances in infant-handling contexts. There are studies in the literature that imply contagion is stronger between individuals with stronger relationships (De Marco et al., 2011; Palagi et al., 2014). This could fit with the selectivity of production of vocal comments even if it is due to contagion at large distances.

Instances of emotional contagion have been reported in several primate species such as chimpanzees (Okamoto et al., 2001) or Sulawesi and Tonkean macaques (Thierry et al., 2000; De Marco et al., 2011). An interesting example of emotional contagion in non-human primates is collective arousal/excitement where more than two individuals engage in bouts of intense affiliation (De Marco et al., 2010). During collective excitement, individuals actively greet each other in close-contact interactions accompanied by loud and soft vocalizations (Thierry et al., 2000; De Marco et al., 2010). Collective arousal has been observed in different contexts: during reconciliation or appeasement interactions after conflicts, while awaiting the distribution of food in captive populations or when individuals are reunited after temporary separation (Thierry et al., 2000; De Marco et al., 2011). Greetings exchanged during collective excitement are more likely to occur between closely-bonded partners (De Marco et al., 2014) and may play a role in reinforcing or reaffirming social relations (De Marco et al., 2014), renewing social bonds, reducing social tension and enhancing group cohesion (De Marco et al., 2011). Cases of collective arousal have been observed in macaque species with a tolerant social system (Thierry et al., 2000; De Marco et al., 2011), so it is likely that some forms of collective excitement also take place in the socially-tolerant Barbary macaques (Thierry, 2007).

Vocal comments share most of the characteristics that define collective-arousal behaviour. They involve more than two individuals that engage in close affiliative contacts simultaneously, mainly occur among closely-bonded partners, and are accompanied by soft vocalizations (Thierry et al., 2000).

Moreover, access to infants is important to Barbary macaques' social life because they help regulate social relations (Whiten & Rumsey, 1973; Deag, 1980; Small, 1990; Paul & Kuester, 1996; Paul et al., 1996; Henkel et al., 2010; Kubenova et al., 2017). Individuals with limited access to infants (e.g. low-ranking individuals) must find other strategies to engage in the social life of the group, reinforce or reaffirm their social bonds with higher-ranking individuals or reduce social tension. Vocal comments tended to be uttered by individuals who had a lower social rank than the infant-handlers (mainly, closely-bonded to the commenters). Therefore, vocal comments might function as a form of collective arousal that allows individuals with limited access to infants to benefit from the social services that infants provide to the group.

In summary, my results suggest that vocal comments seem to be triggered by infant-related arousal (proximate explanation) and may ultimately enable individuals to engage in infant-handling interactions either physically (in the mid or long-term by gaining social tolerance near the infant) or at a distance (during the third-party interaction via collective excitement), depending on the affiliative and dominance relationship between callers and third-parties.

4.4.4.2. Vocal comments during agonistic contexts

Vocal comments in affiliative situations were more frequent than in agonistic encounters probably because the risk of retaliation is expected to be much lower during infant-handling interactions than during conflicts (Widdig et al., 2000; Young et al., 2014). This is in line with previous data where commenting behaviour during conflicts represented 10 – 50% of all vocal comments observed, while the rest (50 – 90%) occurred during infant-handling interactions (Brumm et al., 2005).

Results indicate that vocal comments during conflicts seem to be directed towards specific individuals. Vocal comments tended to be produced when callers and aggressors were reliable allies in terms of providing active support during conflicts (as represented by networks of recipient-helper relations where aid-recruitment calls were recorded). Moreover, Barbary macaques mainly produced vocal comments when the victim of the aggression observed was weakly-bonded to them. The likelihood of vocal comments in agonistic contexts increased as the strength of grooming relations between commenter and the third-party victim decreased. As grooming is important to strengthen social bonds, form alliances and exchange coalition behaviours (Watts, 2002; Young et al., 2014), vocal comments seem to function as signals of support directed to allies involved in conflicts against potential competitors of the caller.

Vocalizations uttered when observing others' disputes have been reported in other primate species and labelled as 'vocal alliances' (Silk et al., 2004; Wittig et al., 2007). These vocal behaviours seem to be common in Afro-Eurasian primate species with matrilineal dominance hierarchies and among females who may use them to support kin against lower-ranking individuals to maintain the maternal dominance rank (Wittig et al., 2007). As Barbary macaques are also Afro-Eurasian primates with a matrilineal dominance style (Preuschoft et al., 1998), vocal comments may be understood as an example of 'vocal alliances'. This supposition is further supported by the finding that females generally 'commented on' male aggressors, but also other females, against victims who had the same sex and either the same or lower social rank than themselves, especially in the case of middle-ranking commenters. The lack of kinship data did not allow testing for the influence of maternal-relatedness in these networks, but the patterns observed in terms of sex, rank and social bonds match the findings of previous studies reporting 'vocal alliances' (Silk et al., 2004; Wittig et al., 2007).

4.5. General discussion

In this chapter, I aimed to understand how social bonds established via grooming, huddling and close proximity are relevant to predict the interactions derived from vocal behaviours. On one hand, I studied aid-recruitment calls for which responses are thought to depend on the complex dynamics of relations and alliances that individuals secure through socio-positive interactions. On the other hand, I investigated vocal comments, the production of which may reflect the nature of the social relations between the caller and the individuals involved in a third-party interaction. Although the results correspond well with most of the literature reviewed, they must be taken with caution because they are based on data collected on only one group of Barbary macaques (BDG).

In summary, Barbary macaques did not recruit aid in all agonistic contexts, suggesting that in most cases, the dominance relationship between two individuals seems to be readily accepted by both individuals. Regardless, aid-recruitment calls were mainly uttered when males threatened females and when middle-ranking individuals were attacked by higher-ranking members. Low-ranking subjects, however, normally responded with formal submission. Barbary macaques provided agonistic support to their affiliates. It was generally males who backed up other conspecifics during conflicts, and aid was mainly provided to individuals of the same rank when the opponent was a lower-ranking member. Networks based on grooming, proximity within 1m and a combination of affiliative behaviours (CSI: grooming + huddling + 1m proximity) predicted who provided support to whom. I argued that individuals with strong alliances probably called in order to avoid high aggression and to protect their social status. Results for aid-recruitment networks confirmed most of my initial predictions and matched findings of previous studies (Gouzoules et al., 1984; Widdig et al., 2000; Watts, 2002; Slocombe & Zuberbühler, 2007; Berghänel et al., 2011; Gilby et al., 2013; Young et al., 2014). However, the influence of kinship could not be tested, so I cannot rule out the possibility that the correlation between social bonds and agonistic support would disappear when statistical analyses control for this variable, as has previously been reported (Ventura et al., 2006).

Screams produced during conflicts may also be directed to the aggressor. Fedurek et al. (2015) suggested that chimpanzee (*Pan troglodytes*) screams did not only serve to solicit help from an audience but also to signal the victim's submission and discourage the aggressor from continuing the assault. Accordingly, chimpanzees produced sequences of screams more often when the rank distance between the aggressor and the victim was large than when it was small (Fedurek et al., 2015). My results also indicate that aid-recruitment calls were more likely to be uttered when individuals confronted aggressors higher in rank than themselves in comparison to aggressors of the same or lower rank. Therefore, I cannot rule out the possibility that aid-recruitment calls collected in this thesis have also the function to display submission and repel aggressors. Although screams may have a repelling function, Fedurek et al. (2015) found that another vocalization (namely the 'waa' bark) was mainly responsible for discouraging attackers from future aggression. 'Waa' barks were directed to aggressors and were always uttered after aid-recruitment screams and, generally, after receiving support (Fedurek et al., 2015). Similarly, Barbary macaques sometimes uttered isolated pant barks after screaming during conflicts (see ***Appendix I*** for further details). It is likely that the pant barks of Barbary macaques have the same function as the 'waa' barks of chimpanzees.

Only screams accompanied by searching behaviours (i.e. standing up and/or stretching neck while looking around or orienting head or gaze towards particular conspecifics) were considered as aid-recruitment calls in this study. This operational definition avoided confusion with other vocalizations that may have a different purpose in similar agonistic contexts (Fischer & Hammershcmidt, 2002). As described in ***Appendix I*** different call types could be identified during vocalizing conflicts. However, all the calls recorded were accompanied by searching behaviours and 94% of them included noisy and complex screams as the main acoustic element (see ***Appendix I***). Overall, the qualitative sound analysis (***Appendix I***) indicated that aid-recruitment calls that were responded to by allies with agonistic support contained clear and modulated tonal screams plus long and high-pitched screeches as main call types. In contrast, most calls not responded to with aid mainly included one of the aforementioned call types accompanied by acoustic elements lower in frequency than the responded to calls (i.e. rasping squeaks and hoarse screams). Motivational theory states that increased arousal due to increased aggression leads to the production of longer calls of higher frequency and calls that are more chaotic than those produced during less severe attacks (Gouzoles et al., 1984; Berry et al. 1996; Fitch et al. 2002). Support for this theory has been found in nonhuman primates (rhesus macaques, *Macaca mulatta*, Gouzoles et al., 1984; chimpanzees, Slocombe & Zuberbühler, 2007; Geoffroy's spider monkeys, *Ateles geoffroyi*, Ordóñez-Gómez et al., 2015). It is likely that the intensity of the attacks in

Barbary macaques also influenced the production of certain call types, with high-frequency vocalizations uttered during high aggression and increasing the probability of recruiting agonistic support. However, my data does not allow me to test the impact of aggression intensity on the production of these calls and the responses they elicit.

As found in chimpanzees (Fedurek et al., 2015) and other macaques (*Macaca mulatta*, Gouzoules et al., 1984; Gouzoules & Gouzoules, 1990), my data seems to indicate that screams uttered during conflicts mainly served to recruit aid. The vocalizations here analysed were always accompanied by searching behaviours. Audio recordings collected in this thesis were contrasted with recordings of vocalizations collected in other Barbary macaque groups and showed resemblance with calls described as aid-recruitment vocalizations (see ***Appendix I***). Moreover, aggressors were never observed moving away from the victim during the production of these calls as would be expected if these calls served to repel rivals, but they generally continued or increased the aggression. Only, in one occasion, the initiator of the aggression (GH, a high-ranking male) directed submissive/appeasement behaviours (i.e. teeth-chattering) to the victim (AR, a juvenile male) while looking around, after the victim started screaming, likely to avoid retaliation from potential allies of the victim. Finally, in accordance with previous studies on aid-recruitment calls, the production of these calls in my study group was more likely when aggressors had a higher rank than the caller and the same or lower rank than the helper, and mainly recruited aid from affiliates (i.e. allies) and, particularly, from males, who are more likely to provide support during conflicts than females (Widdig et al., 2000; Slocombe & Zuberbühler, 2007; Fedurket et al., 2015).

The analyses of vocal comments collected in this thesis showed that vocal comments uttered during infant-handling contexts are acoustically and functionally different from those uttered during agonistic contexts, as indicated by previous studies (Fischer & Hammerschmidt, 2002; Brumm et al., 2005; see ***Appendix I***). During the observation of third-party agonistic interactions, individuals uttered raspy vocalizations whereas individuals produced soft pants and pant barks while observing other parties engaged in infant-handling. Even though vocal comments are low-frequency vocalizations in both contexts, these calls are of longer duration in agonistic than in infant-handling situations (see ***Appendix I*** for further details). Functionally, these calls are produced in opposite situations and, as my data suggests, the affiliative and dominance relationships between callers and third-parties are different for each context. Accordingly, we may assume that the proximate and ultimate purpose of vocal comments in infant-handling contexts is different to that of vocal comments uttered during conflicts between third-parties.

The occurrence of vocal comments in infant-handling contexts was predicted by huddling bonds between callers and the participants of the infant-handling interaction, and grooming interactions between commenters and the mothers of the infants being handled. Normally, individuals commented when observing higher-ranking conspecifics handling infants, and it was the females who vocalized more often when other females were involved. I argued that vocal comments in infant-handling contexts may function as a signal to elicit social tolerance near the infant during infant-handling interactions. However, the fact that these vocalizations were sometimes uttered at long distances does not fully support this hypothesis and the alternative (but not mutually exclusive) theory that vocal comments are a small-scale version of the so-called instances of 'collective shared joy' (Thierry et al., 2000; De Marco et al., 2011) cannot be ruled out. Here, commenting would not have signalling intent but would reflect arousal by the observation of closely-bonded partners interacting with infants of closely-bonded mothers. Even though arousal can be deemed as an epiphenomenon that may trigger the production of these calls, 'collective arousal' may have the ultimate function of allowing individuals with limited access to infants to benefit from the social services they provide by vocally joining (at a distance) infant-handling interactions (De Marco et al., 2011).

Vocal comments during agonistic encounters seem to represent a form of 'vocal alliances' observed in other primate species (Silk et al., 2004; Wittig et al., 2007) because they occurred when allies were aggressors in third party interactions and the victims were not close affiliates. Moreover, the relation between helpers of third parties and the opponent of the individual helped (helper-opponent network) did not correspond to the relations between commenters and third-party victims of aggression (commenter-victim network), despite support, in both cases, being provided to strong allies. I tentatively propose that aid-recruitment calls serve to encourage physical defence by an ally against a potential aggressor, while vocal comments are used to display support (a vocal alliance) to an ally who is confronting a mutual competitor. However, I am unable (with my data) to rule out the possibility that the intensity of conflicts differed between the two contexts (see ***Chapter 6*** for further discussion).

Overall, results obtained for both types of vocalizations (aid-recruitment calls and vocal comments) suggest that Barbary macaques have a high degree of triadic awareness and evaluate the complex alliances and social relations of their conspecifics to assess the risks and opportunities that may arise from producing vocalizations in particular contexts. Aid-recruitment calls and vocal comments may also serve to draw the attention of others in the audience to the interaction via eavesdropping effects. However, this does not seem to be the main function of these calls, but a by-product due to the salience of vocal behaviours (McGregor, 2005), since the occurrence of these calls seems to be selective (ie) predicted by the dominance and affiliative relations established between callers and allies (aid-recruitment calls) or commenters and third parties (vocal comments). Nonetheless, these vocalized interactions may provide important information regarding triadic relations to eavesdroppers that may help them navigate the complexities of social life in their group (Slocombe & Zuberbühler, 2007; Snijders & Naguib, 2017).

In the previous chapter, I illustrated how affiliative relations may predict who learns from whom. Many studies have highlighted that social learning can be predicted from the dyadic interactions established via socio-positive behaviours (Coussi-Korbel & Fragaszy, 1995; Dindo, 2009; Franz & Nunn, 2009, 2010; Hobaiter et al., 2014; Coelho, 2015). Results of this chapter also suggest that the interactions that take place during vocalized events may also tell us something about how individuals would behave in a social learning context. Communication networks based on both aid-recruitment calls and vocal comments seem to mirror the strength of affiliative relations between callers and other conspecifics. The strength of social bonds that callers establish with allies via socio-positive interactions is indirectly represented in helper-recipient and commenter-aggressor networks. Therefore, communication networks based on aid-recruitment calls and vocal comments uttered during conflicts may be used as a proxy of affiliative relations leading to social alliances. The commenter-victim network, however, seems to be a proxy for caller-competitor relationships. Vocal comments uttered during infant-handling contexts apparently represent strong affiliative bonds in terms of huddle membership (commenter-handler network) and access to commodities (commenter-mother network). In all cases, communication networks used in this thesis indirectly mirror the strength of affiliative relations, which ultimately are thought to represent social learning opportunities (Coussi-Korbel & Fragaszy, 1995).

Even though communication networks in this thesis were mainly built to depict the relationships between callers and potential receivers to which the calls might be directed to, they might take different forms. Aid-recruitment networks that illustrate the relationship between call production (callers) and call response (allies providing agonistic support) can be viewed as a proxy for a social support network, since they do not include all potential receivers. However, vocal comments in infant-handling contexts which, in the case of signalling social tolerance near the infant would depict the relationship between emitters and all potential receivers, would better represent signalling interactions (i.e. communication) per se. Note that communication networks based on vocal comments in infant-handling contexts were only built to test the relationship between callers and those involved in the third-party interaction observed, while other individuals in the audience were excluded (except mothers of infants when not engaged in the third-party).

Individuals producing vocal comments in infant-handling contexts do not face the dangers of those who produce aid-recruitment calls, who seem to assess the risk of retaliation of producing these calls in each agonistic context. Therefore, communication networks used as a proxy of social support (e.g.

aid-recruitment networks) may include information on individuals' decisions based on awaraness of triadic relations that may represent the risks and opportunities of social learning during task presentations more realistically than signalling networks (e.g. vocal comments in infant-handling contexts). In addition, if vocal comments serve to gain access to infants, only those with strong social bonds (i.e. those with a high chance to gain social tolerance near infants) will likely utter these calls. My results confirmed that the occurrence of vocal comments in infant-handling contexts was more likely when the chances to gain access to infants were higher (i.e. stronger social bonds with infant-handlers and mothers of infants). Accordingly, communication interactions may add extra information about the quality of social relations (and social tolerance) that is not captured by affiliation, but may be crucial to represent social learning opportunities (Snijders & Naguib, 2017). Had my data on communication networks and social learning been collected on the same group, I could have tested these proposals.

Consequently, communication contexts can provide relevant information about the risks and chances individuals have to evaluate when they attempt to approach and observe others in a social learning context. Therefore, it may be useful to consider the relationships established in communication networks, in conjunction with affiliative networks, when we investigate social learning dynamics in a species or group.

Chapter 5

Social learning: how affiliative and communication interactions may influence who learns from whom

Abstract

In the previous chapters, I described how socio-positive relations may provide opportunities for learning in the social context in which Barbary macaques live, and how these social bonds predict communication interactions. In this chapter, I combine social learning field experiments with analytical tools developed to identify the diffusion of social information in naturalistic contexts, to investigate social learning of a novel food resource in free-ranging Barbary macaques. Moreover, I use linear regressions between communication networks and networks based on who observed whom during task introductions to discuss whether communication interactions also reflect social learning opportunities in this species.

I found that Barbary macaques socially learned from each other only when presented with difficult tasks. Results suggest that social transmission most likely occurred via indirect social learning processes such as stimulus/local enhancement, social facilitation or response facilitation. Who observed whom within 1m during task introductions predicted social diffusion for the most difficult task. Observations within 5m and affiliative relations, outside of task introduction periods, predicted social learning for the task of medium difficulty. Finally, communication interactions observed in affiliative contexts, outside of task presentations, also predicted who observed whom during task presentations. Communication networks may represent opportunities for social learning in these macaques and provide an extra layer of information to complement affiliative networks in order to increase the power of detecting social learning.

Rachel Kendal (RK), Jeremy Kendal (JK) and Cara Evans (CE) designed the tasks tested in one of the groups: TG. CE conducted the open-diffusion experiments in TG with her research assistant, Mallory Owen (MO). Erin Morton (EM) was my research assistant during task introductions in BDG.

5.1. Introduction

Social learning is defined as ‘learning influenced by the observation of, or interaction with, a conspecific, or its products’ and, when it occurs, it shapes the diffusion of social information within a group (Heyes, 1994, p. 207; Hoppitt & Laland, 2008, p. 105). Social learning is, therefore, required for the maintenance of animal traditions, or culture, and it is important to survival (Kendal, 2008). Early on in the field, one of the most widely used methods to test for the spread of new behavioural traits within a group of animals was diffusion curve analysis (DCA). In DCA, the cumulative number of animals that learn a new behavioural trait is plotted against time. The shape of the resultant curve was thought to represent a particular learning mechanism (Franz & Nunn, 2009). This method assumes that animals interact randomly in a learning context and, therefore, social learning is not biased by individual attributes (e.g. sex, age, social rank) (Reader, 2004). However, recent research has demonstrated otherwise (Lonsdorf & Bonnie, 2010). Consequently, DCA likely fails to predict social learning in most cases where learning is influenced by specific individual attributes and/or social dynamics (Reader, 2004; Franz & Nunn, 2009).

The relationship between social dynamics and social learning was first predicted by Coussi-Korbel & Fragaszy (1995, see ***Chapter 3***) and later demonstrated in many animal species (Lonsdorf & Bonnie, 2010). Based on Coussi-Korbel & Fragaszy (1995)’s theoretical framework, Franz & Nunn (2009) developed the network-based diffusion analysis (NBDA), a statistical method to test for the social diffusion of information in groups of animals, as an alternative to diffusion curves. NBDA has been improved and extended several times (Hoppitt et al., 2010; Hoppitt & Laland, 2011) since its original version (Franz & Nunn, 2009). As a result, NBDA can now be either based on the order in which individuals acquire a novel trait (OADA – order of acquisition diffusion analysis) or the time of each individual’s trait acquisition (TADA – time of acquisition diffusion analysis). The analysis assumes that the diffusion of the trait will be faster between individuals that have strong social connections (Coussi-Korbel & Fragaszy, 1995). Therefore, the order or time of acquisition of the trait is compared with the patterns of connections of a social network representing potential social learning opportunities (Coussi-Korbel & Fragaszy, 1995; Franz & Nunn, 2009).

In the last decade, NBDA has proven to be a useful tool to test for social learning in animal societies (Hoppitt et al., 2010). Most of the studies that have used NBDA to test for social learning in primates informed the analysis with social networks based on affiliative interactions (wild redfronted lemurs, *Eulemur rufifrons*, Schnoell & Fitchell, 2012; wild-bearded capuchins, *Sapajus libidinosus*, Coelho, 2015; bonobos, *Pan paniscus*, van Leeuwen et al., 2020), associations (squirrel monkeys, *Saimiri sciureus*, Claidière et al., 2013; wild-bearded capuchins, Coelho, 2015; bonobos, van Leeuwen et al., 2020), relations of similarity (rank similarity in ring-tailed lemurs, *Lemur catta*, Kendal et al., 2010; group membership in bonobos, van Leeuwen et al., 2020) or observation events (i.e. who observes whom) during task introduction times (chimpanzees, *Pan troglodytes schweinfurthii*, Hobaiter et al., 2014; vervet monkeys, *Chlorocebus plygerythrus*, Canteloup et al., 2020). However, little attention has been paid to the potential power of communication networks to predict who has the opportunity to learn from whom.

The relationship between communication and social learning was already hinted at by Coussi-Korbel & Fragaszy (1995) and later highlighted by Heyes & Galef (1996). If communication can be understood as acts where the sender inadvertently provides information to one or more receivers (Font & Carazo, 2010), communication relations might well represent social learning opportunities. In fact, social learning studies, unless focused on 'teaching', suggest that observers may extract information from signals or cues that demonstrators may have not intended to provide (known as 'inadvertent social learning' Hoppitt & Laland 2008; Hoppitt et al., 2008; Leadbeater, 2015; Font & Carazo, 2010). Moreover, Schaefer & Ruxton (2012) argued that learning acquired from cues (a form of by-product information) might have even shaped the evolution of communication, suggesting that a natural and historical feedback exists between the development of animal communication systems and the evolution of social learning.

Some researchers have tried to fill the gaps between the fields of primate communication and social learning. For instance, it has been demonstrated that social learning is crucial for the production, use and comprehension of vocal signals in several primate species (Snowdon, 2009; Watson et al., 2015; Lameira, 2017; Cheney & Seyfarth, 2018; Seyfarth & Cheney, 2018; Fischer et al., 2020). Also, Snowdon & Boe (2003) demonstrated that cotton-top tamarins (*Saguinus oedipus*) rely on facial expressions and vocalizations of conspecifics to learn about food palatability. In these examples, communication is at the core of the information that is being transmitted, and communication relations describe the pathways through which the information that will be learned is directly transmitted.

However, communication interactions may also indirectly represent the pathways through which a new trait is passed (Webster & Laland, 2013; Snijders & Naguib, 2017). For instance, the frequency and intensity by which an individual responds to the calls of others might indicate whom they find more reliable in terms of providing new and vital information (Silk et al., 2000; Searcy & Nowicki, 2005; Wheeler et al., 2011). Also, Kulahci et al. (2015) demonstrated that ring-tailed lemurs are socially selective, generally responding to the contact calls of those with whom they share stronger grooming bonds. Accordingly, communication networks can sometimes reflect affiliative relations or even represent aspects of socio-positive relations that are not fully captured by other behaviours (e.g.

grooming, Snijders & Naguib, 2017). This potential quality of communication networks will be considered when I aim to assess the occurrence of social transmission of information using NBDA. Hasenjager et al. (2020) recently used NBDA to investigate the social diffusion relative to novel foraging sites using dance-based communication networks in honeybees (*Apis mellifera*). To the best of my knowledge, no other study has used communication networks and NBDA to test for social learning in another animal species.

Modern methods to test for social learning make use of open-diffusion experiments in which extractive foraging tasks with two possible actions to access rewards are presented (Dindo, 2009; Reader & Biro, 2010; Hoppitt & Laland, 2013). The two-action paradigm allows testing for option preferences at the individual or group level. Open diffusion experiments allow testing for the spread of novel behaviours within a social group in a more ecologically valid context than captivity and beyond the artificial dyadic context (Dindo, 2009; Hoppitt & Laland, 2013). Moreover, tasks need to be difficult enough to require social learning (Kendal et al., 2010a). In a study with several tamarin species, Kendal et al. (2009) showed that individuals significantly produced fewer successful manipulations in total and more unsuccessful than successful manipulations in the most difficult task compared to the other tasks. In addition, learning time (i.e. latency between first contact and first successful manipulation) was significantly shorter for the easiest task than for the difficult tasks (Kendal et al., 2009).

Finally, Hoppitt (2017) highlights the importance of using observation networks during task introductions in social learning studies that use NBDA. Observation networks are useful for two main reasons: a) they have the advantage that even when there is no social structure and other social networks cannot provide evidence for social learning, social transmission can still be inferred if the order in which individuals observe others perform the task predicts the order of diffusion (Hoppitt, 2017), b) they can be used to conduct linear regressions with other networks allowing to assess whether the social relationship quantified in the other network is important to determine learning opportunities (Hoppitt, 2017).

In the present study, I first used social networks based on affiliative relations (e.g. grooming and proximity) and NBDA to test whether Barbary macaques learn from each other in a series of open-diffusion trials involving exposure to a different foraging task. Each extractive foraging task had two possible actions. The manipulations involved to complete the actions in each task differed in complexity from one task to another. As a result, I tested three tasks of different difficulty: easy, medium and high. I hypothesise for Hypothesis 1 that the evidence for social learning will vary according to task difficulty (as indicated by increased learning time and reduced number of successful manipulations, Kendal et al. 2009). Accordingly, I predict that (a) socio-positive networks outside of task presentation times, and (b) observation networks during task presentations, will indicate more evidence for social learning in NBDA analysis for the difficult tasks versus easier tasks.

Affiliative and observation networks during task introductions were collected in both study groups (BDG & TG). However, social diffusion data were only sufficient for NBDA in TG while data on communication interactions were only collected in BDG. Therefore, I cannot directly test whether communication networks predict the paths of social diffusion using NBDA. I hypothesize in Hypothesis 2 that affiliative relations and communication interactions will represent social learning opportunities in a novel foraging context. Accordingly, I expect that a) affiliative networks will predict observation networks during task introductions in both groups, and b) as affiliative relations predicted communication interactions in BDG (see ***Chapter 4***), I expect that communication networks will predict who observes whom in a social learning context.

5.2. Methods

5.2.1. Study sites and subjects

Open-diffusion experiments were carried out in two groups of Barbary macaques: one in Trentham Monkey Forest (TG, N = 61) and one in Blair Drummond Safari Park (BDG, N = 29) (for more details see ***Chapter 2***).

Experiments with TG were carried out by CE and a research assistant (MO) between the 4th of July and the 26th of August of 2011. Task introductions with BDG were carried out by me and my research assistant (EM) between the 26th of April and the 29th of May of 2018.

5.2.2. Description of the tasks

Three extractive foraging tasks were presented to the TG. Raisins were used as rewards. The first task (blue/yellow task) could be solved by reaching for raisins into one of two identical holes painted in two different colours (blue or yellow). The second task (push/lift-up task) consisted of a swing door that could be pushed inwards or lifted up outwards to reach for the raisins inside. The third task (rotating-door task) involved a rotating door that could be spun clockwise or counter-clockwise to uncover a hole through which raisins could be reached. Pilot tests established that the tasks were of increasing difficulty for the monkeys to solve, being Task 1 (blue/yellow task) the easiest one and Task 3 (rotating-door task) the most difficult out of the three.

Task experiments with the BDG could not be finished but data on who observes whom during task introductions were used to build observation networks for this group (further details are given in

section 5.2.5 below). Observation data on BDG were obtained during the presentation of an extractive foraging task (twin-door task) similar to the rotating-door task presented to TG.

All tasks were made of sturdy materials (wood) and were fixed to the ground to avoid monkeys from getting harmed or breaking the task and accessing the rewards without using the intended actions. Likewise, the tasks were designed with the monkeys' safety in mind and, accordingly, no moving parts were able to trap hands/digits and no parts were removable. Many rewards were placed inside the tasks at the beginning of each session to avoid, as much as possible, having to refill the tasks during a session. Tasks were checked when possible to see if refilling was necessary. Researchers tried to obscure the tasks during refilling. If this was not possible, the identity of the monkeys that observed the refilling was noted to control for potential biases. Interference with the natural dynamics of monkeys interacting with the tasks was kept to a minimum. In all cases, the two actions led to the same quantity and quality of food rewards.

Task 1: Blue/yellow task

This consisted of a rectangular wooden box 28 (w) x 16 (h) x 16 (d) cm with two option holes in the top (6x6 cm). One of the square option holes was marked with a yellow frame and the other one was marked with a blue frame. These colours were chosen because they are equally visible to di and tri-chromatic individuals. Between the two holes, inside the box, two connected pendulum doors hung (***Figure 5.1***). When a monkey introduced its hand inside one of the holes, the pendulum on that side was pushed to the centre of the box causing the other pendulum to covering the other hole. This mechanism ensured that only one monkey at a time was able to manipulate the task and access the raisins. When necessary, the task was refilled using the two option holes.

Colours were used to distinguish both options. Afro-Eurasian primates like Barbary macaques have trichromatic vision (Jacobs, 1996; Onishi et al., 1999; Carvalho et al., 2017), so they are capable of distinguishing blue from yellow, green or red. Only a preference for red items has been found in macaque species (Skalníková et al., 2020), supporting the foraging hypothesis, that states that trichromatic vision is an adaptation to facilitate visual detection of ripe fruit (Mollon, 1989; Bowmaker et al., 1991). In order to prevent colour biases, red was avoided in the tasks.

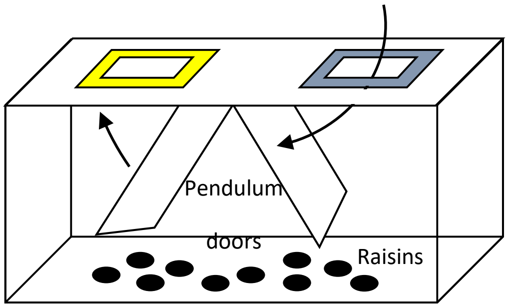


Figure 5.1. Illustration of task 1 that shows the two option holes (blue and yellow), the internal mechanism of the pendulum doors and where the raisins were placed.

The task was fixed to the ground using long U-shaped metal anchor stakes.

Task 2: Push/Lift-up task

This consisted of a wooden square-box 21 (w) x 21 (h) x 21 (d) cm with a swing door at the front that could be pushed inwards or lifted up outwards. A gap of 3 cm between the bottom of the door and the bottom of the box allowed monkeys to manipulate the swing door. The task was refilled through a hole in the back that was covered with a wooden lid screwed to the box. By unscrewing one of the two screws in the lid, the researcher could swing the lid to one side and refill the task. The raisins were placed at the back of the box (***Figure 5.2***).

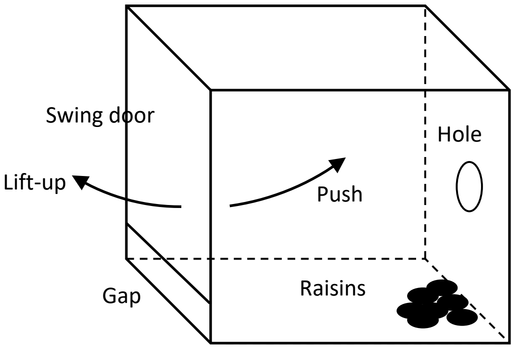


Figure 5.2. Illustration of task 2 that shows the swing door with the two possible actions (lift-up or push), the refilling hole, the door gap and where the raisins were placed.

The task was attached to a metal cylinder that was already fixed to the ground in the enclosure.

Task 3: Rotating-door task

This consisted of a square-wooden box 23 (w) x 23 (h) x 23 (d) cm with a circular retrieval hole (8 cm in diameter) that was covered by a circular rotating door (9.5 cm in diameter). The rotating door could be rotated clockwise or counter-clockwise to uncover the hole that gave access to the raisins (***Figure 5.3***). Once uncovered, the monkeys could stretch their arms through the retrieval hole to reach the raisins placed inside at the bottom of the box. The task was refilled using the circular retrieval hole.

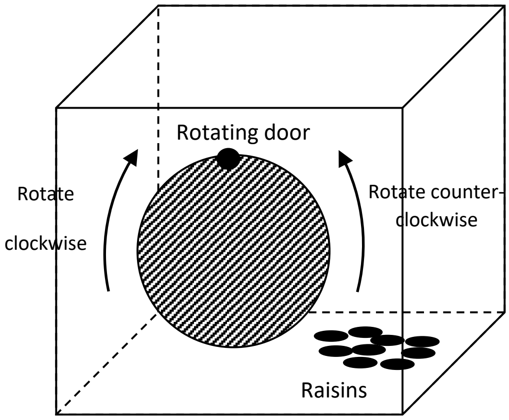


Figure 5.3. Illustration of task 3 that shows the rotating door with the two possible actions (rotate clockwise or counter-clockwise) and where the raisins were placed. The circular retrieval hole was behind the rotating door and it was concentric to this same door.

The task was fixed to the ground using long U-shaped metal anchor stakes.

BDG task: Rotating door twin-box

The task presented to the group at Blair Drummond Safari Park consisted of a wooden box 90 (w) x 30 (h) x 30 (d) cm formed by three modules attached to each other: two identical squared-modules (interactive modules) with a manipulandum similar to task 3 (a rotating door) separated by a third module (separation module) of the same dimensions 30 (w) x 30 (h) x 30 (d) cm (***Figure 5.4***). In this case, the rotating doors could be spun clockwise or counter-clockwise, but the task could only be solved when the doors were spun clockwise. Each door was covering a hole (7.5 cm in diameter) that gave access to the rewards placed inside the modules. The door also had a hole of the same size (7.5 cm in diameter) that had to be matched with the hole underneath to be able to reach the rewards. Two long screws acted as doorstops to (a) prevent the task being solved by rotating the door counter-clockwise and to (b) ease solving the task by spinning the door clockwise.

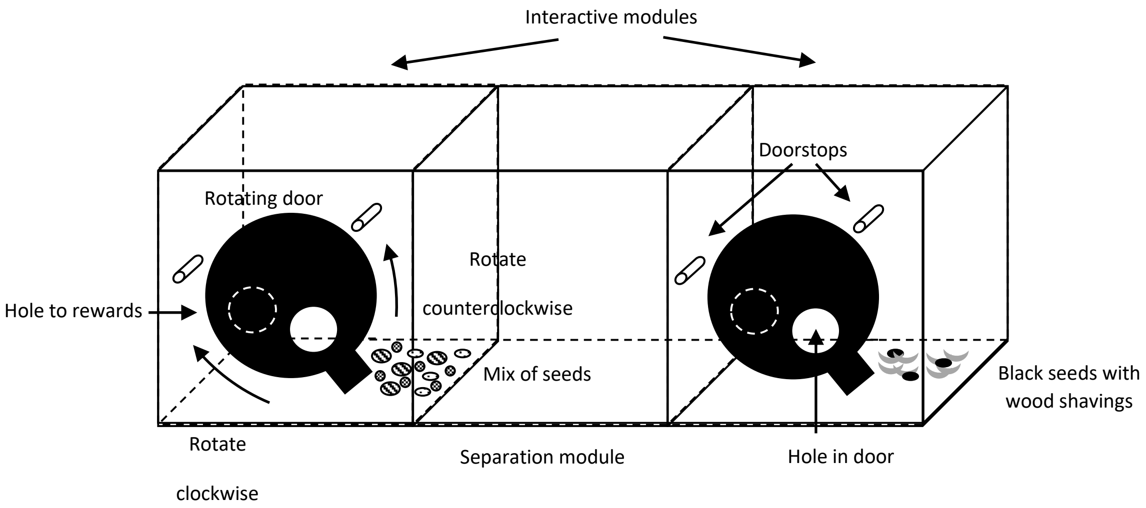


Figure 5.4. Illustration of BDG task that shows the rotating doors, the blocking mechanisms (doorstops) and where the rewards were placed. The circular retrieval hole covered by the rotating door had to match the hole in the rotating door in order for the monkeys to reach the rewards inside the interactive modules.

The interactive modules contained different contingencies: one with abundant and high quality rewards (i.e. a mix of seeds; the rich module) and one with few low quality rewards (i.e. one type of less desired seeds mixed with wood shavings; the poor module). The aim of the task was to test for a 'rich' preference, reinforce use of the preferred interactive module and, later, reverse contingencies to determine how fast macaques learned to reverse their interactive module preference in four different conditions: a) when there is no sound associated with the rich module, b) when an artificial sound is associated with the rich module, c) when a Barbary macaque vocalization is associated with the rich module: a 'play' call (socio-positive context) or a scream (negative/agonistic context). The third separation module, was built to provide enough distance to allow monkeys to discriminate from which of the two interactive modules the sounds were coming from (pilot studies were carried out in Mona Sanctuary with 4 Barbary macaques to find the minimum distance to discriminate two close sounds).

The task was designed to test whether Barbary macaques' vocalizations acted as social cues that enhance learning, since the contribution of vocalisations in social learning contexts has been understudied (Snowdon & Boe, 2003; Snowdon, 2009; Watson et al., 2015; Snijders & Naguib, 2017). However, the study could not be finished due to the changes in management of the safari park, but data on who observed whom during task introductions in BDG was used in subsequent chapters (see ***section 5.2.5*** for more details).

5.2.3. Experimental procedure

Prior to data collection, tasks were piloted with other groups to: a) test the feasibility and sturdiness of the tasks and the level of monopolisation by high-ranking individuals, b) evaluate the level of interest of macaques in the task, c) determine whether the order of task difficulty was as anticipated.

Two separate groups of Barbary macaques live in Trentham Monkey Forest: the German group (N = 61) and the French group (N = 75). Tasks tested in Trentham were piloted in the French group, while experiments were conducted with the German group. The twin-door task tested with the only group at Blair Drummond Safari Park was previously piloted in a group of 25 wild Barbary macaques (Middle Hill Group, MHG) that live in the Gibraltar Upper Rock Nature Reserve.

The final version of the tasks were feasible and resistant to the manipulation of the individuals tested during the pilot experiments. Individuals showed continued interest in the piloted tasks and low levels of monopolisation (i.e. eventually, all subjects had the chance to interact with the tasks).

Many rewards were placed inside the experimental tasks before each session. Tasks were checked when possible during sessions to see if refilling was necessary. Researchers tried to obscure the task from the monkeys during refilling. If this was not possible, the identity of the monkeys that observed the refilling was noted to control for potential biases. Interference with the natural dynamics of monkeys interacting with the tasks was kept to a minimum. In all TG tasks, the two actions led to the same quantity and quality of food rewards (in BDG, there was only one action per module leading to rewards).

Open diffusion experiments

One middle-ranking female (OR) was trained as a demonstrator in BDG using the rich module. No monkeys were trained and no option was seeded in TG for any of the tasks. In TG and BDG, three and two different locations, respectively, were used for task introductions (see ***Chapter 2***, ***Figures 2.5*** & ***2.6***). Task presentations were rotated around these locations to increase the likelihood that most individuals encountered, and had the chance to interact with, the tasks.

Tasks were presented twice per day in both groups (but not during heavy rain): one session in the morning and one in the afternoon (counterbalanced for each task location). Each session was scheduled to last 1 hour and took place in areas far away from the public paths in Trentham Monkey Forest or when visitors numbers were zero or low in Blair Drummond Safari Park. Tasks introductions were carried out between 9 a.m. until park closing time except when tested in Test Area 3 (Valley) with TG (see ***Figure 2.6*** in ***Chapter 2***), which was only available between 9 and 10 a.m.

Tasks were introduced for a total of 34 days (~51 hours) in the order of increasing difficulty in TG and for a total of 26 days (~44 hours) in BDG. The differences in duration of task presentation in TG (***Table 5.1***) enabled a familiarisation period for the macaques to experimental set ups with foraging tasks.

Table 5.1. Calendar of task-introduction sessions with TG.

	Day 1 to 14		**Day 15 to 24**		**Day 25 to 30**		**Day 31 to 34**		
Task	AM	PM	AM	PM	AM	PM	AM	PM	**Total days (time)**
Blue/yellow task	✓	✓	✓						23d (32h 25’)
Push/lift-up task				✓	✓				14d (12h 39’)
Rotating-door task						✓	✓	✓	10d (06h 13’)

Task presentations in TG were filmed with one video camera placed at 5m from the task and zoomed in on the apparatuses. In BDG, the camera zoomed in on the front of the task was placed at 10m. One researcher (CE in TG and the assistant in BDG) stood behind this camera, narrating who was approaching and manipulating the task, which actions (e.g. push or lift-up door) or modules (rich or poor for the twin-door task) were being used and whether monkeys were successful in retrieving rewards. At BDG, a second camera was placed at 5m behind the task covering a 10m radius of view. I stood behind this camera narrating: (a) who was approaching and interacting with the task, (b) the identity and distance from the task of the monkeys within a 10m radius and (c) who was presumed to be attending (head orientation) to each task manipulation. CE provided all this information to the single camera for TG. The assistant in TG stood at 5m on the other side of the task, facing the camera, taking notes on the task manipulations, the identity of those within 10m of the task and which were presumed to be attending, in order to: a) ensure no data were missed and b) enable cross-validation of the data recorded by the video camera and CE.

5.2.4. Data collection

I coded all task introduction videos. For each session, I collected (i) date and time, (ii) task being used and its location, (iii) the identity of the individuals interacting with the task, (iv) the time and type of each interaction with the task (event) and its duration, (v) which of the two task options/actions were used, (vi) the number of successful and unsuccessful manipulations of the task, (vii) the identity of the individuals within a 10m radius of the task, whether they were attending to the task and from what distance they observed the task being solved (see ***Table 5.2*** and ***Appendix G***).

Table 5.2. Ethogram of events recorded during task introductions.

Event	**Description**
Bout	A bout started when an individual approached within 0.5m of the task and ended when the individual moved further than 0.5m of the task
Task contact	Exploratory behaviours involving inspecting, touching, biting, leaning-on and pulling the task that do not involve solving the actions and retrieving rewards from the task.

Unsuccessful manipulation	A monkey manipulates the moving parts of the tasks (e.g. the door or rotating disc) and/or places hand(s) into the retrieving hole but does not retrieve raisins from the task.
Successful manipulation	A manipulation of the task that results in raisins being retrieved from inside the task.
Displaced from task	Individual at task moves away when a nearby individual directs agonistic behaviours towards them (i.e. face threat, chase off, hit, bite) or another individual approaches the task (an approach being within 0.5m of the task).
Leaves task	Animal who is at task moves back or away (animal's whole body is beyond 0.5m) from it of its own accord (i.e. without being displaced, or the session ending or task being broken/refilled). If the animal moves away to threaten or chase off another individual who is in proximity or approaching but then returns immediately back to the task, the animal was not recorded as leaving the task.
Observing	Individuals within 5m of the task attend (i.e. head and/or gaze oriented towards) the individual at task (i.e. within 0.5m of the task) or manipulating the task. Distance from task of observers was noted as within 1m or between 1-5m.
Refill	Researcher approaches task (0.5m) and inserts rewards inside. If individuals were able to observe the refill, their identity and distance from the task was noted.

Data on first successful task interaction for each individual were used to establish the order and time of acquisition of the novel trait (i.e. solving the task). Data collected during task introductions were also used to calculate a series of individual-level variables that were included in the NBDA to control for potential biases (that could indicate social learning when it was not actually present) in the diffusion of the novel trait. Thirteen variables were used to inform the NBDA at the individual level (data on these variables are listed in ***Appendix J***). As *individual attributes*, I included sex, age and kinship since they can influence the rate of acquisition of the trait (Hoppitt & Laland, 2011) and two measures of social rank (Jenks Natural Breaks Classification and the median of all ranking methods, see ***Appendix A***) to control for monopolisation due to differences in social rank (Kendal et al., 2010a). As t*ask-related* factors, I included the 8 individual-level variables listed in ***Table 5.3***. Neophobia and monopolisation may slow down the rate of diffusion of the trait, causing an erroneous identification of social learning (Kendal et al., 2010a; Hoppitt & Laland, 2011; Coelho, 2015). Therefore, it is important to include variables to control for these factors (***Table 5.3***). Two variables (*total refills observed* and *B/Y proportion refill*, see ***Table 5.3***) were calculated and included in the NBDA to control for the few instances where task refilling could not be obscured and monkeys were reported observing the refills. Finally, the rate of performance was included in the NBDA to control for individual differences in the likelihood of transmission of the trait to others (Hoppitt, 2011).

Table 5.3. Task-related interactions used to control for individual-level confounding factors in the network-based diffusion analysis (NBDA).

Variable	Definition	Measure/Control for
Contact latency	Time between first approach within 0.5m of the task (start of a bout) and first physical contact with the task.	Normalized continuous variable indicating the degree of fear of the novel task (neophobia).
Contact level	Contact latency transformed into	Level of neophobia.

	a categorical variable: 1: < 10 s; 2: 10-60 s; 3: 1-3 min; 4: > 3 min.	
Option preference	Category assigned to each of the available options to solve each task. Blue/yellow task: 1: Yellow, 2: Blue; Push/lift-up task: 1: Push, 2: Lift-up; Rotating-door task: 1: Clockwise, 2: Counter-clockwise. In all cases, category 3 = No preference.	Only when individuals chose one of the options in > 60% of their task interactions, did I consider they showed a preference for that option. This enables measurement of option-bias learning preferences.
Total refills observed	Sum of all the task refilling events for which each individual has been reported as 'attending'.	Controls for learning biases caused by the observation of humans using the options to place rewards inside (see ***2.2.2. Description of the tasks*** in ***Chapter 2***).
B/Y proportion refill	Only for blue/yellow task. Total number of refills observed using the blue option divided by the total number of refills observed using the yellow option.	Blue/yellow task is the only task where refills needed to be done from two separated parts of the task (the blue and the yellow holes). This controls for biases introduced by observing humans refilling one hole more times than the other.
Frequency of attention at distance	Number of bouts individuals observed others interacting with the task but did not approach it (i.e. did not initiate a bout) divided by the total number of bouts individuals were observed within 10m of the task (not interacting with the task, whether attending or not).	When individuals are interested in the task (attend to the task when this is being used by others) but do not approach the task, it is likely that the task is being monopolised and the observer remains at a distance because it is receiving threats from the demonstrator or is inhibited from approaching the task. This controls for monopolisation.
Frequency of access to the task	Number of bouts where individuals approached within 1m of the task divided by the total number of bouts individuals were present within 10m of the task (as demonstrators or observers, interacting or not, attending or not).	This variable indicates variation in the likelihood with which individuals approach the task. It controls for neophobia, monopolisation and other unknown factors.
Rate of performance with the task or transmission of the trait	An individual's number of successful interactions divided by the total time interacting with the task	Individuals that keep succeeding with the task are reinforced to keep interacting with it, increasing their rate of performance and, thus, potentially influencing transmission of the trait to other group members more than other task-interacting individuals in the group (Hoppitt, 2011; Hoppitt & Laland, 2011).

Data on who observes whom during task introductions were collected in both groups to build observation networks. Evidence of social transmission in NBDA depends on whether the observation networks used to inform the model are representative of the type of social learning process/processes occurring (Hoppitt & Laland, 2011). If the task requires a social learning process where detailed information of the actions needs to be transmitted, it is more likely that evidence for social learning will be found using a network based on observations at a close distance than at a long distance. For that reason, two observation networks at two different distances from the task (within 1 and within 5m) were built for each group.

Behavioural data collected outside task introduction sessions were used to build: a) social networks based on grooming, proximity within 1m, proximity within 5m and a combination of affiliative behaviours using the Composite Social Index (CSI = grooming + proximity within 1m + huddling), b) communication networks based on who backed up whom after aid-recruitment calls (helper-recipient network) and vocal comments produced in affiliative contexts (commenter-handler network) (see ***Chapter 4***). Data on communication interactions was only available for BDG (for further details on how data was collected and how the networks were constructed see sections ***3.2*** and ***4.2***, respectively).

5.2.5. Statistical methods

All the statistical analyses were performed in R. All the p-values obtained in multiple comparisons were adjusted using a Benjamini-Hochberg correction with a False Discovery Rate (FDR) of 5%.

Inter-observer reliability

CE coded ~23% of the videos in TG to test for inter-observer reliability using Cohen's Kappa. Reliability was measured for (i) identity of monkeys interacting with the task, (ii) task options being used, (iii) number and type of events or interactions with the task, (iv) identity of observers (see ***Table 5.2***). Interpretation of the level of agreement was made using the rules established by Fleiss et al. (2003) and McHugh (2012).

For BDG, I coded the videos to collect data on who observes whom with the narration turned off, and then checked these data against my oral comments. Prior to my experiments, I spent 4 weeks learning (and was tested by keepers) to identify the monkeys up to 30m.

Analysis of option preferences

A chi-square goodness-of-fit analysis was conducted to determine group biases in the preference for one action (option) which might influence the diffusion of social information. The percentage of successful interactions with each option was calculated per individual. Accordingly, individuals were classified in the following categories: a) shows preference (>60% use) for option 1, b) shows preference (>60% use) for option 2, c) shows no preference for any of the options. A comparative analysis with different threshold percentages was carried out to justify the use of the >60% criterion (see ***Table 5.3*** & ***Appendix H***).

To investigate option biases that may be naturally present in the species or may have arisen asocially in the group, option preferences were calculated for the whole group and for a subset of individuals that solved the task without previous observation of demonstrators (i.e. potential asocial learners). Primacy and recency effects were described for each task, using only individuals that had observed both options being solved before their first successful interaction. As primacy effects I considered cases where individuals solved the task using the first successful option they observed being used. As recency effects I considered cases where individuals solved the task using the option of the most recent successful interaction they had observed.

Three additional effects were explored when individual option preferences were not explained by primacy or recency effects: a) ***copying the most successful:*** individuals copying the option of the individual observed with the highest proportion of successful manipulations, b) ***frequent exposure:*** individuals copying the preferred option (>60% criterion) of the demonstrator most frequently observed (in terms of number of bouts), c) ***first option:*** individuals sticking to the option used in their own first successful manipulation. Effects were only measured in observers who manipulated the task >5 times in total. For *copying the most successful* and *frequent exposure* effects, only demonstrators whom had produced >5 task manipulations prior to the first successful interaction of the observer were considered. Asocial learners were excluded in the exploration of all effects, except for *first option effect*.

Task difficulty

I calculated, for each individual, (i) the learning time (difference between the time of first contact with the task and time of first successful interaction) and (ii) the rate of successful and unsuccessful manipulations (i.e. number of successful or unsuccessful manipulations divided by time spent at task) (see ***Appendix K***). Learning time controls for time to first contact, and so differences found will not be attributed to variation in task salience or neophobia. According to normality results using Shapiro-Wilk tests, non-parametric analyses were used to test for task difficulty (see ***Appendix E***).

First, I compared the number of successful manipulations, given the duration of presentation, among tasks. Then, I compared the frequency of successful versus unsuccessful manipulations within each task for the whole group and for the subset of asocial learners (i.e. innovators). Finally, I compared learning time among tasks. I used a Kruskal-Wallis test and a post-hoc Dunn test analysis with Benjamini-Hochberg correction to compare all these measures among tasks. For comparisons within tasks, only a Kruskal-Wallis test was used.

Network-based diffusion analysis

OADA was used in addition to TADA versions of NBDA because of the potential fluctuating variable of attempts to solve the task being unsuccessful due to the rewards being exhausted (Hoppitt et al., 2010). Both agent-based models (***purely asocial model*** and ***asocial + social learning model***) were calculated using both NBDA versions (OADA & TADA) and modelled using additive and multiplicative approaches. The additive approach assumes that social transmission occurs as an independent process from asocial learning by which individuals can acquire the trait, and then the total rate of acquisition will be the sum of the rates of asocial learning and social transmission (i.e. social influence adds to the chances of individual learning). The additive model is, therefore, likely to be appropriate if individuals can acquire the trait as a direct consequence of observation (Hoppitt & Laland, 2008), for instance, by imitation or some other form of observational learning. Conversely, the multiplicative approach assumes that the behaviour of the informed (knowledgeable) individual influences the naïve individual's behaviour in a manner that leads indirectly to learning (i.e., social influence of the model multiplies the chances of individual learning, for instance, by increasing exploratory behaviours at task). As I cannot predict 'a priori' the type of social learning process, both approaches were used (Hoppitt & Laland 2011).

Maximum likelihood methods (AICc and Akaike weights) were used to determine which of the asocial or asocial + social learning models (see ***Chapter 2***) better explained the observed diffusion data. Social transmission was said to occur when the asocial + social learning model had an AICc value, at least, 2 units lower than the pure asocial learning model. In addition a ΔAICc > 4 constituted strong evidence and a ΔAICc > 10, very strong evidence for social learning (Hoppitt & Laland, 2011).

Different combinations of individual-level variables were tested using forward selection and backward elimination in order to find both the asocial and asocial + social learning models with the lowest AICc (Hoppitt & Laland, 2011). The variance inflation factor (VIF) was used to test for multicollinearity of these variables. Those variables with a VIF > 4 were considered collinear (Hair et al., 2010). The variable with the greatest VIF > 4 was removed before testing for multicollinearity again. This procedure was performed until all the remaining variables had a VIF < 4, and these variables were used to inform the network based diffusion analyses.

Following Hoppitt & Laland (2011)'s guidelines, the analyses were conducted considering (a) a constant and non-constant rate of transmission of the novel trait (see ***Table 5.3***), and (b) a constant and non-constant rate of asocial acquisition, modelled using a baseline rate function corresponding to a gamma distribution (Hoppitt & Laland, 2011). NBDA was only conducted in TG and was done so for each task separately and using each affiliative and observation network collected.

Observation networks

Data on who observes whom was only accurate at the bout (see ***Table 5.2***) level in TG meaning I did not have accurate data on who observed whom during every individual task interaction. However, the number of bouts per individual was not sufficient to calculate a representative weighted network, so all observation networks in TG were unweighted. To aid comparisons between groups, observation networks of BDG were also unweighted, despite more accurate data availability.

Observation networks in both groups were built as directed networks using NetDraw and analysed using SNA metrics: a) density, b) component ratio, c) average degree, d) clustering coefficient, e) Network Centralization Index (NCI), and f) assortative mixing, indicative of the social learning context. For each task and group, SNA metrics were compared between both observation networks (within 1 and 5m) to determine if there were significant differences in the network structure and the patterns of connections that might influence or help explain the diffusion of novel traits. A bootstrap procedure, analogous to the classical paired-sample t-test was used to compare all the network-based measures (Snijders & Borgatti, 1999). A randomization procedure was conducted to compare the results for assortative mixing (see ***section 2.4.7*** in ***Chapter 2***).

Permutation-based mixed models

To test whether affiliative networks and communication networks predicted who observed whom during task introductions, I used permutation-based linear/logistic mixed models (see ***Chapter 2***). The regression model was informed with fixed effects (i.e. sex, age, social rank and kinship) and random effects (i.e. individual identity). The Akaike Information Criterion (AICc) was used to determine which model better explained the data.

A network based on a combination of grooming, huddling and proximity within 1m (Composite Sociality Index – CSI) is a good representation of socio-positive relations in Barbary macaques (see ***Chapter 4***), and was used to test whether affiliative relations predict who observes whom in a social learning context in both groups. In BDG, two communication networks (helper-recipient, commenter-handler, see ***Chapter 4***) were also used to run regressions with observation networks to explore whether communication interactions may be informative of social learning opportunities.

5.3 Results

5.3.1. Inter-observer reliability

CE coded 19 sessions out of a total of 84 (22.62% of all sessions), which accounts for a total of 15 h and 17 minutes (55,000 seconds out of a total of 184,590 seconds = 29.79% of all the observed time). There was generally a high degree of inter-observer agreement (see ***Table 5.4***). Sessions coded by CE included missing and additional information on who observed whom that were not available when I coded the videos. This difference might explain the lowest level of agreement for this variable (***Table 5.4***), which does not make the data I coded on *who observes whom* less reliable but more conservative.

Table 5.4. Measures of agreement for inter-observer reliability using Cohen's kappa.

Variable	Cohen's Kappa	ASE	p-value	C.I. low 95%	C.I. high 95%	Level of agreement	
						Fleiss et al. (2003)	McHugh (2012)
Monkey identity	U: 0.99 W: 0.99	U: 0.003 W: 0.006	U: 0 (z: 336.8) W: 0 (z: 161.4)	U: 0.99 W: 0.98	U: 1 W: 1	Excellent	Almost perfect
Action performed	U: 0.96 W: 0.98	U: 0.012 W: 0.009	U: 0 (z: 81.95) W: 0 (z: 111.64)	U: 0.94 W: 0.96	U: 0.98 W: 0.99	Excellent	Almost perfect
Events	U: 0.88 W: 0.89	U: 0.014 W: 0.013	U: 0 (z: 64.11) W: 0 (z: 66.83)	U: 0.85 W: 0.86	U: 0.91 W: 0.92	Excellent	Strong
Who observes whom	U: 0.70 W: 0.66	U: 0.046 W: 0.059	U: <0.001 (z: 15.26) W: <0.001 (z: 11.01)	U: 0.61 W: 0.54	U: 0.79 W: 0.77	Good	Moderate

ASE: Assymetric Standard Error. p-value: null hypothesis = agreement is the same as chance agreement (kappa = 0), alternative hypothesis = agreement is different from chance agreement (kappa ≠ 0). C.I.: confidence intervals. Both unweighted (U) and weighted (W) versions of Cohen's kappa were measured. The difference between unweighted and weighted kappa is that weighted kappa incorporates the magnitude of each disagreement and provides partial credit for disagreements when agreement is not complete (Maclure and Willet, 1987).

5.3.2. Option preferences

Task 1: Blue/yellow task

The diffusion pattern for the blue/yellow task is shown in ***Figure 5.5*** where the proportion of knowledgeable individuals is plotted against time. Thirty-four out of 56 individuals (61% of TG) solved the task successfully at least once (only one individual, BB, solved the task only once), with 6 of these appearing to do so asocially.

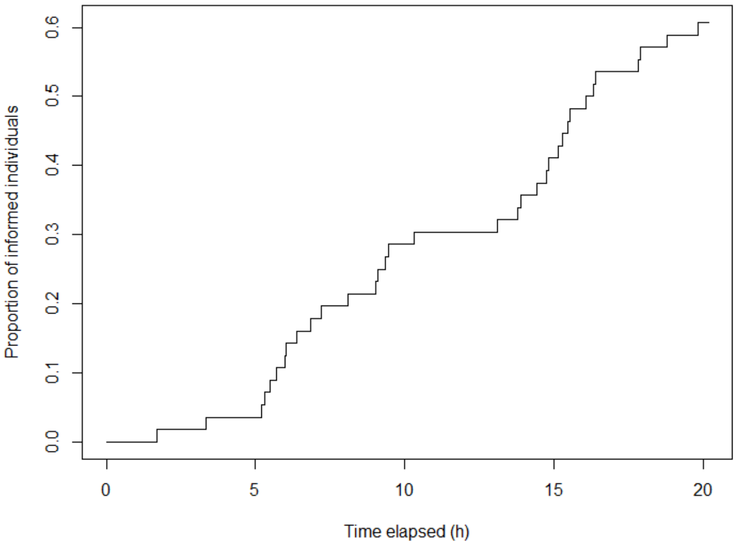


Figure 5.5. Proportion of informed individuals over time elapsed of experimentation for TG in blue/yellow task.

The χ^2 analysis showed differences among preference categories (χ^2 = 11.53, df = 2, p-value = 0.003). Post hoc analyses indicated no option preference at the group-level (Blue-Yellow: p=0.109; Blue-No preference: p = 0.003; Yellow-No preference: p = 0.102, see ***Appendix H*** and ***Figure 5.6***). For the asocial learners, no option preference was apparent ($\chi^2 = 3$, df = 2, p-value = 0.223).

Primacy and recency effects were investigated for the 27 individuals that had observed both options being solved before their first successful task interaction. For 14 of these, the first successful action and the most recent successful action seen were the same ($N_{yellow} = 9$, $N_{blue} = 5$). For the remaining 13 individuals, 5 used the most recent action seen in their first successful interaction and 8 used the same action as the first successful action observed. Option preferences were almost uniform with a majority of individuals (20 out of 34) showing no preference for any of the two options (***Figure 5.6***). No other effects were tested for this task.

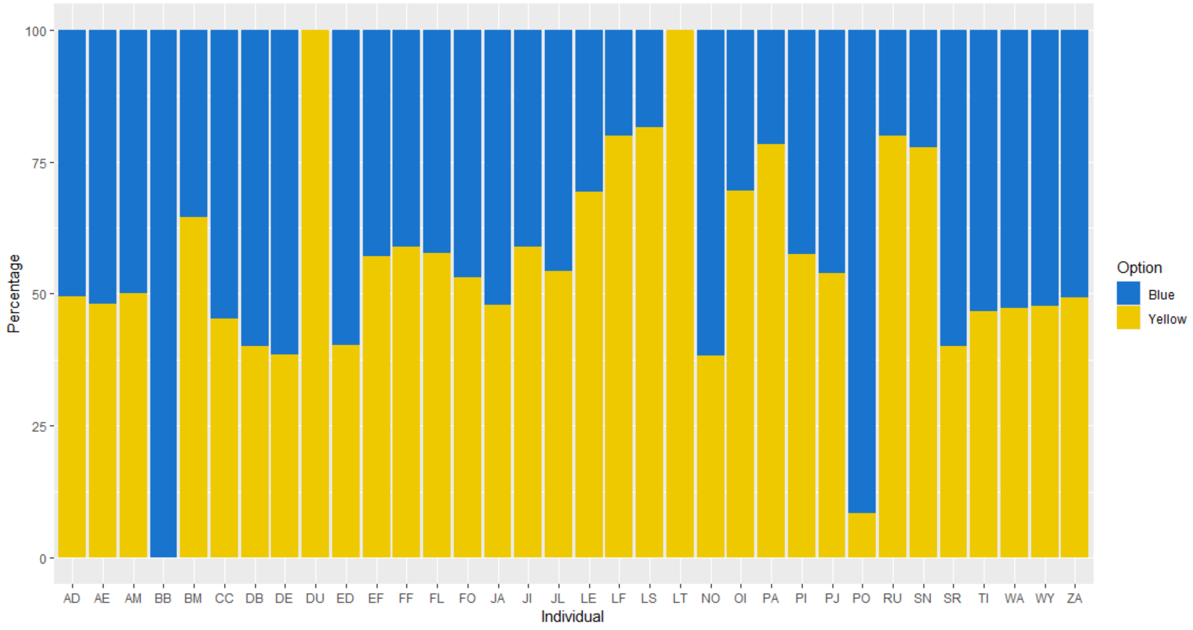


Figure 5.6. Percentage of options that each individual used to solve blue/yellow task.

Task 2: Push/Lift-up task

The diffusion pattern for the push/lift-up task is shown in ***Figure 5.7.*** A total of 28 out of 56 individuals (50% of the group) solved the push/lift-up task successfully more than once (asocial learners: 9 individuals).

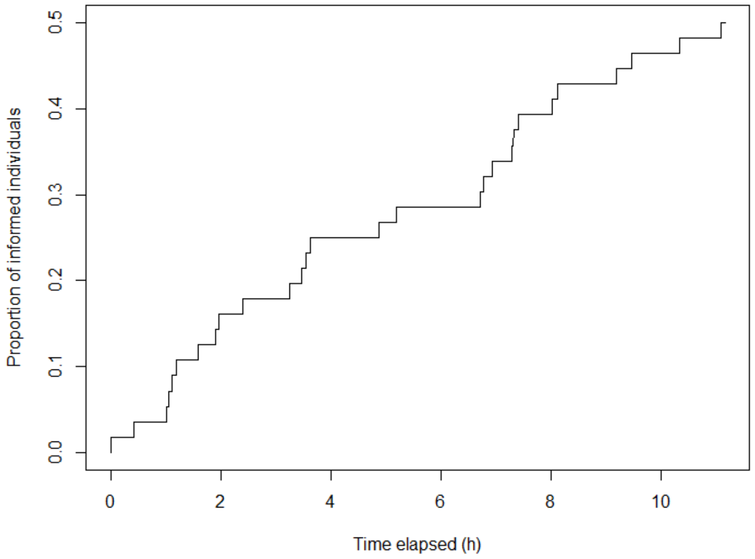


Figure 5.7. Proportion of informed individuals over time elapsed of experimentation for TG in push/lift-up task.

The χ^2 analysis showed differences among preference categories ($\chi^2 = 8.86$, df = 2, p-value = 0.012). Post hoc analyses indicated no group-level option preference (Push-Lift-up: p=0.695; Push-No preference: p = 0.008; Lift-up-No preference: p = 0.011, see ***Appendix H*** and ***Figure 5.8***). Asocial learners, also showed no option preference ($\chi^2 = 2.67$, df = 2, p-value = 0.264).

Primacy and recency effects could be investigated for 14 individuals. Despite seven of these subjects observing the same action as first and most recent, five of them used the opposite action as their first successful option. Of the other seven individuals, two used the most recent action observed, and five the first observed action, as their first successful action.

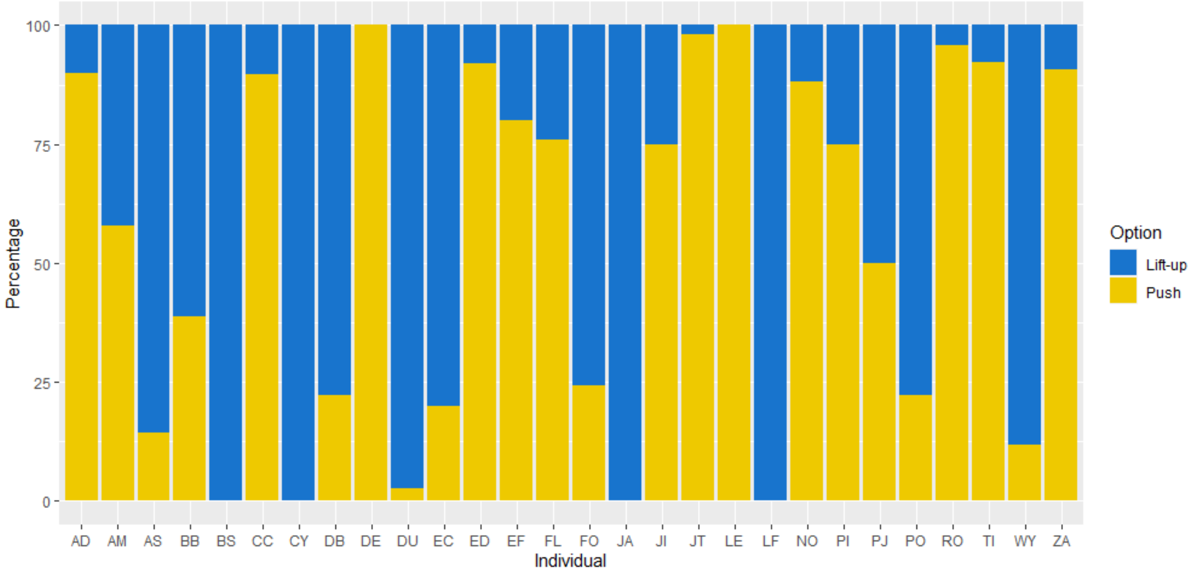


Figure 5.8. Percentage of options that each individual used to solve push/lift-up task.

Almost half of the individuals that solved the task (~43 %) showed a preference for the *Lift-up* option (N = 12) and half a preference for the *Push* option (N = 14; ***Figure 5.8***) indicating option preferences at the individual level. As primacy and recency effects do not explain this, other effects were explored. Excluding asocial learners (9 of 28), (i) a potential *copy the most successful* effect was observed in 47% of the individuals (9 of 19) and (ii) a potential *frequent exposure* effect was observed in 26% (5 of 19) of the individuals (for 3 individuals, the preferred option of the most frequently observed individual was also the preferred option of the most successful demonstrator observed). Finally, 82% of the individuals (23 of 28) retained their first successful option as their preferred option.

Task 3: Rotating-door task

Sixteen out of 56 individuals (29% of the group) solved the task (***Figure 5.9***) at least once (only one individual, TI, solved the task only once), with seven of these appearing to be asocial learners.

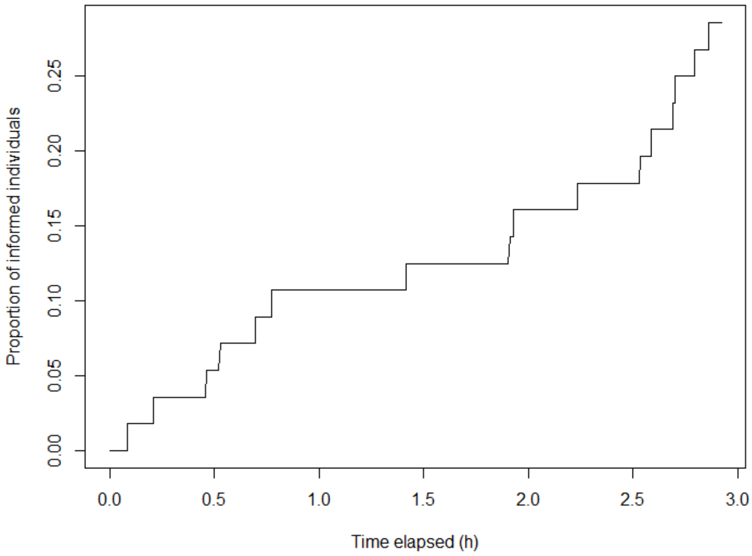


Figure 5.9. Proportion of informed individuals over time elapsed of experimentation for TG in rotating-door task.

There were differences between preference categories ($\chi^2 = 6.13$, df = 2, p-value = 0.047) and post hoc analyses indicated no option preference at the group-level (Clockwise-Counterclockwise: p=0.439; Clockwise-No preference: p = 0.088; Counterclockwise-No preference: p = 0.034, see ***Appendix H*** and ***Figure 5.10***). There was also no option preference for the seven apparent asocial learners ($\chi^2 = 3.71$, df = 2, p-value = 0.156).

Only six individuals observed both actions being used before their first successful interaction, three of which observed the same action being solved as first and most recent action observed. Of the other three individuals, two used the most recent action observed, while one used the same action as first observed, in their first successful action. Data were insufficient to test for primacy or recency effects.

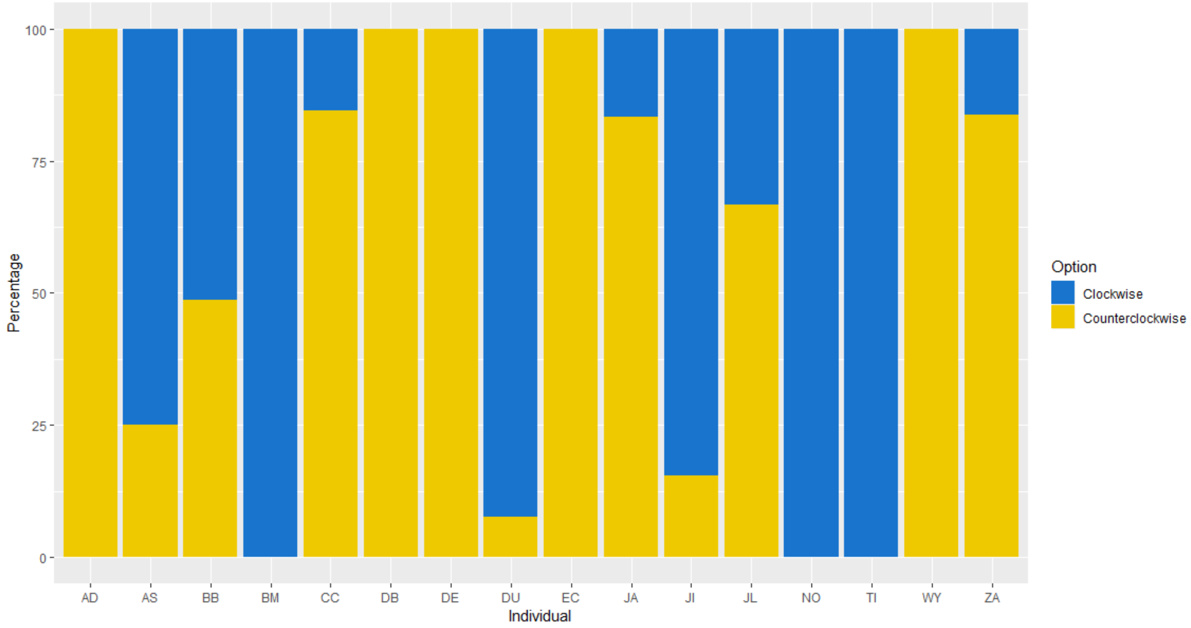


Figure 5.10. Percentage of options that each individual used to solve rotating-door task.

Thirty-seven percent (N = 6) of the individuals that successfully solved the task (N = 16) preferred the *Clockwise* option while 56% (N = 9) preferred the alternative option (***Figure 5.10***). Seven out of nine individuals (78% of all successful subjects, excluding asocial learners) preferred the option used by the most successful individual they had observed. A potential frequent exposure effect was only found for two of the individuals that copied the most successful individual observed, who also was the most frequently observed individual. Finally, 87.5% of the subjects (14 of 16) retained their first successful option choice as their preferred option.

5.3.3. Task difficulty

The rate of successful manipulations differed among the three tasks (Kruskal-Wallis $\chi^2 = 20.585$, df = 2, p-value < 0.001), with a higher rate of successful manipulations in the blue/yellow task (***Table 5.5***) than in the push/lift-up (Dunn test: p = 0.013) and the rotating-door (Dunn test: p < 0.001) tasks. Rate of successful manipulations was also greater in the push/lift task than in the rotating-door task (Dunn test: p = 0.009). The rate of unsuccessful manipulations was significantly different among tasks (Kruskal-Wallis $\chi^2 = 37.741$, df = 2, p-value < 0.001) with higher rates in the blue/yellow task than in the push/lift-up task (Dunn test: p < 0.001) and the rotating-door task (Dunn test: p < 0.001), and no difference between these two latter tasks (Dunn test: p = 0.288). The rate of successful task manipulations indicates that task difficulty varied as anticipated. These results were inconsistent with those obtained when the rate of unsuccessful manipulations was considered, for which the blue/yellow task appeared to be more difficult than the other tasks. However, introductions of the blue/yellow task presented a series of flaws that affected the successful retrieval of raisins but not the manipulation of the actions (consisting in stretching one hand through a hole, a component that was also present in the other tasks). These problems included: a) an internal mechanism of pendulum doors that hindered the extraction of rewards, b) the impossibility to know when the task was empty, causing monkeys to attempt to solve it when successful was not possible, c) a period of habituation to extractive foraging tasks, a novel context for this group of monkeys. All these issues, that most likely increased the number of unsuccessful manipulations and latency to first success, were solved for and/or not observed in push/lift-up and rotating-door tasks.

Table 5.5. Mean and median values of measures used to test task difficulty.

Task	Rate of successful manipulations	Rate of unsuccessful manipulations	Learning time (s)
Blue/yellow	Mean: 0.093 Median: 0.086	Mean: 0.061 Median: 0.063	Mean: 58.53 Median: 25.50
Push/lift-up	Mean: 0.064 Median: 0.065	Mean: 0.016 Median: 0.016	Mean: 42.04 Median: 18.50
Rotating-door	Mean: 0.042 Median: 0.033	Mean: 0.021 Median: 0.008	Mean: 86.50 Median: 55.50

*: indicates significant results. Data can be found in ***Appendix K***.

For all tasks, individuals performed significantly more successful than unsuccessful manipulations (see ***Table 5.6***). Amongst apparent asocial learners, individuals performed more successful than unsuccessful interactions for push/lift-up and rotating-door tasks only (see ***Table 5.7***).

Table 5.6. Kruskal-Wallis tests comparing the frequency of unsuccessful and successful manipulations per task.

Task	Estimate (median)	Statistic (V)	5%CI	95%CI	p-value
Blue/yellow	-0.025	126	-0.044	-0.007	0.006*
Push/lift-up	-0.049	13	-0.062	-0.037	< 0.001*
Rotating-door	-0.023	31	-0.039	-0.009	0.019*

*: indicates significant results. Data can be found in ***Appendix K***.

Table 5.7. Kruskal-Wallis tests comparing the frequency of unsuccessful and successful manipulations per task for apparent asocial learners only.

Task	Estimate (median)	Statistic (V)	5%CI	95%CI	p-value
Blue/yellow	-0.006	10	-0.051	0.037	1
Push/lift-up	-0.056	0	-0.082	-0.031	0.004*
Rotating-door	-0.043	0	-0.131	-0.018	0.016*

*: indicates significant results. Data can be found in ***Appendix K***.

Finally, differences in learning time among tasks were not significant (Kruskal-Wallis χ^2 = 4.2253, df = 2, p-value = 0.12). However, post-hoc tests revealed a significantly longer learning time for the rotating-door task compared to push/lift-up (Dunn test: p = 0.048) and the blue/yellow (Dunn test: p = 0.089) tasks although the latter only approached significance.

5.3.4. Observation networks

All networks were unweighted and directed.

TG (N = 56)

For blue/yellow task, a total of 294 observation bouts were recorded. The observation network within 1m was built from 68 bouts. The observation network within 5m was built from 257 bouts. All the individuals observed during the task introduction formed one component in both networks (***Figures 5.11*** and ***5.12***).

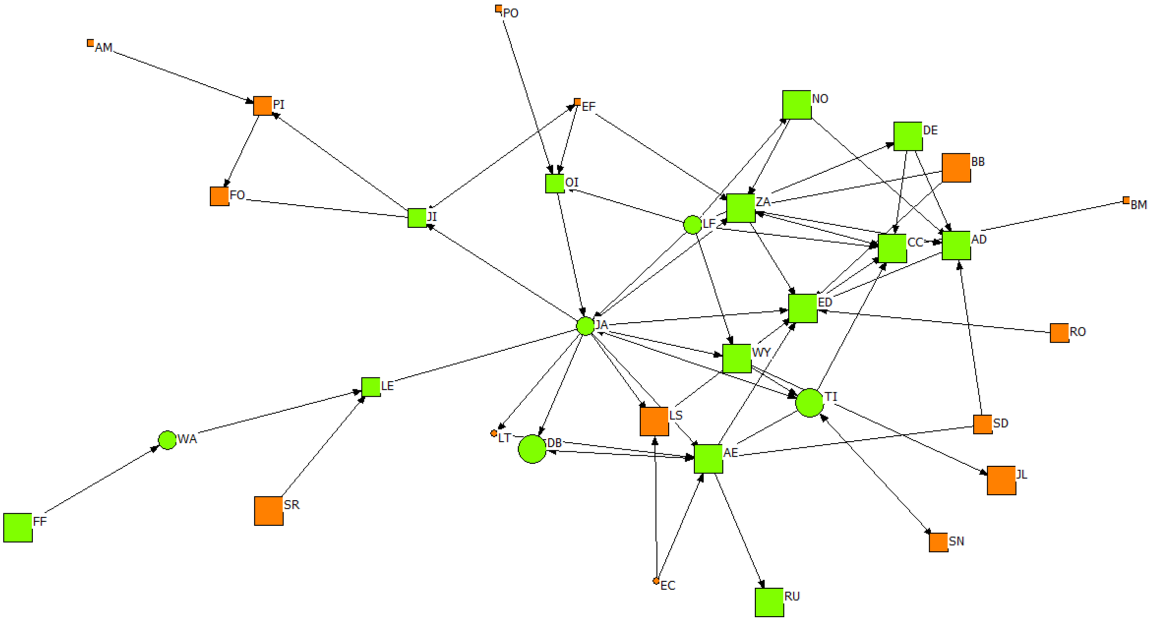


Figure 5.11. Graph representation of the observation network within 1m for blue/yellow task and TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The direction of the arrows indicates who observed whom.

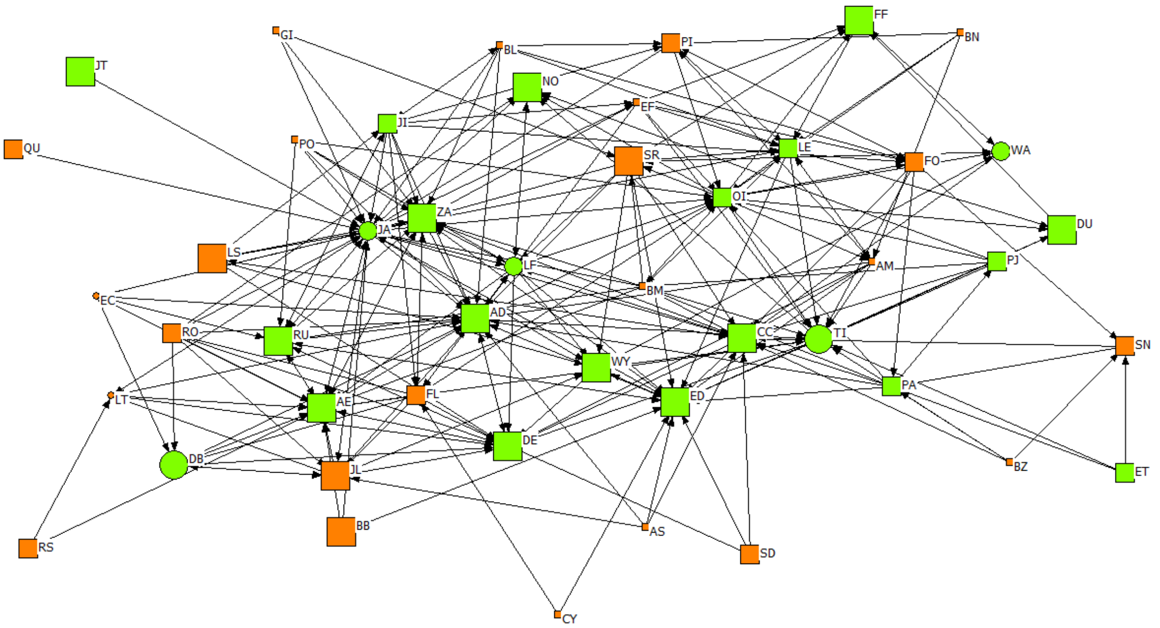


Figure 5.12. Graph representation of the observation network within 5m for blue/yellow task and TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The direction of the arrows indicates who observed whom.

The observation networks significantly differed in density, average degree and NCI (***Table 5.8***) as in the within 5m network, individuals were more densely connected, observed and were observed by more individuals on average and the network was less centralized than 1m network.

For push/lift-up task, 206 observation bouts were collected in total, the observation network within 1m was based on data from 42 bouts, and the within 5m network on 184 bouts. All individuals were connected in one component for who observes whom within 5m (***Figure 5.14***), but within 1m the network was formed by two separate components (***Figure 5.13***). The observation networks significantly differed in density and average degree (***Table 5.8***), again suggesting more connections with more individuals within 5m compared to 1m.

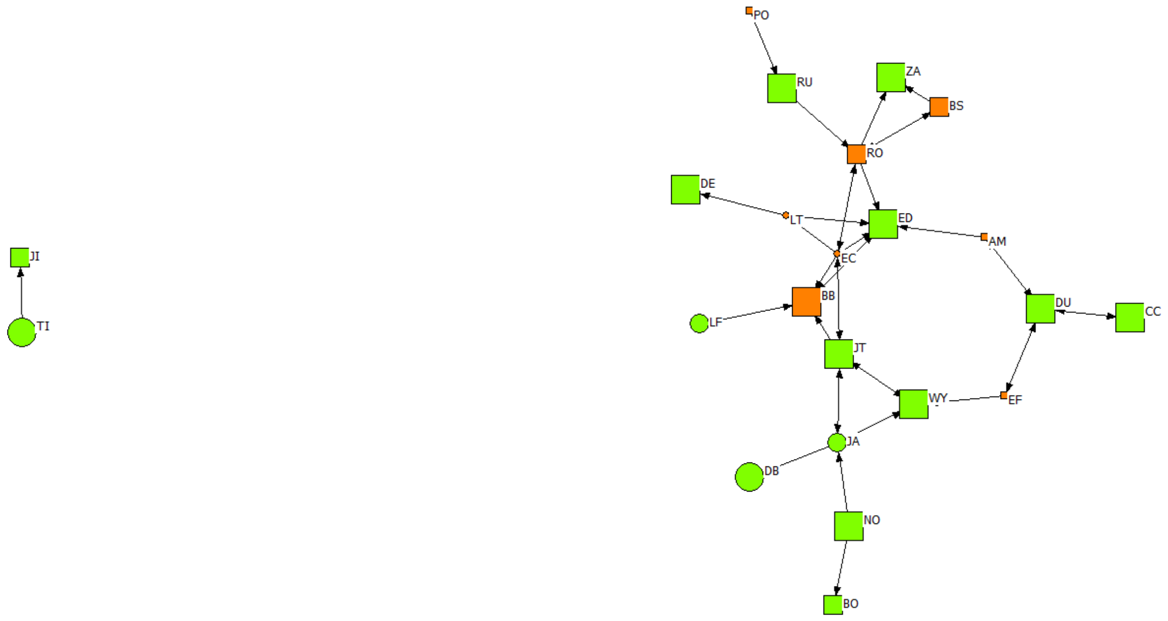


Figure 5.13. Graph representation of the observation network within 1m for push/lift-up task and TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The direction of the arrows indicates who observed whom.

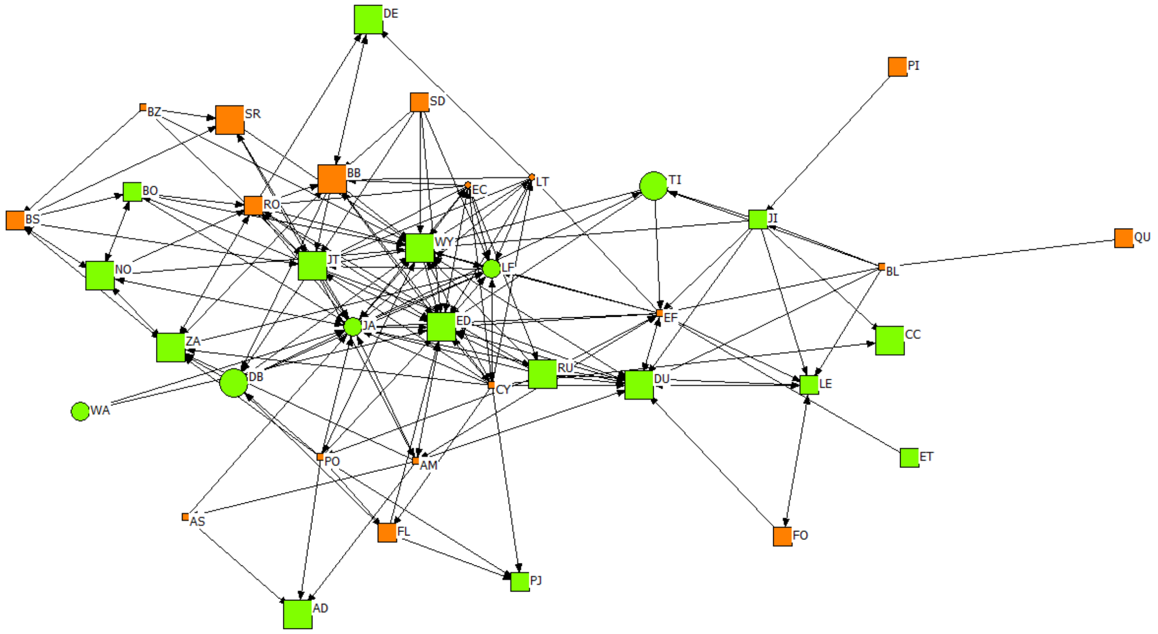


Figure 5.14. Graph representation of the observation network within 5m for push/lift-up task and TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The direction of the arrows indicates who observed whom.

For rotating-door task, observation networks were built based on a total of 17 (1m network, ***Figure 5.15***) and 57 bouts (5m network, ***Figure 5.16***) out of 57 total bouts recorded. Note that within each bout, individuals generally observed several task manipulations by the same demonstrator. Accordingly, the 1m network is based on more task observations than the unit used to represent it (i.e. the bout). Despite this, results of this network must be taken with caution. Five separate components were observed for the observation network within 1m while individuals formed two different components for the within 5m network. Networks significantly differed in density, average degree and clustering coefficient (***Table 5.8***) as, again, there were more connections with more individuals in the observation network within 5m compared to within 1m. Also, observations within 1m seemed to occur in more and smaller units (clusters of individuals) than observations within 5m.

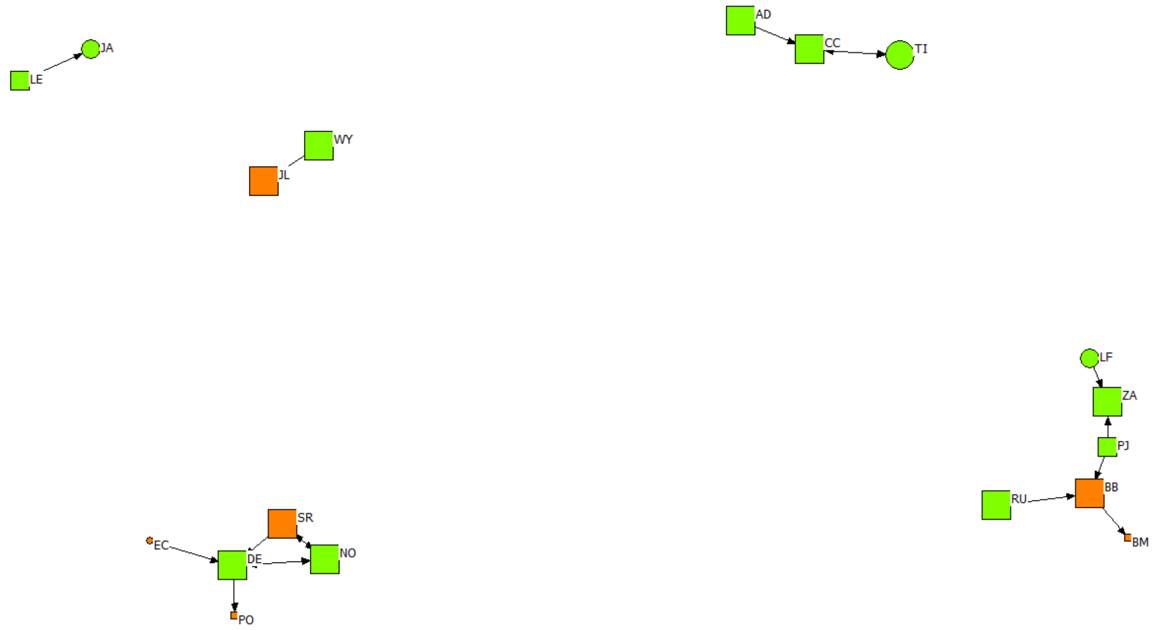


Figure 5.15. Graph representation of the observation network within 1m for rotating-door task and TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The direction of the arrows indicates who observed whom.

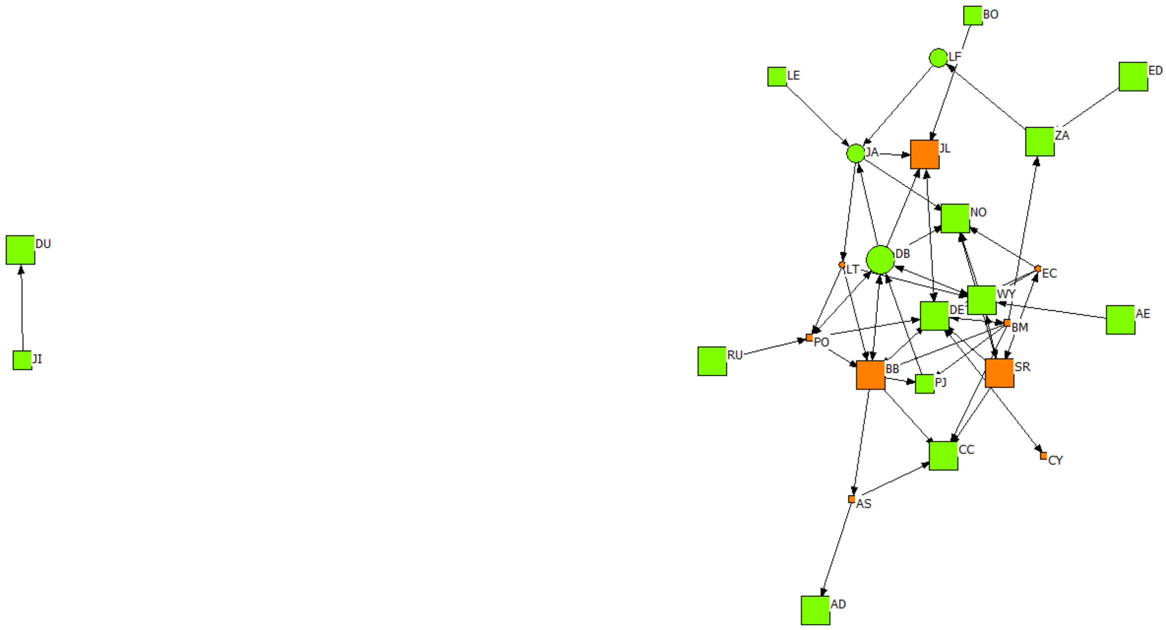


Figure 5.16. Graph representation of the observation network within 5m for rotating-door task and TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The direction of the arrows indicates who observed whom.

Table 5.8. Values of the SNA metrics and results of the metric comparisons between observation networks in TG.

Task	SNA metric	Observation 1m	Observation 5m	p-value
Blue/yellow	D	0.022	0.083	**< *0.001****
	CR	0.418	0.164	0.507
	AD	2	7.46	**< *0.001****
	CC	0.309	0.504	0.999
	NCI	8.31	4.77	***0.018****
Push/lift-up	D	0.013	0.059	**< *0.001****
	CR	0.618	0.327	0.611
	AD	1	5.21	**< *0.001****
	CC	0.293	0.545	0.982
	NCI	2.29	3.66	0.540
Rotating-door	D	0.006	0.019	***0.031****
	CR	0.764	0.564	0.507
	AD	0.50	1.64	***0.033****
	CC	0.309	0.307	***0.002****
	NCI	0.18	3.44	0.993

D: Density. CR: Component ratio. AD: Average Degree (Proportion). CC: Clustering Coefficient. NCI: Network Centralization Index. The p-value indicates if the difference between the values of each SNA metric were significant in the bootstrap procedure. *: indicates significant results.

Results for assortative mixing are tentative and must be taken with caution due to the small sample size of some networks and the fact that these values are based on unweighted data (see ***Appendix D***). In general, females tended to observe males (and males observed females only in the 5m network for the push/lift-up task), although a general trend for sex homophily was observed for the 1m network in the blue/yellow task (***Figure 5.17***).

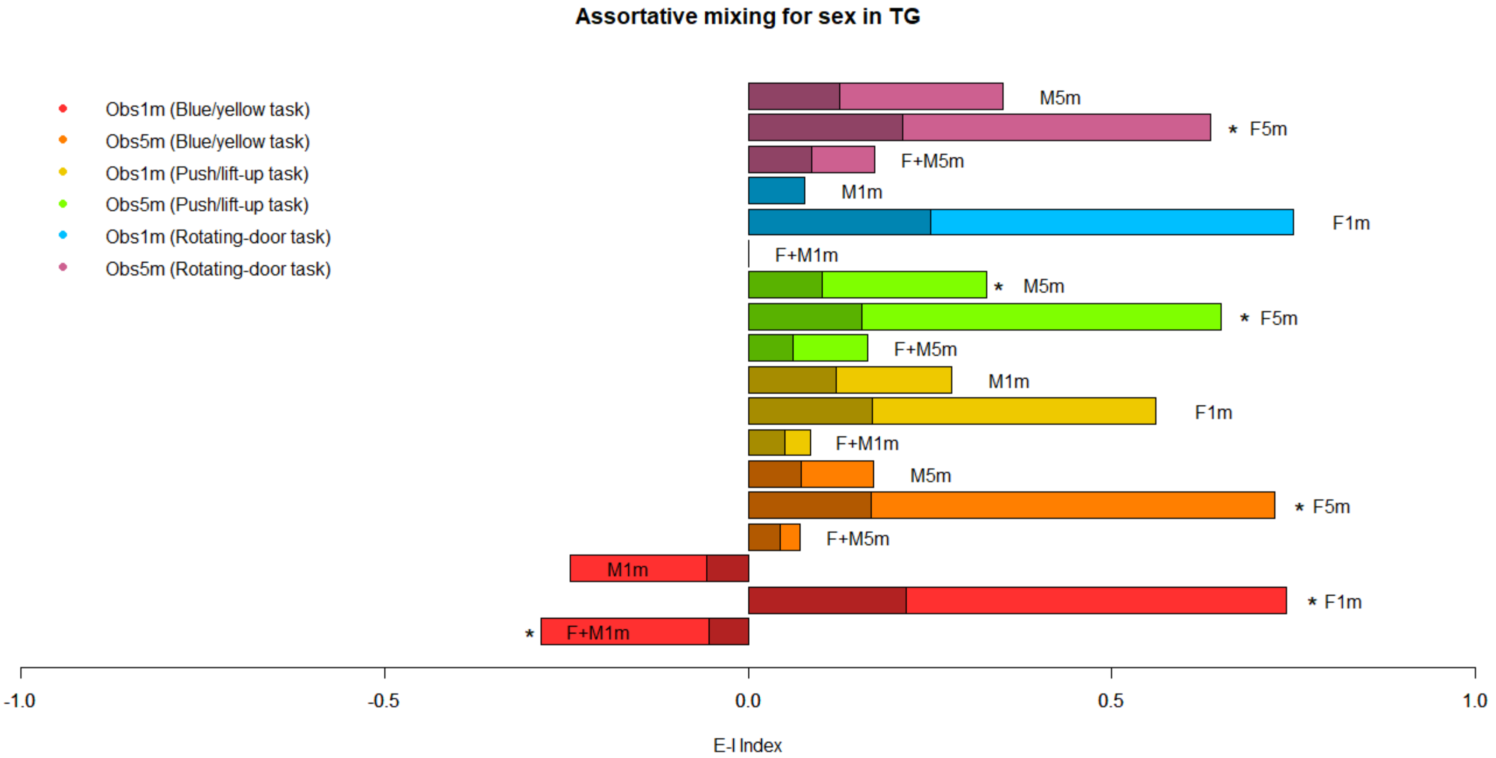


Figure 5.17. Assortative mixing for sex (observation networks, TG). Obs1m: Observation network within 1m. Obs5m: Observation network within 5m. F+M1m/5m: E-I index measures of all possible observations between males and females within 1 or 5m. F1m/5m: E-I index measures of observations within 1 or 5m involving females (i.e. excluding M-M interactions). M1m/5m: E-I index measures of observations within 1 or 5m involving males (i.e. excluding F-F interactions). The grey bars (darker shades when overlap with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability of obtaining the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

Regarding age, adults tended to observe sub-adults at all distances in blue/yellow task and within 5m in push/lift-up task. Sub-adults tended to observe adults except for observation networks within 1m for push/lift-up and rotating-door tasks (***Figure 5.18***). In terms of social rank, the measure for the overall network of observation within 1m in blue/yellow task indicated a preference for those of the same rank, but this seems to be driven by the low rankers (***Figure 5.19***). Middle-ranking individuals in the observation network within 5m in blue/yellow task and all rank classes in the observation network within 5m in push/lift-up task showed a significant level of heterophily (***Figure 5.19***). As of kinship, individuals, generally, tend to interact with those of a different kin less than would be expected by chance, although this was only significant for the 5m network in the blue/yellow task (***Figure 5.20***).

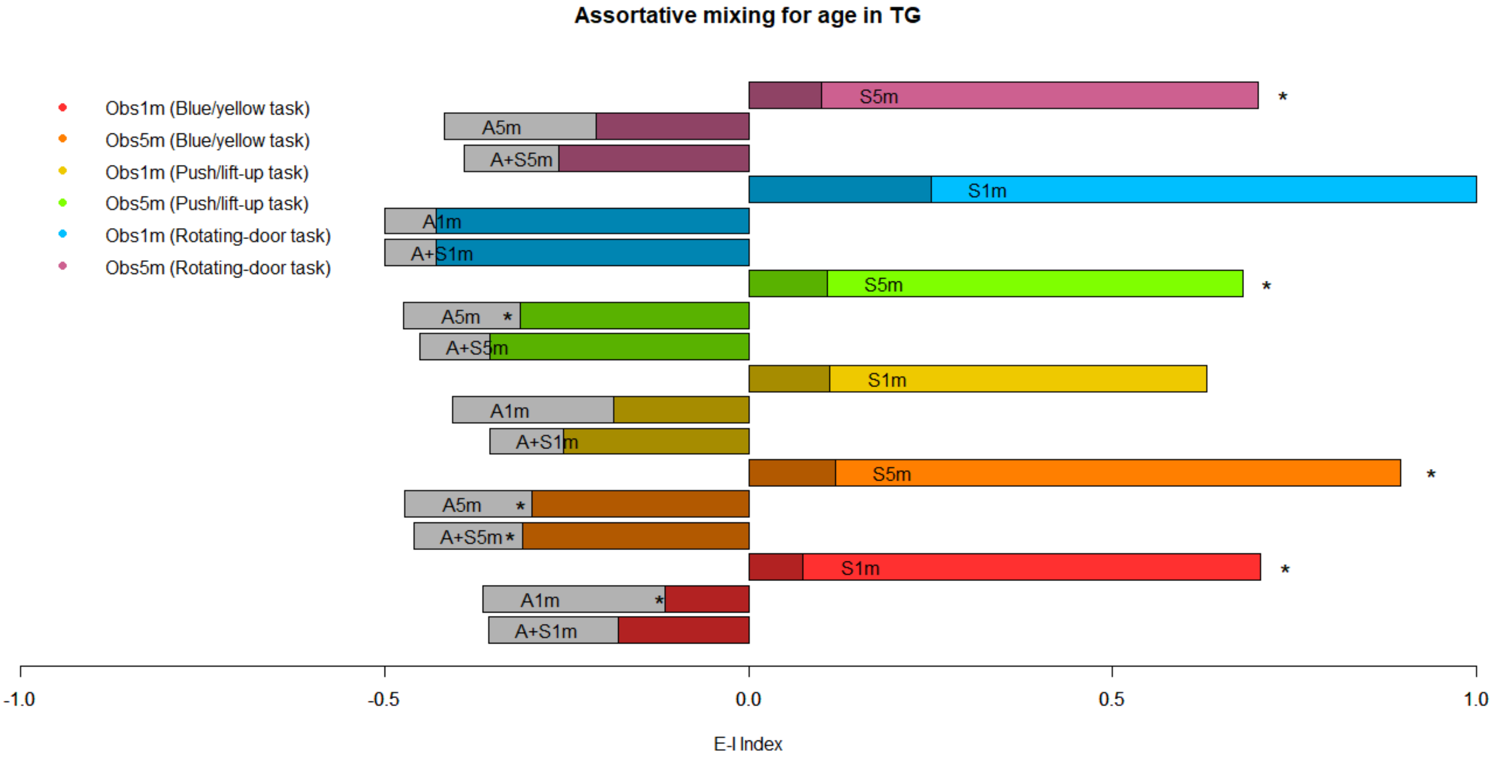


Figure 5.18. Assortative mixing for age (observation networks, TG). Obs1m: Observation network within 1m. Obs5m: Observation network within 5m. A+S1m/5m: E-I index measures of all possible observations between adults and sub-adults within 1 or 5m. A1m/5m: E-I index measures of observations within 1 or 5m involving adults (i.e. excluding S-S interactions). S1m/5m: E-I index measures of observations within 1 or 5m involving sub-adults (i.e. excluding A-A interactions). The grey bars (darker shades when overlap with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance is < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

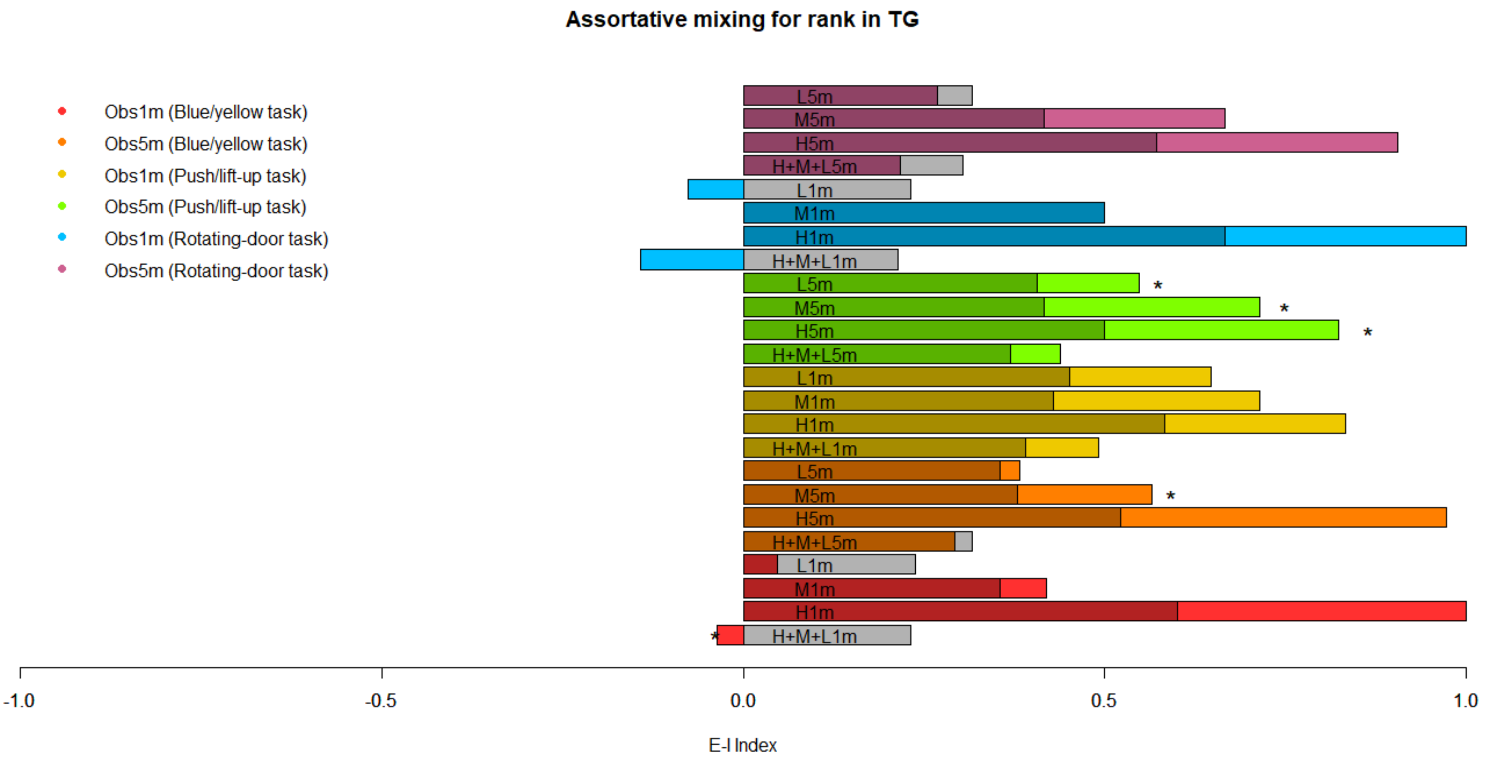


Figure 5.19. Assortative mixing for social rank (observation networks, TG). Obs1m: Observation network within 1m. Obs5m: Observation network within 5m. H+M+L1m/5m: E-I index measures of all possible observations between high, middle and low-ranking individuals within 1 or 5m. H1m/5m: E-I index measures of observations within 1 or 5m involving high-ranking individuals. M1m/5m: E-I index measures of observations within 1 or 5m involving middle-ranking individuals. L1m/5m: E-I index measures of observations within 1 or 5m involving low-ranking individuals. The grey bars (darker shades when overlap with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance is < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

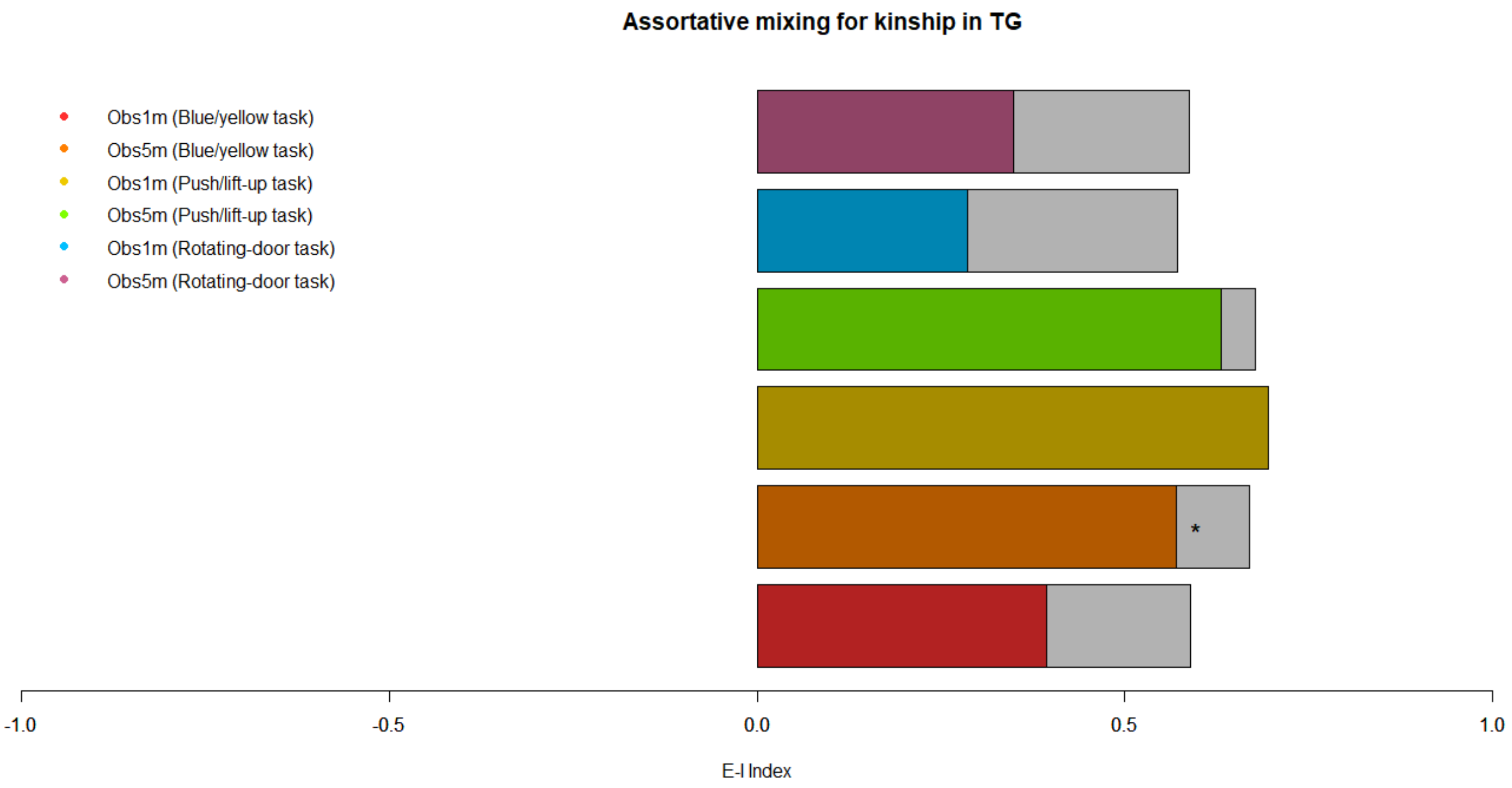


Figure 5.20. Assortative mixing for kinship (observation networks, TG). Obs1m: Observation network within 1m. Obs5m: Observation network within 5m. The grey bars (darker shades when overlap with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance is < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

BDG (N = 25)

A total of 558 instances of individuals observing another interacting with the twin-door task within 1m were collected, and 1590 within 5m of the task. Two components were obtained for the observation network within 1m (***Figure 5.21***), while within 5m all individuals formed a single unit (***Figure 5.22***). Both networks significantly differed in component ratio, clustering coefficient and NCI (***Table 5.9***), as individual relations in the observation network within 5m were less centralized and more cliqued than those within 1m, despite individuals forming a single component in the former network (***Figures 5.21*** & ***5.22***).

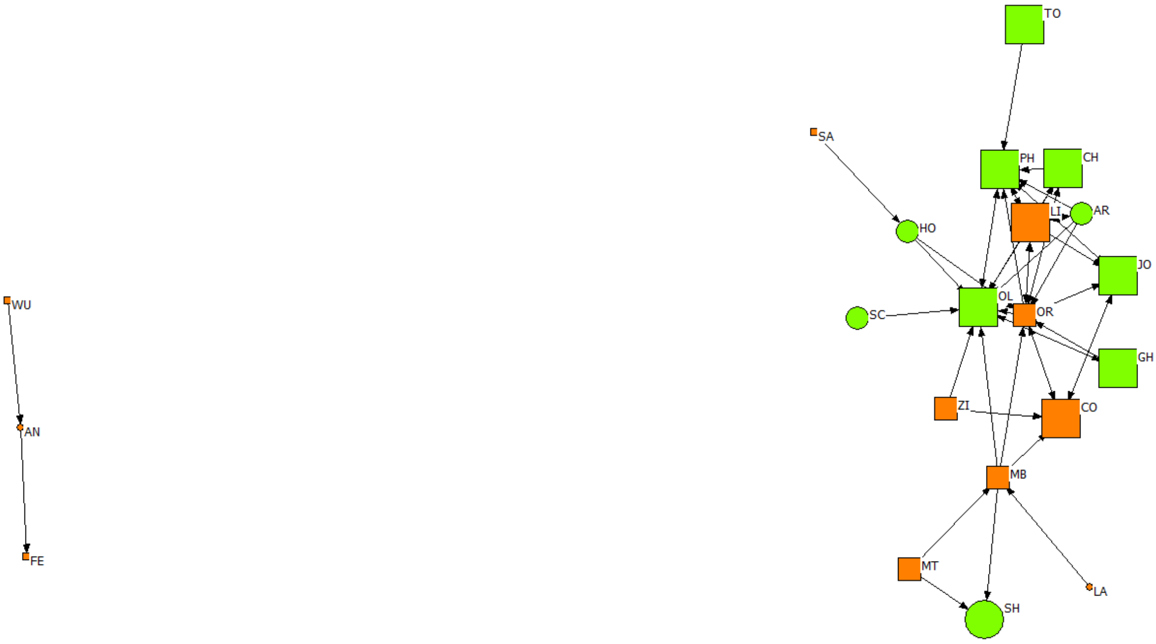


Figure 5.21. Graph representation of the observation network within 1m during twin-door task introductions in BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The direction of the arrows indicates who observed whom.

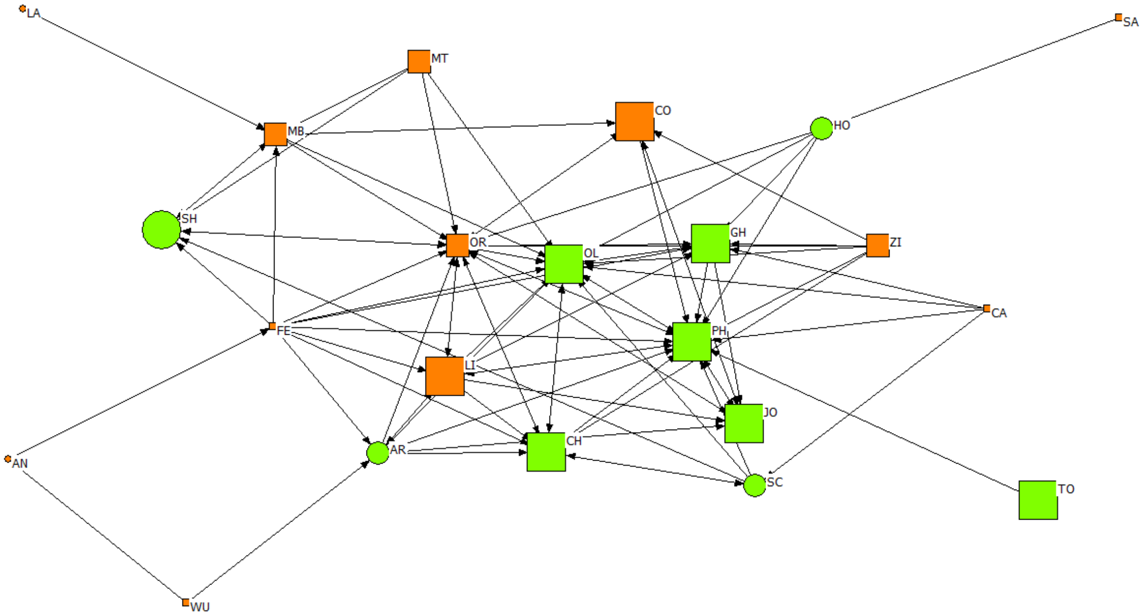


Figure 5.22. Graph representation of the observation network within 5m during twin-door task introductions in BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The direction of the arrows indicates who observed whom.

Results for assortative mixing are also tentative for BDG but suggest individuals tended to observe adults (only significant for sub-adults in the 5m network) and individuals of the opposite sex (only significant for females in the 5m network, see ***Figure 5.23***). Even though Barbary macaques observed more frequently those of different social rank than those of the same rank, these differences were not greater than chance in any case (see ***Figure 5.23*** and ***Appendix D***).

Table 5.9. Values of the SNA metrics and results of the metric comparisons between observation networks during twin-door task introductions in BDG.

SNA metric	Observation 1m	Observation 5m	p-value
D	0.114	0.190	1
CR	0.059	0	***< 0.001****
AD	3.52	6.27	1
CC	0.561	0.544	***< 0.001****
NCI	8.35	6.32	***< 0.001****

D: Density. CR: Component ratio. AD: Average Degree (Proportion). CC: Clustering Coefficient. NCI: Network Centralization Index. The p-value indicates if the difference between the values of each SNA metric were significant in the bootstrap procedure. *: indicates significant results.

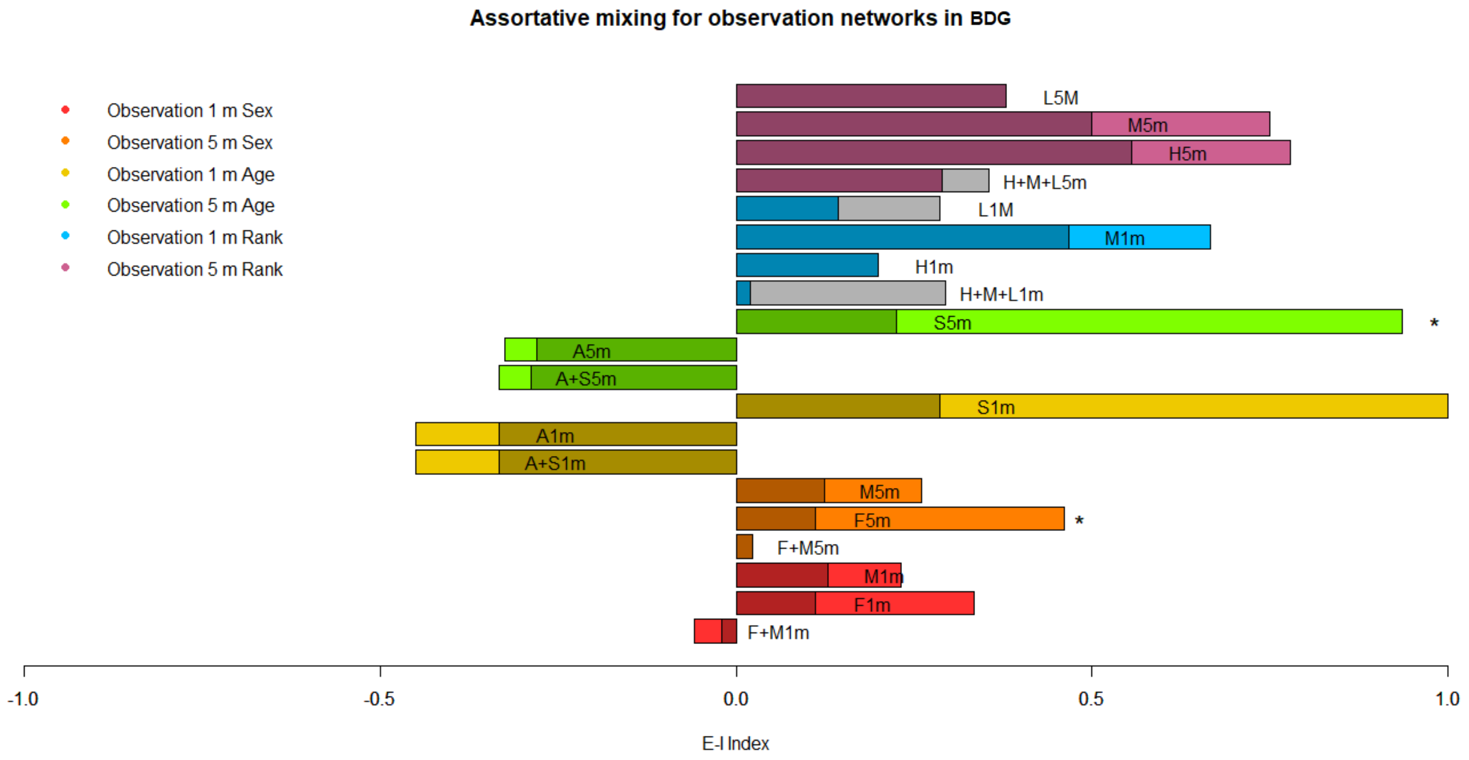


Figure 5.23. Assortative mixing for observation networks during twin-door task introductions in BDG. For each network, the first bar represents E-I index measures considering all possible relations between class categories. The second and third bar of each network represent E-I index measures for all relations of individuals of one class category (i.e. excluding relations that do not involve those of the selected class): a) females (F) and males (M) for sex, b) adults (A) and sub-adults (S) for age, c) high (H), middle (M) and low (L) for social rank (in that order from bottom to top). The grey bars (darker shades when overlap with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance is < 0.05. Regardless of whether the E-I Index is negative or positive (i)

heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

5.3.5. Network-based diffusion analysis (NBDA)

Due to collinearity, *social rank order*, *contact latency* and *preferred option* were removed from the analysis for blue/yellow task, and *contact level* and *social rank order* were not included in the NBDA for push/lift-up and rotating-door tasks. Since *contact level* and *social rank order* are variables that measure similar attributes as *contact latency* and *social rank class*, respectively, they were used instead when errors of convergence in the optimization algorithm persisted even after the optimization method used in the regression model was changed. Confidence intervals were measured for the social parameter (see ***Appendix L***). The narrowest confidence intervals were obtained for the CSI and the observation networks, suggesting that these networks had more power to detect a social transmission effect than the other networks (Hoppitt & Laland, 2011).

OADA

In all cases, the best models controlled for neophobia as well as for individual option preferences and/or potential introduced biases (i.e. refills observed, see ***Table 5.10***). In blue/yellow and push/lift-up tasks, the best models also controlled for monopolisation. However, controlling for this factor provided a worst fit (ΔAICc > 2) for the rotating-door task, suggesting monopolisation had only a weak effect on the order of acquisition of the trait compared to with the blue/yellow and push/lift-up tasks.

Results for OADA can be seen in ***Table 5.10.*** No evidence of social transmission was found in OADA models for any of the affiliative and observation networks for any of the tasks.

TADA

In all cases, measures of neophobia improved model fit (***Table 5.11***). However, measures of monopolisation apparently had a greater effect in the time of acquisition of the trait in the blue/yellow task (improving all models) than in the push/lift-up (improving 2 models, best null model for proximity within 1m and best social model for observation within 5m) and the rotating-door (improving no models) tasks (***Table 5.11***).

Results for TADA can be seen in ***Table 5.11.*** No evidence of social transmission was found for the blue/yellow task with any of the affiliative and observation networks used to inform the analysis. However, there was evidence of social learning in the push/lift-up task when the CSI network (ΔAICc > 2) and the who observed whom within 5m network (ΔAICc > 4) informed the model, and in the rotating-door task when who observes whom within 1m informed the model (ΔAICc > 2).

The best models for the two networks that resulted in evidence for social transmission in the push/lift-up task were multiplicative indicating indirect social learning processes such as local/stimulus enhancement, or social or response facilitation (CSI: ΔAICc = 2.37, 3.85x more likely the best model in comparison with the best additive model; observation within 5m: ΔAICc = 6.55, 1.19x more likely the best model in comparison with the best additive model). Despite this, the additive model for who observes whom within 5m from the push/lift-up task also showed enough evidence of social transmission (see ***Table 5.12***). In the case of the rotating-door task, the best model of the network that resulted in evidence of social transmission was also multiplicative (observation within 1m: ΔAICc = 2.91, 40.5x more likely the best model in comparison with the best additive model, see ***Table 5.12***).

Table 5.10. Results for Order of acquisition diffusion analysis (OADA) for all the networks tested and each task.

		Purely asocial model		**Social + asocial model**			**Individual-level variables included in the models**
Task	Network	AICc	Akaike	AICc	Akaike	ΔAICc	
Blue/yellow	Grooming	183.84	0.81	186.76	0.19	-2.92	Social rank class*, Contact level*, Total refills observed*, B/Y proportion refill*, Frequency of access*
	Proximity 1m	183.84	0.82	186.81	0.18	-2.97	
	Proximity 5m	183.84	0.81	186.77	0.19	-2.93	
	CSI	183.84	0.82	186.81	0.18	-2.97	
	Observation 1m	183.84	0.75	186.00	0.25	-2.16	
	Observation 5m	183.84	0.81	186.76	0.19	-2.92	
Push/lift-up	Grooming	140.87	0.82	143.86	0.18	-2.99	Contact latency*, Option preference*, Total refills observed*, Frequency of access*
	Proximity 1m	140.87	0.82	143.86	0.18	-2.99	
	Proximity 5m	140.87	0.82	143.86	0.18	-2.99	
	CSI	140.87	0.82	143.86	0.18	-2.99	
	Observation 1m	140.87	0.82	143.86	0.18	-2.99	
	Observation 5m	140.87	0.41	140.13	0.59	0.74	Contact latency*, Option preference*, Total refills observed, Frequency of access*
Rotating-door	Grooming	75.365	0.82	78.442	0.18	-3.077	Contact latency*, Option preference*
	Proximity 1m	75.365	0.82	78.442	0.18	-3.077	
	Proximity 5m	75.365	0.82	78.442	0.18	-3.077	
	CSI	75.365	0.82	78.442	0.18	-3.077	
	Observation 1m	75.365	0.82	78.442	0.18	-3.077	
	Observation 5m	75.365	0.82	78.442	0.18	-3.077	

ΔAICc: Difference between the AICc of the purely asocial model – the AICc of the social + asocial model. Akaike: Akaike weights. By default, the individual-level variables reported are those included in the purely asocial model. Those marked with an * indicate those included in the social + asocial model. CSI: Network combining grooming, huddling and proximity within 1m.

Table 5.11. Results for Time of acquisition diffusion analysis (TADA) for all the networks tested and each task.

		Purely asocial model		**Social + asocial model**			**Individual-level variables included in the models**
Task	Network	AICc	Akaike	AICc	Akaike	ΔAICc	
Blue/yellow task	Grooming	780.80	0.82	783.85	0.18	-3.05	Contact level*, Total refills observed*, B/Y proportion refill*, Frequency of access*
	Proximity 1m	780.80	0.81	783.67	0.19	-2.87	Contact level*, Total refills observed*, B/Y proportion refill*, Frequency of access*
	Proximity 5m	780.80	0.79	783.42	0.21	-2.62	Contact level*, Total refills observed*, B/Y proportion refill*, Frequency of access*
	CSI	780.80	0.81	783.69	0.19	-2.89	Contact level*, Total refills observed*, B/Y proportion refill*, Frequency of access*
	Observation 1m	780.80	0.71	782.62	0.29	-1.82	Contact level*, Total refills observed*, B/Y proportion refill*, Frequency of access
	Observation 5m	780.80	0.80	783.59	0.20	-2.79	Contact level*, Total refills observed*, B/Y proportion refill*, Frequency of access*
Push/Lift-up task	Grooming	617.78	0.39	616.89	0.61	0.89	Contact level*, Total refills observed*
	Proximity 1m	615.83	0.65	617.05	0.35	-1.22	Contact latency*, Option preference, Total refills observed*, Frequency of access
	Proximity 5m	617.78	0.58	618.46	0.42	-0.68	Contact level*, Total refills observed*
	CSI	617.78	0.23	**615.41***	**0.77***	**2.37***	Contact level*, Total refills observed*
	Observation 1m	617.78	0.44	617.30	0.56	0.48	Contact level*, Total refills observed*
	Observation 5m	617.78	0.04	**611.23***	**0.96***	**6.55***	Contact level*, *Option preference**, Total refills observed*, *Frequency of access**
Rotating-door task	Grooming	327.55	0.49	327.43	0.51	0.12	Contact latency*, Option preference
	Proximity 1m	327.55	0.87	331.40	0.13	-3.85	Contact latency*, Option preference
	Proximity 5m	328.53	0.84	331.88	0.16	-3.35	Contact latency*
	CSI	327.55	0.75	329.70	0.25	-2.15	Contact latency*, Option preference
	Observation 1m	327.55	0.19	**324.64***	**0.81***	**2.91***	Contact latency*, Option preference
	Observation 5m	327.55	0.29	*325.77*[1]	*0.71*[1]	*1.78*[1]	Contact latency*, Option preference

ΔAICc: Difference between the AICc of the purely asocial model – the AICc of the social + asocial model. Akaike: Akaike weights. Results in bold with * indicate relevant results in terms of evidence of social transmission. [1] Evidence of social transmission is close to the threshold (ΔAICc > 2) but not enough to consider that the social model was significantly better then the null. By default, the individual-level variables reported are those included in the purely asocial model. Those marked with an * indicate those included in the social + asocial model, while those in *italics* indicate that only were included in the social + asocial model. CSI: Network combining grooming, huddling and proximity within 1m.

Table 5.12. NBDA results for additive and multiplicative approaches of models and networks that provided evidence of social transmission.

		Additive				**Multiplicative**				
Task	**Network**	Null AICc	Social AICc	ΔAICc	Akaike	Null AICc	Social AICc	ΔAICc	Akaike	**Ratio**
Push/lift-up	CSI	617.78	620.52	-2.74	0.20	617.78	615.41	2.37	0.77	3.85
	OBS5	617.78	614.90	2.88	0.81	617.78	611.23	6.55	0.96	1.19
Rotating-door	OBS1	327.55	335.54	-7.99	0.02	327.55	324.64	2.91	0.81	40.5

Null AICc: AICc of the purely asocial model. Social AICc: AICc of the social + asocial learning model. ΔAICc: Difference between the AICc of the purely social model – the AICc of the social + asocial model. Akaike: Akaike weights. Ratio: Calculates the ratio between the akaike weights of both models (Akaike multiplicative/Akaike additive, Wagenmakers & Farrell, 2004). CSI: Network combining grooming, huddling and proximity within 1m. OBS5: 5m observation network. OBS1: 1m observation network.

5.3.6. Permutation-based linear mixed models

The CSI network predicted who observed whom within 1 and 5m during interactions with all tasks at TG, excepting rotating-door task within 1m (***Table 5.13***). Likewise, at BDG, affiliative networks predicted observation networks in all cases (***Tables 5.14*** & ***5.15***). Regressions between observation networks and the communication network based on who backs up whom in social conflicts (helper-recipient) at BDG were not significant. However, relations established through vocal comments produced in affiliative contexts (commenter-handler) at BDG predicted who observed whom within 5m using both weighted and unweighted versions of the observation network and who observed whom within 1m for the weighted version of the network (***Tables 5.14*** & ***5.15***).

Table 5.13. Results of the permutation-based linear mixed model regressions between CSI and observation networks of TG for each task.

Observation network	**Blue/Yellow task**	**Push/Lift-up task**	**Rotating-door task**
Within 1m	$r_{CSI} = 0.078$	$r_{CSI} = 0.150$	$r_{CSI} = 0.054$
	_p = 0.023*_	**_p < 0.001*_**	p = 0.190
Within 5m	$r_{CSI} = 0.081$	$r_{CSI} = 0.172$	$r_{CSI} = 0.105$
	_p = 0.004*_	**_p < 0.001*_**	**_p = 0.019*_**

*: indicates significant resuts.

Table 5.14. Results of the permutation-based linear mixed model regressions for BDG using unweighted observation networks.

Observation network	**CSI**	**Helper-recipient**	**Commenter-handler**
Within 1m	$r_{CSI} = 0.157$	r = 14.355	r = 3.057
	_p = 0.039*_	p = 0.138	p = 0.506
Within 5m	$r_{CSI} = 0.172$	r = 0.916	r = 19.723
	_p = 0.028*_	p = 0.799	**_p = 0.039*_**

In all cases, communication networks had to be scaled up by a factor of 10 in order to overcome errors of convergence of the optimization algorithm used in the linear mixed models. *: indicates significant results.

Table 5.15. Results of the permutation-based linear mixed model regressions for BDG using weighted observation networks.

Observation network	CSI	Helper-recipient	Commenter-handler
Within 1m	r_{CSI} = 2.27E04	r = - 0.005	r = 6.08E-05
	_p = 0.006*_	p = 0.503	**_p = 0.009*_**
Within 5m	r_{CSI} = 2.00E04	r = 0.076	r = 0.166
	_p = 0.030*_	p = 0.381	**_p = 0.003*_**

In all cases, communication networks had to be scaled up by a factor of 10 in order to overcome errors of convergence of the optimization algorithm used in the linear mixed models. *: indicates significant results.

5.4. Discussion

In this chapter, I first aimed to understand whether Barbary macaques rely on social learning in foraging contexts for which individual learning is challenging (Hypothesis 1). First, I investigated whether Barbary macaques rely on social learning when presented with difficult tasks. Affiliative relations only predicted the patterns of social diffusion for the task of medium difficulty, but not for the most difficult task as indicated in prediction a. Confirming prediction b, observation networks during task introductions provided evidence of social transmission for tasks of medium and high difficulty.

Secondly, I explored whether communication interactions in Barbary macaques may represent patterns of relations through which social diffusion of information can occur (Hypothesis 2). I investigated whether: a) affiliative networks predict who observes whom during task introduction times, and b) communication networks that predict affiliative networks also predict who observes whom during task introduction times. Socio-positive relations predicted observation networks in all tasks, confirming prediction a. Regarding prediction b, only the communication network based on vocal comments produced in affiliative contexts predicted who observed whom during task introductions.

5.4.1. Task difficulty

Tasks were designed to be of increasing difficulty: blue/yellow task (low), push/lift-up task (medium), rotating-door task (high). Outcomes confirmed that the rotating-door task required more learning time and, therefore, was more difficult than the push/lift-up and blue/yellow tasks, as expected. Also, the rate of successful manipulations indicated that blue/yellow task was the easiest task and rotating-door task was the most difficult of the three. Finally, the blue/yellow task was identical to the round-box task used by Kendal et al. (2009) with callitrichids, the easiest task tested in their study, in which they used a more difficult task (flip-top box) similar to push/lift-up task. In conclusion, I determine that blue/yellow task was the easiest task of this study, push/lift-up task was of medium difficulty and rotating-door was the most difficult task tested.

5.4.2. Evidence of task solution option preferences

Results indicated that no option preference was observed at the group-level for any of the three tasks tested in TG. No primacy or recency effects were observed for the blue/yellow and push/lift up tasks, indicating that individuals did not copy the first or most recent successful action observed. Data for the rotating-door task were not sufficient to test for primacy or recency effects. In contrast, the study of individual-bias effects indicated that for (i) the blue/yellow task, Barbary macaques did not seem to prefer one option over the other, (ii) the push/lift up task, individuals seemed to prefer one option or the other based on their own individual experience with the task, (iii) the rotating-door task, option preferences seemed to have been influenced by the rate of success of the individuals they observed plus their own task experience. Given the established order of task difficulty, these findings align with an increasing reliance on social information as task difficulty increases.

Primates tend to rely more on social learning as problem-solving contexts become more challenging or difficult (Byrne & Russon, 1998; Kendal et al., 2009, 2010a). This might explain why in the most difficult task (i.e. rotating-door) individuals seemed to copy the most successful demonstrator observed. Alternatively, it is likely that the underlying social learning process required to solve the rotating-door task involved the evaluation of the payoffs associated with the alternatives presented by the demonstrators' manipulations (Laland, 2004; van Leeuwen et al., 2013; Vale et al., 2014; see below). This would be deemed as a "direct bias" where individuals adopt the choice they perceived as more valuable or effective (Kendal et al., 2018). However, my data did not allow me to discriminate between these two strategies since data on the exact number of successful task manipulations that each individual observed was not available. The push/lift-up task was difficult enough to yield an individual preference, but not enough to yield a social influence on solution choice. However, it is likely that some form of social learning (see next section) played a role in the diffusion of the solving of this task of medium difficulty. Finally, Barbary macaques seemed to interact randomly with both options in the easiest task (i.e. blue/yellow task), showing that the action used did not influence their performance with the task.

5.4.3. Evidence of social diffusion of task solution using NBDA

This analysis determines whether the order or time of first solution (regardless of option used) was related to the relationships between individuals in the group. OADA showed no evidence of social transmission for any of the tasks or social networks tested. OADA is useful when the baseline rate of acquisition of the trait is influenced by fluctuating variables (e.g. monopolisation, variable availability of resources, scrounging strategies, Hoppitt et al., 2010; Hoppitt & Laland, 2011) and, hence, difficult to model. Results indicated that these variables did not have much influence on social diffusion in any case. Since TADA is more powerful than OADA (Hoppitt & Laland, 2011), I here only discuss results for TADA.

No evidence of social transmission was found for the easiest task (blue/yellow task). For the push/lift-up task (medium difficulty), the affiliative (CSI) network showed evidence, and the network based on who observed whom within 5m strong evidence, of social transmission. The CSI network predicted the 5m observation network for push/lift-up task, indicating that affiliates were included among those observing within 5m. Variables measuring monopolisation and option preference were included in the best social model for the 5m observation network but not for the affiliative (CSI) network. Thus, in the 5m observation network, it is likely that social tolerance was higher between demonstrators and strongly bonded partners (Coussi-Korbel & Fragaszy, 1995) than for other individuals, so that affiliates were less constrained by monopolisation than other observers. Such accords with reports that affiliative behaviours like grooming are generally exchanged for commodities such as priority access to resources in primates (Barrett et al., 1999, Henzi et al., 2003; Barelli et al., 2011; Schülke et al., 2020). Moreover, the fact that the variable 'option preference' improved the social learning model in the NBDA for the 5m observation network but not for the affiliative network in the push/lift-up task, suggests that this variable was only important for the non-affiliates. The absence of a significant option-bias effect at the individual level in the option preference analysis (see ***section 5.4.2***) was probably due to the small subset of non-affiliates in the 5m network (i.e. a greater proportion of affiliates in the 5m network probably obscured this potential bias).

For the rotating-door task (most difficult task), only the network based on who observes whom within 1m showed evidence for social transmission. Monopolisation did not seem to have influenced social transmission in the rotating-door task, suggesting that those observing within 1m were highly tolerated by demonstrators near the task. Although it appears to be inconsistent that affiliative networks did not predict the 1m observation network for the rotating-door task, this result may be due to the small sample size of the 1m network. I would argue that demonstrators and observers at 1m probably had a strong socio-positive relation (see ***section 5.4.6***). Consistent with this interpretation is the finding that the 1m observation network predicted the communication networks in affiliative contexts in BDG (see ***section 5.4.6***) and that grooming relations may have had some influence in tolerance required for social transmission in this difficult task (see ***Appendix L***).

Overall, evidence for social learning was obtained for the most difficult tasks, as expected based on theory (Boyd & Richerson, 1985) and previous studies with other primate species (Kendal et al., 2009, 2010a). Moreover, affiliative relations predicted the diffusion of social information in one of the tasks, indicating that bonds established through socio-positive interactions can represent opportunities of social learning in Barbary macaques (Coussi-Korbel & Fragaszy, 1995; Franz & Nunn, 2009, see ***Chapter 3***), as previously reported in other nonhuman primates (Schnoell & Fitchell, 2012; Claidière et al., 2013; Coelho, 2015; van Leeuwen et al., 2020).

5.4.4. Evidence of social learning processes of task solution using NBDA

NBDA allows for the prediction of social learning mechanisms using diffusion networks. The mathematical approaches used to model the interaction between asocial and social learning might indicate whether individuals were more likely to learn vida direct or indirect social learning processes (Hoppitt & Laland 2011). If social and asocial learning interact additively (i.e. social influence adds to the chances of learning asocially), individuals presumably acquired the novel trait as a direct consequence of observation (e.g. by imitation or observational learning, Hoppitt & Laland, 2008). Conversely, if social and asocial learning interact multiplicatively (i.e. social influence multiplies the chances of learning asocially), novel trait acquisition is probably due to indirect social learning mechanisms (e.g. stimulus/local enhancement or social/response facilitation, Hoppitt & Laland, 2008). Task-action design, group or individual-level option preferences and the type of diffusion networks that provide evidence for social learning may help refine the interpretation of results by narrowing down conclusions to one or a few social learning mechanisms within each class (i.e. direct versus indirect social learning).

For both networks (CSI and observation within 5m) in the push/lift-up task, the best NBDA models were obtained using multiplicative approaches indicating that social transmission occurred through an indirect social learning process (Hoppitt & Laland, 2011). The fact that no evidence of social transmission was obtained for the 1m observation network, implies that attention only needed to be attracted to the task and not the specific actions which may only have been visible when within 1m of the task. Therefore, I would argue that social learning occurred via stimulus/local enhancement or social facilitation, as response facilitation seems unlikely as there was no evidence that individuals performed the same rewarding actions that they observed (see ***section 5.4.2***) with the push/lift-up task (Hoppitt & Laland, 2011).

The best NBDA models for who observed whom within 1m of the rotating-door task were again obtained using multiplicative approaches, indicating asocial + indirect social learning processes (Hoppitt & Laland, 2008). Close-proximity observations (1m) allow the transmission of detailed information. The fact that individuals copied the preferred action of the most successful individual observed in the rotating-door task (see ***section 5.4.2***) suggests that a transient effect of the action observed might have led Barbary macaques to perform the same successful actions observed via response facilitation (Hoppitt & Laland, 2008), but not observational learning as the best model was not additive. In addition, option choice was probably reinforced by individual experience with the task (see ***section 5.4.2***).

5.4.5. On the role of observation networks in social learning

For all tasks, SNA showed that individuals were selective with whom they tolerate at close proximity in a task context. Observation networks within 5m included more individuals, who were more connected to each other and, generally, less centralized than within 1m, indicating more potential for identity dependent 'directed social learning' within 1m than within 5m (Coussi-Korbel & Fragaszy, 1995). However, no significant results for assortative mixing by any of the individual attributes tested (sex, age, social rank, kinship) were obtained for observation networks within 1m in the tasks of medium (push/lift-up) and high difficulty (rotating-door). This suggests that other factors (e.g. social bonds, task payoffs, conspecifics' success) likely influenced whom to observe, as indicated by option-preference and NBDA (see above). The observation of individuals of particular characteristics may be due to learning purposes (e.g. a social learning strategy) or monitoring others (e.g. social dynamics, fear of attack). Data collected in this thesis does not allow me to distinguish between these alternatives. However, observing others may play a significant role in information diffusion in task-related learning contexts (Borgatti et al., 2013; Kulahci, 2014), with individuals selectively directing attention towards those from which relevant information about social events can be obtained in order to cope with complex and challenging social lives (Seyfarth & Cheney, 2003; van de Waal et al., 2010; Micheletta, 2012; Kulahci et al., 2016). Several studies have shown that individual attributes (i.e. sex, age, rank, kinship) influence visual attention in despotic macaque species (e.g. rhesus macaques) but less so in tolerant species like Barbary macaques (Thierry, 2007; Teufel et al., 2010; Micheletta, 2012; Rosati & Santos, 2017). This might explain the lack of results for assortative mixing in the 1m observation network of the most difficult tasks.

Within this framework, I would argue that social bonds (leading to social tolerance) were relevant for observation networks in the push/lift-up task, while demonstrators' success was important for observation networks in the rotating-door task. Results of previous analyses support this reasoning. Several studies indicate that visual attention in Barbary macaques is generally drawn to affiliates (Micheletta, 2012; Berthier & Semple, 2018). For the push/lift-up task, affiliative (CSI) and observation relations within 5m predicted each other and provided evidence for social learning. For the rotating-door task, only observing within 1m resulted in social learning seemingly through a tendency to copy the most successful individual observed, as the observation network was not predicted by social bonds.

Coussi-Korbel & Fragaszy (1995) defined isomorphic coordination as one individual's activity drawing the attention of observers to an activity or element of the environment (e.g. task or task manipulations) causing an increase in behavioural similarity. This form of coordination may provide the observer the opportunity to learn general or detailed information from the demonstrator depending on the distance between them (Coussi-Korbel & Fragaszy, 1995). Only the most difficult task (rotating-door) required close proximity to acquire detailed information about demonstrators' manipulations and payoffs in order to learn how to solve it.

Overall, these findings have similarities to findings with wild monkeys. In a task similar to the push/lift-up task used in this thesis there was evidence for indirect social learning (i.e. stimulus and local enhancement), in wild vervets as in the present study (van de Waal et al. 2010). Moreover, there is evidence of a payoff bias in the social learning of wild vervet monkeys (when task contingencies varied in quantity between options, Bono et al. 2018) and capuchin monkeys (when learning about extractive foraging techniques to process structurally protected fruits, Barrett et al. 2017).

5.4.6. On the role of communication networks in social learning

The network based on who is backing up whom (helper-recipient) did not predict observation networks in any case in BDG. This network represents coalitions/alliances formed via affiliative behaviours. However, not only the affiliative relation with the aided individual but also the identity of the opponent will have influenced the relations observed in this communication network (see ***Chapter 4***). Accordingly, the helper-recipient network may have not captured all the socio-positive relations and, thus, was probably not representative of all social observation opportunities. Although this network alone may not be useful in making predictions about who observes whom in a social learning context, it may provide additional information to complement other affiliative networks when testing for social diffusion of information (Snijders & Naguib, 2017). Moreover, this communication network can be understood as a proxy of social relations between individuals that exchange commodities (e.g. coalitionary support, access to resources like a foraging task) and which interconnections are the result of the strength of social bonds and risk assessments based on triadic awareness. Therefore, the helper-recipient network may be more representative (than other communication networks such as vocal comments in infant-handling contexts, see below) of actual social learning opportunities which do not only depend on the chance to observe others interacting with the task but also on social dominance dynamics that may constrain opportunities to access the task. Accordingly, this network may be useful to directly test for social learning using NBDA. My study did not allow me to test for this since data on communication networks and social learning were unfortunately obtained in different groups.

The network based on vocal comments produced during affiliative contexts (commenter-handler) in BDG did predict observation networks within 5m. This suggests that communication networks that represent affiliative relations may also depict social learning opportunities. Interestingly, the commenter-handler network only predicted observations within 1m when the strength of connections were considered (weighted network). These vocal comments occurred among strongly-bonded partners and were probably uttered to gain access to resources or privileges (i.e. social tolerance, see ***Chapter 4***). Based on this, those in TG that learned how to solve the rotating-door task (high difficulty) probably had strong bonds with the demonstrator which were not only defined by the affiliative behaviours studied. That is, vocal comments uttered in infant-handling contexts can be understood as a proxy for strong affiliative relations that may represent social privileges and/or particularly strong bonds (e.g. if increased infant-related arousal triggers the production of these calls, arousal is expected to be greater when strong affiliates are involved in social interactions, see ***Chapter 4***). I may speculate that in TG other unmeasured socio-positive relations were involved such as those represented by vocal commenting. These social bonds would have granted observers with high levels of social tolerance at 1m, allowing them to acquire detailed task information. I am unable to test this in this thesis as communication networks and data on social learning were obtained in different groups. However, a network combining affiliative relations based on social behaviours (e.g. grooming, proximity) with those based on vocalizations in affiliative contexts would probably be most holistic in capturing all the aspects of social relations, including those related to access to privilege information or resources that influence social learning opportunities (Snijders & Naguib, 2017).

It is likely that the factors influencing social learning when tasks are difficult and therefore learners are 'uncertain' (Kendal et al. 2018), were aspects of social relations not captured in the affiliative networks used in the predictions. A further study using a bigger sample size and combining affiliative plus communication networks might provide further insights into this matter.

Chapter 6

General Discussion

In this chapter, I discuss the evidence provided by the overall findings in this thesis and previous literature that link primate communication, social dynamics and social learning. First, I describe the social learning opportunities that Barbary macaques may have in different contexts (i.e. during- versus outside-task introductions and in different affiliative situations) and how they may vary between groups of different characteristics (i.e. group size, type of enclosure). Second, I discuss the evidence of social intelligence provided by the analysis of the communication networks used in this thesis (i.e. based on aid-recruitment calls and vocal comments) and how communication interactions also represent social learning opportunities and can be used to test for social learning in free-ranging groups of animals. Third, I present a summary of the evidence of social transmission in Barbary macaques provided by my findings. Then, I discuss the social learning processes and social learning strategies of Barbary macaques suggested by my outcomes in comparison with previous evidence in other primate species and the implications of my study for future research on cultural transmission in Barbary macaques. Finally, I detail the limitations of my thesis, its implications in future studies on social dynamics, primate communication, social learning, human language evolution and conservation, and provide several ideas for future directions and methodological improvements.

6.1. The social learning context: on how social networks represent social learning opportunities

Barbary macaques live in multimale-multifemale societies consisting of 12 to 88 individuals (Ménard, 2002; Mittermeier et al., 2013; Wallis et al., 2020) and a complex and diverse array of social relations (Fischer et al., 2017). They have relaxed dominance relationships (with common rank reversals), balanced competition tests (i.e. frequent counter-attacks), high rates of socio-positive interactions and high levels of social tolerance (Thierry, 2004; Thierry, 2007), meaning they are defined as an intermediate species in the egalitarian-despotic spectrum of macaque societies (Thierry, 2007). The description of the social structure (i.e. patterns of social relations) of animal societies allows predictions about opportunities for social learning (Coussi-Korbel & Fragaszy, 1995; Voelkl & Noë, 2008; Carter et al., 2015; Coelho, 2015). When individuals within a group are loosely connected with each other, the group is clustered or fragmented and/or social relations are heterogeneous (asymmetric) in terms of occurrence or strength, individuals are likely to learn via directed social learning (Coussi-Korbel & Fragaszy, 1995). When group cohesion is high, all individuals are connected with each other or form one single component and/or social relations are homogeneous (symmetric), social information will be likely acquired via non-specific social learning (Coussi-Korbel & Fragaszy, 1995). Accordingly, the study of the social learning context in which Barbary macaques live conducted in this thesis confirmed the prediction that societies with an intermediate style of social dynamics (i.e. social tolerance but strict hierarchies) will provide evidence of both non-specific and directed social learning (Coussi-Korbel & Fragaszy, 1995).

The findings presented in this thesis provided an empirical description of the social organization of two groups of Barbary macaques in terms of group cohesion, level of connectivity among individuals and symmetry of relations to test the predictions about directed or non-specific social learning opportunities stated by Coussi-Korbel & Fragaszy (1995). The highest levels of group cohesion were found in long-distance associations between individuals (networks based on proximity within 5m) where the social structure was defined as saturated and fairly homogenous, resulting in predominance of non-specific social learning. The other affiliative networks (grooming, huddling and proximity within 1m) and all communication and observation networks during task introductions resulted in less cohesive and more asymmetric relations than proximity within 5m, enabling the prediction of directed social learning in these contexts.

Although I found some significant differences in the social structure among grooming, huddling and close proximity (1m) networks within groups, these three types of networks were the most similar at the network level among all networks considered. This corresponds to the findings of Carter et al. (2015) that grooming and other affiliative networks (such as those based on lip-smacking) in chacma baboons (*Papio ursinus*) did not significantly differ at the network level. It, however, contrasts previous evidence in other primates and animal societies (olive baboons, *Papio anubis*, Lehmann & Ross, 2011; meerkats, *Suricata suricatta*, Madden et al., 2011). I note, however, that the lack of significant correlations for most centrality measures among grooming, huddling and close proximity in my study indicated that each of these networks, despite predicting each other, likely represented slightly different aspects of affiliative relations. Accordingly, one socio-positive behaviour was probably insufficient to accurately illustrate all social bonds in the group (Lehmann & Ross, 2011; Madden et al., 2011). This was confirmed when a network based on a combination of grooming, huddling and close proximity (using the Composite Sociality Index – CSI) predicted communication networks and provided evidence for social learning, whereas none of the networks based on single behaviours did so consistently. The findings in this thesis address the need for integrating different kinds of networks (e.g. affiliative interactions, proximity) in the study of animal social networks, as highlighted by several studies (Flack et al., 2006; Castles et al., 2014; reviewed in Snijders & Naguib, 2017).

Castles et al. (2014) found that the position of individuals within proximity networks did not always predict their position in networks based on affiliative interactions (e.g. grooming). The authors argued that proximity cannot always be used as a proxy of interactions – contradicting the arguments of other researchers (Farine, 2015) – and cautioned against this assumption, encouraging researchers to test it before drawing conclusions about the power of proximity in predicting interactions (Castles et al., 2014; Carter et al., 2015). In this thesis, affiliative interactions (grooming, huddling) predicted proximity networks (within 1m & 5m) in both groups of Barbary macaques, supporting the idea that proximity associations may represent opportunities of interaction (Farine, 2015). However, I argued (***Chapter 3***) that the ability of proximity networks to predict interactions may depend on group size and the characteristics of the enclosure (as argued by Carter et al., 2015) as well as the distance considered since regression coefficients between interaction (grooming, huddling) and proximity networks were lower for 5m than for 1m networks.

The social context in which distance is measured may also influence the usefulness of proximity networks in predicting interaction networks. For instance, observations within 5m during task introductions resulted in highly asymmetrical relations and fragmented networks, in contrast to 5m proximity networks outside task introductions, which formed a highly saturated and symmetric social unit. Social tolerance of individuals in proximity will differ between contexts, for instance, when highly valuable resources such as extractive foraging tasks are present or not (Cronin et al., 2014; Fitchel et al., 2018). Social factors like grooming or dominance relations may have a greater influence on social tolerance during feeding on monopolizable resources than outside feeding contexts (Watts, 2006). Moreover, social tolerance is influenced by the capacity of individuals to exclude others or grant them access to the resource, as well as fear of retaliation by dominant individuals monopolizing the resource (Amici et al., 2012; Cronin et al., 2014). Therefore, fewer individuals, and more asymmetric relations within networks are expected to be found in contexts where individuals are competing for valuable resources than in contexts where they are not (Fitchel et al., 2018). In addition, Coussi-Korbel & Fragaszy (1995) stated that the acquisition of social information is mediated by social dynamics in two manners: by proximity (i.e. the closer the proximity, the more likely individuals will acquire specific social information) and by the influence of affiliative bonds on visual attention (i.e. attention biases towards affiliates). Accordingly, measures of proximity in different contexts represented different opportunities for social interaction in my study that resulted in different patterns of social learning: 'directed' in 5m proximity networks during task introductions and 'non-specific' in 5m proximity networks outside of task introduction times.

Similarities and differences in the social structure between huddling and close proximity networks within groups were consistent across BDG and TG groups. That was not the case for grooming networks. In BDG, grooming networks were more saturated and symmetric than huddling and close proximity networks, while the opposite was found for grooming networks in TG. Grooming is an affiliative behaviour that serves as a conflict-solving and tension-reducing behaviour (Schino et al., 1988). In studies of primate social relations, those individuals that exchange high rates of grooming also exchange high rates of aggression (Silk, 1982; Perry, 1996; Schino et al., 2005; McFarland & Majolo, 2011). Barbary macaques in Trentham Monkey Forest live in a wide and densely forested area, ~8 times larger than the macaque enclosure at Blair Drummond Safari Park, which is an open field.

Therefore, resources in Trentham Monkey Forest are expected to be more widespread than in Blair Drummond, reducing the likelihood of fights to gain access to them in TG. Moreover, the complexity of TG's environment may enable avoidance behaviours effectively reducing the frequency of conflicts within the group. In fact, proximity was not collected at ranges >5m in TG because it was not possible to observe or track the subjects through the dense vegetation beyond that distance. In Blair Drummond Safari Park, however, individuals were in sight of each other most of the time and initiated agonistic or socio-positive interactions at any time and at distances >20 m (*personal observation*). Consequently, the probability of agonistic encounters that may lead to appeasement or reconciliatory behaviours such as grooming was expected to be lower in TG than in BDG.

Kudo & Dunbar (2001) showed that large groups tend to be more sub-structured (cliqued) and less cohesively connected in grooming networks than small groups. Therefore, it is expected that a smaller fraction of all possible dyadic interactions occur in a larger group like TG (N=56) in comparison to a smaller group like BDG (N=25), resulting in less saturated and more asymmetric grooming networks in TG than in BDG. Accordingly, the characteristics of the enclosures (as stated before) plus group size would have made less likely the occurrence of agonistic and affiliative encounters in TG than in BDG, explaining the differences at the network-level found between groups. Moreover, grooming was the only affiliative behaviour here studied that is known to be directly linked to the occurrence of agonistic encounters as a conciliatory behaviour (Schino et al., 1988). Huddling and close proximity, however, are rarely subjected to a direct response to aggressions and generally depend on other factors such as climate conditions (i.e. cold temperatures in the formation of huddles, Campbell et al., 2018) or social-related factors like social organization (i.e. fission-fussion societies), social events (i.e. presence of newborns), gregariousness (i.e. propensity to be in proximity of others) or sociality (i.e. propensity to interact with others when in proximity to them) of the group or taxa (proximity, Matsumura & Okamoto, 1997; Carter et al., 2015). Consequently, partner selection in grooming networks was probably more constrained than huddling and close proximity networks in TG by the characteristics of the environment, group size and the presence of cliques in the social structure (Aureli & de Waal, 1997; Kudo & Dunbar, 2001; Palagi et al., 2007; Lehmann et al., 2007). However, since I only studied one large group (TG) and one small group (BDG), it is possible that the group differences found in this thesis are due to factors other than group size and habitat/enclosure characteristics, so further comparisons with more groups of different sizes and from different environments are necessary (see ***section 6.5***).

Barbary macaques may establish a wide variety of strong to weak bonds with their peers when they can freely choose their counterparts out of the full set of potential partners, while the frequent exposure to a limited subset of conspecifics will limit the diversity of social bonds that can be formed. In BDG, individuals were constantly in sight of each other and so could freely pick their grooming, huddling and close proximity partners. However, being in sight of other members of the group may increase third-party interventions that interrupt or constrain the occurrence of socio-positive interactions between particular individuals due to competition for access to dominant conspecifics or mating partners (Flack et al., 2006; Schneider & Krueger, 2012), increasing the disparity of social bonds within the group. This might explain why disparity was not significantly different among grooming, huddling and close proximity in TG (but it was in BDG), showing that the strength of social relations for these networks was more evenly distributed in TG than in BDG.

Supporting evidence of all the differences found in grooming, huddling and close proximity networks between both groups is provided by the results obtained for average degree and the total amount of agonistic encounters collected in each group. Despite BDG (N=25) being half the size of TG (N=56), individuals had an average number of grooming partners in BDG (Average Degree=12.4) that was twice the value obtained in TG (Average Degree=6.7). However, for huddling and close proximity, both groups had a similar average of partners (see ***Table 3.1***). Note that average degree increased proportionally with increasing group size as distance between individuals increased (proximity 1m vs 5m), but was the same for proximity within 1m in both groups (***Table 3.1***). Several authors have demonstrated that the total number of partners primates interact or associate with is influenced by group size until a certain limit where individuals cannot maintain more social relations (Dunbar, 1992; Lehmann et al., 2007) or it is fixed relative to group size and biased towards preferred partners (Kudo & Dunbar, 2001). Accordingly, we would expect that average degree in TG for all affiliative networks was similar or greater than that of BDG. This only seems to be true for huddling and close proximity. Therefore, I argue that the size and complexity of the Trentham Monkey Forest reduced the number of agonistic encounters in TG that would have led to reduction of tension via grooming interactions with more conspecifics.

In accordance with the above argument, even though sampling effort of agonistic interactions, using the same sampling methods and rules, was almost double in TG (532 h) compared to BDG (299 h), the total amount of agonistic encounters observed in TG (343 events) was half that in BDG (696 events). Moreover, 56.7% of all the possible grooming interactions occurred in BDG, while only 12.2% were observed in TG. These results support the previous idea regarding the influence of the environment in the occurrence of grooming interactions as conciliatory behaviours. Some studies have highlighted that the nature of the habitat influences the level of dispersion of a group, so that individuals tend to gather together in open habitats, which increases agonistic competition for resources (Wrangham, 1980; Cibien et al., 1989; Marino & Baldi, 2014). This supports the idea that tension-reducing behaviours like grooming would be more frequent and widespread among all individuals in BDG than in TG. The low values (closer to zero) of average clustering coefficients, especially for grooming networks in TG also suggest that individuals in this group were more cliqued than in BDG, limiting interactions to a small subset of the group (Whitehead, 2008).

The differences in the social structure of grooming networks between groups were also reflected in partner preferences (i.e. assortative mixing). BDG and TG showed opposed partner preferences for sex. Females in BDG clearly preferred to exchange grooming with other females, whereas no significant preference for females was found in TG. I argued (***Chapter 3***) that the social and environmental constraints in TG resulted in the formation of cliques defined by mother relatedness, within which, sex composition was subjected to kinship. This may explain the absence of sex partner preferences for females in TG. In BDG, social structure was less cliqued, forming a more cohesive unit, than in TG. Therefore, the preferences of females for other females in BDG may be due to males being the dispersing sex (Thierry et al., 2004), resulting in females having more opportunities to establish social bonds among them (McFarland & Majolo, 2011; Roubová et al., 2015). The preference of males for the philopatric sex (females) in grooming networks may be explained by grooming coercion. In Barbary macaques, where males outrank females (Maestripieri, 1997, Bayne, 2005), males may use their rank status to direct aggression towards females that refuse to provide them with social services like grooming to force grooming interactions (McFarland & Majolo, 2011), as happens in other primate species (Smuts & Smuts, 1993; Colmenares et al., 2002).

Grooming and huddling showed the highest similarity among all affiliative networks in both groups in terms of social structure, including individual centrality (representing the position and role of individuals in the network). The patterns of relations and partner preferences observed in grooming networks were reflected in huddling networks, supporting previous findings that indicate a correlation between these two affiliative behaviours (Campbell et al., 2018; Ueno & Nakamichi, 2018). The fact that grooming formed a more cohesive, connected and homogenous (i.e. less disparity in the strength of connections) network than huddling in BDG supports the idea that huddling partners in Barbary macaques may be chosen based on the strength of grooming bonds (Campbell et al., 2018). This suggests a higher partner selectivity in huddling than in grooming interactions in BDG (Campbell et al., 2018) and it is likely that huddling was being exchanged as a commodity for grooming (Ueno & Nakamichi, 2018). Results for TG do not support these statements. Again, individuals in TG seemed to be constrained by the characteristics of their environment, probably reducing the number of agonistic encounters that led to reconciliatory behaviours like grooming. I suggest that the higher number of conflicts in BDG than in TG provided more opportunities for individuals in this group to establish or strengthen social bonds through grooming interactions, allowing them to select their huddling partners based on their grooming relations. In TG where individuals were constrained by proximity due to their environment and clustered in mother-related cliques, partner selection for huddling was probably limited most times to the small subset of individuals within the clique.

Differences in partner preference between affiliation at a close distance (grooming, huddling and proximity within 1m) and proximity within 5m indicate which individuals (in terms of sex, age, social rank and kinship) enjoyed higher levels of social tolerance from their conspecifics across contexts. My results (particularly in TG) for affiliative networks outside task introductions indicated that, in a social learning context, individuals will tend to observe (within 5m radius) those of different sex, age and social rank classes to themselves. Observation networks supported this idea. Significant results for assortative mixing (indicating partner preferences) were mainly obtained for task observations within 5m. In presence of a highly valuable resource, social tolerance is expected to be lower near to rather than far from the resource (Cronin & Sánchez, 2012; Schnöll, 2014; Fitchel et al., 2018). Therefore, observers are likely to be found at a distance that allows high social tolerance by those exploiting the resource, as is the case with proximity within 5m. Results of assortative mixing for 5m observation networks were similar to those obtained in grooming, huddling and close proximity networks in both groups, confirming that most social learning opportunities depicted by affiliative relations will be represented by observations at a distance from the valuable resource.

Overall, the social context in which Barbary macaques live represents different levels of social tolerance among individuals. Coussi-Korbel & Fragaszy (1995) already stated that social tolerance is influenced by the levels of behavioural coordination in space and/or time (e.g. proximity) between individuals, and may vary between groups and within species depending on the social dynamics of each animal society and their environment. My results suggest that the distance considered between individuals and the environmental constraints faced by each group may have led to different social dynamics that influenced how conspecifics tolerated each other (but this is based on a comparison between one group of each size and environment, so other factors may also explain these group differences in social dynamics, see ***section 6.5***). Ultimately, social tolerance represents opportunities for individuals to acquire social information, which can be transmitted following different patterns (directed or non-specific social learning, Coussi-Korbel & Fragaszy, 1995). The social networks studied in this thesis provided social contexts where information was more likely to be acquired from specific individuals (grooming, huddling, close proximity, communication and observation networks) and social contexts where all individuals had the same contribution to the flow of information (proximity within 5m). Moreover, the results of this thesis highlight the importance of considering different social behaviours to better capture the social context within which individuals can socially learn from each other (Snijders & Naguib, 2017). Accordingly, an affiliative network combining grooming, huddling and close proximity was built to further test for social learning and investigate the role of communication in social learning.

6.2. Communication networks and social intelligence

Several studies have demonstrated that sociality and communication coevolved in primate species (McComb & Semple, 2005; Gustison et al., 2012). Freeberg et al. (2012) showed that the complexity and diversity of communication systems in nonhuman primates increased with group size, and that species with dynamic interactions and relaxed dominance structures (i.e. complex and flexible social relations) were also more flexible in signal production and sensitive to vocal signals than societies with rigid social and dominance relations. Accordingly, social relations, especially in egalitarian species like Barbary macaques (Thierry, 2001; Rebout et al., 2017), are expected to influence, and be influenced by, communication interactions. The findings of this thesis support this statement. Social bonds predicted communication networks based on responses to aid-recruitment calls. Also, the production of vocal comments was predicted by the strength of affiliative relations between callers and individuals involved in the third-party interactions triggering these calls.

Outcomes highlighted that Barbary macaques did not recruit aid in all agonistic contexts, suggesting that in most cases, the dominance relationship between dyads was readily accepted by both individuals (Drews, 1993). Regardless, aid-recruitment calls were more likely when males (who normally outrank females in this species, Maestripieri, 1997; Bayne, 2005) threatened females and when middle-ranking individuals were attacked by higher-ranking members. Low-ranking subjects, however, normally responded with formal submission. Accordingly, I argued (***Chapter 4***) that only individuals with strong alliances produced aid-recruitment calls in order to avoid high aggression and protect their social status. Yet, many of the aid-recruitment calls were not responded to, most likely because individuals assessed the triadic relationships among those involved in the conflict and in the audience, and evaluated the risk of retaliation of providing agonistic support as high (Widdig et al., 2000, Young et al., 2014). In line with this, Barbary macaques mainly provided agonistic support to their affiliates (partners in grooming, close proximity and affiliative CSI networks) when affiliates had the same rank, and when the opponent had the same or a lower rank, than the helper, corroborating previous literature (Widdig et al., 2000; Young et al., 2014).

Vocal comments in agonistic encounters seemed to function as the so-called ‘vocal alliances’ observed in other primate species because they occurred between allies and against weakly-bonded group members (Silk et al., 2004; Wittig et al., 2007). Agonistic support was generally provided by males to both sexes and also between females when aid-recruitment calls were produced. Similarly, when vocal comments were produced in agonistic contexts, it was females who vocalized in support of males or other females when the victims of the aggression were individuals of the same sex and of the same or lower rank than the caller. In the case of aid-recruitment calls, the helper generally had the same or a higher rank than the individuals involved in the conflict, whereas vocal comments where frequently uttered when callers had the same or lower rank than one or both individuals involved. Therefore, it is likely that vocal comments in agonistic contexts ultimately serve to provide support when the risk of retaliation for joining the conflict is high (Silk et al., 2004). Moreover, commenters and aggressors in the vocal comment network were predicted by the strong alliances depicted in the aid-recruitment network representing relations between recipients of support and helpers. Accordingly, vocal comments may also serve to strengthen the alliance and/or return the favour of help provided in the past to a higher ranking ally going against a strong competitor (Schino & Aureli, 2009; Young et al., 2014; Duboscq et al., 2017).

Some studies highlight that 'vocal alliances' are low-cost displays that function to signal the willingness to physically intervene in the conflict if the dispute is not settled quickly (Wittig et al., 2007). In addition, the intensity of aggression may be related to the occurrence of agonistic support in Barbary macaques (Prud'homme & Chapais, 1993) and other primate species (Pereira & Kappeler, 1997; but see Pallante et al., 2016). Moreover, it has been suggested that primates can modify the acoustic structure of vocalizations produced during conflicts to exaggerate the severity of aggression in order to increase the chances of eliciting help from potential allies (Slocombe & Zuberbühler, 2007). Consequently, it is possible that the intensity of the conflict (or the level of perceived aggression by the victim) influences the decision of providing physical (as in aid-recruitment contexts) or vocal (using vocal comments) support. Further research is necessary to investigate this question.

The occurrence of vocal comments in infant-handling contexts was predicted by the huddling bonds between callers and the third parties, and by the grooming ties established between callers and mothers of the infants involved in the third-party interaction. Normally, individuals called when higher-ranking conspecifics were observed handling infants, and it was the females who mainly vocalized when other females were involved in the third-party interaction. These infant-centred affiliative interactions represent important opportunities for adults to establish or strengthen their social bonds and play an important role in the social dynamics of the group, especially among females (Maestripieri, 1994; Whitham et al., 2007). The strong social bonds between callers, infant-handlers and mothers of handled infants might be taken to suggest that Barbary macaques produced vocal comments when the chances to join the infant-handling interaction were high. However, based on the fact that vocal comments were sometimes uttered at long distances (Brumm et al., 2005), I discussed in ***Chapter 4*** that these vocalizations may also be an expression of collective arousal (Thierry et al., 2000, De Marco et al., 2011). Both explanations (signalling benign intentions and collective arousal) are not mutually exclusive.

The 'social brain hypothesis' suggests that nonhuman primates live in social groups to overcome ecological problems like predation or finding food and mating partners (Dunbar, 2009). However, to overcome the stresses of living in close proximity (e.g. conflicts that arise from sharing space and resources), primates maintain group cohesion and stability through complex social relations that involve the formation of coalitions and alliances (Dunbar 1998, 2016). In order to do that, primates require high cognitive abilities to anticipate their future needs and the consequences of their actions, and they do it by evaluating their social and natural environment (Slocombe & Zuberbühler, 2007; Dunbar, 2016). Overall, the patterns of relations observed in communication networks suggest that Barbary macaques have a high degree of triadic awareness. Accordingly, Barbary macaques evaluate the complex alliances and social relations of their conspecifics to assess the risks and opportunities that may arise from producing or responding to vocalizations in particular contexts. Both aid-recruitment calls and vocal comments may provide important information regarding triadic relations to eavesdroppers that may help them navigate the complexities of social life in their group (Slocombe & Zuberbühler, 2007; Snijers & Naguib, 2017). This use of coalitions, alliances and understanding of third party relations is a key sign of social intelligence (i.e. social brain hypothesis, Byrne & Whiten, 1988; Dunbar, 1998, 2009, 2016).

Social intelligence in primates has also been associated with high rates of tactical deception (Byrne & Corp, 2004; Dunbar, 2016). Deception can be defined as manipulation of the behaviour of others without the use of force (Byrne & Corp, 2004) and it is an indication of sophisticated cognitive skills (Mitchell & Thompson, 1986; Whiten & Byrne, 1988; Wheeler et al., 2011). Deceptive communication (i.e. the production of false signals from which the signaller derives some fitness benefits, Hauser, 1996; Searcy & Nowicki, 2005) is common in primate species (Wheeler et al., 2011). Past experience with deceptive signals may tell receivers who in their group is reliable in terms of conveying relevant social information (Silk et al., 2000; Searcy & Nowicki, 2005). Accordingly, communication networks may represent social relations established based on awareness of who is likely to provide reliable information about the social or natural environment. Similarly, the communication networks studied in this thesis also showed that individuals are aware of potential alliances and evaluate the risks of retaliation of intervening in a third-party interaction (***Chapter 4***)**.** Awareness of triadic relations and reliable informants is important in social learning contexts where individuals may compete for social information and access to food resources (i.e. foraging task) (Coussi-Korbel & Fragaszy, 1995; Dunbar, 2010; Duboscq et al., 2016). Therefore, the patterns of relations observed in communication networks are useful to predict who is likely to observe whom in a social learning context.

6.3 Communication networks and their role in social learning

In this thesis, I found that communication networks based on vocal comments, but not aid-recruitment calls, were predictive of observation opportunities. However, I argue that both types of communication may be instructive in outlining overall social learning opportunities in groups, despite this conclusion must be taken with caution since the role of communication networks was only conducted in one group of Barbary macaques (BDG).

The relationship between callers (vocal comments) and infant-handlers predicted observation networks. Likewise, the relationship between commenters and infant-handlers was predicted by huddling relations. Huddling events represent instances of closer physical proximity (i.e. higher social tolerance) and stronger bonds between individuals than grooming (Takahashi, 1997; Campbell et al., 2018; Ueno & Nakamichi, 2018, see ***Chapter 3***), whereas grooming is used as a tension-reducing behaviour or in exchange for commodities (Barrett et al., 1999; Henzi et al., 2003). Accordingly, huddling relations may represent social relations based on higher partner reliance/alliance than other affiliative behaviours (e.g. grooming). In addition, callers and mothers of the infants involved in the third-party interaction were strong grooming partners. This suggests that the communication network based on vocal comments during infant-handling interactions may also represent instances of individuals trying to gain access to, or paying attention to, individuals with privilege access to a resource (i.e. the infant). Therefore, the patterns of relations depicted in this communication network seem to be representative of social interactions occurring in similar contexts (i.e. competition for resource access), such as who observed whom during foraging-task introductions, as my results indicate.

The communication network based on the relationship between aid-recruiters and their allies (helpers) did not predict observation networks in my study. Support provided in conflicts did not only depend on the strength of affiliative relations between callers and helpers but also on the dominance relations among all individuals involved (callers, helpers and opponents, see ***Chapter 4***). Consequently, the communication network based on who provided support to whom probably did not represent all the alliances that individuals actually had. However, this network did depict strong affiliative relations (i.e. it was predicted by grooming, close proximity and affiliative CSI networks), which are known to represent social learning opportunities. Therefore, I argued (***Chapter 4***) that this communication network can be useful to test for social learning if combined with other affiliative behaviours to create a more representative network of the social bonds in the group. Nonetheless, I would argue that this communication network can also be used alone to indicate social learning opportunities. This is because observation networks during social learning experiments do not necessarily indicate who is going to learn from whom (Hoppitt, 2017). Social learning does not only depend on the opportunities to observe others but also on the complex dominance and tolerance relations that individuals have established with the demonstrator of the novel behaviour and the audience that will grant them access to the task (Franz & Nunn, 2009; Kendal et al., 2010; Hoppitt & Laland, 2011;). Accordingly, approaching and interacting with the task will be influenced by social factors such as the risk of retaliation and the occurrence of displacements directed from individuals at or near the task. Therefore, the relations observed in the recipient-helper network that depicted higher levels of triadic awareness, may be more representative of actual learning opportunities than networks based on vocal comments during infant-handling interactions or observation networks.

The observation of conspecifics' behaviours during foraging-task interactions represent opportunities for individuals to extract social information relevant to survival. Accordingly, the behaviour of others at task can be understood as social cues from which observers may learn something about the task. In this case, observation networks may represent the transmission of social cues and, therefore, be considered cue networks. Interestingly, only communication networks based on vocal comments in infant-handling contexts, and not aid-recruitment networks, predicted observation (cue) networks. This is likely because networks based on aid-recruitment calls can be viewed as a proxy of a social support network instead of a communication network per se. Indeed, the helper-recipient network represented the relationship between callers and those who responded with aid to the vocalization but not all the pathways through which the communication signal (aid-recruitment call) was transmitted. However, networks based on vocal comments in infant-handling contexts, which apparently signalled for social tolerance near the infant, would represent all the diffusion ways between callers and potential receivers. Moreover, the production of vocal comments were the result of attention paid to socially-bonded partners engaged in affiliative infant-handling interactions. Observation networks also represented attention biases towards affiliates. Consequently, vocal-comment networks would have represented observation biases influencing the acquisition of novel information via social cues (i.e. social learning opportunities), just like observation (cue) networks. As aforementioned, social learning opportunities do not necessarly convey in social learning events, and the factors that influence actual social learning seem to be captured by aid-recruitment (helper-recipient) networks more than by networks based on vocal comments in infant-handling contexts.

In conclusion, the evidence of social intelligence suggested by the analysis of communication networks in this thesis indicates that communication interactions represent aspects of social complexity (e.g. triadic awareness) that are relevant to social learning. It is not clear whether social learning is a driver or a by-product of animal social intelligence (Reader & Laland, 2002; Reader et al., 2011; Dunbar, 2016) but it is clear that the sophisticated cognition that underpins social intelligence is required for social learning (Dunbar, 2016). Social complexity in primates did not only co-evolve with communication (McComb & Semple, 2005; Freeberg et al., 2012; Gustison et al., 2012) but also with social learning (Street et al., 2017), indirectly linking the co-evolution of communication and social learning. In Chapter 1, I presented a framework that illustrates a parallelism between theories of communication and social learning evolution (Hoppitt et al., 2008; Schaefer & Ruxton, 2012). I argue that social learning and communication evolved from cues (by-product forms of inadvertent information) so that the selection and evolution of inadvertent cues into active communication signals acted upon the evolution of inadvertent forms of social information into more efficient learning processes (e.g. teaching), and vice versa (Hoppitt et al., 2008; Schaefer & Ruxton, 2012). According to this, the social structure of communication interactions in a group of primates may well mirror the patterns of social information diffusion, confirming the usefulness of communication networks in the study of social learning (Snijders & Naguib, 2017).

6.4. Evidence of social learning in Barbary macaques

In the present study, evidence of social transmission in Barbary macaques was only found for the most difficult tasks. These results are consistent with the predictions and findings of previous studies that support the hypothesis that animals rely on social learning when asocial learning is costly in terms of time and energy investment ('costly information hypothesis', Boyd & Richerson, 1985, 1988; Byrne & Russon, 1998; Kendal et al., 2009, 2010). Accordingly, animals face the trade-offs of acquiring costly but accurate information through trial-and-error (asocial learning) or less reliable but cheap (safe, easy and less costly-to-obtain) information through social learning (Kendal et al., 2005, 2009). The results presented in this thesis indicate that, for the task of medium difficulty (push/lift-up task), only social relations represented in affiliative (CSI) and 5m task observation networks provided evidence of social diffusion. For the most difficult task (rotating-door task), evidence of social learning was only found in 1m task observation networks perhaps because individuals needed to acquire detailed information about task manipulations in order to learn how to solve it. As would be expected (Hoppitt, 2017), a network based on who observed whom during task introductions provided stronger evidence of social learning, using NBDA analysis, than any other networks in this study.

Affiliative relations may represent social learning opportunities because they occur within the proximity range between individuals at which observation necessary for social learning can happen (Coussi-Korbel & Fragaszy, 1995; Franz & Nunn, 2009; Hoppitt, 2017). Although affiliation (e.g. interactions like grooming or associations based on proximity) can be used as a proxy of who is likely to observe whom, it is not always representative of all social diffusion patterns (Hoppitt, 2017). When affiliation is measured using associations, the distance considered between individuals (proximity) may not include all potential observers (Hoppitt, 2007). For instance, a measure of association based on proximity within 1000 square miles to study social learning in humpback whales may be a good approach to capture all the potential observations between individuals (Allen et al., 2013). However, proximity based on nearest neighbour to investigate social learning in starlings housed in an enclosure of a few square meters, may leave out many instances where individuals not considered associated can observe and learn from each other (Boogert et al., 2014; Hoppitt, 2017). This links with the previous idea that associations may not always be used as a proxy of interactions since it depends on the measure of proximity (e.g. scale) considered, the research question and the characteristics of the study species, group or population as well as the environment they live in (Castles et al., 2014; Carter et al., 2015). Carter et al. (2016) also demonstrated in chacma baboons (*Papio ursinus*) that evidence of social learning depends on the measure of affiliation (e.g. grooming interactions, proximity measured with different methods and at different scales) that we use.

Hoppitt (2017) empirically demonstrated that observation networks are a direct and powerful way to detect social transmission, even when there is no social structure information or when other networks (e.g. affiliative) cannot provide evidence of social learning. This is because network-based diffusion analyses (NBDA) can provide evidence for social learning if the order in which individuals observe each other follows the order of diffusion (Hoppitt, 2017). Observation networks are also useful to assess whether the relationships quantified in another network (e.g. affiliative) are representative of opportunities for observation (Hoppitt, 2017). The lower predictive power (AICc) in NBDA of the affiliative (CSI) network relative to the 5m observation network plus the significant regression between these two networks for the task of medium difficulty (push/lift-up task) suggest that affiliative relations only explained, in part, the pathway of social diffusion of information in this case.

For the most difficult task (rotating-door task), the affiliative (CSI) network predicted 5m observation networks but not 1m observation networks. In order to learn this task, individuals needed to be socially tolerated at a close distance (as indicated by the absence of influence of task monopolisation on 1m observers, see ***Chapter 5***) to acquire detailed information about how to solve the task. It seems that individuals copied the action of the most successful individual observed. Copying others' actions may have a transient effect constraining learning when no immediate access to the task after observation of a demonstrator is granted (Hoppitt & Laland, 2008). Therefore, the small size of the 1m observation network and the low number of learners for the rotating-door task may be due to the specific conditions required for observers to learn the task. It is likely that this also limited the power of the affiliative (CSI) network to predict 1m observation networks and provide evidence of social transmission. In addition, observation networks in TG (the group of Barbary macaques for which social learning was tested) were unweighted, meaning that they only depicted whether individuals observed each other but not how often observations occurred. This might have also reduced the predictive power of the affiliative (CSI) network in the regression analysis. Despite this, the high levels of social tolerance observed between demonstrators and learners (observing within 1m) suggest that some form of affiliation (i.e. strong social bonds) was relevant in this task for social learning to occur.

The affiliative (CSI) network predicted observation networks even when observation networks provided no evidence of social learning (see ***Chapter 5***). This supports the previous idea that affiliative networks do not always approximate the pathways of social diffusion (Carter et al., 2016; Hoppitt, 2017). The lack of evidence of social learning provided by most of the affiliative networks (grooming, 1m and 5m proximity, CSI) in all three tasks suggests that the measures of affiliation used in this study probably were not representative enough of social learning opportunities. Hoppitt (2017) suggests that a 'diffusion-specific network' where interactions or associations among individuals are captured during the diffusion phase of the novel behaviour may be a better approach to test for social learning than social relations collected in a period preceding the diffusion. Therefore, networks based on observations during task introductions or associations measured as time spent together in the task area may be more powerful for detecting and quantifying social diffusion of information than social networks outside task introductions (Claidière et al., 2013; Hoppitt, 2017). Furthermore, it has been observed that dynamic networks may be substantially more powerful for NBDA than static networks (Hobaiter et al., 2014). Since social dynamics may vary over the course of a study, the patterns of social relations (e.g. grooming interactions, associations based on proximity) collected previous to the diffusion of novel behaviours or at different periods during the diffusion may be different from those at the end of the diffusion experiment (Hoppitt, 2017). Consequently, I cannot rule out the possibility that the lack of evidence of social learning provided by the affiliative networks used in this thesis was due to the static nature of the networks.

For both push/lift-up and rotating-door tasks, results indicate that individuals acquired the new information via indirect social learning processes since evidence of social transmission was provided by the NBDA multiplicative, rather than additive, approach (i.e. Hoppitt & Laland, 2011). In addition, macaques used different social learning strategies (Kendal et al. 2018) to learn how to solve each task. There was no evidence that individuals needed to acquire detailed information or copy others' actions in order to learn the push/lift-up task. This is supported by the fact that the actions required for this task (i.e. pushing, lifting up) are said to belong to the natural behavioural repertoire of the species and have been tested in Barbary macaques in foraging tasks resulting in no social learning (Amici et al., 2020). Based on the significant evidence of social diffusion for the push/lift-up task, I argued (***Chapter 5***) that social learning of this task probably occurred via stimulus/local enhancement or social facilitation. Accordingly, individuals could have been attracted to the task and/or increased their rate of task exploration due to the mere presence of another individual interacting with it (Hoppitt & Laland, 2008). Previous studies have also found evidence of stimulus/local enhancement and social facilitation in macaque species (lion-tailed macaques, *Macaca silenus*, Westergaard & Lindquist, 1986; long-tailed macaques, *Macaca fascicularis*, Zuberbühler et al., 1996; Schmitt et al., 2014; Japanese macaques, *Macaca fuscata*, Leca et al., 2010) and other primate species (Custance et al., 2001; van de Waal et al., 2010; see Bandini & Tennie, 2020).

Results for the most difficult, rotating-door, task indicate that individuals needed to obtain detailed information about the specific actions used in task manipulations and the demonstrators' task payoffs in order to learn how to solve this task. Apparently, Barbary macaques copied the action of the most successful individual observed, suggesting that they used a 'who' (model-based) strategy for the most difficult task (Kendal, 2008; Kendal et al., 2009, 2018; Rendell et al, 2011). This provides extra support to the 'costly information hypothesis' outlined above (Boyd & Richerson, 1985, 1988; Rieucau & Giraldeau, 2011) because results indicate that the costs of exploring this task (the most difficult of the three) to asocially learn the actions that led to rewards were higher than in the push/lift-up task (medium difficulty). Among all the indirect social learning processes described, response facilitation is the only one that predicts individuals performing the same action observed by a demonstrator (Hoppitt & Laland, 2008). In response facilitation, individuals perform a motor action already in the species behavioural repertoire or the use of a familiar action in a novel context is socially transmitted (Hoppitt & Laland, 2008). Barbary macaques used the rotating door by pushing it aside (i.e. making the door rotate clockwise or counter-clockwise around a screw; novel context). Pushing is a motor action already in the behavioural repertoire of Barbary macaques (Amici et al., 2020). Therefore, I suggest that social learning of the rotating-door task occurred via response facilitation. Evidence for response facilitation has also been found in macaques (pig-tailed macaques, *Macaca nemestrina*, Ferrari et al., 2005; long-tailed macaques, Brotcorne et al., 2020) and other primate species (great apes, Amici et al., 2014). Similarly, 'who' strategies have also been reported in macaques (Japanese macaques, Hikami et al., 1990; Tanaka 1995, 1998; rhesus macaques, *Macaca mulatta*, Deaner et al., 2005; *Macaca sp.*, Gariépy et al., 2014) and other primates (Horner & Whiten, 2005; Wood, 2013; Coelho et al., 2015; Kendal et al., 2015). For instance, it has been demonstrated that nonhuman primates may pay attention to the demonstrators' payoffs in task-related contexts and copy the option of the most proficient individual observed (Tan et al., 2018).

The inclusion of individual-level variables (e.g. sex, age, social rank, kinship, task neophobia and monopolisation) in NBDA allows investigation of the effect of these variables in asocial versus asocial+social learning models (Hasenjager et al., 2021). Comparisons of the individual-level variables that explained asocial and asocial+social diffusion models in the NBDA help explain most of the findings discussed above in this section. In the push/lift-up task, both best asocial and asocial+social learning models controlled for neophobia when informed with affiliative (CSI) and 5m observation networks, but monopolisation (measured as frequency of attention and access to the task) only improved the model fit for 5m observation networks in both learning models. This indicates that learners included individuals highly tolerated near the task (affiliates) plus other less socially-tolerated individuals within 5m, confirming that affiliation only partly explained the diffusion of social information. Regarding the rotating-door task, controlling for neophobia improved both asocial and asocial+social learning models for the 1m observation network, but controlling for observers' option preferences only improved the asocial learning model for this network. This indicates that individual option preferences were a good predictor of the order of acquisition when considering no social effect (asocial learning), but not when considering social transmission (social learning). This makes sense when considered alongside the finding that individuals copied the option of the most successful demonstrator observed (not simply the demonstrator preceding them in the diffusion) in order to learn how to solve the task. Accordingly, option preferences represent socially copied options, required for learning this particular task. Therefore, option preferences will indicate that individuals have learned the task, so these preferences are likely to follow the order or time of acquisition in the asocial learning model. However, if we consider social transmission, the order or time of acquisition will be influenced by option preferences only when the demonstrator is the most successful individual observed by the observer in each case. Consequently, considering option preferences in general will not improve the asocial+social learning model in this case.

Observation networks in my study indicated directionality (who observed whom). 'Peering' is defined as 'attentive and sustained close-range watching of the activities of a conspecific' (Schuppli & van Schaik, 2019) and it is predicted by the complexity and difficulty of the procedures observed and the acquisition of novel skills (Whiten, 2019). The prediction of social learning in 1m observation networks for the most difficult task concurs with the idea of 'peering' suggested by Schuppli and colleagues (Schuppli et al., 2016; Schuppli & van Schaik, 2019; Whiten, 2019) and it is a trait worth exploring in depth in future research with Barbary macaques and other species where NBDA is used. Overall, the results of this thesis are consistent with the theory of directed social learning (Coussi-Korbel & Fragaszy, 1995). The social context of the networks that predicted social learning in TG indicated that individuals will acquire information from particular conspecifics. Moreover, these networks in TG had a cliqued social structure, suggesting that interactions and associations were more frequent among those individuals within the clique. Also, the fact that individuals copied the actions when observing task interactions within 1m also suggests that selective social tolerance towards particular subjects influenced social diffusion. Evidence for directed social learning has been found in other primate species classified as despotic (ring-tailed lemurs, *Lemur catta*, Kendal et al., 2010) or intermediate in the despotic-egalitarian spectrum (wild-bearded capuchins, *Sapajus libidinosus*, Coelho, 2015) where social diffusion or learning opportunities seemed to be influenced by the cliqued social structure of the populations studied.

Piaget (1962) defined sensorimotor intelligence as knowledge obtained from sensory perception and motor actions involving objects in the environment. The results presented in this thesis are consistent with previous research on complex object manipulation that indicate that macaque species possess advanced sensorimotor abilities (e.g. searching for hidden objects, pulling, rotating) indicative of sensorimotor intelligence (Antinucci et al., 1982; Gibson, 1986; Antinucci, 1989; Parker, 2015). The data reported here also provides support to the hypothesis that omnivorous extractive foraging patterns are associated with advanced sensorimotor intelligence (Parker & Gibson, 1977; Westergaard & Fragaszy, 1987; Westergaard, 1988; Parker, 2015; Bandini & Tennie, 2020). Even though, sensorimotor intelligence is commonly associated in nonhuman animals with the use of tools in extractive foraging, not all extractive foragers are tool users (Parker, 2015). Animals may use specialized anatomical parts (e.g. heavy beaks, specialized teeth for cracking) or dexterous hands (like Barbary macaques do) for the extraction of food (Gibson, 1986; Parker, 2015). To date, most of the evidence of social learning in macaque species has been reported for the transmission of foraging techniques involving the manufacturing and/or use of tools (Zuberbühler et al., 1996; Drapier & Thierry, 2002; Leca et al., 2007; Watanabe et al., 2007; Gumert et al., 2009; Huffman et al., 2010; Leca et al., 2010; Macellini et al., 2012; Tan et al., 2018). To my knowledge, my study is the first to provide evidence of social diffusion in Barbary macaques, a non-tool-user macaque species. Moreover, my results are consistent with the observation that the transmission of extractive foraging patterns in monkeys are said to occur via social facilitation and observational learning rather than through imitation (Whiten, 2000).

The social disposition to observe others is required for the social transmission of novel motor behaviours, allowing the mapping and reproduction of motor acts (Westergaard & Fragaszy, 1987). Therefore, sensorimotor intelligence is correlated to social learning abilities (Parker, 2015). My results indicate that individuals copied demonstrators' actions in the most difficult task, indicating that specific sensorimotor abilities were required for social transmission in this case. Reader et al. (2011) found that cognitive abilities of nonhuman primates expressed in social learning arose as adaptations for extractive foraging tasks, providing support to the 'extractive foraging hypothesis' proposed by Dunbar (1992) to explain primate intelligence. Dunbar (1992) proposed that primate intelligence could be explained by social ('social brain hypothesis' outlined above) or ecological (e.g. 'extractive foraging hypothesis') adaptations. Although Dunbar (1992) only found evidence for the 'social brain hypothesis'

(Dunbar, 1993, 1998), evidence for the 'extractive foraging hypothesis' has been found in many primate species suggesting that the evolution of primate intelligence was influenced by both social and ecological processes (Reader & Laland, 2002; Parker, 2015; Powell et al, 2017). Similarly, culture has been defined as a source of adaptive behaviour that allows individuals to efficiently acquire information about foraging or mating opportunities by copying others (Laland, 2008). In addition, social learning may have been instrumental in promoting the evolution of social intelligence and cognitive abilities in primates (Whiten & van Schaik, 2007), as well as the transmission of animal behavioural traditions or culture (Kendal, 2008). The results presented in this thesis suggest that Barbary macaques possess all the socio-cognitive and motor skills necessary for cultural transmission of behaviours.

6.5. Limitations of the study and future directions

Implications on primate communication, social dynamics and social learning

Data reported in this thesis must be taken with caution, especially, all the analyses of communication networks (***Chapter 4***) and on social learning (***Chapter 5***) that were conducted in only one group of Barbary macaques. Although the results of Chapters 4 and 5 were mostly consistent with the research literature, repetition of the methods and analyses should be carried out in, at least, a second population of the same species to account for differences due to within-group and between-group variation and validate the results of this thesis. In ***Chapter 3***, where the social learning context was compared between two groups of Barbary macaques, differences in the social structure of affiliative networks between groups were attributed to differences in the group size and the characteristics of the environment. The most striking difference between groups was found for the grooming network, a tension-reducing behaviour that seems to be highly influenced by dominance and other triadic relations (Barrett et al., 1999; Henzi et al., 2003). Further research is necessary to investigate the influence of group size and habitat features in shaping the social learning context of a species' population.

In this thesis, I only studied one large (TG) and one small (BDG) group of Barbary macaques, each living in a different environment: TG lived in a large and highly densely forested area, while BDG lived in a small open field. Although, literature and the evidence provided in this thesis suggest that group differences were probably due to differences in group size and enclosure characteristics, further comparisons with more groups of different sizes and from different environments are necessary to confirm this. These comparisons of multiple groups could also compare evidence of directed and non-specific social learning in small versus large groups living in different environments (e.g. complex versus open habitats, wild versus captivity). Factors other than group size and habitat features can also explain group differences in social dynamics. For instance, Sapolsky & Share (2004) found that the patterns of high affiliation with females and relaxed dominance relations characteristic of unaggressive male baboons that survived after an outbreak of tuberculosis that mostly killed all aggressive males, were adopted by immigrant males and the 'pacific culture' persisted over time within the troop. Investigating the presence of behavioural variants or traditions in future studies may help understand group differences in social dynamics beyond the influence of socio-ecological factors like group size or environmental constraints.

Analyses of data adequacy indicated that the social networks used in this thesis were representative of the population (see ***Appendix C***). However, data were sparse in most cases and caution must be taken in the interpretation of results of these networks. Repetition of the analyses with a bigger sample may confirm the findings reported in my study. In addition, the results reported here indicated that networks combining different affiliative relations are more representative of social relations, and support the idea that communication networks may be used alone or to complement other networks in order to test for social learning using NBDA (Snijders & Naguib, 2017). Relations among individuals in animal societies are typically 'multi-dimensional' since interactions occur across different social contexts (e.g. affiliation, agonism, communication), connecting individuals of different sex, age or rank classes and may vary in space and over time (Croft et al., 2008; Finn et al., 2019). These interdependencies are often not properly captured by single layer networks (Aleta & Moreno, 2018), such as the ones used in this thesis. In recent years, advances have been made in the analysis of multilayer networks that assemble distinct networks by organising them in different levels or layers and coupling them with interlayer connections (Boccaletti et al., 2014; Kivelä et al., 2014; Finn et al., 2019). Consequently, future research on social learning may benefit from the integration of multilayer network analysis in NBDA, using networks representing different affiliative and/or communication relations.

The study of communication networks presented in this thesis provides a more realistic approach (than dyadic studies) to investigate the function of communication signals (McGregor&Peake, 2000; Krause et al., 2014). The use of SNA to study communication allows depicting all the triadic relations that take place within the social environment where communication interactions occur (McGregor & Peake, 2000; McGregor, 2005). My results provide a new layer of understanding of two Barbary macaque vocalizations: aid-recruitment calls and vocal comments. However, some aspects of these calls are still unclear (***Chapter 4***). Further research might help to elucidate whether (i) aid-recruitment calls serve to avoid high aggression, protect individual's social status or both and (ii) the intensity of the conflict predicts the occurrence of aid-recruitment calls (e.g. if aggression is perceived as high) and 'vocal alliances' (e.g. vocal comments produced in agonistic contexts if aggression is perceived as low). In the case of vocal comments produced during infant-handling interactions, detailed studies of the relations between callers and third parties after the production of vocal comments, in the short and long-term, may provide more information on the function of these calls (Brumm et al., 2005). For instance, the observation that callers gain privileged access to the infants in future infant-handling interactions would support the benign intention hypothesis. If callers also strengthen their bonds with infant-handlers in other contexts, or vocal comments occur after conflicts with infant-handlers, support for the collective arousal hypothesis would be provided.

Some information about the underlying social learning processes and strategies that Barbary macaques used in this study was suggested from the approaches used in the NBDA and the analysis of task-option preferences. However, the investigation of social learning processes and social learning strategies was beyond the scope of this thesis. Further experiments are necessary to explore what cognitive mechanisms and learning biases characterise Barbary macaques during the acquisition of social information. In addition, results presented here indicate that social learning is responsible for the spread of novel behaviours in Barbary macaques. Fischer et al. (1998) reported a local variation in the vocalizations of two different populations of Barbary macaques. A group of Barbary macaques in Affenberg Salem (Germany) arising from an original founder population in La Forêt des Singes (France) and separated for 20-30 years was observed to develop novel acoustic variations of shrill-bark vocalizations (i.e. alarm calls produced in response to a dog, Fischer et al., 1998). In playback experiments, individuals provided similar responses to the calls of both groups, even though they responded significantly longer to the calls of the other group, indicating that Barbary macaques could discriminate calls from different origins (Fischer et al., 1998). This finding suggests that Barbary macaques may have population-specific (local) variations (at least, in the vocal domain) that individuals in each group may have innovated and acquired via social learning, and maintained over the years through cultural transmission (i.e. social traditions, Gupta et al., 2015). Accordingly, further study of behavioural traditions and cultural transmission in this primate species could prove fruitful.

Implications in human language evolution

Dunbar (2004) suggested that human language evolved as a form of grooming-at-distance, allowing our species to buffer the costs of living in large social groups. Social intelligence is necessary to navigate the complexities of social life (Byrne & Whiten, 1988; Dunbar, 1998, 2009, 2016). Human language, like social learning, are indicators of social intelligence (Dunbar, 1998; Reader & Laland, 2002; Reader et al., 2011; Parker, 2015; Dunbar, 2016). My study provided evidence of social intelligence in Barbary macaques by the observation of high levels of triadic awareness in communication networks and the significant results of social information diffusion. In a similar way that human language is said to function to establish social bonds and maintain group cohesion (Dunbar, 2004), communication networks may operate likewise, since they are, usually, predicted by affiliative networks (Micheletta, 2012; Kulahci et al., 2015; Roberts & Roberts, 2019a,b, see ***Chapter 4***). For instance, alliances established via grooming may be tested during conflicts where agonistic support is requested (e.g. by aid-recruitment calls or 'vocal alliances'). Similarly, vocal comments during infant-handling interactions, whether they signal benign intentions and/or collective arousal, seem to help to maintain or strengthen social bonds (Whitham et al., 2007). In both human and nonhuman primates (as suggested by my study), communication interactions seem to represent opportunities to acquire or exchange social information about the natural or social environment, such as learning about a new food source or about changes in social dynamics and triadic relations (Dunbar, 2004; Wheeler et al., 2011). Accordingly, this thesis indicates that human and nonhuman primate communication share similarities in terms of function and cognition.

Dunbar (2004) proposed that human language evolved as a substitute to grooming when social groups became large enough so that grooming was insufficient to maintain group cohesion. However, the coevolution of social and communication complexity (McComb & Semple, 2005; Freeberg et al., 2012; Gustison et al., 2012) suggests that primate communication may have been useful to complement the social bonding function of grooming in nonhuman primate species. It is likely that once human language evolved, it became the main social bonding mechanism in our species, with close contact (grooming-like) gestures (e.g. rubbing, stroking, petting, patting) acquiring a complementary role as social-bonding behaviours along with other forms of language (Dunbar, 2004). In addition, social complexity also coevolved with social learning (Street et al., 2017), suggesting a co-evolution of primate sociality, communication and social/cultural transmission. The parallelism between social learning and communication evolution theories suggests a constant feedback between the selective pressures shaping cues into active communication signals and the selective pressures acting on inadvertent forms of social learning for the evolution of active or more efficient forms of social transmission like teaching (Hoppitt et al., 2008; Schaefer & Ruxton, 2012, see ***Chapter 1***). This framework supports the hypothesis of an evolutionary continuity between human and nonhuman primate communication (Arbib et al., 2008; Fedurek & Slocombe, 2011; Wheeler et al., 2011; Liebal et al., 2013; Moore, 2016). This hypothesis also highlights that social learning is key in the acquisition of some communication signals during ontogeny in both human and nonhuman primate species (Arbib et al., 2008; Wheeler et al., 2011; Liebal et al., 2013). Those that argue against this hypothesis suggest that human language evolved as an exaptation of increased social intelligence (Reboul, 2015; Scott-Phillips, 2015). However, the same explanation has been proposed for the evolution of social learning (Leadbeater, 2015) and, yet, it is present in many animal species, including nonhuman primates

(Hoppitt & Laland, 2008; Kendal et al., 2010; van de Waal et al., 2010; Schnoell & Fitchell, 2012; Claidière et al., 2013; Hobaiter et al., 2014; Coelho, 2015; Kendal et al., 2015; Canteloup et al., 2020; van Leeuwen et al., 2020).

The multicausal theory and the socio-cognitive niche hypothesis for the evolution of human language provide a holistic conceptual framework for the continuity between primate communication systems and human language. According to this framework, genetic and socio-ecological factors changed the lifestyle of primate ancestors influencing the development of a series of cognitive adaptations that resulted in the evolution of human language and related socio-cognitive mechanisms (Pinker, 2010; Whiten & Erdal, 2012; Prieur et al., 2020). This enrichment and diversification of cognitive abilities responded to an increase in the size, complexity and dynamics of primate societies that, at the same time, were also influenced by the development of these new socio-cognitive skills (Prieur et al., 2020). Socio-cognitive elements such as cooperation, egalitarianism, theory of mind, culture or language, which are highly developed in humans, were the result of this evolutionary process, in which one element influenced and was influenced by the evolution of the others (Whiten & Erdal, 2012). Indeed, all these socio-cognitive skills are so intertwined in their evolution and the underlying mechanisms that it is possible that they may represent different levels of the same trait (Whiten & Erdal, 2012; Gontier, 2013). Accordingly, we may understand language evolution within the evolution of cooperation, mindreading, resource sharing, cultural transmission or other socio-cognitive mechanisms (e.g. meta-cognitive abilities). This theoretical framework links the intercorrelations between sociality, communication and social learning highlighted in the previous paragraphs of this section.

My results provide a few insights within the multicausal/socio-cognitive framework for the evolution of human language condensed above. For instance, language is used in hunting-gathering human societies to coordinate and plan physical attacks on prey as well as to make joint decisions about foraging strategies and locations (Prieur et al., 2020). These plans and decisions require knowledge about each individual (e.g. hunting abilities, social and health status, prestige, reputation) and their socio-ecological context (e.g. demographics, outcomes of previous hunting and gathering activities, availability of resources), all information that is socially transmitted during social gatherigs (Prieur et al., 2020). Therefore, these human populations use triadic awareness, social learning and assessments of the social and ecological environment to make cooperative decisions about their hunting and gathering plans and strategies. Chimpanzees, for instance, also use communication signals (vocalizations, gaze and movements) to collaborate when it is necessary to obtain food in the wild (e.g. hunting) or in captivity (e.g. experimental setups), to initiate and coordinate border patrols or to form alliances and coalitions to dominate others or provide support in conflicts (Boesch & Boesch, 1989; Boesch, 1994; Mitani & Watts, 2005; Mitani, 2009). The multicausal/socio-cognitive framework states that language was necessary for the evolution of cooperation and vice versa (Pinker, 2010; Whiten & Erdal, 2012; Prieur et al., 2020). The outcomes of this thesis indicate that triadic awareness and social transmission of information that influences foraging decisions are also present in Barbary macaques. Moreover, forms of cooperation such as agonistic support, which result from the production of communication signals (aid-recruitment calls and 'vocal alliances'), also occur in Barbary macaques.

Egalitarian distribution of resources is common in humans and it is a function of interpersonal negotiations. In fact, egalitarianism and cooperation can be considered mutually reinforcing adaptations since egalitarian sharing is the rewarded outcome of cooperative efforts, with language acting as a facilitator of these interpersonal exchanges (Prieur et al., 2020). Again, egalitarianism would have been another socio-cognitive element crucial in the evolution of human language (Prieur et al., 2020). Egalitarianism has also been observed in other primates. For instance, chimpanzees are observed directly handing pieces of hunted prey to individuals whom use communication signals to beg for it. These sharing episodes reflect social ties since they are frequently observed between males who are allies, preferred male and female sexual partners, and between mothers and their offspring (Boesch & Boesch, 1989; Boesch, 1994; Melis et al., 2006). The high levels of social tolerance observed in this study of macaques, especially during highly competitive contexts such as the presentation of foraging tasks (i.e. low levels of monopolisation, individuals of all sex, age and rank classes allowed to interact with the task), indicate a tendency of Barbary macaques towards egalitarianism. Moreover, this social tolerance near the task was also influenced by social bonds or alliances (e.g. affiliative and communication networks mirroring affilative bonds predicted who observed whom during task interactions) and regulated with communication signals (e.g. teeth-chattering to show submission when approaching the task, facial threats to dissuade others from approaching the task; *personal observation*).

The coevolution of cooperation and egalitarianism allows for the free sharing of social information (via language) that is crucial for cultural transmission, innovation and cultural evolution which, at the same time, allow for the development of technology and generalized ideas that support cooperation and egalitarianism (Prieur et al., 2020). In this study, social tolerance based on social alliances or bonds and regulated through communication signals (i.e. facial threats, signals of submission of affiliation such as teeth-chattering; *personal observation*) allowed the acquisition of social information during task introductions in Barbary macaques. Moreover, Barbary macaques made use of different social learning strategies and responded with different social learning processes depending on the characteristics of the novel task (e.g. acquisition difficulty, familiarity with the actions) they faced. This suggests that Barbary macaques possess traits necessary for cultural transmission and cultural evolution.

All the evidence on cooperation-related skills, social biases towards egalitarianism and cultural transmission properties provided by my results, indicate that Barbary macaques apparently navigate in a socio-cognitive niche where they seem to evaluate and extract some socio-ecological information (e.g. awareness of triadic relations, social information of novel traits) that helps them achive proximate goals (e.g. recruitment of support, social tolerance) that correlate with fitness (e.g. avoidance of aggression, access to resources). Therefore, my results indicate that most of the socio-cognitive abilities that prompted the evolution of human language may already be present in a non-ape primate species. According to the evolutionary hypothesis, all these aspects of social cognition, seemingly present in Barbary macaques, may have added selective pressures on primate societies, promoting the development of these and new socio-cognitive abilities and their mutual feedback up to the emergence of all the different cognitive mechanisms associated to the origin of human language (Pinker, 2010; Whiten & Erdal, 2012; Prieur et al., 2020). It is likely that all or some of these social skills of Barbary macaques can be explained by factors other than cognition. For instance, Butovskaya (2020) found that post-conflict affiliation behaviours such as consolation or appeasement of aggressors and bystanders, which have been traditionally interpreted as an expression of cognitive empathy, may develop without any increase in cognition and likely emerged in Tonkean macaques (*Macaca tonkeana*) as side of effect of spatial distribution. Although evidence is still controversial, recent research based on primate comparative studies (including humans, great apes, American and Afro-Eurasian monkeys) points to a continuity in the evolution of social cognition between human and non-human primates that may have its origins in the common ancestor between apes and humans or, even, before that, in a non-ape ancestor that evolved within a socio-cognitive niche (Isler & van Schaik, 2014; Whiten, 2016; Killin, 2017; Whiten & van de Waal, 2017; Dein, 2019; Butovskaya, 2020; Prieur et al., 2020).

In this thesis, I followed a holistic approach linking social dynamics, communication and social learning that might be useful to fill the gaps of evolutionary theories in favour of a continuity between human language and primate communication systems. Further studies using the methods presented in this thesis, to investigate specific questions regarding human language evolution, may be fruitful. This is especially so if more realistic multimodal-multifactorial approaches (in comparison with unimodal approaches or the one used in this thesis) were used for the construction of social/communication networks (Partan & Marler, 1999, 2005; Slocombe et al., 2011; Semple & Higham, 2013; Waller et al., 2013; Genty et al., 2014; Clay et al., 2016).

Implications in primate conservation

This thesis may lay down the foundations of further studies on conservation since social affiliation, communication and learning in non-human primates may become a useful tool in determining well-being, group stability and the potential effects of environmental threats such as habitat fragmentation or tourism (McCowan et al., 2007; Kendal, 2008; Kendal et al., 2010; Reader & Biro, 2010; Maréchal et al., 2011; Sueur et al., 2011). Social network analysis (SNA) allows exploration and simulation of the removal of certain individuals to determine the robustness of social and communication networks and which individuals are keystone individuals in the maintenance of group stability (Kasper & Voelkl, 2009). Wild and captive populations may experience increased within-group food competition and aggression due to an increase in group size or environmental constraints (e.g. human barriers like agricultural expansion or habitat fragmentation, Sueur et al., 2011). Managers of captive or wild populations may use information provided by social network analyses to manipulate group composition and matriline configuration of social groups (e.g. by splitting captive groups or circumventing the obstacles that hinder natural group fission) promoting group cohesion and stability, and reducing the levels of aggression, morbidity and mortality (McCowan et al., 2007; Sueur et al., 2011). Also, studying innovation and social learning in managed populations may facilitate identification of those individuals that may have successful responses to environmental changes, a key conservation issue in habitats facing the threats of anthropogenic changes and invasive species (Clavero et al., 2009). Similarly, knowledge on how captive individuals process social information are relevant to improve husbandry procedures (Bethell et al., 2012).

Understanding interactions between group members in different contexts (e.g. agonism, communication, social learning) can be used in conservation and reintroduction programs to (i) train individuals in foraging techniques or survival skills before reintroduction, (ii) remove problem individuals from the group (i.e. animals that have a negative impact on group cohesion or welfare, or that are highly likely to spread conflict-inducing behaviours) and (iii) select which animals can be relocated to other captive populations (e.g. transferred between zoos or sanctuaries) or reintroduced to the wild without affecting the group stability of the original group (McCowan et al., 2008; Clark, 2011; Sueur et al., 2011). In addition, understanding the environmental and social factors involved in communication may help to elucidate other previously unidentified effects of habitat fragmentation, as well as identifying the most knowledgeable individuals that can provide crucial social and environmental information to other conspecifics, improving the fitness of wild or reintroduced populations (Sueur et al., 2011). Similarly, social network analysis and the study of within-group social diffusion may provide relevant information regarding disease transmission, allowing managers to isolate or treat those individuals that contribute the most in the transmission of the disease (Kendal, 2008; Sueur et al., 2011). Finally, understanding of social learning may influence conservation priorities by increasing awareness of the importance to protect, not only genetic, but also cultural animal diversity (Whitehead, 2010; Gruber et al. 2019).

The methods used in this thesis provide a wide set of tools that managers and conservationists can use to make decisions that improve their conservation and reintroduction programs. Moreover, the results presented in this thesis provide evidence of the social complexity and communication and cognitive abilities of Barbary macaques, adding to the amount of data that blurs the line between humans and other nonhuman primate species. Because it is politicians and managers who make conservation decisions, scientists are bound to rely on public awareness through diffusion of their work to contribute in the protection of animal species and their habitats (Whitehead, 2010). The conclusions drawn from this thesis stress the similarities between humans and nonhuman animals serving to change people's perceptions of species and increase their willingness to protect them.

Since 2008, Barbary macaques have been considered 'Endangered' by the IUCN Red List (Wallis et al., 2020). The destruction and degradation of their habitats due to the (i) domestic and industrial consumption of wood, (ii) use of fire, (iii) land clearing for agriculture and (iv) over-grazing by livestock is causing a rapid decrease of wild Barbary macaque populations. In addition, the expansion of human populations has generated conflicts between local people and Barbary macaques that look for other sources of food as their habitat is constrained and fragmented by human activities. The shooting of Barbary macaques by farmers as a result of crop raiding is seen as an ongoing threat to the future of this species. Finally, the illegal pet trade and wildlife trafficking is also depleting the populations of Barbary macaques in Morocco and Algeria (Wallis et al., 2020). Overall, in the last 24 years, wild populations of Barbary macaques have declined >50%. It is estimated that less than 7,000 individuals remain in the wild, apart from a population in Gibraltar (~300 individuals) that is not considered threatened (Mittermeier et al., 2013; Wallis et al., 2020).

My findings can be compared to the wild (as the groups were free-ranging and TG in a particularly ecologically valid context), but also to captive welfare of Barbary macaque populations. Although requiring further replication, group differences in social dynamics and social transmission, attributed to differences in group size, habitat constraints, demographics or cultural variants, may help with management decisions of wild and captive populations. For instance, my findings suggest that large groups inhabiting densely forested areas like TG, are likely to have a more cliqued social structure and, therefore, fewer agonistic encounters than small groups living in open habitats like BDG. Accordingly, deforestation and habitat fragmentation may negatively impact the stability and survival of wild populations as agonism may increase. Likewise, the complexity of captive environments may help maintain group cohesion, stability and welfare of captive Barbary macaques and better prepare individuals for any future reintroduction attempts. However, the higher group cohesion and homogeneity of social relation strengths in BDG compared to TG indicate that social information may be transmitted faster within small and cohesive populations like BDG than within large and cliqued societies like TG. This is relevant to pre-release phases of reintroduction programs (Baker, 2002; Beck et al., 2007) where individuals learn about their wild environment (e.g. edible foods, response to predators, etc.) from previously introduced conspecifics or through introductions of learning opportunities by caregivers.

My analysis of flow betweenness and social learning indicated that the individuals that most contribute to social diffusion depend on the social context (e.g. level of social tolerance required, whether detailed information needs to be transmitted or not, etc.) and the type of social relations they have with each other. Therefore, it is crucial to obtain this sort of information in order to choose which individuals may be more successful (in learning new behaviours and enabling their transmission to conspecifics) in training phases within conservation programs, or which individuals need to be removed to control the spread of diseases in captive populations. Finally, my study provides evidence of social intelligence in Barbary macaques in many different contexts (i.e. affiliative and agonistic encounters, communication interactions, social learning of tasks of different difficulty) that stress the similarities between humans and this species. Therefore, the findings of this thesis have the potential to inspire the publics’ sympathy for the plight of Barbary macaques and increase their contribution to the conservation of this unique primate species.

Appendices

APPENDIX A – Dominance hierarchy and ranking

Dominance ranks of Blair Drummond group (BDG)

There are different approaches and statistical methods to determine dominance ranks. After reviewing research literature, Funkhauser et al. (2018) defined four main behavioural measures or contexts that are generally used as approaches to estimate dominance ranks: a) agonistic competitions (win/lose fights), b) formal dominance or lack of aggressiveness (flee-upon-approach, submissive or displacement behaviours), c) priority access to resources, d) privileged roles. Dominance relationships based on privileged roles can be measured by the directionality or asymmetry of dyadic relations related to access to valuable commodities, such as the exchange of grooming. Priority access to resources as a mean to measure dominance can only be measured in specific situations, such as in experimental conditions like foraging task introductions (Funkhauser et al., 2018). In this thesis, I aimed to determine the influence of dominance ranks in grooming and other socio-positive networks and in networks based on social learning contexts where individuals compete to access a resource (i.e. the foraging task). To avoid biased measures of dominance, I calculated social ranks for BDG in contexts that do not depict privileged roles or priority access to resources. Consequently, dominance ranks were measured using agonistic competitions and formal dominance (Funkhauser et al., 2018).

Agonistic competitions are referred as dyadic interactions where one subject (the winner) directs an agonistic behaviour (e.g. hit, slap, bite, threat) towards another subject (the loser) who displays a submissive behaviour (e.g. flee, silent-bared teeth display, submissive grin, see ***Table 2.3*** in ***Chapter 2***). These agonistic encounters are characterized by the asymmetry of the outcome (i.e. win or lose, Drews, 1993). On the other hand, lack of aggressiveness/agonism refers to those instances where conflicts are resolved using non-agonistic assessments (i.e. submissive behaviour) and escalated fights do not take place (Drews, 1993). In these contexts, it is assumed that one subject (the subordinate) has learned from previous encounters with a conspecific or recognizes some dominance features on its opponent that bias its behaviour towards fleeing-upon-approach responses or submission/yielding when receiving threats (Vessey, 1981). Therefore, the subordinate recognizes its inferior position, so the dominance relationship is readily accepted instead of agonistically challenged. This dominance context is termed ‘formal dominance’ (Funkhauser et al., 2018). Data on agonistic encounters was collected using behavioural measures based on agonistic competitions and formal dominance (see ***Table 2.3*** in ***Chapter 2***).

Dominance ranks can be calculated using different statistical methods. Here, I followed the recommendations of Funkhauser et al. (2018) for calculating dominance ranks using different approaches, correlate the scores obtained across methods and, if there are no significant differences, calculate median ranks across all these ranking procedures, which minimizes errors and takes conservative interpretations of dominance hierarchy with minimal data.

Traditionally, there are two main types of methods to measure dominance ranks. The first one uses a numerical criterion that is maximized or minimized in the re-organization of a data matrix of dominance relations (i.e. dominance matrix). The second type calculates the individual overall success and ranks the subjects in order according to this measure (de Vries & Appleby, 2000). The **I&SI method** belongs to the first type and is one of the most commonly used methods to rank subjects in a hierarchy. It is a non-parametric method since it makes no assumptions on the probability distribution of wins and losses, and serves to order the subjects according to a dominance rank after linearity has been confirmed (i.e. linearity of the hierarchy order must be statistically significant). It was developed by de Vries (1998) and later improved by Schmid & de Vries (2013). For my analyses, I used the improved I&SI method (Schmid & de Vries, 2013) and the improved Landau h' test of linearity (de Vries, 1995). In combination with the I&SI method, I also measured **David's scores** (David, 1987) which have been widely used since Gammell et al. (2003) recommended this index to measure dominance ranks. David's scores belong to the second type of methods to measure dominance ranks and its algorithm has been improved several times (de Vries, 1998; Gammell et al., 2003; de Vries et al., 2006). Moreover, normalized David's scores are used to estimate steepness, a complementary measure to linearity that estimates the degree to which individuals differ from each other in winning dominance encounters (de Vries et al., 2006). I used the improved algorithm to estimate David's scores, the hierarchy steepness and the randomization test to determine the significance of steepness (a similar procedure used by de Vries, 1995, to find the p-values for h'). Both I&SI method and David's scores assume linearity of dominance ranks (Gammell et al., 2003; Schmid & de Vries, 2013).

Following Funkhauser et al. (2018) guidelines, I also measured dominance ranks using three other methods: a) **Elo-ratings**, a non-matrix based technique to determine dominance ranks assuming linearity (Albers & de Vries, 2000), b) **ADAGIO** (Douglas et al., 2017) and **PERC** (Fushing et al., 2011), two different methods that analyse dominance without making structural assumptions of the hierarchy (i.e. network-based methods). Elo-ratings also provides a stability measure of the hierarchy that calculates the ratio of rank changes per individual over a given period of time (large variation = low stability with score closer to 0, no/small variation in individuals' ranks = high stability with score closer to 1). The stability characteristic is useful to assess the consistency of the hierarchy, especially when h' results in a statistically significant linearity but of low degree. More information about hierarchy methods used in this thesis can be found in ***Table A.1*** and in Funkhauser et al. (2018). Finally, I used Spearman rank correlations with Benjamini-Hochberg corrections to determine the reliability across rankings provided by the different methods.

Table A.1. Description of the methods and calculations used to determine the dominance hierarchies of BDG and TG.

I&SI method	
Description	The method is based in the re-organization of individuals assuming a linear hierarchy by minimizing the number of inconsistencies (I) and the total strength of inconsistencies (SI) in a matrix of dominance relations (de Vries, 1995, 1998; Schmid & de Vries, 2013).
Calculations	I used DomiCalc, which is a series of Excel macros (the script is the same applied in R by Leiva et al., 2010 using the ISI.method function). In contrast to the R function, DomiCalc provides all the alternative optimal ranking solutions and uses the differences between numbers of dominations and subordinations (Dom-Sub) and the proportion of dominations (PD) in the last step of the procedure to break ties and decide the final ranking order (optimization of the method, Schmid & de Vries, 2013). Linearity was measured using the improved Landau h' test with the linear.hierarchy.test function in R.
David's scores	
Description	The method derives a dominance index based on the overall success of each individual and the relative strenght of its opponents. It calculates the proportion of wins over losses in agonsitic encounters relative to the total number of observed interactions and corrected for chance occurrences of observed outcomes (David, 1987; Gammell et al., 2013).
Calculations	I used the R function steeptest (package 'steepness') which calculates steepness and derives David's scores using the improved algorithm with the correction of chance probabilities suggested by Gammell et al. (2003). I estimated normalized and non-normalized David's scores. Steepness of a dominance hierarchy refers to the size of the absolute differences between adjacently ranked individuals and their overall success in winning dominance encounters. Steepness is the absolute slope of the straight line fitted to the normalized David's scores plotted against individual ranks (de Vries, 2006).
Elo-ratings	
Description	The method provides sequential estimations of individual dominance strengths based on the actual sequence of dominance interactions. It is based on the assumption that the chance of individual A winning B is a function of the difference in current ratings of the two contestants. Therefore, the method takes into account the sequence of interactions and updates the rating of each individual after each contest until the last contest observed to provide the final ranking scores (Albers & de Vries, 2000; de Vries, 2009).

Calculations	I use the R package 'EloOptimized' to calculate Elo-ratings using the traditional method (eloratingfixed function) and the optimized method (eloratingopt function). The traditional method considers the parameter k (which determines the number of rating points that an individual wins or loses after each encounter) as constant and assigns the same initial Elo-scores to all the individuals (1000 by default). The optimized method uses the maximum likelihood approach to calculate the values of k that better fit the data and the initial Elo-ratings (using AIC measures of model fit). Rank stability was measured using the ratio of rank changes per individuals present over a given time period (Neumann et al., 2010). The stability index is formally expressed as: $S = \frac{\sum_{I=1}^{d}(C_i \; x \; w_i)}{\sum_{i=1}^{d} N_i}$ where C_i is the sum of absolute differences between rankings of two consecutive days, w_i is a weighting factor determined as the standardized Elo-rating of the highest-ranking individual involved in a rank change, and N_i is the number of individuals present on both days.
PERC (Percolation-conductance)	
Description	The method is a network-based ranking model. It attempts to determine dominance ranks of individuals in a group under the assumption that the hierarchy structure may not be linear, so dominance relations are not completely transitive, meaning that if A dominates B and B dominates C, A does not necessarily dominates C (Fushing et al., 2011). The method follows two main steps. First, a series of matrices are calculated based on pairwise interactions plus transitive dominance inferred from interactions with common third-parties in order to estimate dominance potential probabilities. Then, individuals are assigned a rank according to the final matrix calculated in step one and a simulated annealing algorithm (see Fushing et al., 2011) is used to minimize the number of inconsistencies to provide a final rank (confident bounds of individual ranks are derived).
Calculations	I used the R package 'Perc' and the guidelines developed by **Fushing & McCowan labs**. Calculations were based on a matrix that combines information from direct win/loss interactions with information from indirect pathways between individuals to calculate a matrix of probabilities where each row individual outranks the column individual. The analysis provides heat maps of the individual ranks to identify non-linear dominance structures and takes into account the uncertainty of the data due to potential intransitivities. The annealing algorithm seeks to minimize the costs of potential inconsistencies due to these intransitivities by re-ordering the matrix (with values of dominant subjects above the diagonal and values of subordinate subjects below the diagonal) so that the total sum of the probability values below the diagonal is reduced to the maximum (Fushing et al., 2011).

ADAGIO (Approach for Dominance Assessment in Gregarious species)	
Description	This method represents dominance hierarchies using directed acyclic graphs (DAG). A DAG is a network free of cycles (i.e. there is no path from one node back again to the same node). This method does not assume linearity (but it can detect it) and assumes there are no circular triads and that dominance relations are irreflexive (no individual is dominant over itself), transitive (if A>B and B>C, then A>C) and asymmetric (if A>B, B cannot be > A). ADAGIO uses dyadic dominance relationships to extract a dominance hierarchy in the form of a DAG for a given dominance network. If the network is not a DAG, ADAGIO transforms the network into a DAG by detecting the largest strongly connected components (cycles) and extracting the weakest link of this cycle. ADAGIO predicts linear and non-linear hierarchies much better than other methods. Also, observational zeros do not influence the performance of the analysis, and it is so versatile that it can be used for large groups where most relationships are unknown and for small (N < 6) sample sizes (Douglas et al., 2017).
Calculations	I used the **Adagiov1.1 package (ADAGIO Release 1.1)** provided by Douglas et al. (2017). This package uses a script performed in the Windows command line and Java 1.8. I performed the four versions of the analysis: a) no pre-processing + bottom-up approach, b) no pre-processing + top-down approach, c) pre-processing + bottom-up approach and d) pre-processing + top-down approach. Pre-processing allows breaking symmetry at the dyadic level: for a given dominance, the weight (strength) of the edge between two individuals, where one appears to be dominant to the other, is set to the difference in the number of interactions won by the dominant one, and the reciprocal edge is removed. In the case of a tie, both edges are not considered in the analysis. Top-down and bottom-up approaches serve to compute ranks. The top-down approach sets the ranks of all the roots of the network at 1 (roots = individuals that give but do not receive edges), and the ranks of all the other subjects depend on how many edges they receive +1. The bottom-up approach is the converse method and it starts with leaves (nodes that are not the source of any edge). Different measures are used to decide which ADAGIO version provides better results: a) relative error (proportion of number of interactions removed after pre-processing), b) weight (strength of the relation) and edges removed (proportion of weight or edges of dominance relations removed, respectively, due to pre-processing and DAG conversion), c) Directional Consistency Index (DCI) as estimated by van Hooff & Wensing (1987) which reflects the frequency with which the behaviour occurred in its more frequent direction relative to the total number of times the behaviour occurred.

In total, 838 agonistic encounters were recorded in BDG. Dominance ranks were calculated for all individuals in the group excluding infants. After removing infants from the analysis and including observations of formal submission, 696 agonistic interactions were used for hierarchy analyses in BDG.

Linearity was low but significant (h' = 0.419, p<0.001) indicating dominance relations in BDG follow a linear or near-linear structure. Steepness was also low but significant (stp = 0.327, p<0.001) indicating that the size of the absolute differences between adjacently ranked individuals in their overall success in winning dominance encounters is small but significant (***Figure A.1***). A species with a hierarchy that is weakly linear and shallow is termed as egalitarian, while a species with a hierarchy that is strongly linear and steep is termed as despotic (van Schaik, 1989). Low but significant linearity and steepness is typical of species classified as intermediate in the despotic-egalitarian spectrum, such it is the case of Barbary macaques (van Schaik, 1989; Thierry, 2007).

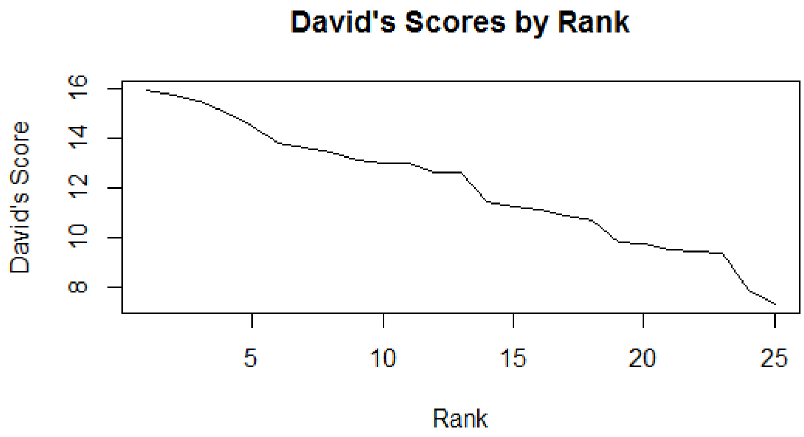


Figure A.1. Normalized David's scores plotted against individual ranks for BDG outside task introductions. The continuous line represents steepeness of dominance relations.

Eight similar alternative optimal solutions were obtained in the I&SI method. The final rank provided by the I&SI method is the median of the ranks of these eight optimal outcomes (Funkhauser et al., 2018). Normalized David's scores were only used to calculate steepness. Non-normalized David's scores were used for Spearman correlations to test reliability among ranking methods. Regarding Elo-ratings, only scores obtained for the optimized function were considered. The traditional function presented several issues (see ***Table A.1***). First, the problem with assigning a random and constant *k* is that it might affect how much a single win or loss influences the outcome. Small values of *k* assume that a single loss or win are not predictive of future outcomes, while large values of *k* tend to have a greater impact on the Elo-scores (Franz et al., 2015). Therefore, the appropriate value of *k* is unknown with the traditional function. Second, assigning the same initial Elo-score to all subjects might be problematic because long periods of observations are required for this value to be corrected.

Therefore, the first Elo-scores calculated for the first interactions might not be representative of the individual ranks until a certain amount of observations have been analysed, a greater issue when we are dealing with sparse datasets as the ones used in this thesis (Foerster et al., 2016). The optimized method solves all these issues using maximum likelihood to calculate *k* and a burn-in period of 100 interactions (a default measure that assumes a period of time at which the initial Elo-scores would have changed and become representative of the individual ranks). This burn-in period is also relevant to measure stability since several observations are needed to have a representative sample of dominance relations. Accordingly, stability was measured from interaction 100 until the end of the study (a total of 130 days). No rank changes were observed during this time period (S = 0, see ***Table A.1***), indicating a stable hierarchy with identical rankings on each day. The Elo-rating function also provides results for the Jenks Natural Breaks Classification, a method that determines the best arrangement of values into different classes by reducing the variance of values within classes and maximizing this variance between classes (Jenks, 1967). This method allowed classifying individuals in three main ranking classes: high, middle and low.

Results of the PERC method showed 657 transitive triangles, 2 intransitive triangles and a transitivity measure of 0.99, indicating that dominance relations followed a linear (transitive) structure (hierarchy). Due to the high transitivity of the data, the algorithm provided the same rank order with the exact same value of the costs of inconsistencies in all permutations (cost = 4.351644), indicating that only one optimal solution for the rank order was possible for the PERC method. Heat maps in PERC indicate measures of dominance probability between dyads (ranging from 0 to 1, with 1 indicating the individual in the row always outranks the individual in the column). The heat map (***Figure A.2***) showed that most of the dominance relationships were well defined (certain) and the hierarchy was clearly and strongly transitive (linear). The heat map probabilities were transformed into measures of dominance certainty between dyads (values ranging between 0.5 and 1, with 0.5 indicating total uncertainty and 1 indicating total certainty). I considered values <0.70 as uncertain (Fushing et al., 2011), resulting in a total of 16 uncertain relationships of 300 possible dyads (5.3% of the data) and confirming that most dominance relations were well-defined.

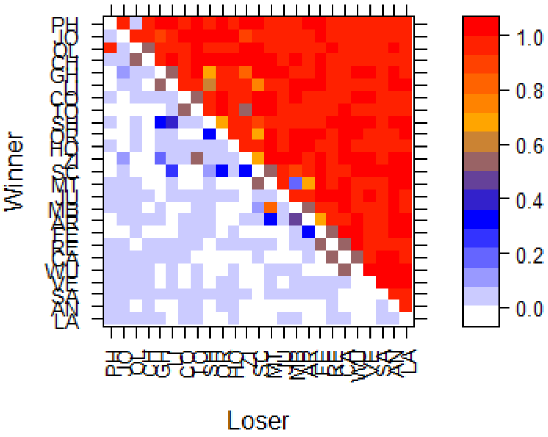


Figure A.2. Heat map of dominance probabilities between winners and losers in BDG outside task introductions. Individuals in the diagonal with values closer to 0.5 indicate uncertain relationships.

Regarding ADAGIO, pre-processed versions resulted in lower values (than no pre-processed versions) of relative error (pre-processed: 0.047, no pre-processed: 0.113), weight removed (pre-processed: 0.006, no pre-processed: 0.065) and edges removed (pre-processed: 0.010, no pre-processed: 0.192). This suggests that pre-processed versions lost less information and, therefore, were more powerful than non-processed versions (Douglas et al., 2017). The DCI (DCI=0.963) indicated that data mostly contained unidirectional relations, meaning that in most cases, the dominance relationships between individuals were well-defined and there were very few cases of tied dominance relations. Douglas et al. (2017) demonstrated that bottom-up approaches performed best in simulations, but they also highlighted that ADAGIO asymptotically performs best with the top-down rank approach. Both bottom-up and top-down approaches provided similar results, so I estimated the median of ranks between both results for further analyses, following Funkhauser et al. (2018) recommendations.

Results of all ranking methods are found in ***Table A.2***. Correlations of ranks across ranking methods were calculated using the R function cor.test (which is adapted to handle ties in the data). All correlations resulted in high and significant coefficients (***Table A.3***), indicating that all methods provided highly similar results and differences in individual ranks were not significant. Since all methods were equally reliable, a median of ranks across methods was calculated and used in the thesis as a measure of ordinal social ranks. Jenks Natural Breaks Classification was used as a measure of categorical social ranks.

Table A.2. Dominance ranks of BDG obtained for all ranking methods outside task introductions.

Individuals	I&SI median	DS rank	Elo ranks	PERC rank	ADAGIO median rank	Median ranks all methods	Jenks Natural Breaks Classification
JO	1.5	1	2	2	2	2	High
PH	2	2	1	1	1	1	High
OL	2.5	5	3	3	3	3	High
CH	4	3	4	4	3	4	High
GH	5	4	5	5	4	5	High
CO	6	7	7	7	5	7	High
LI	7	6	6	6	4	6	High
SH	8	8	9	9	5	8	High
TO	9	10	8	8	5	8	High
OR	10	9	11	10	6	10	Mid
HO	11	11	10	11	7	11	Mid
SC	12	13	13	13	7	13	Mid
ZI	13	12	12	12	8	12	Mid
JU	14.5	14	16	15	11	14	Mid
MT	15	15	15	14	10	15	Mid
MB	15.5	18	14	16	9	16	Mid
AR	17	16	17	17	10	17	Mid
FE	18	21	18	18	12	18	Low
RE	19.5	17	19	19	12	19	Low
CA	20	22	20	20	13	20	Low
WU	20.5	19	21	21	13	21	Low
VE	22	20	22	22	14	22	Low
SA	23	23	23	23	15	23	Low
AN	24	25	24	24	16	24	Low
LA	25	24	25	25	17	25	Low

DS rank: Rank obtained from David's scores. Elo ranks: Rank obtained from Elo-ratings. Median ranks all methods: Median of ranks calculated across all ranking methods.

Table A.3. Correlations of dominance ranks of BDG between ranking methods outside task introductions.

Correlations	**Spearman's rho**
I&SI - David's scores	rho = 0.9831 p = < 0.001
I&SI - Elo-ratings	rho = 0.9931 p = < 0.001
David's scores - Elo-ratings	rho = 0.9746 p = < 0.001
PERC - I&SI	rho = 0.9961 p = < 0.001
PERC - David's scores	rho = 0.9815 p = < 0.001
PERC - Elo-ratings	rho = 0.9969 p = < 0.001
ADAGIO - I&SI	rho = 0.9896 p = < 0.001
ADAGIO - David's scores	rho = 0.9765 p = < 0.001
ADAGIO - Elo-ratings	rho = 0.9946 p = < 0.001
ADAGIO - PERC	rho = 0.9923 p = < 0.001

Dominance ranks during task introduction contexts in BDG:

Due to the big size of the Trentham Group (N = 56) and the characteristics of the environment that hindered field observations of dyadic interactions (e.g. natural barriers that limit view range), data on agonistic interactions in this group was incomplete and insufficient to draw a clear social hierarchy (i.e.

most dominance relations were unknown). Therefore, researchers (CE and MO) completed this data with observations of agonistic displays collected during task introductions. As stated before, the inclusion of observations collected in task contexts may lead to biased dominance ranks in TG that compromise the use of these measures in the analyses conducted in this thesis. To test that is not the case, I repeated all the hierarchy analyses in BDG using, this time, agonistic data collected only in task introduction contexts in this group.

I collected the following data on dominance encounters during task introduction times:

- Individuals displacing conspecifics from the task.
- Individuals shooing away other conspecifics from the task.
- Individuals that reacted with a submissive behaviour by the presence or actions of other individuals showing no apparent agonism.

All these cases account for instances of priority access to a resource (i.e. the foraging task): the winner of a displacement, the actor of shooing behaviours and the receiver of submissive behaviours with no apparent agonism can be deemed as individuals that have priority access to the task over the loser of these encounters.

A total of 464 agonistic encounters were obtained during task introductions in BDG, which resulted in a total of 269 encounters after removing infants. I also removed those cases where aggression was not responded by the receiver (the receiver ignores the actor of the aggression). Moreover, since the task is a valuable resource, most individuals will not dare, or have the chance, to approach or manipulate the task, while others will tend to monopolize it using agonistic displays. This suggests that many of the possible agonistic interactions between dyads will not take place. Confirmation of this was obtained when data showed that only 26% of all possible dyadic interactions were observed in agonisitic displays during task introductions (null dyads = 74%, 222 out of 300 possible dyads). Accordingly, I decided to remove those interactions involving subjects that did not have, at least, one win and one loss, to avoid over or underestimate the dominance ranks of some individuals (Foerster et al., 2016). This led to the exclusion of 8 individuals from the analysis: CA, LA, JU, RE, SA, TO, VE and WU (see ***Table 2.1*** in ***Chapter 2***). Accordingly, hierarchy analyses were based on a total of 241 agonistic interactions during task introductions among the other 17 Barbary macaques in the group.

Linearity was low but significant (h' = 0.363, p = 0.018) as well as steepness (stp = 0.216, p<0.001, ***Figure A.3***). Only one final optimal ranking order solution was obtained for the I&SI method. Elo-ratings could not be computed using the optimized method due to the burn-in period of 100 interactions that removed most of the relevant agonistic interactions collected in this context, leading to a result that only ranked two dominant males (GH and PH). Therefore, ranks for Elo-ratings were derived from the traditional method. Stability was measured for two periods: a) period 1 comprises a total of 16 days and it is based on the optimized method with a burn-in period of 100 interactions, b) period 2 comprises a total of 31 days and it is the minimum period that the function allows to measure since it requires a minimum of interactions to compute the analysis. Stability for period 1 (rank differences = 74, S = 0.173) and period 2 (rank differences = 203.5, S = 0.315) can be considered low, indicating that the hierarchy derived from the analysis was fairly stable during the whole study, despite stability requires a longer sample period to provide accurate measures (Neumann et al., 2010).

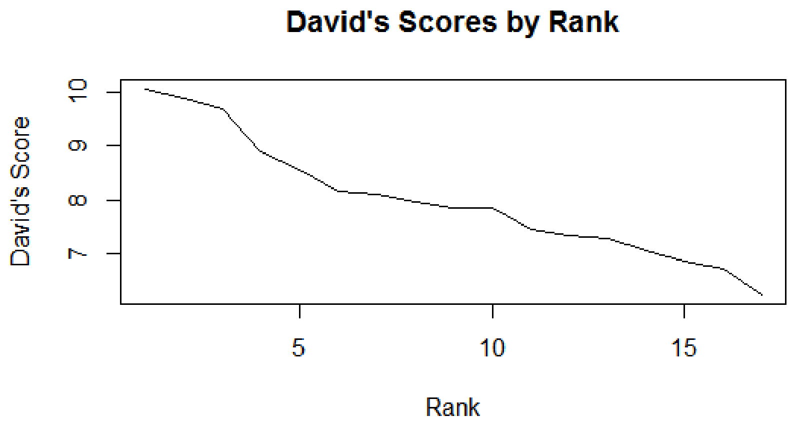


Figure A.3. Normalized David's scores plotted against individual ranks for BDG during task introductions. The continuous line represents steepeness of dominance relations.

The PERC method resulted in 105 transitive triangles, 0 intransitive triangles and a transitivity value of 1, indicating a fully transitive (linear) hierarchy. A total of 10 similar optimal solutions were obtained, so the final rank provided for PERC is the median of all these optimal solutions. Here, I used a conservative threshold for uncertainty values (<0.60). A total of 16 out of 135 dyads (11.8%) were deemed as uncertain dominance relationships (***Figure A.4***).

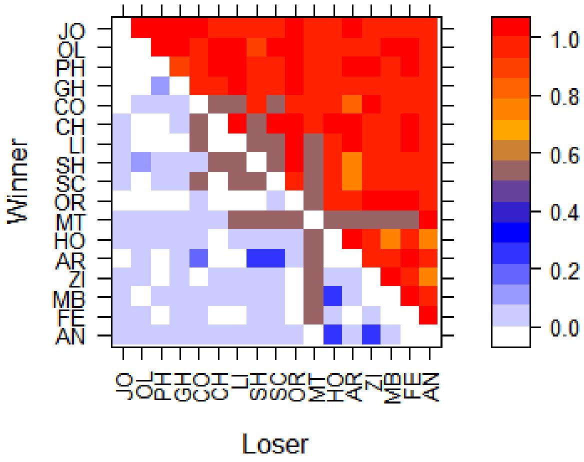


Figure A.4. Heat map of dominance probabilities between winners and losers in BDG during task introductions. Individuals in the diagonal with values closer to 0.5 indicate uncertain relationships.

No results were obtained from ADAGIO. This was probably due to the fact that data was fully transitive but presented many zeros in the matrix (unknown dominance relationships), as was reported in simulations run by the creators of the method (Douglas et al., 2017). When ADAGIO detects a linear hierarchy but the input data contains many zeros, the analysis deems some individuals as incomparable and does not return a rank ordering (Douglas et al., 2017).

Spearman rank correlations (corrected using Benjamni-Hochberg corrections) were conducted to compare ranks obtained across methods during task introductions. Median ranks across methods during and outside task introductions were also compared using correlations. Correlations among the methods used for dominance relations during task introductions in BDG were significant in all cases (***Table A.5***). Overall, results indicate that the ranks derived during and outside task introductions are highly similar and show no significant differences in individual ranking positions (***Table A.4*** & ***Table A.5***). This indicates that the inclusion of agonistic interactions occurring during task introductions does not seem to significantly influence the results of the linear hierarchy.

Table A.4. Dominance ranks of BDG obtained for all ranking methods during task introductions.

Individuals	I&SI rank	DS rank	Elo ranks	PERC rank	Median ranks during task all methods	Jenks Natural Breaks Classification	Median ranks out of task
JO	1	1	1	1	1	high	2
OL	2	2	2	2	2	high	3
PH	3	3	3	3	3	high	1
CH	4	4	4	5	4	high	4
GH	5	5	5	4	5	mid	5
CO	6	6	7	6	6	mid	7
SH	7	7	6	8	7	mid	8
LI	8	8	10	8	8	mid	6
SC	9	10	8	9	9	mid	13
MT	10	9	9	10.5	9.5	mid	15

OR	11	14	11	10.5	11	mid	10
HO	12	11	12	12	12	mid	11
AR	13	13	13	13	13	low	17
ZI	14	16	16	14	15	low	12
MB	15	15	14	15	15	low	16
FE	16	17	15	16	16	low	18
AN	17	12	17	17	17	low	24

DS rank: Rank obtained from David's scores. Elo ranks: Rank obtained from Elo-ratings. Median ranks out of task: Median of ranks calculated across all ranking methods outside task introductions.

Table A.5. Correlations of dominance ranks of BDG between ranking methods during task introductions.

Correlations	**Spearman's rho**
I&SI - David's scores	rho = 0.9485 p = 0.0000
I&SI - Elo-ratings	rho = 0.9828 p = 0.0000
I&SI - PERC	rho = 0.9963 p = 0.0000
David's scores - Elo-ratings	rho = 0.9387 p = 0.0000
David's scores - PERC	rho = 0.9399 p = 0.0000
Elo-ratings - PERC	rho = 0.9742 p = 0.0000
Median ranks during vs out of task	rho = 0.9332 p = 0.0000

Dominance ranks of Trentham group (TG):

A total of 343 encounters outside task introductions + 485 encounters during task introductions (828 agonistic encounters in total) were used in the hierarchy analyses for TG. I used the same methods used to determine social (dominance) ranks in BDG. Linearity was low and significant (h' = 0.112, p<0.001), as well as steepness (stp = 0.049, p<0.001, ***Figure A.5***), as expected in Barbary macaques which are intermediate in the despotic-egalitarian spectrum (van Schaik, 1989; Thierry, 2007).

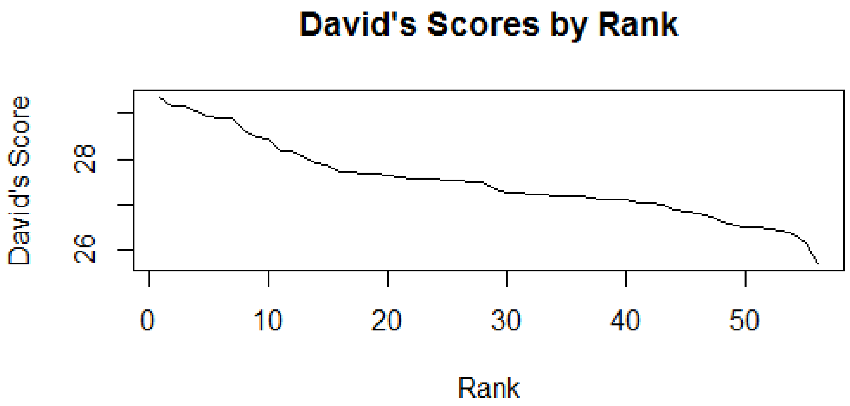


Figure A.5. Normalized David's scores plotted against individual ranks for TG. The continuous line represents steepeness of dominance relations.

Only one optimal ranking order was obtained for the I&SI method (I: 6, SI: 62). Elo-ratings were calculated using the optimized algorithm with a burn-in period of 100 interactions. On the first 100 interactions, only information of social rank for 31 out of 56 individuals was available (55% of the group). Therefore, I calculated stability from the moment information on dominance relations for all individuals was available until the end of the study (a total of 45 days). Results indicate that the hierarchy is somehow stable but changes in dominance relations are not rare (rank differences = 1165, S = 0.397). This may be due to the sample size, since the group is large and the complexity of the environment hinders the observation and occurrence of agonistic encounters (see ***Chapter 6*** for further details).

PERC resulted in 642 transitive triangles, 11 intransitive triangles and a transitivity value of 0.98, indicating that dominance relations were linear. Since some intransitivities were present, some optimal solutions of the PERC simulations have greater costs than others (cost range: 54.99 – 67.62). Therefore, the best ranking order is the one provided by the simulation with a lower cost value. Uncertainty measures indicated that 14.8% of all possible dyads (458 out of 3080) were not clearly defined (i.e. uncertainty probability <0.60, ***Figure A.6***). Again, the large and complex environment and group size of this group of Barbary macaques makes highly likely that most of the possible dyadic interactions do not take place or are so infrequent that can rarely be observed. This can make that some dominance relations are not well established and even change depending on a different audience at the moment of the encounter.

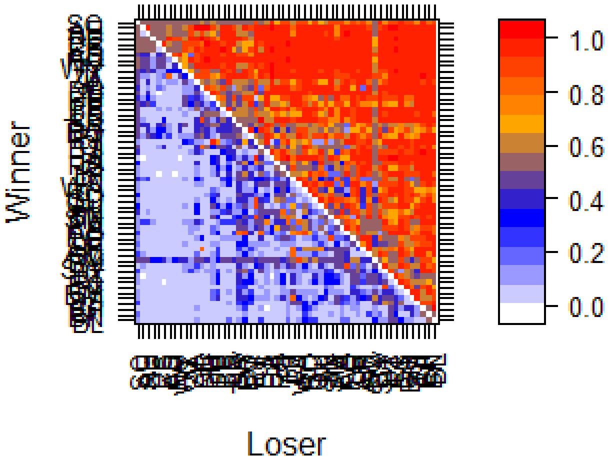


Figure A.6. Heat map of dominance probabilities between winners and losers in TG. Individuals in the diagonal with values closer to 0.5 indicate uncertain relationships.

Due to the presence of intransitivities and the small sample size, pre-processing approaches were used in ADAGIO to break symmetries and potential ties of dominance relations at the dyadic level (Douglas et al., 2017). DCI (DCI=0.963) indicated that data mostly contained unidirectional relations, meaning that in most cases, the dominance relationships between individuals were well-defined and there were few cases of tied dominance relations (Douglas et al., 2017). Both top-down and bottom-up approaches led to the same ranking order.

Results of the ranking orders obtained for all methods can be seen in ***Table A.6***. Correlations among ranking methods were high and significant in all cases (***Table A.7***). Since all methods were equally reliable, a median of ranks across methods was calculated and used in the thesis as a measure of ordinal social ranks. Jenks Natural Breaks Classification was used as a measure of categorical social ranks.

Table A.6. Dominance ranks of TG obtained for all ranking methods.

Individuals	I&SI method	DS	Elo ranks	PERC	ADAGIO	Jenks Natural Breaks Classification	Median ranks all methods
DE	1	2	2	4	1	high	2
CC	2	5	1	5	2	high	2
ZA	3	1	9	11	3	high	3
AD	4	3	7	7	2	high	4
NO	5	4	6	8	3	high	5
ED	6	6	4	6	3	high	6
AE	7	8	3	2	3	high	3
RU	8	9	10	3	4	high	8
WY	9	7	5	9	3	high	7
JT	10	10	8	10	3	high	10
SR	11	11	12	19	6	high	11
SQ	12	19	17	1	5	mid	12
JL	13	15	15	12	5	high	13
BO	14	26	23	21	6	mid	21
DB	15	14	11	13	5	high	13
BB	16	12	16	17	6	mid	16
TI	17	13	13	14	4	high	13
LS	18	23	29	18	7	mid	18
BS	19	30	37	24	7	low	24
TW	20	21	27	20	4	mid	20
JA	21	24	26	26	6	mid	24
OI	22	22	22	23	4	mid	22
DU	23	16	14	15	5	high	15
FF	24	17	19	16	6	mid	17
ET	25	20	25	22	4	mid	22
JI	26	18	28	25	5	mid	25
PJ	27	25	31	30	9	mid	27
PI	28	29	21	28	10	mid	28
WA	29	39	32	31	7	mid	31
LE	30	38	40	41	12	low	38
RO	31	44	35	32	8	mid	32
LF	32	47	46	29	8	low	32
SD	33	41	36	33	12	mid	33
QU	34	36	30	34	7	mid	34
SM	35	31	20	37	13	mid	31
RS	36	34	34	27	12	mid	34
FL	37	37	44	35	8	low	37

AM	38	51	49	43	11	low	43
SN	39	32	41	36	11	low	36
AS	40	43	42	39	13	low	40
BY	41	27	18	45	13	mid	27
SF	42	45	47	42	13	low	42
FO	43	33	33	44	10	mid	33
SW	44	35	38	46	11	low	38
PA	45	28	24	38	10	mid	28
PO	46	52	45	40	9	low	45
LT	47	54	51	48	8	low	48
EC	48	55	54	49	9	low	49
CY	49	56	56	50	10	low	50
BZ	50	40	48	47	11	low	47
BM	51	50	39	51	12	low	50
SS	52	42	43	52	11	low	43
GI	53	46	50	53	12	low	50
EF	54	53	52	54	12	low	53
BL	55	48	55	56	13	low	55
BN	56	49	53	55	13	low	53

DS rank: Rank obtained from David's scores. Elo ranks: Rank obtained from Elo-ratings. Median ranks all methods: Median of ranks calculated across all ranking methods.

Table A.7. Correlations of dominance ranks of TG between ranking methods.

Correlations	**Spearman's rho**
I&SI - David's scores	rho = 0.9084 p = < 0.001
I&SI - Elo-ratings	rho = 0.8918 p = < 0.001
David's scores - Elo-ratings	rho = 0.9513 p = < 0.001
PERC - I&SI	rho = 0.9666 p = < 0.001
PERC - David's scores	rho = 0.9033 p = < 0.001
PERC - Elo-ratings	rho = 0.8923 p = < 0.001
ADAGIO - I&SI	rho = 0.8713 p = < 0.001
ADAGIO - David's scores	rho = 0.8175 p = < 0.001
ADAGIO - Elo-ratings	rho = 0.7809 p = < 0.001
ADAGIO - PERC	rho = 0.8764 p = < 0.001

APPENDIX B – Partner preferences in non-vocalized events

Kruskal-Wallis and Dunn tests were carried out to investigate the directionality of partner preferences in terms of sex, age and social rank in agonistic contexts in BDG where aid-recruitment calls were not produced. These results were used for comparisons with those obtained in aid-recruitment contexts (see ***Chapter 4***).

Results showed that there were sex, age and social rank differences when directing agonistic displays in silent agonistic contexts. Females significantly directed more aggression towards other females than towards males. Males directed more aggression towards both sexes than females towards males. Adults directed more aggression towards individuals of all ages than sub-adults towards adults. High-ranking individuals directed more aggression than lower (mid and low) ranking individuals towards high-ranking individuals. Middle-ranking individuals preferably received aggression from individuals of the same or higher rank. Low-ranking individuals seemed to significantly receive more aggression from higher-ranking individuals than from other low-ranking partners (***Table B.1*** and ***Figure B.1***).

Table B.1. Kruskal-Wallis and Dunn test results for non-vocalized agonistic interactions and each individual attribute.

	Kruskal-Wallis test	**Dunn test**
Sex	χ^2 = 20.105, df = 3, p < 0.001*	FF-FM: -1.09 (0.330) FF-MF: -4.37 (p < 0.001)* FF-MM: -1.71 (p = 0.131) FM-MF: -3.39 (p = 0.002)* FM-MM: -0.74 (p = 0.463) MF-MM = 2.43 (p = 0.031)*
Age	χ^2 = 23.737, df = 3, p < 0.001*	AA-AJ: -4.34 (p<0.001)* AA-JA: 0.49 (p = 0.628) AA-JJ: -1.82 (p = 0.104) AJ-JA = 3.49 (p = 0.001)* AJ-JJ = 1.19 (p = 0.280) JA-JJ: -1.87 (p = 0.104)
High vs lower	χ^2 = 13.574, df = 1, p < 0.001*	HH-HMid: -2.93 (p = 0.009)* HH-HL: -3.29 (p = 0.005)* HL-HMid: 0.35 (p = 0.870)
Middle vs high	χ^2 = 0.893, df = 1, p = 0.345	MidH-MidL: -3.67 (p = 0.001)* MidH-MidMid: -0.93 (p = 0.550) MidL-MidMid: 2.74 (p = 0.013)*
Low vs higher	χ^2 = 4.418, df = 3, p = 0.036*	LH-LL: -0.35 (p = 0.870) LH-LMid: 0.94 (p = 0.550) LL-LMid: 1.29 (p = 0.355)

Higher vs lower: Comparison of high-ranking individuals directing behaviours to other high-ranking individuals vs high ranking individuals directing behaviours to lower-ranking classes. Middle vs high: Comparison of middle ranking individuals directing behaviours to high ranking individuals vs middle ranking individuals directing behaviours to middle and low ranking partners. Low vs higher: Comparison of low ranking individuals directing behaviours to other low ranking individuals vs low ranking individuals directing behaviours to higher-ranking partners. F: Females. M: Males. A: Adults. J: Sub-adults/Juveniles. H: High-ranking. Mid: Middle-ranking. L: Low-ranking. * indicates significant p-values.

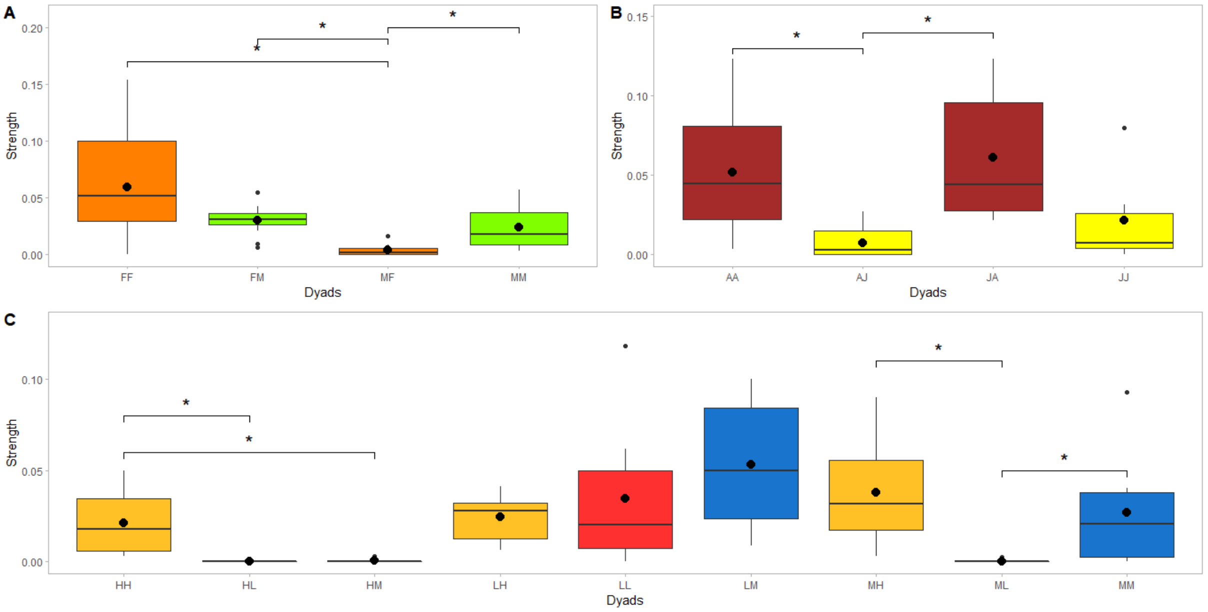


Figure B.1. Box-plot of the strength of interactions in agonistic encounters for sex (**A**), age (**B**) and social rank (**C**) categories. F: Females. M: Males. A: Adults. J: Sub-adults/Juveniles. H: High-ranking individuals. M: Middle-ranking individuals. L: Low-ranking individuals. Dyads names describe who the victim (first letter) is and who the aggressor (second letter) is. For instance, FM indicates that males direct aggression towards females, AJ indicates that sub-adults direct aggression to adults and LH indicates that high-ranking individuals direct aggression towards low-ranking conspecifics.

APPENDIX C – Adequacy of datasets

Datasets for each social network were described in terms of a series of attributes (see ***Table 2.6*** and ***Table C.1***) following guidelines provided by Whitehead (2008). This first exploration of the datasets determines whether the amount of data collected is sufficient to investigate the social structure of the population or more data are required (Whitehead, 2008). A description of the datasets can be found in ***Table C.1.***

Table C.1. Description of the datasets for the attributes described by Whitehead (2008).

Network	Size of population	Rate of identification	Sampling periods per dyad	Associations per individual	Length of dataset
Grooming BDG	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 2.98)	Some (mean = 48.64)	Long (1029 sessions in total)
Grooming TG	Intermediate (N = 56+5 infants)	Complete (all individuals identified)	Some (mean = 1.49)	Some (mean = 13.20)	Long (1568 sessions in total)
Huddling BDG	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 3.18)	Some (mean = 34.25)	Long (1029 sessions in total)
Huddling TG	Intermediate (N = 56+5 infants)	Complete (all individuals identified)	Some (mean = 1.66)	Some (mean = 16.47)	Long (1568 sessions in total)
Proximity 1m BDG	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 1.66)	Some (mean = 18.32)	Long (1029 sessions in total)
Proximity 1m TG	Intermediate (N = 56+5 infants)	Complete (all individuals identified)	Some (mean = 1.29)	Some (mean = 11.47)	Long (1568 sessions in total)
Proximity 5m BDG	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 3.45)	Many (mean = 134.24)	Long (1029 sessions in total)
Proximity 5m TG	Intermediate (N = 56+5 infants)	Complete (all individuals identified)	Some (mean = 2.16)	Many (mean = 142.60)	Long (1568 sessions in total)
Recruiter-aggressor	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 1.84)	Some (mean = 17.52)	Long (1292 sessions in total)
Helper-recipient	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 1.51)	Few (mean = 9.92)	Long (1292 sessions in total)
Helper-opponent	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 1.58)	Some (mean = 10.17)	Long (1292 sessions in total)
Commenter-handler BDG	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 2.02)	Some (mean = 15.00)	Long (1292 sessions in total)
Commenter-mother BDG	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 2.38)	Few (mean = 9.91)	Long (1292 sessions in total)
Commenter-aggressor BDG	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 1.28)	Few (mean = 7.65)	Long (1292 sessions in total)
Commenter-victim BDG	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 1.29)	Few (mean = 7.04)	Long (1292 sessions in total)
Observation 1m blue/yellow task TG	Intermediate (N = 56+5 infants)	Complete (all individuals identified)	Some (mean = 1.16)	Few (mean = 4.85)	Long (294 sessions in total)
Observation 5m blue/yellow task TG	Intermediate (N = 56+5 infants)	Complete (all individuals identified)	Some (mean = 1.59)	Some (mean = 17.83)	Long (294 sessions in total)
Observation 1m push/lift-up task TG	Intermediate (N = 56+5 infants)	Complete (all individuals identified)	Some (mean = 1.21)	Few (mean = 4.43)	Long (206 sessions in total)
Observation 5m push/lift-up task TG	Intermediate (N = 56+5 infants)	Complete (all individuals identified)	Some (mean = 1.67)	Some (mean = 16.97)	Long (206 sessions in total)
Observation 1m rotating-door task TG	Intermediate (N = 56+5 infants)	Complete (all individuals identified)	Some (mean = 1.06)	Few (mean = 2)	Medium (57 sessions in total)

Observation 5m rotating-door task TG	Intermediate (N = 56+5 infants)	Complete (all individuals identified)	Some (mean = 1.21)	Few (mean = 5.31)	Medium (57 sessions in total)
Observation 1m twin-door task BDG	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Some (mean = 6.98)	Some (mean = 41.24)	Long (1590 sessions in total)
Observation 5m twin-door task BDG	Intermediate (N = 25+4 infants)	Complete (all individuals identified)	Many (mean = 11.61)	Many (mean = 128.64)	Long (1590 sessions in total)

Sampling periods per dyad: Number of sampling periods during which a dyad is observed associated. For the interpretation of these measures see Whitehead (2008, p. 80-81) or ***Table 2.6*** in ***Chapter 2***.

The measures of population size, rate of identification and length of datasets indicates that a long study (i.e. a great sampling effort) was carried out to collect each social behaviour in both groups. Despite this, data can be considered sparse in most cases since only some or few observations per dyad were available at the end of the study (***Table C.1***). This is common in animal social networks (Croft et al., 2008; Whitehead, 2008). However, more analyses are required to explore the uncertainty of the datasets in terms of representing the social structure of the population (Whitehead, 2008; Farine & Strandburg-Peshkin, 2015).

In order to determine whether my datasets were representative of the social structure of the population, I followed the approach and guidelines proposed by Farine & Strandburg-Peshkin (2015). This approach calculates edge weights (strength of interactions) using the Simple Ratio Index (SRI, see ***Chapter 2***) and provides different measures of uncertainty for the edge weights of the datasets. Bootstrap and Bayesian methods were used to generate new datasets that were compared to the original ones. The non-parametric bootstrap re-samples the sampling periods of the original data to generate new datasets for which edge weights are calculated. By generating 1000 bootstrapped datasets we obtain a distribution of measures that can be used as a representation of the social structure of the population (i.e. true estimates). Bayesian methods use maximum likelihood probability to generate these new datasets. For both methods, 95% confidence intervals were estimated. A third approach to calculate 95% confidence intervals, the Clopper-Pearson method, was also used (Farine & Strandburg-Peshkin, 2015). Three measures of precision and accuracy were calculated in R to estimate the levels of uncertainty of the edge weights in the original datasets:

a) **Absolute error:** Absolute difference between the mean of inferred edge weights and the mean of observed edge weights.

b) **Relative accuracy:** Mantel rank correlations between inferred edge weights and observed edge weights.

c) **Precision of uncertainty estimates:** Rate of underestimated values (where observed values lie below the estimated 95% interval of the inferred networks) and the rate of overestimated values (where observed values lie above the estimated 95% interval of inferred networks).

For further details on the methods see Farine & Strandburg-Peshkin (2015) and ***section 2.4.3. Adequacy of data*** in ***Chapter 2***. Results of these measures of uncertainty can be found in ***Table C.2***.

Table C.2. Absolute error, relative accuracy and precision of uncertainty estimates calculated for all datasets following the guidelines described by Farine & Strandburg-Peshkin (2015).

Dataset	Mean ± SD	Coefficient of variation	Absolute error	Relative accuracy	Rate of UEV	Rate of OEV
Grooming BDG	0.006203511 ± 0.01415789 (Obs) 0.005226803 ± 0.01182928 (b) 0.004577041 ± 0.01143489 (B)	2.282239 (Obs) 2.263196 (b) 2.498315 (B)	0.0009767077 (b) 0.00162647 (B)	0.9598412 (b) 0.9986022 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0 (B) 0 (CP)
Huddling BDG	0.004286306 ± 0.0140455 (Obs) 0.00357436 ± 0.01144978 (b) 0.003312144 ± 0.01204761 (B)	3.27683 (Obs) 3.203308 (b) 3.637404 (B)	0.0007119462 (b) 0.000974162 (B)	0.9616201 (b) 0.9984333 (B)	0 (b) 0 (B) 0 (CP)	0.003333333 (b) 0 (B) 0 (CP)
Proximity 1m BDG	0.002374172 ± 0.004782954 (Obs) 0.001999854 ± 0.00453419 (b) 0.001226628 ± 0.00271699 (B)	2.014578 (Obs) 2.26726 (b) 2.215006 (B)	0.0003743176 (b) 0.001147543 (B)	0.8745909 (b) 0.9944045 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0 (B) 0 (CP)
Proximity 5m BDG	0.01664881 ± 0.01652946 (Obs) 0.01430794 ± 0.01451193 (b) 0.01427974 ± 0.01306179 (B)	0.9928315 (Obs) 1.014257 (b) 0.9147079 (B)	0.002340863 (b) 0.002369065 (B)	0.9008598 (b) 0.9989755 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0 (B) 0 (CP)
Grooming TG	0.001134268 ± 0.00427026 (Obs) 0.001053694 ± 0.004483159 (b) 0.0004721071 ± 0.00216655 (B)	3.764771 (Obs) 4.254707 (b) 4.589107 (B)	8.05741e-05 (b) 0.0006621611 (B)	0.8244869 (b) 0.9814426 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0.0006493506 (B) 0 (CP)
Huddling TG	0.001312125 ± 0.00483661 (Obs) 0.001206272 ± 0.004892068 (b) 0.0005749196 ± 0.002684262 (B)	3.68609 (Obs) 4.055527 (b) 4.668935 (B)	0.0001058527 (b) 0.0007372051 (B)	0.8768328 (b) 0.9798606 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0 (B) 0 (CP)
Proximity 1m TG	0.001073504 ± 0.003249092 (Obs) 0.0009926956 ± 0.003573732 (b) 0.0003010039 ± 0.001139401 (B)	3.026624 (Obs) 3.600028 (b) 3.785337 (B)	8.080802e-05 (b) 0.0007724997 (B)	0.7872513 (b) 0.9702436 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0.003246753 (B) 0 (CP)
Proximity 5m TG	0.01261497 ± 0.01543967 (Obs) 0.01189713 ± 0.01541573 (b) 0.009247432 ± 0.009934572 (B)	1.223917 (Obs) 1.295751 (b) 1.074306 (B)	0.0007178315 (b) 0.003367534 (B)	0.8763096 (b) 0.9898341 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0.002597403 (B) 0 (CP)
Recruiter-aggressor BDG	0.001207179 ± 0.00226383 (Obs) 0.0007980473 ± 0.001761292 (b)	1.875305 (Obs) 2.207002 (b) 2.077747 (B)	0.0004091319 (b) 0.0006276986 (B)	0.8654055 (b) 0.9947803 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0 (B) 0 (CP)

	0.0005794806 ± 0.001204014 (B)					
Helper-recipient BDG	0.0006817294 ± 0.00172773 (Obs) 0.0004477481 ± 0.001322572 (b) 0.0002579998 ± 0.0007893237 (B)	2.534334 (Obs) 2.95383 (b) 3.059397 (B)	0.0002339813 (b) 0.0004237296 (B)	0.8958925 (b) 0.9876244 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0.003333333 (B) 0 (CP)
Helper-opponent BDG	0.0006724078 ± 0.001597978 (Obs) 0.0004443516 ± 0.001253864 (b) 0.0002456175 ± 0.0006720555 (B)	2.376502 (Obs) 2.821784 (b) 2.736188 (B)	0.0002280562 (b) 0.0004267904 (B)	0.7102934 (b) 0.9904415 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0.003333333 (B) 0 (CP)
Commenter-handler BDG	0.0009641869 ± 0.002235554 (Obs) 0.0006389256 ± 0.001686576 (b) 0.0004650993 ± 0.00127833 (B)	2.31859 (Obs) 2.639707 (b) 2.748509 (B)	0.0003252613 (b) 0.0004990875 (B)	0.8657294 (b) 0.9897838 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0 (B) 0 (CP)
Commenter-mother BDG	0.0006013269 ± 0.00210705 (Obs) 0.0003972235 ± 0.001524953 (b) 0.0003247379 ± 0.001404939 (B)	3.504001 (Obs) 3.839029 (b) 4.326378 (B)	0.0002041035 (b) 0.0002765891 (B)	0.9232986 (b) 0.9863564 (B)	0 (b) 0 (B) 0 (CP)	0.003333333 (b) 0 (B) 0 (CP)
Commenter-aggressor BDG	0.0004830426 ± 0.001117689 (Obs) 0.0003191415 ± 0.0009413346 (b) 0.0001378882 ± 0.0003455289 (B)	2.313851 (Obs) 2.949583 (b) 2.505863 (B)	0.000163901 (b) 0.0003451544 (B)	0.8170532 (b) 0.9908628 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0.006666667 (B) 0 (CP)
Commenter-victim BDG	0.0004543348 ± 0.001028197 (Obs) 0.0003038846 ± 0.0008983358 (b) 0.0001084693 ± 0.0002469903 (B)	2.263082 (Obs) 2.956174 (b) 2.277053 (B)	0.0001504503 (b) 0.0003458655 (B)	0.7436031 (b) 0.9982614 (B)	0 (b) 0 (B) 0 (CP)	0 (b) 0.05333333 (B) 0 (CP)
Observation 1m twin-door task BDG	0.002758448 ± 0.01049536 (Obs) 0.002320011 ± 0.00897322 (b) 0.002065074 ± 0.008588787 (B)	3.804807 (Obs) 3.86775 (b) 4.159069 (B)	0.0004384374 (b) 0.0006933735 (B)	0.9591736 (b) 0.983272 (B)	0 (b) 0 (B) 0 (CP)	0.006666667 (b) 0 (B) 0 (CP)
Observation 5m twin-door task BDG	0.008308268 ± 0.02610146 (Obs) 0.006873002 ± 0.02047758 (b) 0.00759703 ± 0.02528359 (B)	3.141625 (Obs) 2.979423 (b) 3.328088 (B)	0.001435267 (b) 0.0007112378 (B)	0.9880048 (b) 0.9978919 (B)	0 (b) 0 (B) 0 (CP)	0.0224 (b) 0 (B) 0 (CP)

UEV: Under-estimated values. OEV: Over-estimated values. Obs: Observed network. b: bootstrap method. B: Bayesian method. CP: Clopper-Pearson method

The analysis of uncertainty of the datasets only concerns to the strength of relations of the networks (i.e. edge weights, Farine & Strandburg-Peshkin, 2015). Therefore, observation networks in TG were not included in the analysis because they were all unweighted, meaning that the strength of relations was not considered in the dataset, only the occurrence of the event. As highlighted by Farine & Strandburg-Peshkin (2015), the bootstrap method performs poorly at quantifying uncertainty for sparse data because many edges are binary (i.e. the index-based edge weight will be either 0 or 1, and it will not have any uncertainty under a bootstrapped estimate). In these cases, the Bayesian method provides more realistic uncertainty measures (Farine & Strandburg-Peshkin, 2015). Since most of the datasets can be considered sparse, the Bayesian method was considered the most reliable method to measure uncertainty.

Generally, results (see ***Table C.2***) showed that the absolute error is always lower than the observed means and standard deviations for both bootstrap and Bayesian methods, which indicates that the absolute error is low and the sampling effort made was enough to capture a fairly reliable estimate of the true edge weights (Farine & Strandburg-Peshkin, 2015). The high relative accuracy obtained in all cases indicates that the observed values are representative of the true estimates of edge weights of the population. The highest values of relative accuracy were obtained in the most reliable method for sparse data: the Bayesian method. Underestimated values (i.e. observed values that fall below the 95% confidence interval of the true estimates) were not observed in any case. Some overestimated measures were obtained for the Bayesian method in affiliative networks of TG and some communication networks. Despite this, these overestimated values represent less than 0.06% of the observed cases, suggesting that the levels of uncertainty of the datasets were low. Overall, absolute error was low, relative accuracy was high and there were none or negligible over and underestimated values. Therefore, the levels of uncertainty in the datasets used in this thesis for the construction of affiliative, communication and observation networks were low and observed edge weights can be considered representative of the true estimates of the population.

For associations, I included an extra measure included in the software SOCPROG developed by Whitehead (2008): social differentiation. Association data differs from interaction data in that associations may occur by chance. When we consider that two or more individuals are associated we assume that they are in a situation in which interactions usually take place (Whitehead & Dufault, 1999). However, this does not mean that the subjects will ever interact or that the association we observe is a real indication of bonds between individuals. To ensure that data represents preferred or avoided companions, Whitehead (2008) proposed to determine whether observed associations are significantly greater or lower than associations occurred by chance. Bejder's (MBFB) permutation test, as described by Whitehead (2008), is useful to test that. However, before testing the hypothesis of preferred/avoided companionship, it is necessary to ensure the datasets are large enough for the permutation test to be able to reject the null hypothesis of no preferred companionship. Whitehead (2008) suggested the following criteria: S^2 x H > 5, where S is social differentiation measured as the coefficient of variation of the true association indices calculated using maximum likelihood, and H is the mean number of observed associations per individual. Accordingly, if the value of that calculation is > 5, the Bejder's permutation test has the ability to reject the null hypothesis of no preferred companionship.

I considered each 5-minute data collection session as a sampling period and calculated SRI corrected for gregariousness to obtain the measure of social differentiation. Social differentiation was calculated as the coefficient of variation (CV) of the true association indices (SRI) among pairs of individuals in terms of the actual time spent together. A value of social differentiation (S) lower than ~0.3 indicates rather homogenous societies, S greater than ~0.5 indicates well-differentiated societies, and S greater than ~2 indicates extremely differentiated societies (Whitehead 2008). Moreover, I also calculated the correlation between true and estimated (from observed data) association indices (*r*) to test if datasets accurately described the social structure of the population. This correlation index *r* is an indicator of the power of the analysis to detect the true social system where values ~1 indicate an "excellent" representation of the population in the datasets, values ~0.8 indicate a "good" representation, values ~0.4 indicate a "somewhat" representative pattern of true social relations and values ~0 indicate unreliable datasets (Whitehead 2008). Whitehead (2008) also tabulated the minimum values of social differentiation, mean associations per dyad and mean associations per individual necessary for each value of *r* (see Table 3.15 in Whitehead, 2008, p. 84).

According to Table 3.15 in Whitehead (2008, p. 84), all cases except proximity within 1m in TG showed a "somewhat" to "good" representation of the social structure of the population, and the mean number of associations per dyad and individual were higher than the minimum values required for the correlation index *r* and social differentiation S (***Table C.3***). Even though TG was fairly differentiated for proximity 1m (S = 0.545), the correlation between true and estimated association indices was poor (r = 0.181), indicating that this dataset is insufficient (i.e. more data is required) to obtain a representative structure of the population (***Table C.3***, Whitehead, 2008). This contradicts the results for the correlation between true and observed estimates of association indices for proximity within 1m in TG calculated as relative accuracy (see ***Table C.1***). The difference between the measure of relative accuracy calculated in R and the correlation index (*r*) calculated in SOCPROG is that the first one correlates the ranks of the association indices while the second one correlates the absolute values of these edge weights. As Farine & Strandburg-Peshkin (2015) highlighted, relative accuracy is important in studies of animal social networks because researchers often care more about the relative rankings of association strengths or other social traits within a given network than their absolute values. This is also true in this thesis because the aim was to make network comparisons of relative measures. Therefore, it was safe to use the data on proximity within 1m collected in TG for the purposes of this thesis. Overall, all datasets (except proximity within 1m in TG) had enough power to reject the null hypothesis of no preferred companionship in the Bejder's permutation test. The values obtained in

SOCPROG for proximity within 1m in TG are borderline in terms of dataset power to reject the null hypothesis of no preferred companionship (Whitehead, 2008, p. 84). Therefore, results of the Bejder's permutation test for proximity 1m in TG must be taken with caution.

Table C.3. Measures of social differentiation and correlation indices calculated in SOCPROG for association datasets.

	Blair Drummond Group	Trentham Group
Proximity 1m	Mean associations/dyad: 0.75	Mean associations/dyad: 0.22
	Mean associations/individual: 17.92	Mean ass/individual: 12.32
	S (SE): 0.915 (0.039)	S (SE): 0.545 (0.032)
	r (SE): 0.454 (0.027)	r (SE): 0.181 (0.013)
	S^2 x H: 15	S^2 x H: 3.66
Proximity 5m	Mean associations/dyad: 5.09	Mean associations/dyad: 2.41
	Mean associations/individual: 122.24	Mean associations/individual: 132.75
	S (SE): 0.763 (0.028)	S (SE): 0.803 (0.025)
	r (SE): 0.768 (0.014)	r (SE): 0.723 (0.018)
	S^2 x H: 71.16	S^2 x H: 85.59

S: Social differentiation estimate (coefficient of variation of true association indices calculated using maximum likelihood). SE: standard error. r: estimate correlation between true and estimated association indices using likelihood method. H: mean number of associations per individual

Finally, Bejder's permutation tests (also called MBFB permutation tests) were used in all datasets based on socio-positive behaviours (grooming, huddling and proximity) to determine whether individuals have preferred/avoided companions. This was necessary to draw conclusions about the social learning context depicted by affiliative networks. Before describing whether social learning opportunities were directed or non-specific, it was necessary to rule out the possibility that interactions/associations between dyads observed were not random (see ***Chapter 3***). The Bejder's or MBFB permutation test uses the original data to create a series of randomized networks that are compared to the observed network. By comparing the same statistic between the observed and randomized networks, the test provides a measure of significance of the difference between both datasets. I used the coefficient of variance of the association indices as the statistic since it is easier to interpret and has the advantage of presenting a measure of effect size (Farine & Whitehead, 2015). I performed the permutation tests with a 2-tailed significance level of 0.05, running 1000 permutations tests and 1000 trials per permutation using the method 'Permute associations within samples' which is the most robust method available in SOCPROG and accounts for differences in gregariousness (see Whitehead, 2008, 2009, 2017). Results of preferred/avoided companions can be found in ***Table C.4***.

Table C.4. Results of the Bejder's permutation test for datasets based on affiliation, communication and task observations.

	Dataset	CV obs	CV random	p-value
Blair Drummond Group	Grooming	2.338164	1.77806	<0.001*
	Huddling	3.350523	2.55512	<0.001*
	Proximity 1m	2.066175	1.497168	<0.001*
	Proximity 5m	1.033659	0.9781955	<0.001*
	Recruiter-aggressor	1.875305	1.639751	<0.001*
	Helper-recipient	2.534334	1.829959	<0.001*
	Helper-opponent	2.376502	1.926446	<0.001*
	Commenter-handler	2.31859	2.115378	0.001*
	Commenter-mother	3.504001	3.279688	0.069
	Commenter-aggressor	2.313851	2.071382	0.006*
	Commenter-victim	2.263082	2.205485	0.166
	Observation 1m	3.888505	3.206846	0.002*
	Observation 5m	3.141625	3.017514	<0.001*
Trentham Group	Grooming	3.801224	2.907974	<0.001*
	Huddling	3.721883	2.917871	<0.001*
	Proximity 1m	4.89087	3.17242	0.001*
	Proximity 5m	1.46015	0.69962	<0.001*

CV obs: coefficient of variation of our dataset. CV random: coefficient of variation of a random sample obtained using Bejder's permutation test. *: Indicates significant results.

Results provided evidence against the null hypothesis of no preferred companions, indicating that the interactions and associations observed in datasets based on affiliative behaviours were not the result of random relations (***Table C.4***). In case of insufficient data, such as proximity within 1m in TG, Whitehead (2008) argued that simulations normally reject the null hypothesis when S^2 x H is > 5 and fail to reject it when S^2 x H is < 5. Despite S^2 x H was < 5 in the proximity 1m dataset of the Trentham group, the test rejects the hypothesis. According to simulations run by Whitehead (2008), it seems that this dataset had enough power to detect social partner preferences. In conclusion, grooming, huddling and proximity relations of Barbary macaques in both groups were not the result of random interactions/associations but of preferred/avoided companionships. Regarding communication datasets, all networks except commenter-mother and commenter-victim were significant for the Bejder's permutation test (for further details of these results refer to ***Chapter 4***). Weighted observation networks (only BDG) were also the result of non-random interactions (***Table C.4***).

APPENDIX D – E-I index results (assortative mixing)

Assortative mixing (i.e. preferred partners of certain classes) was measured using the E-I index which estimates whether individuals prefer to interact or associate with individuals of the same or a different class (i.e. individuals of the same or different sex, age, rank or kin).

E-I index for sex, age and social rank was measured for each network as a whole and for class subsets of the networks. For instance, E-I index for sex was measured considering all the external and internal connections for both classes (males and females) simultaneously (whole network) and for each of these classes (e.g. for females, male-male interactions were removed to calculate the E-I index and only female-female and male-female dyads were considered). Kinship was only measured for the whole network and not for each of the several matrilines (i.e. small sample size per matriline).

For significant results we must consider that: (i) if the E-I index is greater than chance, whether positive or negative, this indicates a preference for external connections (heterophily), (ii) if the E-I index is lower than chance, whether positive or negative, this indicates a preference for internal connections (homophily). See ***section 2.4.7*** for more details on the interpretation of the E-I index.

Table D.1. E-I index measures and p-values for assortative mixing in BDG.

Network	Attribute	Dyads	Type of network	E-I index	Median bootstrap	Adjusted p-value
Grooming	Sex	All	Unweighted	-0.16129	-0.01935	0.033113
			Weighted	-0.47039	-0.30592	0.017397
		Females (excl. M-M)	Unweighted	0.015625	-0.01563	0.240352
			Weighted	-0.4026	-0.30983	0.017397
		Males (excl. F-F)	Unweighted	0.413043	0.130435	0.033113
			Weighted	0.4	0.13913	0.033113
	Age	All	Unweighted	-0.30323	-0.26452	0.179064
			Weighted	-0.25	-0.26974	0.208518
		Adults (excl. J-J)	Unweighted	-0.28947	-0.28947	0.510898
			Weighted	-0.23618	-0.27303	0.179064
		Sub-adults (excl. A-A)	Unweighted	0.894737	0.140351	0.025795
			Weighted	0.90795	0.179916	0.021596
	Rank	All	Unweighted	0.303226	0.367742	0.065387
			Weighted	0.069079	0.190789	0.05119
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.535354	0.424242	0.065387
			Weighted	0.522659	0.407855	0.065387
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.613636	0.443182	0.065387
			Weighted	0.590062	0.428571	0.065387
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.594203	0.463768	0.065387
			Weighted	0.014286	0.178571	0.065387
Huddling	Sex	All	Unweighted	-0.50562	-0.08989	0.017996
			Weighted	-0.78102	-0.36253	0.010198
		Females (excl. M-M)	Unweighted	-0.41333	-0.09333	0.024895
			Weighted	-0.7619	-0.35979	0.010198
		Males (excl. F-F)	Unweighted	0.222222	0.111111	0.269226
			Weighted	0.153846	0.102564	0.339332

	Age	All	Unweighted	-0.37079	-0.29213	0.194361
			Weighted	-0.19221	-0.19221	0.513297
		Adults (excl. J-J)	Unweighted	-0.35632	-0.29885	0.19844
			Weighted	-0.14872	-0.17949	0.194361
		Sub-adults (excl. A-A)	Unweighted	0.866667	0.166667	0.057588
			Weighted	0.775401	0.165775	0.046791
	Rank	All	Unweighted	0.078652	0.325843	0.045858
			Weighted	-0.24574	0.080292	0.020796
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.370787	0.393258	0.4979
			Weighted	0.521739	0.434783	0.156769
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.659574	0.468085	0.081584
			Weighted	0.46875	0.385417	0.119709
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.155556	0.355556	0.081584
			Weighted	-0.45763	0.025424	0.020796
Proximity 1m	Sex	All	Unweighted	-0.19231	-0.02885	0.071386
			Weighted	-0.29258	-0.05677	0.071386
		Females (excl. M-M)	Unweighted	0.183099	0.042254	0.104379
			Weighted	0.006211	-0.01863	0.516697
		Males (excl. F-F)	Unweighted	0.12	0.093333	0.516697
			Weighted	0.087248	0.087248	0.516697
	Age	All	Unweighted	-0.25	-0.25	0.524095
			Weighted	-0.19651	-0.22271	0.409118
		Adults (excl. J-J)	Unweighted	-0.20408	-0.23469	0.353029
			Weighted	-0.12381	-0.21905	0.155169
		Sub-adults (excl. A-A)	Unweighted	0.733333	0.155556	0.061788
			Weighted	0.657658	0.135135	0.061788
	Rank	All	Unweighted	0.192308	0.355769	0.064254
			Weighted	0.004367	0.292576	0.064254
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.386667	0.4	0.473505
			Weighted	0.337662	0.376623	0.331591
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.661017	0.474576	0.064254
			Weighted	0.641026	0.452991	0.064254
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.661017	0.474576	0.064254
			Weighted	-0.15068	0.232877	0.064254
Proximity 5m	Sex	All	Unweighted	-0.01099	0.007326	0.068586
			Weighted	-0.10489	-0.09535	0.014877
		Females (excl. M-M)	Unweighted	0.184211	0.013158	0.012398
			Weighted	0.203526	0.136218	0.012398
		Males (excl. F-F)	Unweighted	0.5	0.083333	0.012597
			Weighted	0.271804	0.11939	0.012398
	Age	All	Unweighted	-0.23077	-0.2381	0.291742
			Weighted	-0.21335	-0.21692	0.139652
		Adults (excl. J-J)	Unweighted	-0.18919	-0.25097	0.018596
			Weighted	-0.14839	-0.17548	0.005999
		Sub-adults (excl. A-A)	Unweighted	0.764706	0.067227	0.013197
			Weighted	0.675127	0.266497	0.005999
	Rank	All	Unweighted	0.355311	0.373626	0.027461
			Weighted	0.15733	0.169249	0.019196
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.566265	0.373494	0.030622
			Weighted	0.433303	0.348666	0.027461
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.633987	0.398693	0.027461
			Weighted	0.574597	0.459677	0.026395
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.654676	0.42446	0.027461
			Weighted	0.340351	0.2	0.032993
	Sex	All	Unweighted	0	0	0.52009598

Recruiter-aggressor			Weighted	0.150685	0.077626	0.08818236
		Females (excl. M-M)	Unweighted	0.235955	0.044944	0.0239952
			Weighted	0.384615	0.087912	0.01339732
		Males (excl. F-F)	Unweighted	0.447368	0.131579	0.024995
			Weighted	0.546012	0.165644	0.01359728
	Age	All	Unweighted	-0.34545	-0.27273	0.08618276
			Weighted	-0.40639	-0.2968	0.05318936
		Adults (excl. J-J)	Unweighted	-0.30097	-0.27184	0.29954009
			Weighted	-0.35644	-0.29703	0.19676065
		Sub-adults (excl. A-A)	Unweighted	0.674419	0.116279	0.02839432
			Weighted	0.585366	0.121951	0.04079184
	Rank	All	Unweighted	0.254545	0.354545	0.05458908
			Weighted	0.296804	0.369863	0.08278344
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.492958	0.422535	0.15896821
			Weighted	0.462069	0.42069	0.23795241
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.661538	0.461538	0.03639272
			Weighted	0.700787	0.480315	0.03279344
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.44186	0.418605	0.44811038
			Weighted	0.573034	0.460674	0.13537293
Helper-recipient	Sex	All	Unweighted	-0.02703	0	0.33393321
			Weighted	0.080645	0.048387	0.3795241
		Females (excl. M-M)	Unweighted	0.384615	0.076923	0.03119376
			Weighted	0.55814	0.139535	0.0229954
		Males (excl. F-F)	Unweighted	0.241379	0.12069	0.14957009
			Weighted	0.27619	0.12381	0.13997201
	Age	All	Unweighted	-0.27027	-0.24324	0.3845231
			Weighted	-0.40323	-0.30645	0.11817636
		Adults (excl. J-J)	Unweighted	-0.25	-0.25	0.55128974
			Weighted	-0.38333	-0.31667	0.20555889
		Sub-adults (excl. A-A)	Unweighted	0.862069	0.172414	0.02539492
			Weighted	0.804878	0.170732	0.03519296
	Rank	All	Unweighted	0.027027	0.310811	0.01819636
			Weighted	0	0.306452	0.02179564
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.294118	0.372549	0.21235753
			Weighted	0.225806	0.333333	0.11937612
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.47619	0.428571	0.34833033
			Weighted	0.409836	0.409836	0.56588682
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.263158	0.368421	0.32333533
			Weighted	0.5	0.4375	0.4345131
Helper-opponent	Sex	All	Unweighted	-0.18919	-0.04054	0.0459908
			Weighted	-0.34426	-0.08197	0.02059588
		Females (excl. M-M)	Unweighted	0.132075	0.037736	0.12937413
			Weighted	0.111111	0.027778	0.21615677
		Males (excl. F-F)	Unweighted	0.176471	0.117647	0.29374125
			Weighted	-0.11111	0	0.1229754
	Age	All	Unweighted	-0.2973	-0.27027	0.31873625
			Weighted	-0.32787	-0.27869	0.24615077
		Adults (excl. J-J)	Unweighted	-0.26761	-0.26761	0.50929814
			Weighted	-0.30508	-0.27119	0.36152769
		Sub-adults (excl. A-A)	Unweighted	0.793103	0.172414	0.02779444
			Weighted	0.822222	0.2	0.02979404
	Rank	All	Unweighted	0.081081	0.324324	0.02819436
			Weighted	-0.08197	0.278689	0.01839632
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.2	0.333333	0.09918016
			Weighted	-0.09756	0.243902	0.03159368

		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.609756	0.463415	0.09778044
			Weighted	0.633333	0.466667	0.12077584
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.428571	0.428571	0.51689662
			Weighted	0.444444	0.444444	0.53509298
Commenter-handler	Sex	All	Unweighted	-0.37209	-0.06977	0.018796
			Weighted	-0.51111	-0.13333	0.010198
		Females (excl. M-M)	Unweighted	-0.19403	-0.0597	0.071386
			Weighted	-0.38028	-0.14085	0.029794
		Males (excl. F-F)	Unweighted	0.173913	0.108696	0.297341
			Weighted	0.073171	0.073171	0.557089
	Age	All	Unweighted	-0.39535	-0.30233	0.089582
			Weighted	-0.55556	-0.38889	0.038792
		Adults (excl. J-J)	Unweighted	-0.36585	-0.30488	0.186963
			Weighted	-0.54023	-0.4023	0.056989
		Sub-adults (excl. A-A)	Unweighted	0.733333	0.166667	0.033593
			Weighted	0.73913	0.173913	0.038392
	Rank	All	Unweighted	0.325581	0.360465	0.24815
			Weighted	0.411111	0.411111	0.54789
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.4	0.383333	0.471106
			Weighted	0.457627	0.40678	0.283943
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.708333	0.479167	0.039992
			Weighted	0.729167	0.479167	0.042791
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.771429	0.485714	0.043391
			Weighted	0.827957	0.526882	0.023995
Commenter-mother	Sex	All	Unweighted	-0.34783	-0.1087	0.040392
			Weighted	-0.5614	-0.17544	0.022595
		Females (excl. M-M)	Unweighted	-0.34783	-0.1087	0.040392
			Weighted	-0.5614	-0.17544	0.022595
		Males (excl. F-F)	Unweighted	1	0.266667	0.033993
			Weighted	1	0.28	0.036993
	Age	All	Unweighted	-0.43478	-0.32609	0.178764
			Weighted	-0.5614	-0.40351	0.077984
		Adults (excl. J-J)	Unweighted	-0.43478	-0.32609	0.178764
			Weighted	-0.5614	-0.40351	0.077984
		Sub-adults (excl. A-A)	Unweighted	1	0.153846	0.035593
			Weighted	1	0.2	0.035193
	Rank	All	Unweighted	0.304348	0.347826	0.331534
			Weighted	0.473684	0.421053	0.237552
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.428571	0.392857	0.418916
			Weighted	0.636364	0.454545	0.076985
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.642857	0.464286	0.114377
			Weighted	0.69697	0.484848	0.061588
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.7	0.5	0.121176
			Weighted	0.757576	0.515152	0.04859
Commenter-aggressor	Sex	All	Unweighted	0.066667	0.033333	0.329534
			Weighted	-0.04545	-0.02273	0.431114
		Females (excl. M-M)	Unweighted	0.28	0.06	0.04919
			Weighted	0.12	0.013333	0.20156
		Males (excl. F-F)	Unweighted	0.52381	0.166667	0.032793
			Weighted	0.527273	0.163636	0.054989
	Age	All	Unweighted	-0.43333	-0.3	0.083183
			Weighted	-0.56818	-0.34091	0.058788
		Adults (excl. J-J)	Unweighted	-0.40351	-0.29825	0.158168
			Weighted	-0.54762	-0.35714	0.090782
		Sub-adults (excl. A-A)	Unweighted	0.7	0.15	0.05159

			Weighted	0.652174	0.217391	0.09838
	Rank	All	Unweighted	0.266667	0.35	0.146371
			Weighted	0.227273	0.340909	0.155969
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.315789	0.368421	0.342332
			Weighted	0.283019	0.358491	0.325935
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.65	0.475	0.075385
			Weighted	0.59322	0.457627	0.152969
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.8	0.5	0.073785
			Weighted	0.8	0.533333	0.095581
Commenter-victim	Sex	All	Unweighted	-0.40984	-0.09836	0.025795
			Weighted	-0.45679	-0.11111	0.028194
		Females (excl. M-M)	Unweighted	-0.34545	-0.09091	0.040992
			Weighted	-0.39726	-0.12329	0.05239
		Males (excl. F-F)	Unweighted	0.5	0.166667	0.071986
			Weighted	0.466667	0.2	0.119576
	Age	All	Unweighted	-0.2459	-0.2459	0.532094
			Weighted	-0.30864	-0.25926	0.376525
		Adults (excl. J-J)	Unweighted	-0.22034	-0.23729	0.440712
			Weighted	-0.29114	-0.26582	0.475105
		Sub-adults (excl. A-A)	Unweighted	0.84	0.16	0.029994
			Weighted	0.866667	0.2	0.043991
	Rank	All	Unweighted	0.213115	0.344262	0.081184
			Weighted	0.037037	0.283951	0.052989
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.36	0.36	0.505099
			Weighted	0.16129	0.290323	0.243351
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.6	0.457143	0.120776
			Weighted	0.609756	0.463415	0.205359
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.526316	0.447368	0.224355
			Weighted	0.294118	0.372549	0.334733
Observation 1m	Sex	All	Unweighted	-0.05882	-0.01961	0.389522
		Females (excl. M-M)	Unweighted	0.333333	0.111111	0.10098
		Males (excl. F-F)	Unweighted	0.230769	0.128205	0.29774
	Age	All	Unweighted	-0.45098	-0.33333	0.242152
		Adults (excl. J-J)	Unweighted	-0.45098	-0.33333	0.242152
		Sub-adults (excl. A-A)	Unweighted	1	0.285714	0.066587
	Rank	All	Unweighted	0.019608	0.294118	0.068786
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.2	0.2	0.580884
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.666667	0.466667	0.176965
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.142857	0.285714	0.170566
Observation 5m	Sex	All	Unweighted	0.022222	0.022222	0.552689
		Females (excl. M-M)	Unweighted	0.460317	0.111111	0.035793
		Males (excl. F-F)	Unweighted	0.260274	0.123288	0.173365
	Age	All	Unweighted	-0.33333	-0.28889	0.330334
		Adults (excl. J-J)	Unweighted	-0.32584	-0.2809	0.369326
		Sub-adults (excl. A-A)	Unweighted	0.935484	0.225806	0.034993
	Rank	All	Unweighted	0.288889	0.355556	0.257748
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.777778	0.555556	0.173165
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.75	0.5	0.057788
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.378378	0.378378	0.553489

All: E-I index measures of all possible interactions among sex, age or rank classes. Females (F): E-I index measures of interactions involving females (i.e. excluding Male-Male interactions). Males (M): E-I index measures of interactions involving males (i.e. excluding Female-Female interactions). Adults (A): E-I index measures of interactions involving adults (i.e. excluding Sub-adult-Sub-adult interactions). Sub-adults (S): E-I index measures of interactions involving sub-adults (i.e. excluding Adult-Adult interactions). High: E-I index measures of interactions involving high-ranking individuals (excluding those not involving high-ranking individuals). Middle (Mid): E-I index measures of interactions involving middle-ranking individuals (excluding those not involving middle-ranking individuals). Low: E-I index measures of interactions involving low-ranking individuals (excluding those not involving low-ranking individuals). Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

Table D.2. E-I index measures and p-values for assortative mixing in TG.

Network	Attribute	Dyads	Type of network	E-I index	Median bootstrap	Adjusted p-value
Grooming	Sex	All	Unweighted	0.031915	0.021277	0.429114
			Weighted	0.039773	0.028409	0.429114
		Females (excl. M-M)	Unweighted	0.220126	0.075472	0.071386
			Weighted	0.192182	0.068404	0.071386
		Males (excl. F-F)	Unweighted	0.539683	0.150794	0.029394
			Weighted	0.605263	0.157895	0.029394
	Age	All	Unweighted	-0.52128	-0.53723	0.338132
			Weighted	-0.49432	-0.52273	0.313137
		Adults (excl. J-J)	Unweighted	-0.51087	-0.54348	0.291842
			Weighted	-0.48105	-0.5277	0.275545
		Sub-adults (excl. A-A)	Unweighted	0.836735	0.102041	0.053989
			Weighted	0.816327	0.102041	0.053989
	Rank	All	Unweighted	0.351064	0.340426	0.424915
			Weighted	0.284091	0.3125	0.297052
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.738095	0.47619	0.057703
			Weighted	0.679487	0.474359	0.057703
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.555556	0.37963	0.057703
			Weighted	0.400966	0.333333	0.191462
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.577236	0.414634	0.057703
			Weighted	0.637209	0.432558	0.057703
	Kinship	All	Unweighted	0.510638	0.654255	0.057703
			Weighted	0.295455	0.596591	0.057703
Huddling	Sex	All	Unweighted	0.087558	0.041475	0.184523
			Weighted	0.038095	0.02381	0.381124
		Females (excl. M-M)	Unweighted	0.325843	0.089888	0.031194
			Weighted	0.224719	0.067416	0.046491
		Males (excl. F-F)	Unweighted	0.503185	0.127389	0.031194
			Weighted	0.546099	0.148936	0.031194
	Age	All	Unweighted	-0.54839	-0.54839	0.503499
			Weighted	-0.51429	-0.52381	0.503499
		Adults (excl. J-J)	Unweighted	-0.53333	-0.55238	0.441812
			Weighted	-0.49127	-0.53117	0.272745
		Sub-adults (excl. A-A)	Unweighted	0.75	0.089286	0.064187
			Weighted	0.68595	0.090909	0.064187
	Rank	All	Unweighted	0.290323	0.317972	0.258171

			Weighted	0.304762	0.32619	0.29794
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.747126	0.482759	0.05856
			Weighted	0.701657	0.480663	0.05856
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.520661	0.371901	0.05856
			Weighted	0.513761	0.366972	0.05856
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.503356	0.389262	0.071486
			Weighted	0.552542	0.40339	0.05856
	Kinship	All	Unweighted	0.493088	0.64977	0.05856
			Weighted	0.352381	0.609524	0.05856
Proximity 1m	Sex	All	Unweighted	0.075	0.0375	0.171966
			Weighted	0.147727	0.056818	0.089262
		Females (excl. M-M)	Unweighted	0.387097	0.102151	0.019796
			Weighted	0.442857	0.114286	0.019796
		Males (excl. F-F)	Unweighted	0.409836	0.114754	0.019796
			Weighted	0.474453	0.131387	0.019796
	Age	All	Unweighted	-0.5	-0.52917	0.215157
			Weighted	-0.44886	-0.5	0.196041
		Adults (excl. J-J)	Unweighted	-0.48718	-0.53419	0.134973
			Weighted	-0.42773	-0.51032	0.109978
		Sub-adults (excl. A-A)	Unweighted	0.818182	0.075758	0.04859
			Weighted	0.763636	0.090909	0.04859
	Rank	All	Unweighted	0.208333	0.3	0.083126
			Weighted	0.221591	0.295455	0.10173
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.767442	0.488372	0.082983
			Weighted	0.788618	0.495935	0.082983
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.454545	0.356643	0.083126
			Weighted	0.474747	0.363636	0.083126
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.410256	0.365385	0.222955
			Weighted	0.414634	0.365854	0.222955
	Kinship	All	Unweighted	0.558333	0.670833	0.082983
			Weighted	0.511364	0.647727	0.082983
Proximity 5m	Sex	All	Unweighted	0.049488	0.025597	0.008598
			Weighted	0.06543	0.053397	0.008598
		Females (excl. M-M)	Unweighted	0.332611	0.03792	0.003899
			Weighted	0.384816	0.172369	0.0024
		Males (excl. F-F)	Unweighted	0.423611	0.059028	0.0024
			Weighted	0.395731	0.151396	0.0024
	Age	All	Unweighted	-0.56314	-0.55546	0.133653
			Weighted	-0.53622	-0.5277	0.128974
		Adults (excl. J-J)	Unweighted	-0.55517	-0.56386	0.112777
			Weighted	-0.52258	-0.52723	0.152769
		Sub-adults (excl. A-A)	Unweighted	0.848375	0.045126	0.006599
			Weighted	0.780558	0.006737	0.006599
	Rank	All	Unweighted	0.303754	0.321672	0.016886
			Weighted	0.232389	0.252946	0.007998
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.75048	0.426104	0.007998
			Weighted	0.750787	0.442417	0.007998
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.483266	0.327979	0.007998
			Weighted	0.478261	0.338211	0.007998
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.550898	0.35479	0.016886
			Weighted	0.42498	0.274939	0.027994
	Kinship	All	Unweighted	0.674061	0.701365	0.008855
			Weighted	0.590875	0.615944	0.007998
Observation 1m Blue/Yellow task	Sex	All	Unweighted	-0.28571	-0.05357	0.044991
		Females (excl. M-M)	Unweighted	0.73913	0.217391	0.032394

		Males (excl. F-F)	Unweighted	-0.24528	-0.0566	0.055589
	Age	All	Unweighted	-0.17857	-0.35714	0.090982
		Adults (excl. J-J)	Unweighted	-0.11538	-0.36538	0.040992
		Sub-adults (excl. A-A)	Unweighted	0.703704	0.074074	0.043791
	Rank	All	Unweighted	-0.03571	0.232143	0.046391
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	1	0.6	0.078784
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.419355	0.354839	0.29934
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.047619	0.238095	0.074985
	Kinship	All	Unweighted	0.392857	0.589286	0.058388
Observation 5m Blue/Yellow task	Sex	All	Unweighted	0.07177	0.043062	0.244951
		Females (excl. M-M)	Unweighted	0.723077	0.169231	0.003799
		Males (excl. F-F)	Unweighted	0.172775	0.073298	0.063587
	Age	All	Unweighted	-0.311	-0.45933	0.024795
		Adults (excl. J-J)	Unweighted	-0.29756	-0.47317	0.017796
		Sub-adults (excl. A-A)	Unweighted	0.894737	0.118421	0.009998
	Rank	All	Unweighted	0.291866	0.315789	0.265747
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.971831	0.521127	0.012597
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.564516	0.379032	0.026595
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.38255	0.355705	0.327335
	Kinship	All	Unweighted	0.569378	0.669856	0.034193
Observation 1m Push/Lift-up task	Sex	All	Unweighted	0.084746	0.050847	0.430514
		Females (excl. M-M)	Unweighted	0.560976	0.170732	0.058388
		Males (excl. F-F)	Unweighted	0.28	0.12	0.172366
	Age	All	Unweighted	-0.25424	-0.35593	0.224555
		Adults (excl. J-J)	Unweighted	-0.18519	-0.40741	0.09818
		Sub-adults (excl. A-A)	Unweighted	0.62963	0.111111	0.085983
	Rank	All	Unweighted	0.491525	0.389831	0.256549
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.833333	0.583333	0.132573
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.714286	0.428571	0.118776
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.647059	0.45098	0.10118
	Kinship	All	Unweighted	0.694915	0.694915	0.564487
Observation 5m Push/Lift-up task	Sex	All	Unweighted	0.164384	0.061644	0.069786
		Females (excl. M-M)	Unweighted	0.650485	0.15534	0.008798
		Males (excl. F-F)	Unweighted	0.328125	0.101563	0.026395
	Age	All	Unweighted	-0.35616	-0.45205	0.096781
		Adults (excl. J-J)	Unweighted	-0.31387	-0.47445	0.022396
		Sub-adults (excl. A-A)	Unweighted	0.678571	0.107143	0.026595
	Rank	All	Unweighted	0.438356	0.369863	0.104779
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.823529	0.5	0.022795
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.714286	0.415584	0.016197
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.54717	0.40566	0.04799
	Kinship	All	Unweighted	0.630137	0.678082	0.14997
Observation 1m	Sex	All	Unweighted	0	0	0.552889

Rotating-door task		Females (excl. M-M)	Unweighted	0.75	0.25	0.095781
		Males (excl. F-F)	Unweighted	0.076923	0.076923	0.523495
	Age	All	Unweighted	-0.42857	-0.5	0.419516
		Adults (excl. J-J)	Unweighted	-0.42857	-0.5	0.419516
		Sub-adults (excl. A-A)	Unweighted	1	0.25	0.113977
	Rank	All	Unweighted	-0.14286	0.214286	0.105779
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	1	0.666667	0.310938
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.5	0.5	0.537293
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	-0.07692	0.230769	0.138172
	Kinship	All	Unweighted	0.285714	0.571429	0.142172
Observation 5m Rotating-door task	Sex	All	Unweighted	0.173913	0.086957	0.191162
		Females (excl. M-M)	Unweighted	0.636364	0.212121	0.032194
		Males (excl. F-F)	Unweighted	0.35	0.125	0.068186
	Age	All	Unweighted	-0.26087	-0.3913	0.14997
		Adults (excl. J-J)	Unweighted	-0.2093	-0.4186	0.067986
		Sub-adults (excl. A-A)	Unweighted	0.7	0.1	0.04819
	Rank	All	Unweighted	0.217391	0.304348	0.205559
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.904762	0.571429	0.053389
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.666667	0.416667	0.178164
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.268293	0.317073	0.310138
	Kinship	All	Unweighted	0.347826	0.586957	0.059388

All: E-I index measures of all possible interactions among sex, age, rank or kinship classes. Females (F): E-I index measures of interactions involving females (i.e. excluding Male-Male interactions). Males (M): E-I index measures of interactions involving males (i.e. excluding Female-Female interactions). Adults (A): E-I index measures of interactions involving adults (i.e. excluding Sub-adult-Sub-adult interactions). Sub-adults (S): E-I index measures of interactions involving sub-adults (i.e. excluding Adult-Adult interactions). High: E-I index measures of interactions involving high-ranking individuals (excluding those not involving high-ranking individuals). Middle (Mid): E-I index measures of interactions involving middle-ranking individuals (excluding those not involving middle-ranking individuals). Low: E-I index measures of interactions involving low-ranking individuals (excluding those not involving low-ranking individuals). Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

APPENDIX E – Shapiro-Wilk Normality test results

Shapiro-Wilk normality tests were performed for node strength and all SNA metrics used in this thesis based on individual-level values: degree, disparity, clustering coefficient and flow betweenness. Normality was calculated for all datasets (Rimbach et al., 2015).

Table E.1. Results of the Shapiro-Wilk test for BDG.

Network	Node strength	Degree	Disparity	Clustering coefficient	Flow betweenness
Grooming	W: 0.93, p = 0.081	W: 0.95, p = 0.216	W: 0.61, p < 0.001*	W: 0.90, p = 0.023*	W: 0.94, p = 0.116
Huddling	W: 0.88, p = 0.007*	W: 0.94, p = 0.149	W: 0.93, p = 0.088	W: 0.95, p = 0.305	W: 0.88, p = 0.008*
Proximity 1m	W: 0.98, p = 0.833	W: 0.98, p = 0.787	W: 0.68, p < 0.001*	W: 0.97, p = 0.611	W: 0.89, p = 0.014*
Proximity 5m	W: 0.97, p = 0.665	W: 0.91, p = 0.024*	W: 0.74, p < 0.001*	W: 0.89, p = 0.009*	W: 0.92, p = 0.062
Recruiter-aggressor	W: 0.81, p < 0.001*	W: 0.94, p = 0.160	W: 0.93, p = 0.074	W: 0.96, p = 0.393	W: 0.90, p = 0.019*
Helper-recipient	W: 0.92, p = 0.063	W: 0.94, p = 0.119	W: 0.76, p < 0.001*	W: 0.94, p = 0.137	W: 0.78, p < 0.001*
Helper-opponent	W: 0.93, p = 0.102	W: 0.98, p = 0.958	W: 0.68, p < 0.001*	W: 0.96, p = 0.413	W: 0.88, p = 0.006*
Commenter-handler	W: 0.73, p < 0.001*	W: 0.94, p = 0.174	W: 0.87, p = 0.005*	W: 0.92, p = 0.055	W: 0.66, p < 0.001*
Commenter-mother	W: 0.66, p < 0.001*	W: 0.75, p < 0.001*	W: 0.88, p = 0.007*	W: 0.83, p < 0.001*	W: 0.48, p < 0.001*
Commenter-aggressor	W: 0.92, p = 0.044*	W: 0.93, p = 0.102	W: 0.80, p < 0.001*	W: 0.82, p < 0.001*	W: 0.67, p < 0.001*
Commenter-victim	W: 0.93, p = 0.089	W: 0.91, p = 0.028*	W: 0.85, p = 0.002*	W: 0.74, p < 0.001*	W: 0.57, p < 0.001*
Observation 1m	W: 0.83, p < 0.001*	W: 0.84, p < 0.001*	W: 0.87, p = 0.004*	W: 0.79, p < 0.001*	W: 0.66, p < 0.001*
Observation 5m	W: 0.89, p = 0.012*	W: 0.93, p = 0.082	W: 0.94, p = 0.170	W: 0.86, p = 0.002*	W: 0.85, p = 0.002*

W: Shapiro-Wilk statistic (if W is ~1, data follows a normal distribution; if W < 1, data may not follow a normal distribution). Shapiro-Wilk tests the null hypothesis that data is normally distributed. Therefore, if p < 0.05, the null hypothesis is rejected and there is evidence that the data is not normally distributed. *: indicates significant results.

Table E.2. Results of the Shapiro-Wilk test for TG.

Network	Node strength	Degree	Disparity	Clustering coefficient	Flow betweenness
Grooming	W: 0.95, p = 0.024*	W: 0.98, p = 0.467	W: 0.79, p < 0.001*	W: 0.87, p < 0.001*	W: 0.89, p < 0.001*
Huddling	W: 0.96, p = 0.076	W: 0.96, p = 0.081	W: 0.74, p < 0.001*	W: 0.98, p = 0.299	W: 0.96, p = 0.099
Proximity 1m	W: 0.95, p = 0.029*	W: 0.98, p = 0.443	W: 0.63, p < 0.001*	W: 0.96, p = 0.083	W: 0.94, p = 0.009*
Proximity 5m	W: 0.98, p = 0.383	W: 0.79, p < 0.001*	W: 0.26, p < 0.001*	W: 0.98, p = 0.437	W: 0.96, p = 0.075
Observation 1m blue/yellow task	NA	W: 0.77, p < 0.001*	NA	W: 0.74, p < 0.001*	W: 0.43, p < 0.001*
Observation 5m blue/yellow task	NA	W: 0.92, p = 0.002*	NA	W: 0.98, p = 0.445	W: 0.77, p < 0.001*
Observation 1m push/lift-up task	NA	W: 0.70, p < 0.001*	NA	W: 0.78, p = 0.002*	W: 0.49, p < 0.001*
Observation 5m push/lift-up task	NA	W: 0.85, p < 0.001*	NA	W: 0.97, p = 0.483	W: 0.75, p < 0.001*
Observation 1m rotating-door task	NA	W: 0.63, p < 0.001*	NA	W: 0.66, p = 0.002*	W: 0.27, p < 0.001*
Observation 1m rotating-door task	NA	W: 0.72, p < 0.001*	NA	W: 0.92, p = 0.169	W: 0.52, p < 0.001*

W: Shapiro-Wilk statistic (if W is ~1, data follows a normal distribution; if W < 1, data may not follow a normal distribution). Shapiro-Wilk tests the null hypothesis that data is normally distributed. Therefore, if p < 0.05, the null hypothesis is rejected and there is evidence that the data is not normally distributed. *: indicates significant results. NA: Not applicable (Note that measures of node strength and disparity are based on the strength of connections, a measure that was not available for observation networks in TG).

APPENDIX F – Affiliative network based on the Composite Sociality Index (CSI)

In animal societies, the frequency with which particular dyads engage in different types of socio-positive interactions are sometimes correlated. For instance, individuals that spent more time in proximity may also have frequent grooming interactions (Silk et al., 2013). The Composite Sociality Index (CSI) was originated by Sapolsky et al. (1997) as a solution to combine different interdependent social behaviours in one unbiased measure of sociality. The CSI is based on the relative frequencies of positively correlated affiliative relations and it was originally developed to measure the degree of social integration of individuals (Sapolsky et al., 1997). Later, Silk et al., (2006a) modified the index to measure the strength of dyadic affiliative relations. Since then, the CSI has been used in many primate studies to investigate the strength of dyadic affiliative relations depicted as a combination of different measures of affiliation (Silk et al., 2006a,b, 2009, 2010, 2013; Cheney et al., 2016; McFarland et al., 2017; Molesti & Majolo, 2017).

The CSI was calculated following the formula proposed by Silk et al. (2006a):

$$CSI = \frac{\sum_{i=1}^{d} \frac{SRI_{ixy}}{SRI_i}}{d}$$

where *d* is the number of behaviours that contribute to the index; SRI_{ixy} is the rate (calculated using the Simple Ratio Index or SRI, see ***Chapter 2***) of behaviour *i* for dyad *xy*; and SRI_i is the mean rate (SRI) of behaviour *i* across all dyads. The values of this index range from 0 to ∞. Accordingly, CSI measures the extent to which each dyad deviates from other dyads in their strength of affilative relations (Silk et al., 2009). High values of CSI represent dyads that have more frequent and/or longer lasting affiliative relations than the average dyad in the group. Low values, therefore, represent dyads that have less frequent and/or shorter affiliative relations than the average dyad in the group.

I calculated CSI for both groups of Barbary macaques (BDG and TG) combining measures of grooming, huddling and close proximity (1m). For each group, CSI was used to build a social network representing socio-positive relations as a combination of three interdependent (correlated) measures of affiliation: grooming, huddling and close proximity (see ***Chapter 3***). This new network was named 'affiliative (CSI) network'. Network visualization was conducted using the software NetDraw (see ***Figures F1*** & ***F2***). Affiliative (CSI) networks were described in terms of different SNA metrics: density, average degree, component ratio, disparity, clustering coefficient, Network Centralization Index (NCI) and assortative mixing (see ***Chapter 3*** and ***Table 2.7*** in ***Chapter 2***).

BDG (N = 25)

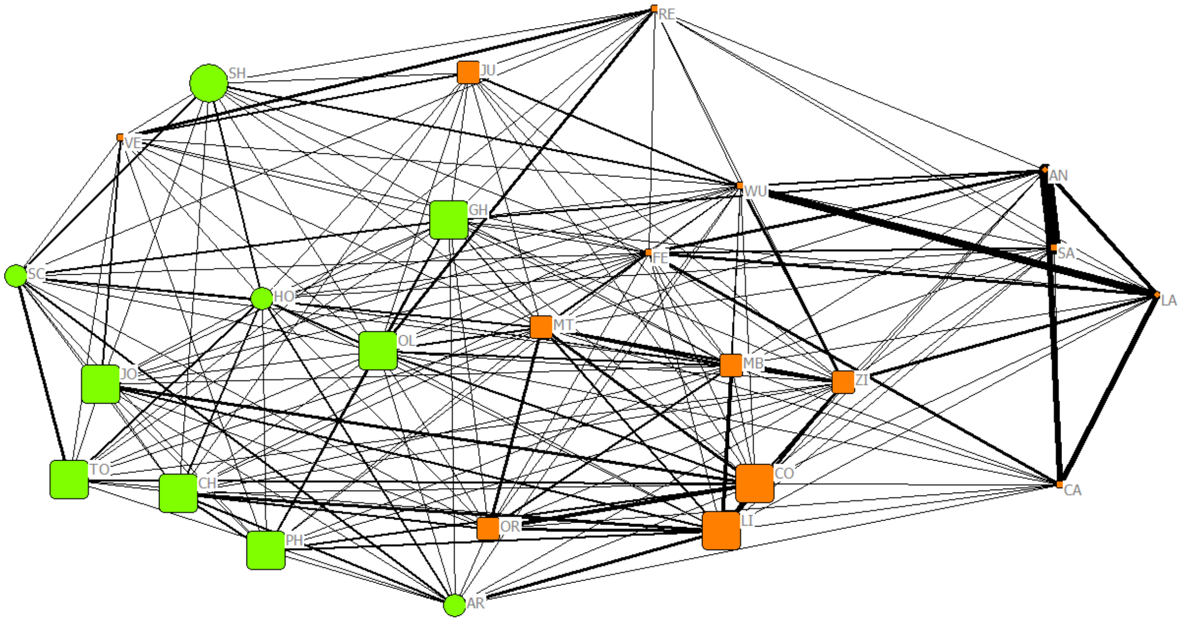


Figure F.1. Graph representation of the affiliative (CSI) network of BDG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads).

TG (N = 56)

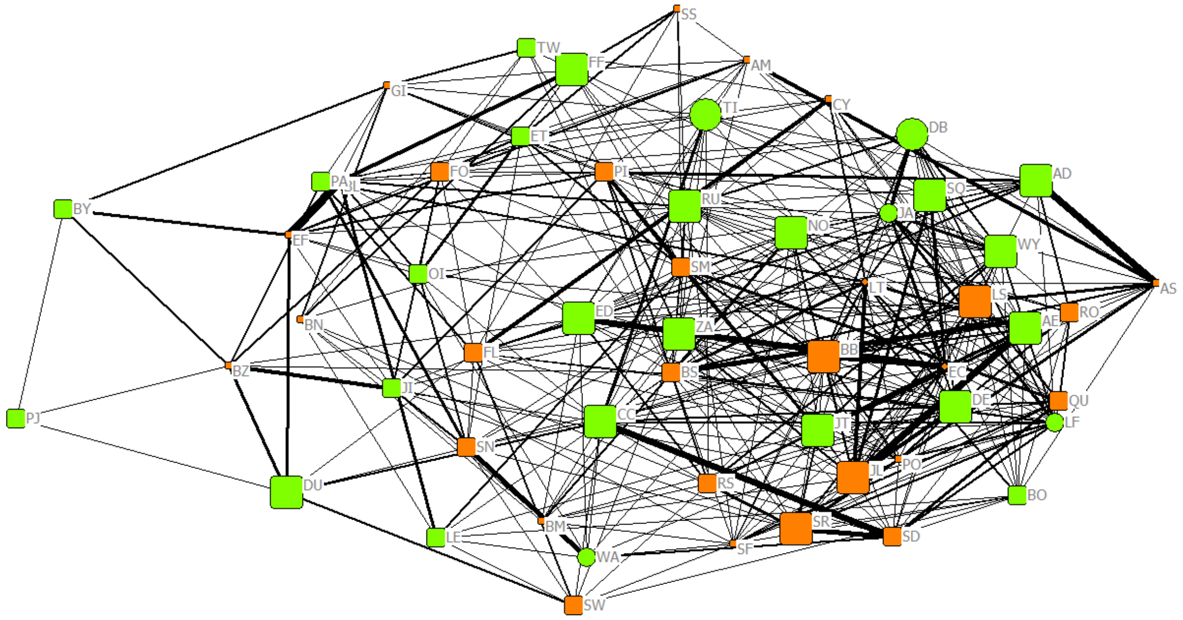


Figure F.2. Graph representation of the affiliative (CSI) network of TG. Colour: green = male, orange = female. Shape: square = adult, circle = sub-adult. Size: large = high rank, mid-size = middle rank, small = low rank. The thickness of the edges represents the strength of the relation (i.e. edge weights between dyads).

Density, average degree and clustering coefficient measures of the affiliative (CSI) networks were higher (indicating more cohesion and connectivity) than those of grooming, huddling and close proximity networks (see ***Table F.1*** and ***Table 3.1*** in ***Chapter 3***). This also suggests that grooming included affiliative relations not present in huddling and close proximity and vice versa, supporting the idea that each single affiliative behaviour represented different aspects of affiliative social relations. The lower disparity and NCI values of the affiliative (CSI) network indicate that social relations were less heterogeneous in this network than in grooming, huddling and close proximity (see ***Table F.1*** and ***Table 3.1*** in ***Chapter 3***). Despite this, the magnitude of these values was more similar to those of grooming, huddling and close proximity than to those of proximity within 5m, indicating that social relations depicted by the affiliative (CSI) network can be considered as asymmetric, suggesting that social diffusion will probably be influenced by individual identity (i.e. directed social learning, Coussi-Korbel & Fragaszy, 1995).

Results of assortative mixing also indicate an asymmetry of social relations (***Figure F.3***). In BDG, there was a general tendency to establish affiliative bonds with individuals of the same sex although this may be due to female-female interactions since males seemed to prefer female partners. Also, adults and sub-adults in BDG preferred to interact with adults and individuals showed a general preference for affiliates of the same rank although this only seems to be true for low-ranking individuals since high and middle-ranking macaques seemed to prefer partners of a different rank (***Table F.2***). In TG, both males and females preferred to interact with individuals of the opposite sex and a trend similar to that of BDG was observed in TG for age and social rank, with the exception that in TG, low-ranking individuals seemed to have stronger affiliative bonds with individuals of other rank classes (***Figure F.3***). Individuals in TG showed a significant preference to affiliate with kin-related conspecifics (***Table F.2***).

Table F.1. Group-level SNA metrics describing the social structure of the affiliative (CSI) network.

Network	Density	Degree	NC	CR	Disparity	CC	NCI (%)
AFF (CSI) BDG	0.657	15.76	1	0	0.1682937	0.733	2.098
AFF (CSI) TG	0.249	13.68	1	0	0.1580326	0.319	1.770

NC: Number of components. CR: Component ratio. CC: Clustering coefficient. NCI: Network Centralization Index. AFF (CSI): Network combining grooming, huddling and proximity within 1m.

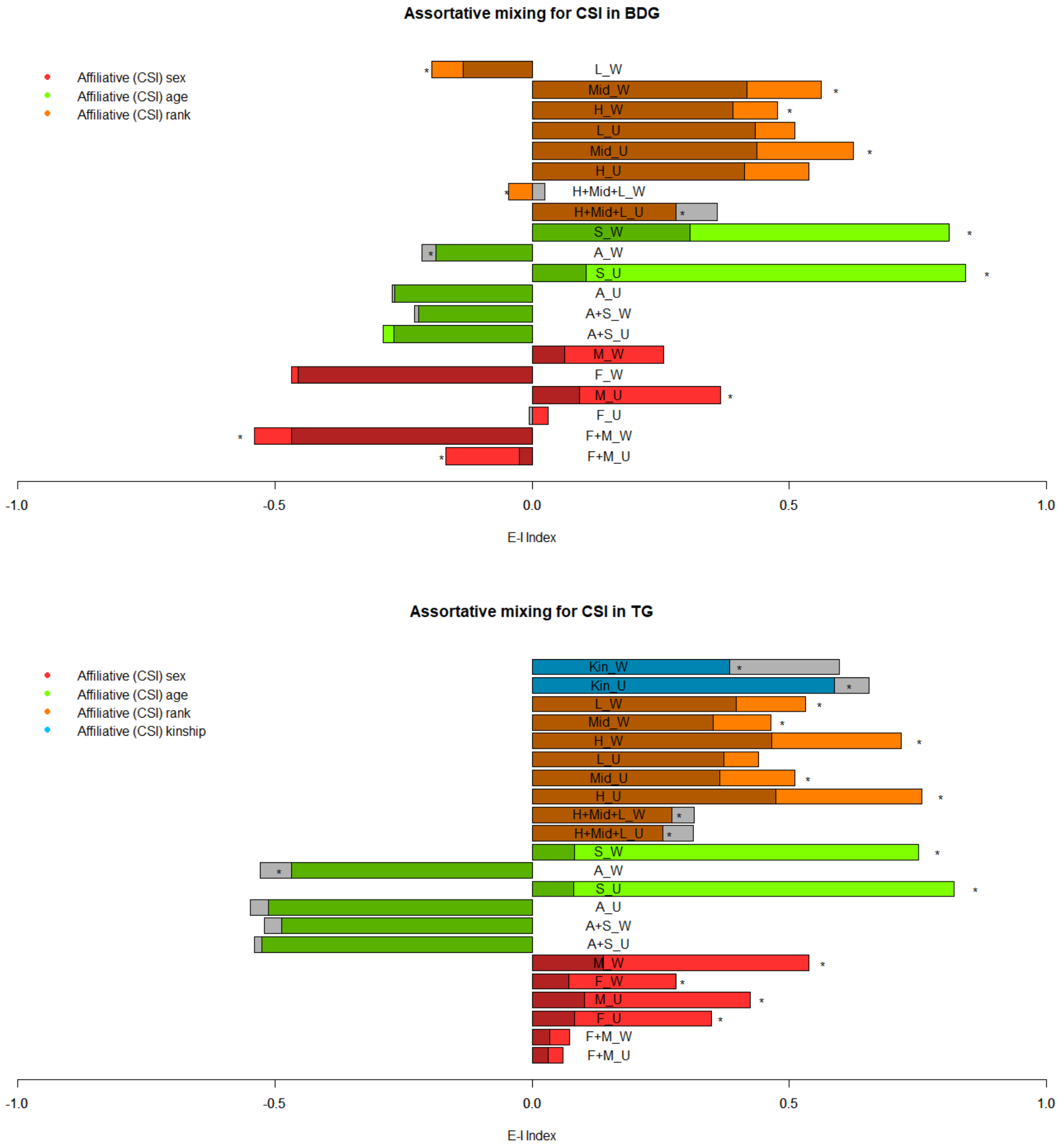


Figure F.3. Assortative mixing for affiliative (CSI) networks. U: Unweighted network. W: Weighted network. F+M: E-I index measures of all possible interactions among males and females. F: E-I index measures of interactions involving females (i.e. excluding M-M interactions). M: E-I index measures of interactions involving males (i.e. excluding F-F interactions). A+S: E-I index measures of all possible interactions among adults and sub-adults. A: E-I index measures of interactions involving adults (i.e. excluding S-S interactions). S: E-I index measures of interactions involving sub-adults (i.e. excluding A-A interactions). H+Mid+L: E-I index measures of all possible interactions among high, mid and low-ranking individuals. H: E-I index measures of interactions involving high-ranking individuals. Mid: E-I index measures of interactions involving middle-ranking individuals. L: E-I index measures of interactions involving low-ranking individuals. Kin: E-I index measures of all possible interactions among kin and non-kin. The grey bars (darker shades when overlapped with the coloured bars) represent the median of the bootstrapped values for the E-I index for each case. The * symbol in the plot indicates that the probability to obtain the observed result by chance was < 0.05. Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

Table F.2. E-I index measures and p-values for assortative mixing of affiliative (CSI) networks.

Network	Attribute	Dyads	Type of network	E-I index	Median bootstrap	Adjusted p-value
Affiliative (CSI) BDG	Sex	All	Unweighted	-0.16751269	-0.02538071	0.00979804
			Weighted	-0.5400641	-0.46794872	0.00219956
		Females (excl. M-M)	Unweighted	0.03144654	-0.00628931	0.14597081
			Weighted	-0.46753247	-0.45454545	0.17656469
		Males (excl. F-F)	Unweighted	0.36666667	0.09166667	0.03819236
			Weighted	0.25601751	0.06345733	0.05018996
	Age	All	Unweighted	-0.2893401	-0.26903553	0.16916617
			Weighted	-0.22115385	-0.22916667	0.15476905
		Adults (excl. J-J)	Unweighted	-0.26701571	-0.27225131	0.43171366
			Weighted	-0.18796992	-0.21470343	0.02339532
		Sub-adults (excl. A-A)	Unweighted	0.84210526	0.10526316	0.01019796
			Weighted	0.81005587	0.30726257	0.00179964
	Rank	All	Unweighted	0.27918782	0.36040609	0.01459708
			Weighted	-0.04647436	0.02403846	0.00159968
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.53719008	0.41322314	0.05918816
			Weighted	0.47672552	0.39004815	0.02559488
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.625	0.4375	0.0259948
			Weighted	0.56259905	0.41679873	0.01519696
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.51111111	0.43333333	0.16216757
			Weighted	-0.19524618	-0.13412564	0.0039992
Affiliative (CSI) TG	Sex	All	Unweighted	0.06005222	0.03133159	0.16016797
			Weighted	0.07295374	0.03380783	0.07878424
		Females (excl. M-M)	Unweighted	0.34883721	0.08305648	0.0059988
			Weighted	0.27889714	0.07104984	0.00779844
		Males (excl. F-F)	Unweighted	0.4245614	0.10175439	0.00759848
			Weighted	0.53826531	0.1377551	0.00339932
	Age	All	Unweighted	-0.52480418	-0.54046997	0.25594881
			Weighted	-0.48754448	-0.52135231	0.12997401
		Adults (excl. J-J)	Unweighted	-0.51336898	-0.54812834	0.07818436
			Weighted	-0.46814404	-0.52908587	0.02819436
		Sub-adults (excl. A-A)	Unweighted	0.82	0.08	0.0079984
			Weighted	0.75075988	0.08206687	0.00619876
	Rank	All	Unweighted	0.25326371	0.31331593	0.04959008
			Weighted	0.27224199	0.31494662	0.04579084
		High (excl. Mid-Mid, Low-Low, Mid-Low)	Unweighted	0.75675676	0.47297297	0.00939812
			Weighted	0.7173913	0.46521739	0.01239752
		Middle (excl. High-High, High-Low, Low-Low)	Unweighted	0.51111111	0.36444444	0.0169966
			Weighted	0.46388443	0.35152488	0.01539692
		Low (excl. High-High, High-Mid, Mid-Mid)	Unweighted	0.44	0.372	0.10077984
			Weighted	0.53174603	0.3968254	0.02419516
	Kinship	All	Unweighted	0.58746736	0.65425532	0.02859428
			Weighted	0.38434164	0.59659091	0.00519896

All: E-I index measures of all possible interactions among sex, age, rank or kinship classes. Females (F): E-I index measures of interactions involving females (i.e. excluding Male-Male interactions). Males (M): E-I index measures of interactions involving males (i.e. excluding Female-Female interactions). Adults (A): E-I index measures of interactions involving adults (i.e. excluding Sub-adult-Sub-adult interactions). Sub-adults (S): E-I index measures of interactions involving sub-adults (i.e. excluding Adult-Adult interactions). High: E-I index measures of interactions involving high-ranking individuals (excluding those not involving high-ranking individuals). Middle (Mid): E-I index measures of interactions involving middle-ranking individuals (excluding those not involving middle-ranking individuals). Low: E-I index measures of interactions involving low-ranking individuals (excluding those not involving low-ranking individuals). Regardless of whether the E-I Index is negative or positive (i) heterophily is indicated when it is greater than chance (i.e. bootstrapped values) and (ii) homophily when it is lower than chance (i.e. bootstrapped values).

CSI calculates the rate A and B are seen engaged in behaviour X compared to the mean rate of all dyads observed engaged in behaviour X. SRI calculates the rate A and B are seen engaged in behaviour X compared to the total number of sessions A and B have been observed but not engaged in that behaviour. Therefore, both CSI and SRI are indices based on relative measures that indicate how much a dyad differs from other dyads in the strength of relations (Whitehead, 2008; Silk et al., 2009). Consequently, networks based on CSI can be compared with networks based on SRI when we study relative differences or ranks (not absolute differences), as it is the case of the analyses used in this thesis (e.g. network regressions).

APPENDIX G – Data recording notes and key (ethogram) used to code task introductions

Event: Behavioural pattern of relatively short duration, which can be approximated as points in time, such as unsuccessful/successful task manipulations, walking by the task, etc. (see ***Table G.1***).

Bout: A bout was defined as the time a monkey approaches the task (within 0.5m from the task) until it leaves the task area (i.e. the monkey moves away further than 0.5m from the task because it is displaced by another monkey, leaves on own accord, task breaks, task is refilled, session ends).

Latency (duration) of recording: For each bout, latency was recorded in relation to initial approach within the task area (0.5m), initial interaction with the task, subsequent interactions with the task and bout duration. Minimum latency value = 1 second (i.e. if the event lasted less than a second it was still recorded as having 1 second latency).

Recording proximity of other monkeys around task: Proximity was recorded as being within 1, 3, 5 or 10m from the task.

- *Event level proximity:* Only recorded for monkeys up to and including a 10m proximity radius. A monkey was regarded as present from the first mention of it being present, until it was recorded as gone. If a monkey was noted coming in to proximity on camera before it was mentioned in the narrative, it was noted as being present from time of camera recorded sighting. If a monkey was mentioned in the proximity sweep that occurs immediately after a session commences, it was regarded as being present from the start of the session. If a monkey was not noted in a proximity sweep by the researcher it was regarded as gone, unless mentioned again as present shortly afterwards (i.e. it was missed during the proximity sweep).

- *Bout level proximity:* Recorded at the end of a bout. It included all monkeys who were in proximity at any point during the bout, even if they were beyond 10m. The proximity recorded at bout level was related to the closest distance that the animal approached to during the bout.

Attending behaviour of others in proximity during task manipulation: Attention was defined as head and/or gaze (if visible) oriented towards the individual manipulating the task. Unless the attending individual was close enough to be picked up by the camera, there was no continuous record of attending behaviours during task manipulation in TG. Attending, therefore, was only recorded for individuals within 10m who are either picked up by the camera or narrated as attending within 10m if camera was zoomed in on task. The experimental setup used in BDG with two cameras allowed recording all attention events of each task manipulation.

Table G.1. Event key

Event category	Shortened version	Description
Setup	Setup	"Setup" was recorded at 0mins if there were monkeys around potentially watching the task setup before filming. Attention and distance from task was recorded for monkeys around the task area during setup.
Arrive at task	Arrive	A monkey arrives at and stops within touching distance (0.5m) of vacant task
Arrive at task while other(s) also at task	Arrive-Oth	A monkey arrives at and stops within touching distance (0.5m) of task that is already occupied by another/others (identity and task manipulations of other individuals at task were recorded).
Leaves task	Leave	Individual at task moves back or away (individual's whole body moves beyond 0.5m from task) without being displaced or the session ending or task being broken/refilled. Time of leaving was recorded as time the monkey moved away 0.5m from the task (if the individual moved away to threaten or chase off another individual who was in proximity or approaching but then returned back to the task within 30s, the animal was not recorded as leaving the task).
Leaves task while other(s) also at task	Leave-Oth	Individual at task (while others at task too) moves back or away (individual's whole body moves beyond 0.5m from task) without being displaced or the session ending or task being broken/refilled. Time of leaving was recorded as time the monkey moved away 0.5m from the task (if the individual moved away to threaten or chase off another individual who was in proximity or approaching but then returned back to the task within 30s, the animal was not recorded as leaving the task). Identity and task manipulations of other individuals at task were recorded.
Leaves task after another approaching	App-leave	The individual currently at task is approached (within 1m) directly by another conspecific. The individual at task leaves task area immediately without showing submission to the approaching individual. Identity of individual approaching and identity and proximity of others in proximity was recorded. Time of leaving was recorded as time animal moves away further than 0.5m from task.
Displaced from task	Disp	Individual at task is displaced (i.e. threatened, chased off, etc., see ***Table 2.3*** in ***Chapter 2***) by another approaching (within 1m) individual. Time of leaving was recorded as time animal moves away further than 0.5m from task. Identity and distance from task of approaching individuals and others in proximity was recorded.
Bout	Bout	The duration in between which an animal arrived at and moved away further than 0.5m from the task area. End of bout can occur due to an individual leaving the task or being displaced, or due to session being ended or task being broken or refilled. Bout duration (latency) was recorded as well as the identity and distance from task of those up to 10m.
Task Broken - undergoes repair	Brok-R	Task is broken but undergoes repair at site. Attention, identity and distance from task of who was in proximity (up to 10m) during repair time was noted. Duration of repairing tasks (latency beginning from when individual is removed from task through to when task becomes re-available) was noted.
Task Broken - session ends	Brok-E	Task is broken and session ends as task has to be taken away for repair.
Refill	Refill	Refill was recorded when the task was being refilled with rewards. Identity and distance from task of individuals in proximity (up to 10m) were recorded. Duration of the refilling was recorded as time researcher approaches within 0.5m from task until researcher completes refill and moves further than 0.5m from task.

Threat	Threat	An individual known to be situated in proximity (up to 10m) to task is threatened by an animal who is at task. Identity, proximity and behaviour (e.g, displays submission, moves away, etc., see ***Table 2.3*** in ***Chapter 2***) of the individual being threatened was recorded.
Walk by- attend to task	Wkby-AT	Individual passes by vacant foraging task and orients gaze in direction of task but does not approach to touching distance (0.5m) and/or stop to inspect/manipulate the task. Proximity (up to 10m) of any nearby individuals to task was recorded. Duration of event was recorded as the time the individual 1st orients its gaze towards task until it stops looking at task.
Walk by- not attend to task	Wkby-NA	Individual passes by touching distance (0.5m) of vacant foraging task but does not orient gaze in direction of task or stop to inspect/manipulate the task. Proximity (up to 10m) of any nearby individuals to task was recorded. Duration of event was recorded as the time the individual reaches touching distance of task until it moves away further than 0.5m from task.
Walk by focal - attend	WkbyFo-AT	Individual passes by an occupied foraging task and orients gaze in direction of task but does not approach to touching distance (0.5m) and/or stop to inspect/manipulate the task. Proximity (up to 10m) of any nearby individuals to task was recorded. Duration of event was recorded as the time the individual 1st orients its gaze towards task until it stops looking at task.
Walk by focal - not attend	WkbyFo-NA	Individual passes by touching distance (0.5m) of an occupied foraging task but does not orient gaze in direction of task or stop to inspect/manipulate the task. Proximity (up to 10m) of any nearby individuals to task was recorded. Duration of event was recorded as the time the individual reaches touching distance of task until it moves away further than 0.5m from task.
Pick-up and eat raisins dropped by previous individual/s	Pic-Eat	An individual was said to pick up and eat raisins dropped by others if when approaching or walking close to the task (within 0.5m of task) it stops, picks up and consumes raisins from the floor or the outside of the task before it manipulates the task for itself. This was recorded for each bout of eating that an animal partakes in during any test session. Also, number of handfuls consumed was noted.
Initial interaction	InInt	Exploratory behaviours involving inspecting, touching, biting, leaning-on and pulling the task (including the option holes) prior to animal's 1st successful retrieval (i.e. contact/inspect but not insert hand inside option hole). A series of initial interactions were possible before a successful task manipulation took place. It begins when an animal first contacts/inspects the task and ends when the animal breaks contact or visual inspection with the task (see qualifier in ***Table G.2*** for initial interactions below). Duration was recorded.
Subsequent interaction	SubInt	Exploratory behaviours involving inspecting, touching, biting, leaning-on and pulling the task (including the option holes) after 1st successful interaction. It begins when an animal contacts/inspects the task at the beginning of each bout or between successful and unsuccessful manipulations, and ends when the animal breaks contact or visual inspection with the task (see qualifier in ***Table G.2*** for initial interactions below). Duration was recorded.
Insert-successful (i.e. successful manipulation of the task)	Ins-S	A manipulation that results in raisins being retrieved from inside the task. It starts at the time the monkey places its hand(s) into an option hole, and ends at the point the monkey removes its hand from within the task and it is observed consuming the reward retrieved.
1st-Insert-successful (i.e. first successful manipulation of the task)	1stIns-S	An animal's 1st manipulation that results in raisins being retrieved from inside the task. It starts at the time the monkey places its hand(s) hand into an option hole, and ends at the point the monkey removes its hand from within the task and it is observed consuming the reward retrieved for the first time.
Insert-unsuccessful (i.e. unsuccessful manipulation of the task)	Ins-U	A monkey places its hand(s) into option hole but does not retrieve raisins from the task. Insert was only recorded if whole hand was placed inside option hole. It starts at the time the monkey places its hand(s) hand into an

		option hole, and ends at the point the monkey removes its hand from within the task but it is not observed consuming any reward.
Insert-unknown	Ins-UK	This category was recorded when the researcher observed a task manipulation but, because of the video angle, it was not possible to determine whether the manipulation was successful or not.
Uknown	UKnwn	A monkey is at the task but due to camera view angle and/or monkey's position it is not possible to discern anything about the monkey's behaviour. Duration of this event was noted.

Table G.2. Qualifier: Task details on initial and subsequent interactions.

Specific actions	Shortened version	Description
NA	NA	NA entered when action data was not available
Visually inspect	VisInsp	An individual orients gaze towards task and appears to visually inspect the task or option holes. The part of the task that was being inspected was noted (front, back, left or right side, option holes). This behavioural category was only noted when visual inspection was unambiguous (i.e. the animal clearly moves head and gaze direction toward task). If the individual moved gaze to a different region of task (e.g. a different option hole), this was recorded as a new event. If the individual diverted gaze away from task then back again to same place, this was also recorded as a new event.
Manual exploration	Man	An individual directs attention/behaviour towards the task box and touches or inspects task box with one or both hands. The part of the task that was being manipulated was noted (front, back, left or right side, option holes). If the individual shifted manual inspection from one area of task to another (e.g. from one option hole to another), this was recorded as a new event. If the individual removed hand from box briefly then put it back in same position, this was recorded as a new event.
Manual exploration and visual inspection	Man&Vis	An individual manually interacts/touches task whilst making clear visual inspection of a separate part of the task (e.g. hand on side of task or blue option hole whilst visually inspecting yellow option hole). The parts of the task that were being inspected and manipulated were noted (front, back, left or right side, option holes). If the individual shifted visual and/or manual inspection from one area of task to another (e.g. from one option hole to another), this was recorded as a new event. If the individual diverted gaze away and/or removed hand from box briefly then put it back to the same place, this was recorded as a new event.
Rest hand(s) on task	Handrest	If animal has hand(s) rested on task but does not appear to focus attention/behaviour towards task (i.e. it is looking to a different direction or focused on itself or another) then where this occurs for longer than 2 seconds was recorded as resting hands on task.
Sit/lean	Sit/lean	An individual sits or leans body on task box.
Mouth/Bite	Mouth/Bite	An individual interacts with task using mouth.
Pull task	Pull	An individual pulls task with hand(s).

APPENDIX H – Comparative analyses of task option preferences to choose a preference criterion threshold

In Chapter 5, I tested whether individuals showed a preference for one of the two available solving-options in each task using a chi-square analysis. The analysis was based on considering that individuals showed a preference for one option if the number of times they used that option (calculated as the percentage of use of that option) was above a threshold. I used the same chi-square analysis used in Chapter 5 to test option preferences using different percentages of use to establish that threshold value. Options used a % of times above the threshold were considered the individual's task-option preference. If none of the options was used a % of times above the threshold considered in each case, individuals were considered to have 'No preference' for any of the task options available. Results of the chi-square tests can be seen in ***Tables H.1*** to ***H.3***.

Table H.1. Chi-square results for the blue/yellow task.

Criteria	Blue	Yellow	No preference	χ^2	p-value	Post-hoc (p-value)
>50%	15	18	1	14.529	0.0006998*	Y-B: 0.60151 Y-N: 0.00029* B-N: 0.00070*
>55%	7	15	22	7.6818	0.02147*	Y-B: 0.132 Y-N: 0.250 B-N: 0.016*
>60%	4	10	20	11.529	0.003136*	Y-B: 0.1088 Y-N: 0.1018 B-N: 0.0033*
>65%	2	9	23	20.176	4.157e-05*	Y-B: 0.035* Y-N: 0.020* B-N: 8e-05*
>70%	2	7	25	25.824	2.469e-06*	Y-B: 0.0956 Y-N: 0.0022* B-N: 2.9e-05*
>75%	2	7	25	25.824	2.469e-06*	Y-B: 0.0956 Y-N: 0.0022* B-N: 2.9e-05*
>80%	2	3	29	41.353	1.048e-09*	Y-B: 0.65 Y-N: 6.5e-06* B-N: 3.7e-06*

B: Blue option. Y: Yellow option. N: No preference. The post-hoc column informs about the p-values after pair-wise comparisons and Benjamini-Hochberg correction. *: indicates significant results.

Table H.2. Chi-square results for the push/lift-up task.

Criteria	Push	Pull	No preference	χ^2	p-value	Post-hoc (p-value)
>50%	15	12	1	11.643	0.002963*	L-P: 0.5637 L-N: 0.0034* P-N: 0.0014*
>55%	15	12	1	11.643	0.002963*	L-P: 0.5637 L-N: 0.0034* P-N: 0.0014*
>60%	14	12	2	8.8571	0.01193*	L-P: 0.6949 L-N: 0.0113* P-N: 0.0081*

>65%	14	11	3	6.9286	0.0313*	L-P: 0.549 L-N: 0.049* P-N: 0.023*
>70%	14	11	3	6.9286	0.0313*	L-P: 0.549 L-N: 0.049* P-N: 0.023*
>75%	12	11	5	3.0714	0.2153	NA
>80%	10	7	11	0.92857	0.6286	NA

P: Push option. L: Lift-up option. N: No preference. The post-hoc column informs about the p-values after pair-wise comparisons and Benjamini-Hochberg correction. *: indicates significant results. NA: Not applicable (chi-square test not significant).

Table H.3. Chi-square results for the rotating-door task.

Criteria	Clockwise	Counter-clockwise	No preference	χ^2	p-value	Post-hoc (p-value)
>50%	7	9	0	8.375	0.01518*	W-C: 0.6171 W-N: 0.0081* C-N: 0.0122*
>55%	6	9	1	6.125	0.04677*	W-C: 0.439 W-N: 0.034* C-N: 0.088
>60%	6	9	1	6.125	0.04677*	W-C: 0.439 W-N: 0.034* C-N: 0.088
>65%	6	9	1	6.125	0.04677*	W-C: 0.439 W-N: 0.034* C-N: 0.088
>70%	6	8	2	3.5	0.1738	NA
>75%	5	8	3	2.375	0.305	NA
>80%	5	8	3	2.375	0.305	NA

C: Clockwise option. W: Counter-clockwise option. N: No preference. The post-hoc column informs about the p-values after pair-wise comparisons and Benjamini-Hochberg correction. *: indicates significant results. NA: Not applicable (chi-square test not significant).

In general, results showed that except for 50% (an extremely optimistic threshold) in the blue/yellow task, outcomes were not overly sensitive to which preference threshold criteria was used. Although option preferences for each category did not differ among the % thresholds tested for the rotating-door task (see ***Table H.3***), the chi-square analysis only did not detect differences among preference categories for the three most conservative values (>70%, >75% and >80%). In general, results indicate that the 60% criterion for option preferences used in this thesis was an intermediate value (not too optimistic like 50% nor too conservative like 80%) that allowed detection of option preferences in all tasks.

APPENDIX I – Detailed description of the qualitative sound analysis of the vocalizations used in the thesis

Aid-recruitment calls

A total of 70 recordings of 20 individuals (80% of the BDG group excluding infants; 7 males and 13 females) were reviewed. Of all these recordings, 50 (ranging from 1 to 11 recordings per subject) of 18 individuals (5 males and 13 females) were classified as of 'good quality' (see ***section 4.2.2*** in ***Chapter 4*** for further details). During the recording sessions subjects were involved in conflicts, which meant that they were constantly moving and, therefore, the distance between the caller and the microphone as well as the direction of the sound from the source varied significantly. Consequently, not all the calls of each 'good quality' recording qualified as measurable in order to be inspected. The number of potentially measurable calls of each 'good quality' recording was counted using the Band Limited Energy Detector (BLED) tool plus a visual and acoustic inspection of the calls in the spectrograms. This made a total of 975 calls (ranging from 4 to 496 calls per subject).

Visual and acoustic inspections suggested that there was some variation in the structure of the calls which might indicate that the monkeys either combined different types of calls or the calls were formed of different acoustic elements (e.g. harmonics or some acoustic phenomena like biphonation or deterministic chaos, Wilden et al., 1998). When the calls were short, the signals showed a harmonic structure, typical of tonal sounds. When the calls were long, they were often preceded by these harmonic elements, but the main part of the structure was chaotic. Some pant barks (as defined in Barbary macaques by Fischer & Kammerschmidt, 2002) were identified, mainly at the end of the call bouts. Oral notes recorded during sessions suggested that the structure of the calls and the presence of some acoustic elements might depend on the level of aggression or the level of arousal (i.e. perceived aggression) of the caller. When the levels of aggression were high (i.e. physical aggression) or perceived as high (i.e. the target of the aggression exhibited fear and submission behaviours), the calls were longer and more chaotic than in other contexts. Pant barks seemed to occur when the aggression had stopped, likely, because the victim was still aroused.

After visual and acoustic inspection of the calls, I classified calls produced during conflicts into two different categories (types) based on small variations in their structure and in how the different acoustic elements were combined:

- **Type 1:** Squeaks and modulated tonal screams accompanied by pants or pant barks, normally at the end of the bout. Variants of this type can be seen in ***Figure I.1***.

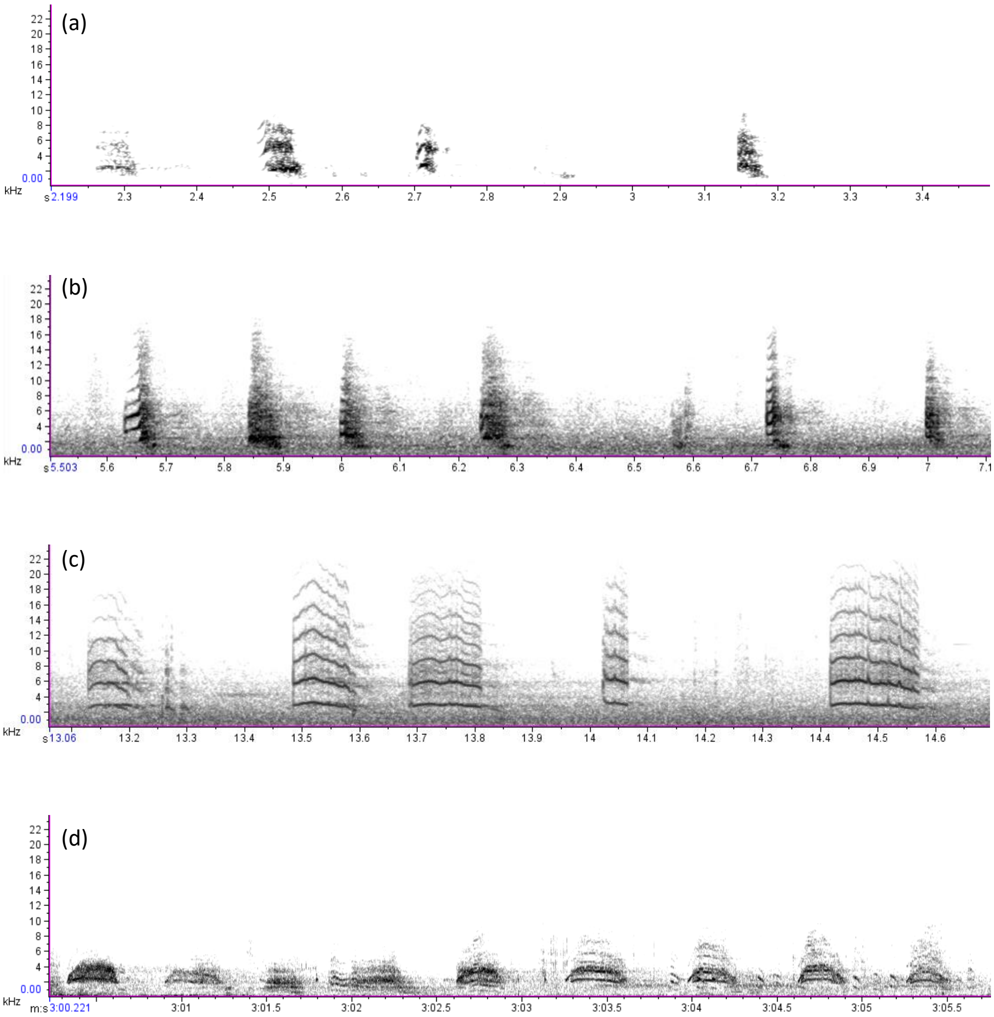


Figure I.1. Type 1 variants (aid-recruitment calls). (a) Type 1.1. Pant barks with some modulation and tonal elements. Context: A middle-ranking adult female (MB) was displaced by a high-ranking adult female (LI). Both females immediately reconciled by performing an anti-parallel position behaviour (as defined by Call & Tomasello, 2007). (b) Type 1.2. Rasping squeaks. Context: A middle-ranking adult female (MB) grooming a high-ranking adult female (LI) was displaced by a high-ranking adult male (CH). The vocalization was accompanied by searching behaviours (i.e. standing up and/or stretching neck while looking around or orienting head or gaze towards particular conspecifics). (c) Type 1.3. Clear and modulated screams. Context: A low-ranking adult female (FE) was threatened by a high-ranking adult male (GH). The low-ranking female was looking around while vocalizing. (d) Type 1.4. Clear squeaks. Context: A high-ranking adult male (GH) threatened a high-ranking sub-adult male (SH).

- **Type 2:** Complex screams, characterized by a rasping sound, sometimes preceded by modulated tonal screams that gradually or abruptly switched into these complex screams. Variants of type 2 are depicted in ***Figure I.2***.

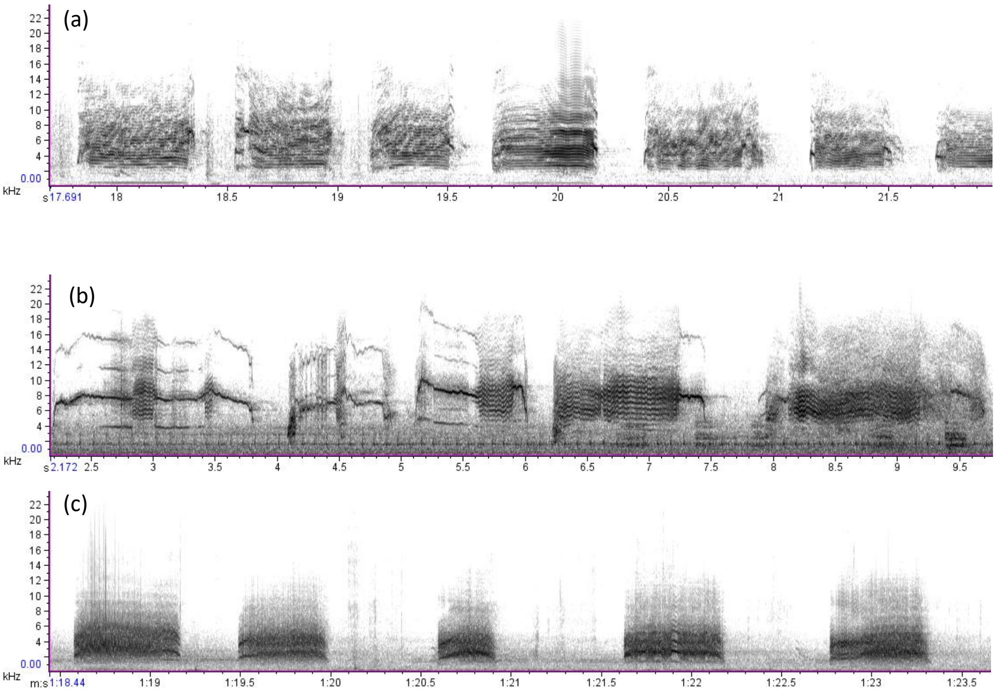


Figure I.2. Type 2 variants (aid-recruitment calls). (a) Type 2.1. Hoarse scream. At a slow rate, it sounds like a long haw (like the bray of a donkey). Context: A low-ranking adult female (FE) was being displaced from a food patch and chased by a high-ranking adult male (GH). The female was backed up by another high-ranking adult male (PH). (b) Type 2.2. High-pitched scream. It occurs at higher frequencies than type 2.1., and it sounds like a high-pitched whistle tone (not hoarse). Context: A middle-ranking juvenile male (AR) challenged a middle-ranking sub-adult male (HO) that had threatened him. (c) Type 2.3. Long and high-pitched screech. It is similar to other types 2, but the rasping element is different. While in types 2.1 and 2.2 the vibration of the sound seems to be placed down the throat (chest sound), in type 2.3 macaques seem to place the vibration up in the throat (nasal sound). This can be detected by slowing down the playback rate of the signal in the software. Context: A high-ranking adult male (PH) screamed at the alpha male (JO) who was threatening him. When the former alpha male (TO, also a high-ranking adult male) approached, the alpha male (JO) teeth-chattered to the caller (PH).

Type 2 variants seemed to occur in contexts where individuals received higher aggression (e.g. being chased instead of receiving facial threats, agonistic encounters occurring between high-ranking individuals or requiring the intervention of third parties) than in contexts where type 1 variants were produced (e.g. displacements or encounters followed by immediate reconciliation). Overall, it seems that when levels of aggression were low or perceived as low, calls characteristically belonged to type 1. Increased levels of aggression or arousal led to types 1 followed by types 2 (***Figure I.3***). In these signals where types 2 followed types 1, it was common to find types 1 isolated or even types 2 without the gradual shift from types 1. The following combinations were the most common ones: a) Type 1.2 starting at low frequencies and going up before turning into a type 2, b) Type 1.3 starting at low frequencies, going up and then down again before turning into type 2.

Type 1.1 was generally found isolated and it is likely a short complaint produced when levels of aggression or arousal were low. Type 1.4 was only seen in males, always isolated (not combined with other types) and in intervals between isolated types 1 or 2, or combinations of these two types. Other call types appeared normally at the end, but also in the middle of these calls, like pant barks or rasping calls. Pant barks were probably produced when the levels of aggression or arousal decreased (most likely, at the end of the conflict). Rasping calls generally occurred when others backed up the victim and challenged the aggressor or when an ally approached (these calls may be vocal comments performed during agonistic encounters, see ***Chapter 4***).

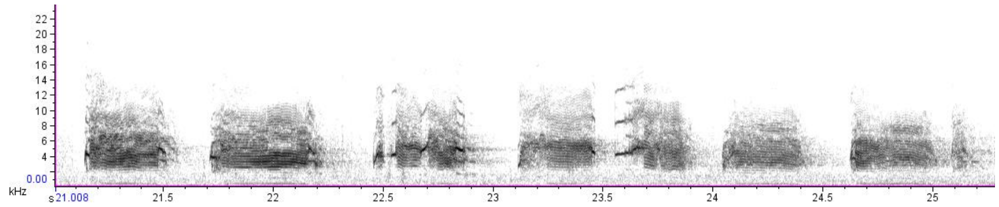
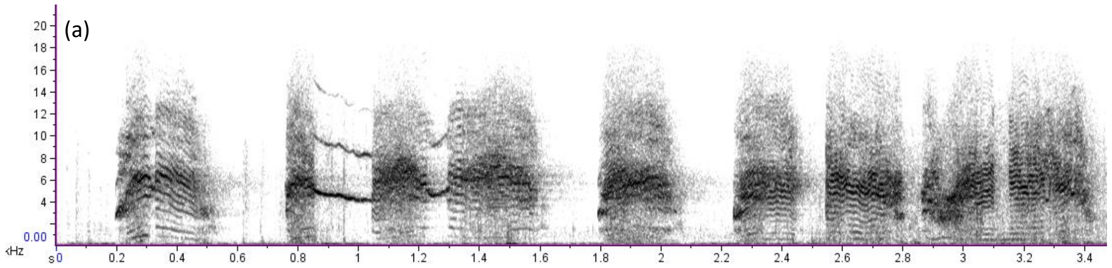


Figure I.3. Aid-recruitment calls that combine elements of types 1 and 2. In this example, a high-ranking adult male (GH) threatened and chased a low-ranking adult female (FE) that screamed while running away and shifting her head and gaze between the aggressor and a high-ranking adult male (PH) present in the vicinity. The high-ranking male in the audience (PH) ended up backing up the female by lunging at her rival.

The recorded calls were compared with the audio files of Barbary macaques provided by Julia Fischer and the spectrograms obtained from these files (***Figure I.4***) and presented in Fischer & Hammerschmidt (2002). Audio and visual inspection of the recordings and the temporal and acoustic features of the spectrograms showed that types 2 highly resembled aid-recruitment calls described in previous studies of this same species (see ***Figures I.2*** & ***I.4***). Types 1, on the other hand, resembled calls that Fischer & Hammerschmidt (2002) described in agonistic contexts performed by individuals that had been chased, attacked, displaced or disturbed, but no searching behaviours were reported during vocalizations.



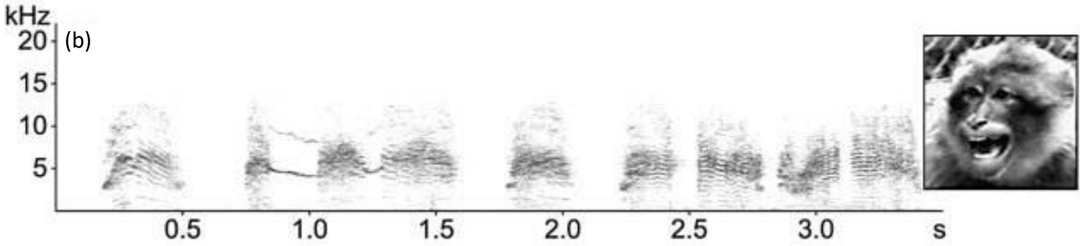


Figure I.4. Spectrogram of an aid-recruitment call described in Fischer & Hammerschmidt (2002). It depicts complex screams from a 3.5-year-old male who challenged a female and appeared to recruit support from allies. (a) A spectrogram of the call obtained using the audio file provided by Julia Fischer and visualized in Raven Pro 1.5 Interactive Sound Analysis Software. (b) A spectrogram of the same vocalization as presented in Fischer & Hammerschmidt (2002).

According to my observations, types 1 seemed to occur during events where levels of aggression were low or perceived as low, so it is likely that no help was required in these situations and the calls were directed at the aggressor (I labelled them as 'complaints'). However, the qualitative analysis here presented, showed that types 1 normally preceded types 2, which suggests that an escalating perception of the tension or aggressiveness generally occurred and, at some point, it triggered the urgency to recruit allies. Since the shift and the distinction between the two call types may be difficult to perceive during observational sessions (especially when calls are of short duration), both types were considered as aid-recruitment calls only if they were accompanied by searching behaviours.

Vocal comments

A total of 50 recordings of vocal comments performed by 17 individuals (68% of the BDG group excluding infants; 13 females and 4 males) were visually and acoustically inspected. This first inspection of the audio files revealed a diversity of call types that fell into the definition of vocal comment (Brumm et al., 2005). Fischer & Hammerschmidt, (2002) described 3 different call types in Barbary macaques that may be considered commenting behaviour: soft pants, rasping calls and pant barks (***Figure I.5***). Brumm et al. (2005) presented spectrograms of 4 types of vocal comments in Barbary macaques (***Figure I.6***) that were only described in terms of their frequency range and duration. The authors highlighted the great variability of the spectral characteristics of these calls and found that vocal comments uttered in agonistic contexts were significantly longer than those produced during affiliative interactions (Brumm et al., 2005).

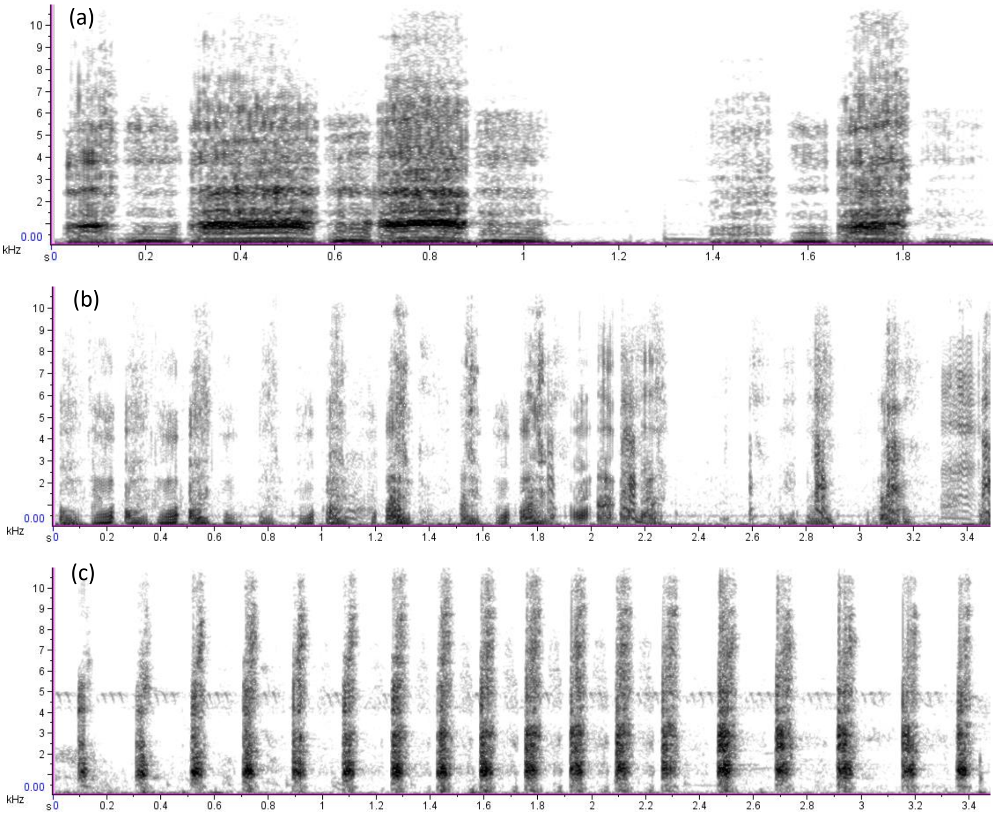


Figure I.5. Call types presented in Fischer & Hammerschmidt (2002) that were defined as commenting behaviour in Barbary macaques. All spectrograms were visualized in Raven Pro 1.5 Interactive Sound Analysis Software using the audio files provided by Julia Fischer. (a) Rasping call of an adult female who observed a fight in a distance. (b) Low frequency soft pants given by a sub-adult female who observed an interaction with an infant. (c) Pant barks from an adult female who observed an interaction with an infant.

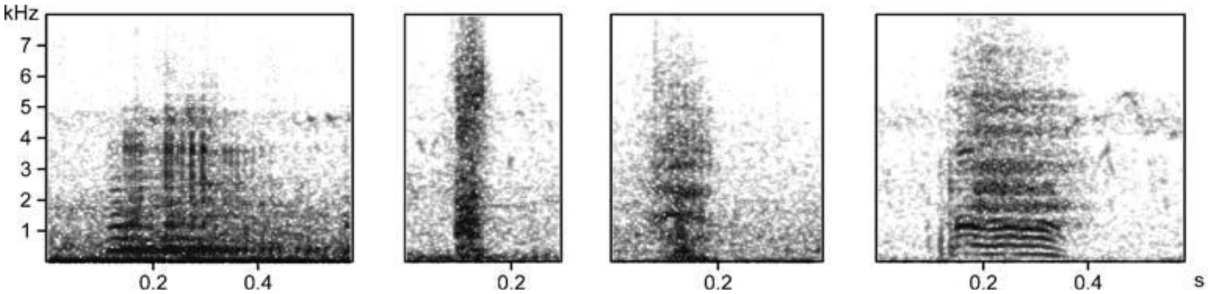


Figure I.6. Spectrograms of vocal comments illustrated in Brumm et al. (2005). According to the authors, the majority of these vocalizations were uttered in series (median of calls/series = 7, interquartile range = 3 – 16) and were of low power.

Due to the low volume of these vocalizations and the difficulty of anticipating their occurrence, some calls were not captured or were recorded too far away from the source. Only 28 of the 50 preliminary recordings could be considered of ‘good quality’. The visual and spectral inspection of the calls in these good quality recordings revealed four main types of vocalizations (***Figure I.7***). In agreement with Brumm et al. (2005)’s findings, vocal comments in agonistic contexts were longer than those produced in affiliative situations (***Figure I.7***). Moreover, audio and visual comparisons of the recordings and the spectrograms indicated that the vocal comments collected during agonistic encounters resembled the rasping calls defined in Fischer & Hammerschmidt (2002) and the long calls described by Brumm et al. (2005) in agonistic contexts (***Figures I.5-I.7***). Also, the vocalizations triggered by the observation of infant-handling interactions could be labelled as soft pants and pant barks as per Fischer & Hammerschmidt (2002) and showed spectral similarities with the short vocal comments Brumm et al.(2005) recorded during affiliative contexts (***Figures I.5-I.7***).

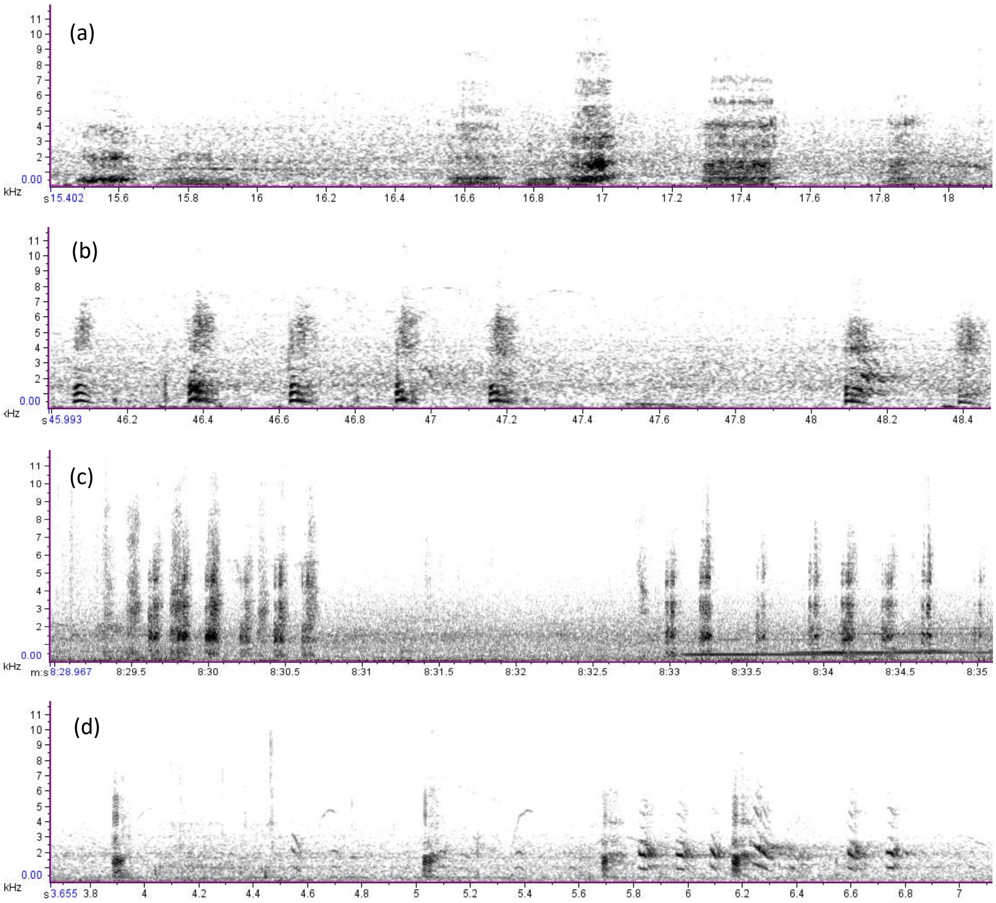


Figure I.7. Main call types of vocal comments collected in BDG during preliminary recording sessions. All spectrograms were visualized in Raven Pro 1.5 Interactive Sound Analysis Software. (a) Rasping call of a low-ranking adult female (WU) observing a middle-ranking adult female (MB) chasing another low-ranking adult female (CA). (b) High-pitched and raspy pant barks of a high-ranking adult female (CO) observing a low-ranking adult female (FE) chasing a low-ranking sub-adult female (LA). (c) Pant bark of a low-ranking sub-adult female (AN) observing a low-ranking adult female (CA) handling her infant. (d) Soft pant of a low-ranking adult female (CA) observing her infant engaging in affiliative behaviours with a middle-ranking adult female (MB).

According to this qualitative analysis, two different call types were found in each context (***Figure I.7***): a) rasping calls and high-pitched raspy pant barks when observing third-party agonistic encounters, b) soft pants and pant barks while observing infant-handling interactions. Personal observations plus an inspection of the datasets suggested that the relative differences in social rank between the caller and the individuals observed might predict which of the two call types is to be used in each context. For instance, rasping calls were generally produced when the victim of the aggression was similar in rank to the caller (a competitor), while raspy pant barks were more likely when the caller was of higher rank than the individuals involved in the interaction. The raspy pant bark was shorter and lower in power than the rasping call, which may suggest that individuals were probably less aroused by these interactions that did not involve 'competitors'. Similarly, pant barks produced when observing affiliative interactions were generally recorded when individuals were more similar in rank, while soft pants seemed to be more likely when the caller was of lower rank than the conspecifics observed. It is likely that macaques evaluate the risks of vocalizing when higher ranking individuals are involved in affiliative interactions and tend to produce more concealing or softer calls (e.g. soft pants) in these situations than in others involving same or lower-ranking conspecifics. Despite these observations, datasets were not sufficient to confirm these ideas, which was also beyond the scope of this thesis. Further research in this direction might provide a better understanding of the usage of these calls and the factors that influence the decision to use one type or another in each context.

APPENDIX J – Individual-level variables used in the network-based diffusion analysis (NBDA)

Values of each individual-level variable used in NBDA to test for social learning of each foraging task introduced in TG can be seen in ***Tables J.1*** to ***J.3***. Sex and age categories were also used to inform the NBDA (values of these variables are found in ***Table 2.2*** in ***Chapter 2***). For further details on how these measures were calculated, see ***Table 5.3*** in ***Chapter 5***.

Table J.1. Individual-level variables used in NBDA to test social learning of the blue/yellow task.

Individual	OA	TA (s)	Social rank		Contact latency		Option preference	Total refills observed	B/Y proportion refill	Frequency of attention at distance	Frequency of access to the task	Rate of transmission
			Class	*Order*	*Level*	*Normalized*						
JA	1	6134	2	24	1	-0.340887185	3	3	2	0.829787234	0.43373494	0.067839729
FL	2	12029	2	37	1	-0.319698584	3	5	0.833333333	0.785714286	0.461538462	0.049010368
OI	3	18758	2	22	1	-0.330292884	1	7	1.142857143	0.568627451	0.215384615	0.046645367
FO	4	19063	2	33	1	-0.309104284	3	4	1.666666667	0.692307692	0.297297297	0.12749004
EF	5	19697	3	53	2	0.178233519	3	0	1	0.545454545	0.137254902	0.037234043
TI	6	20459	1	13	2	-0.213755584	3	14	1.153846154	0.739130435	0.425	0.096897874
RU	7	21541	1	8	2	-0.001869582	1	10	0.9	0.392857143	0.151515152	0.009363296
ZA	8	21712	1	3	1	-0.340887185	3	12	1.2	0.62962963	0.386363636	0.092745638
LF	9	23023	2	32	3	0.835080123	1	6	1.166666667	0.828571429	0.222222222	0.035335689
PO	10	24656	3	45	1	-0.340887185	2	7	1.333333333	0.727272727	0.083333333	0.071856287
AD	11	25872	1	4	1	-0.340887185	3	2	1	0.5	0.466666667	0.081402086
JI	12	29210	2	25	3	0.40071382	3	13	1.4	0.512195122	0.369230769	0.100919989
JL	13	32502	1	13	1	-0.340887185	3	29	0.923076923	0.533333333	0.210526316	0.076754386
WY	14	32790	1	7	1	-0.319698584	3	3	1	0.45	0.285714286	0.053685897
PI	15	33701	2	28	1	-0.287915684	3	16	1.230769231	0.842105263	0.321428571	0.091666667
LE	16	34001	2	38	3	0.803297223	1	2	1	0.533333333	0.4	0.056839475
AM	17	37166	3	43	1	-0.330292884	3	1	1	0.727272727	0.153846154	0.053892216
SR	18	47217	1	11	1	-0.330292884	2	0	1	0.789473684	0.296296296	0.042134831
FF	19	49667	1	17	1	-0.340887185	3	12	1.2	0.571428571	0.416666667	0.154545455

WA	20	50021	2	31	3	0.570222621	3	5	1.25	0.666666667	0.4375	0.09223301
PJ	21	51927	2	27	1	-0.340887185	3	2	1.5	0.8	0.210526316	0.13080895
DU	22	53157	1	15	1	-0.330292884	1	3	1	0.875	0.2	0.052631579
ED	23	53335	1	6	1	-0.340887185	2	4	1.25	0.407407407	0.25	0.090014472
AE	24	54553	1	3	4	5.337657652	3	1	2	0.642857143	0.243243243	0.03742515
NO	25	55085	1	5	1	-0.340887185	2	1	1	0.6	0.5	0.064644852
BM	26	55664	3	50	2	0.061696218	1	0	1	0.684210526	0.208333333	0.076732673
CC	27	55969	1	2	1	-0.330292884	3	1	1	0.642857143	0.333333333	0.062674095
DE	28	57884	1	2	1	-0.298509984	2	0	1	0.8	0.375	0.043333333
PA	29	58811	2	28	2	-0.097218283	1	2	1.5	0.588235294	0.19047619	0.085185185
SN	30	59085	2	36	1	-0.340887185	1	0	1	0.5	0.2	0.098901099
BB	31	64177	1	16	1	-0.340887185	2	2	1	0.416666667	0.076923077	0.25
DB	32	64472	1	13	1	-0.340887185	2	0	1	0.888888889	0.307692308	0.017985612
LT	33	67719	3	48	1	-0.287915684	1	3	0.75	0.6	0.210526316	0.08
LS	34	71395	1	18	1	-0.309104284	1	6	1	0,666666667	0,142857143	0,214285714

OA: Order of acquisition. TA (s): Time of acquisition (in seconds). Individuals with a '-' in OA and TA did not manage to solve the task successfully. Social rank class: It is based on the Jenks Natural Breaks Classification (see ***Appendix A***) where '1' is for high-ranking, '2' is for middle-ranking and '3' is for low-ranking. Social rank order: It is based on the median of all ranking orders across methods (see ***Appendix A***). Contact latency: Normalized = normalized values of continuous contact latency in seconds; Level = contact latency transformed into a categorical variable (1: < 10 s; 2: 10-60 s; 3: 1-3 min; 4: > 3 min; 5: no contact with task). Option preference: 0: No contact with task; 1: Yellow; 2: Blue; 3: No preference.

Table J.2. Individual-level variables used in NBDA to test social learning of the push/lift-up task.

Individual	**OA**	**TA (s)**	**Social rank**		**Contact latency**		**Option preference**	**Total refills observed**	**Frequency of attention at distance**	**Frequency of access to the task**	**Rate of transmission**
			Class	*Order*	*Level*	*Normalized*					
JA	1	20	2	24	1	-0.261491517	2	22	0.615384615	0.303571429	0.030045953
TI	2	1508	1	13	1	-0.237024475	1	14	0.428571429	0.447368421	0.077490775
PI	3	3685	2	28	2	0.117747642	1	0	1	0.25	0.050505051
JI	4	3778	2	25	2	0.044346515	1	10	0.65	0.2	0.060504202
WY	5	4021	1	7	1	-0.273725039	2	15	0.37037037	0.386363636	0.024793388

NO	6	4292	1	5	1	-0.298192081	1	8	0.866666667	0.347826087	0.064487633
RO	7	5718	2	32	2	0.166681727	1	17	0.571428571	0.222222222	0.039800995
BS	8	6852	2	24	1	-0.322659124	2	10	0.833333333	0.333333333	0.013513514
ZA	9	7063	1	3	1	-0.322659124	1	12	0.555555556	0.625	0.076041667
DB	10	8651	1	13	1	-0.322659124	2	3	0.7	0.285714286	0.027111575
FO	11	11704	2	33	1	-0.28595856	2	5	0.4	0.285714286	0.067590988
LE	12	12495	2	38	1	-0.237024475	1	8	0.571428571	0.222222222	0.069364162
EF	13	12807	3	53	2	-0.114689262	1	8	0.56	0.107142857	0.03030303
DU	14	13042	1	15	2	0.105514121	2	12	0.5	0.395348837	0.034519668
AM	15	17569	3	43	1	-0.298192081	3	11	0.363636364	0.195121951	0.049586777
ED	16	18699	1	6	1	-0.322659124	1	16	0.235294118	0.32	0.075078206
JT	17	24215	1	10	1	-0.298192081	1	10	0.695652174	0.148148148	0.066929134
EC	18	24432	3	49	1	-0.310425602	2	7	0.487179487	0.113636364	0.017274472
LF	19	24972	2	32	2	0.166681727	2	12	0.675675676	0.139534884	0.024017467
CY	20	26286	3	50	1	-0.28595856	2	5	0.72	0.038461538	0.090909091
BB	21	26368	1	16	1	-0.28595856	2	11	0.484848485	0.153846154	0.046153846
CC	22	26654	1	2	1	-0.261491517	1	1	0.5	0.333333333	0.081419624
AD	23	28900	1	4	1	-0.310425602	1	1	0	0.125	0.068493151
AS	24	29245	3	40	2	0.276783419	2	1	0.153846154	0.071428571	0.040145985
FL	25	33137	2	37	1	-0.322659124	1	3	1	0.625	0.04084507
PJ	26	34115	2	27	1	-0.322659124	3	2	0.153846154	0.071428571	0.114649682
PO	27	37232	3	45	1	-0.322659124	2	4	0.65	0.166666667	0.088082902
DE	28	39924	1	2	1	-0.322659124	1	1	0.25	0.2	0.05078125

OA: Order of acquisition. TA (s): Time of acquisition (in seconds). Individuals with a '-' in OA and TA did not manage to solve the task successfully. Social rank class: It is based on the Jenks Natural Breaks Classification (see ***Appendix A***) where '1' is for high-ranking, '2' is for middle-ranking and '3' is for low-ranking. Social rank order: It is based on the median of all ranking orders across methods (see ***Appendix A***). Contact latency: Normalized = normalized values of continuous contact latency in seconds; Level = contact latency transformed into a categorical variable (1: < 10 s; 2: 10-60 s; 3: 1-3 min; 4: > 3 min; 5: no contact with task). Option preference: 0: No contact with task; 1: Push; 2: Lift-up; 3: No preference.

Table J.3. Individual-level variables used in NBDA to test social learning of the rotating-door task.

Individual	**OA**	**TA (s)**	**Social rank**		**Contact latency**		**Option preference**	**Total refills observed**	**Frequency of attention at distance**	**Frequency of access to the task**	**Rate of transmission**
			Class	*Order*	*Level*	*Normalized*					
EC	1	304	3	49	1	-0.380048977	2	0	0.75	0.111111111	0.05
NO	2	752	1	5	1	-0.501859547	1	2	0	0.5	0.031746032
JL	3	1660	1	13	1	-0.428773205	2	2	1	0.571428571	0.022522523
DE	4	1902	1	2	2	0.521349238	2	2	0.428571429	0.363636364	0.007915567
JA	5	2499	2	24	1	-0.477497433	2	1	0.4	0.444444444	0.020168067
DU	6	2793	1	15	3	1.008591517	1	2	0	1	0.020708698
JI	7	5106	2	25	1	-0.404411091	1	0	0.5	0.076923077	0.049886621
BM	8	6894	3	50	3	1.885627618	0	2	0.75	0.2	0.00862069
BB	9	6942	1	16	1	-0.501859547	3	1	1	0.333333333	0.06741573
ZA	10	8047	1	3	1	-0.404411091	2	0	0.5	0.333333333	0.062913907
DB	11	9128	1	13	1	-0.428773205	2	5	0.533333333	0.117647059	0.027027027
WY	12	9314	1	7	1	-0.477497433	2	2	0.625	0.8	0.012195122
TI	13	9687	1	13	1	-0.501859547	1	0	0	0.285714286	0.052631579
CC	14	9726	1	2	2	-0.20951418	2	0	0.25	0.333333333	0.038167939
AD	15	10058	1	4	1	-0.453135319	2	0	0.333333333	0.25	0.012578616
AS	16	10311	3	40	1	-0.380048977	1	1	0.666666667	0.25	0.01994302

OA: Order of acquisition. TA (s): Time of acquisition (in seconds). Individuals with a '-' in OA and TA did not manage to solve the task successfully. Social rank class: It is based on the Jenks Natural Breaks Classification (see ***Appendix A***) where '1' is for high-ranking, '2' is for middle-ranking and '3' is for low-ranking. Social rank order: It is based on the median of all ranking orders across methods (see ***Appendix A***). Contact latency: Normalized = normalized values of continuous contact latency in seconds; Level = contact latency transformed into a categorical variable (1: < 10 s; 2: 10-60 s; 3: 1-3 min; 4: > 3 min; 5: no contact with task). Option preference: 0: No contact with task; 1: Clockwise; 2: Counter-clockwise; 3: No preference.

APPENDIX K – Data used to test for task difficulty

Table K.1. Data on learning time and success at task for the blue/yellow task.

Individual	Total unsuccessful manipulations	Total successful manipulations	Total time at task (s)	Rate of unsuccessful manipulations	Rate of successful manipulations	Learning time
AD	126	281	3047	0.041352	0.092222	7
AE	39	75	1662	0.023466	0.045126	506
AM	15	18	206	0.072816	0.087379	8
BB	0	1	4	0	0.25	0
BM	11	31	332	0.033133	0.093373	144
CC	138	135	1779	0.077572	0.075885	27
DB	28	15	675	0.041481	0.022222	2
DE	21	39	706	0.029745	0.055241	119
DU	13	12	194	0.06701	0.061856	52
ED	130	311	3453	0.037648	0.090067	26
EF	41	21	434	0.09447	0.048387	71
FF	31	51	683	0.045388	0.074671	18
FL	66	52	1109	0.059513	0.046889	159
FO	45	64	448	0.100446	0.142857	3
JA	467	320	3980	0.117337	0.080402	18
JI	377	362	3288	0.114659	0.110097	97
JL	10	35	300	0.033333	0.116667	42
LE	117	91	1439	0.081306	0.063238	114
LF	32	20	496	0.064516	0.040323	166
LS	5	27	122	0.040984	0.221311	0
LT	0	4	32	0	0.125	6
NO	55	81	1020	0.053922	0.079412	16
OI	137	73	1308	0.10474	0.05581	132
PA	17	23	254	0.066929	0.090551	25
PI	124	209	1697	0.07307	0.123159	8
PJ	32	76	529	0.060491	0.143667	5
PO	12	12	141	0.085106	0.085106	4
RU	17	5	331	0.05136	0.015106	36
SN	3	9	50	0.06	0.18	2
SR	18	30	563	0.031972	0.053286	16
TI	198	278	2652	0.074661	0.104827	75
WA	54	76	694	0.07781	0.10951	39
WY	76	67	1015	0.074877	0.06601	47
ZA	369	505	4844	0.076177	0.104253	0

Table K.2. Data on learning time and success at task for the push/lift-up task.

Individual	Total unsuccessful manipulations	Total successful manipulations	Total time at task (s)	Rate of unsuccessful manipulations	Rate of successful manipulations	Learning time
AD	0	10	124	0	0.080645	12
AM	8	24	369	0.02168	0.065041	8
AS	7	11	202	0.034653	0.054455	62
BB	10	27	529	0.018904	0.05104	53
BS	4	4	152	0.026316	0.026316	35
CC	7	39	426	0.016432	0.091549	18
CY	0	2	19	0	0.105263	3
DB	4	26	554	0.00722	0.046931	154
DE	10	13	209	0.047847	0.062201	42

DU	24	129	2764	0.008683	0.046671	49
EC	5	9	381	0.013123	0.023622	59
ED	20	144	1912	0.01046	0.075314	202
EF	8	15	397	0.020151	0.037783	8
FL	3	29	481	0.006237	0.060291	41
FO	11	39	528	0.020833	0.073864	14
JA	22	85	2270	0.009692	0.037445	19
JI	14	36	489	0.02863	0.07362	9
JT	12	51	554	0.021661	0.092058	10
LE	1	12	162	0.006173	0.074074	16
LF	1	11	276	0.003623	0.039855	123
LT	3	0	68	0.044118	0	NA
NO	13	73	1071	0.012138	0.068161	15
PI	0	5	60	0	0.083333	0
PJ	3	18	139	0.021583	0.129496	17
PO	1	17	168	0.005952	0.10119	0
RO	9	24	439	0.020501	0.05467	48
TI	35	147	1797	0.019477	0.081803	124
WY	54	96	3164	0.017067	0.030341	12
ZA	23	146	1673	0.013748	0.087268	24

NA: Not applicable = individuals that interacted with the task but never solved it successfully (i.e. never learned the task).

Table K.3. Data on learning time and success at task for the rotating-door task.

Individual	Total unsuccessful manipulations	Total successful manipulations	Total time at task (s)	Rate of unsuccessful manipulations	Rate of successful manipulations	Learning time
AD	7	2	150	0.046667	0.013333	50
AS	3	7	280	0.010714	0.025	91
BB	18	42	550	0.032727	0.076364	31
BM	1	4	321	0.003115	0.012461	184
CC	7	15	338	0.02071	0.044379	58
DB	1	4	117	0.008547	0.034188	53
DE	3	6	726	0.004132	0.008264	212
DU	12	45	1713	0.007005	0.02627	202
EC	0	5	25	0	0.2	18
JA	0	12	355	0	0.033803	0
JI	22	44	847	0.025974	0.051948	0
JL	1	5	154	0.006494	0.032468	40
LE	2	0	11	0.181818	0	NA
LF	1	0	163	0.006135	0	NA
NO	7	32	831	0.008424	0.038508	86
TI	0	1	16	0	0.0625	10
WY	1	7	398	0.002513	0.017588	182
ZA	9	57	735	0.012245	0.077551	167

NA: Not applicable = individuals that interacted with the task but never solved it successfully (i.e. never learned the task).

APPENDIX L – Confidence intervals of the social parameter of each NBDA model

The social parameter (s) is a parameter, fitted to the social network data used to inform the NBDA model, that determines the strength of social transmission relative to asocial learning (Hoppitt et al., 2010). The exact meaning of the s parameter depends on the social network used (e.g. association versus interaction networks) as well as the NBDA model itself (e.g. the individual-level variables entered in the model) when compared with other models using other social networks (Hoppitt, 2017). Therefore, the s parameter varies according to the network and the specific model used in NBDA. When the NBDA model that includes the s parameter is better than the model that does not include this parameter (null model assuming asocial learning), we have evidence of social transmission (see ***Chapter 5*** for further details).

Hoppitt & Laland (2011) highlighted the importance of measuring the confidence intervals for the s parameter to have an idea of the statistical power of the social network data used in NBDA to detect social transmission. The power of network data in terms of providing evidence of social learning depends on the sample size and topography of the network (e.g. homogenous networks have low power to detect social transmission, Hoppitt & Laland, 2011). If the confidence intervals of the s parameter include zero, but are very wide, network data will not have much power to detect social transmission. If the confidence intervals of the s parameter are narrow and include zero, we have evidence that there is little or no social transmission following the social network provided (Hoppitt & Laland, 2011). Hasenjager et al. (2021) provided a clear interpretation of the confidence intervals for the s parameter (see ***Table L.1***).

Table L.1. Interpretation of the 95% confidence intervals (CI) of the s parameter provided by Hasenjager et al. (2021).

Lower limit of the 95% CI	**Upper limit of the 95% CI**	
	Low value	**High value**
0	Little or no social transmission	Weak or no evidence of social transmission, but cannot rule out an important effect either
Low value	A small effect of social transmission	Evidence of social transmission, but uncertain whether the effect is strong or weak
High value	Not possible	Strong evidence of social transmission that has an important effect in the diffusion

Confidence intervals for the s parameter were measured using the profile likelihood technique which provides confidence intervals reflecting any asymmetry in the certainty of the parameter (Hasenjager, 2021). This method reduces the likelihood function to a function of one parameter of interest by treating the other parameters of the model as nuisance and maximizing the likelihood over them (for further details see Royston, 2007 and Morgan, 2010). This likelihood profile technique is useful when the sampling distribution of the parameter is non-normal and models are non-linear, as it is the case of NBDA (Royston, 2007; Franz & Nunn, 2009).

Hoppitt et al. (2010) suggested reporting the bounded parameterisation of the s parameter which provides measures of the strength of social transmission that range from 0 (indicating no social transmission) to 1 (indicating that learning only occurred via social transmission and there was no influence of asocial learning). However, models were difficult to fit in this parameterisation, meaning that measuring confidence intervals using the profile likelihood technique with this parameterisation was not possible (i.e. likelihood profiles required a long computation time and provided profile likelihood graphs that were incomplete or so large that were impossible to visualize to provide accurate measures of CI; the same issue was reported by Atton, 2014). Therefore, confidence intervals were measured for the unbounded parameterisation of the s parameter (s’). ***Tables L.2*** to ***L.4*** are a summary of the tables presented in Chapter 5, but include the results of the s’ parameter and its confidence intervals.

Table L.2. Results for the best OADA and TADA models used to test social learning in the blue/yellow task.

Network	NBDA	Model type	AICc	Akaike weight	Approach	Rate of transmission	Rate of acquisition	Individual-level variables	CI 95%
Grooming	OADA	Best null model	183.84	0.81	Both	Irrelevant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s'=46.73048662 Upper = 866.2913 Lower = 0
		Best social model	186.76	0.19	Multiplicative	Non-constant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s'=46.73048662 Upper = 866.2913 Lower = 0
	TADA	Best null model	780.80	0.82	Multiplicative	Irrelevant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=6.722287e+00 Upper = 94.86816 Lower 0
		Best social model	783.85	0.18	Multiplicative	Constant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=6.722287e+00 Upper = 94.86816 Lower = 0
Proximity 1m	OADA	Best null model	183.84	0.82	Both	Irrelevant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s'=0 Upper = 270.763 Lower = 0
		Best social model	186.81	0.18	Both	Irrelevant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s'=0 Upper = 270.763 Lower = 0
	TADA	Best null model	780.80	0.81	Both	Irrelevant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=8.171911e+01 Upper = 1197.864 Lower = 0
		Best social model	783.67	0.19	Multiplicative	Non-constant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=8.171911e+01 Lower = 0 Upper = 1197.864
Proximity 5m	OADA	Best null model	183.84	0.81	Both	Irrelevant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s’=18.21642525 Upper = ∞ Lower = 0
		Best social model	186.77	0.19	Multiplicative	Non-constant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s’=18.21642525 Upper = ∞ Lower = 0
	TADA	Best null model	780.80	0.79	Both	Irrelevant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=1.174875e+00 Upper = 105.9654 Lower = 0
		Best social model	783.42	0.21	Multiplicative	Constant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=1.174875e+00 Upper = 105.9654 Lower = 0

Affiliative (CSI)	OADA	Best null model	183.84	0.82	Both	Irrelevant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s'=0 Upper = 0.2710376 Lower = 0
		Best social model	186.81	0.18	Both	Irrelevant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s'=0 Upper = 0.2710376 Lower = 0
	TADA	Best null model	780.80	0.81	Both	Irrelevant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=6.684992e-03 Upper = 0.1445493 Lower = 0
		Best social model	783.69	0.19	Multiplicative	Constant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=6.684992e-03 Upper = 0.1445493 Lower = 0
Observation 1m	OADA	Best null model	183.84	0.75	Both	Irrelevant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s’=2.71357580 Upper = 14.81838 Lower = 0
		Best social model	186.00	0.25	Multiplicative	Non-constant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s’=2.71357580 Upper = 14.81838 Lower = 0
	TADA	Best null model	780.80	0.71	Both	Irrelevant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=21.2099202 Upper = 739.863 Lower = 0
		Best social model	782.62	0.29	Additive	Non-constant	Non-constant	contactlevel, refillsobs, BYproprefill	s’=3.221256e+01 Upper = 426.3804 Lower = 0
Observation 5m	OADA	Best null model	183.84	0.81	Both	Irrelevant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s’=0.5043138 Upper = 11.28349 Lower = 0
		Best social model	186.76	0.19	Multiplicative	Non-constant	NA	socialrankclass, contact level, refillsobs, BYprop refill, freqacc	s’=0.5043138 Upper = 11.28349 Lower = 0
	TADA	Best null model	780.80	0.80	Both	Irrelevant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=1.403100e+00 Upper = 5.950102 Lower = 0
		Best social model	783.59	0.20	Multiplicative	Non-constant	Non-constant	contactlevel, refillsobs, BYproprefill, freqacc	s’=1.403100e+00 Upper = 5.950102 Lower = 0

OADA: Order of acquisition diffusion analysis. TADA: Time of acquisition diffusion analysis. Irrelevant: The same result was obtained for constant and non-constant rates. NA: Not applicable = OADA is not sensitive to the baseline rate of acquisition, but TADA is, so this measure was only relevant for TADA (Hoppitt & Laland, 2011). Individual-level variables that better explained the models included social rank class (socialrankclass), contact level (contact level), total number of refills observed (refillsobs), B/Y proportion refill (BYproprefill) and frequency of access to the task (freqacc) (see ***Table 5.3*** in ***Chapter 5***).

Table L.3. Results for the best OADA and TADA models used to test social learning in the push/lift-up task.

Network	NBDA	Model type	AICc	Akaike weight	Approach	Rate of transmission	Rate of acquisition	Individual-level variables	CI 95%
Grooming	OADA	Best null model	140.87	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref, refillsobs, freqacc	s’=0 Lower = 0 Upper = 40.3932
		Best social model	143.86	0.18	Additive	Irrelevant	NA	contactlatencynorm, optionpref, refillsobs, freqacc	s’=0 Lower = 0 Upper = 40.3932
	TADA	Best null model	617.78	0.39	Both	Irrelevant	Constant	contactlevel, refillsobs	s’=49.4430002 Lower = 0 Upper = 187.5994
		Best social model	616.89	0.61	Multiplicative	Constant	Constant	contactlevel, refillsobs	s’=49.4430002 Lower = 0 Upper = 187.59
Proximity 1m	OADA	Best null model	140.87	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref, refillsobs, freqacc	s’=0 Lower = 0 Upper = 23.33602
		Best social model	143.86	0.18	Additive	Irrelevant	NA	contactlatencynorm, optionpref, refillsobs, freqacc	s’=0 Lower = 0 Upper = 23.33602
	TADA	Best null model	615.09	0.49	Multiplicative	Irrelevant	Non-constant	contactlatencynorm, optionpref, refillsobs, freqacc	s’=2.947481e+02 Lower = 0 Upper = 262.1846

		Best social model	615.02	0.51	Multiplicative	Constant	Non-constant	contactlatencynorm, refillsobs	s’=3.327009e+01 Lower = 0 Upper = 157.873
Proximity 5m	OADA	Best null model	140.87	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref, refillsobs, freqacc	s'=0 Upper = 1.420173 Lower = 0
		Best social model	143.86	0.18	Additive	Irrelevant	NA	contactlatencynorm, optionpref, refillsobs, freqacc	s'=0 Upper = 1.420173 Lower = 0
	TADA	Best null model	617.78	0.58	Both	Irrelevant for multiplicative, non-constant for additive	Constant	contactlevel, refillsobs	s’=2.8395769 Upper = 42.13925 Lower = 0
		Best social model	618.46	0.42	Multiplicative	Constant	Constant	contactlevel, refillsobs	s’=2.8395769 Upper = 42.13925 Lower = 0
Affiliative (CSI)	OADA	Best null model	140.87	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref, refillsobs, freqacc	s'=0 Upper = 0.02395578 Lower = 0
		Best social model	143.86	0.18	Additive	Irrelevant	NA	contactlatencynorm, optionpref, refillsobs, freqacc	s'=0 Upper = 0.02395578 Lower = 0
	TADA	Best null model	617.78	0.23	Both	Irrelevant	Constant	contactlevel, refillsobs	s’=4.577039e-02 Upper = 0.3803951 Lower = 0.003973564
		Best social model	615.41	0.77	Multiplicative	Constant	Constant	contactlevel, refillsobs	s’=4.577039e-02 Upper = 0.3803951 Lower = 0.003973564
Observation 1m	OADA	Best null model	140.87	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref, refillsobs, freqacc	s'=0 Upper = 6.835584 Lower = 0
		Best social model	143.86	0.18	Additive	Irrelevant	NA	contactlevel, optionpref, refillsobs, freqacc	s'=0 Upper = 6.835584 Lower = 0
	TADA	Best null model	617.78	0.44	Both	Irrelevant	Constant	contactlevel, refillsobs	s'=0.6521489 Upper = 2.416934 Lower = 0
		Best social model	617.30	0.56	Multiplicative	Constant	Constant	contactlevel, refillsobs	s'=0.6521489 Upper = 2.416934 Lower = 0
Observation 5m	OADA	Best null model	140.87	0.41	Additive	Irrelevant	NA	contactlatencynorm, optionpref, refillsobs, freqacc	s’=0 Upper = 2.356394 Lower = 0
		Best social model	140.13	0.59	Multiplicative	Constant	NA	contactlevel, optionpref, freqacc	s’=5.8565076 Upper = 42.05894 Lower = 1.146447
	TADA	Best null model	617.78	0.04	Both	Irrelevant	Constant	contactlevel, refillsobs	s’=5.9706804 Upper = 169.4736 Lower = 2.553267
		Best social model	611.23	0.96	Multiplicative	Non-constant	Constant	contactlevel, optionpref, refillsobs, freqacc	s’=26.7557683 Upper = 480.0683 Lower = 5.76265

OADA: Order of acquisition diffusion analysis. TADA: Time of acquisition diffusion analysis. Irrelevant: The same result was obtained for constant and non-constant rates. NA: Not applicable = OADA is not sensitive to the baseline rate of acquisition, but TADA is, so this measure was only relevant for TADA (Hoppitt & Laland, 2011). Individual-level variables that better explained the models included contact level (contactlevel), contact latency normalized (contactlatencynorm), preferred option (optionpref), total number of refills observed (refillsobs) and frequency of access to the task (freqacc) (see ***Table 5.3*** in ***Chapter 5***).

Table L.4. Results for the best OADA and TADA models used to test social learning in the rotating-door task.

Network	NBDA	Model type	AICc	Akaike weight	Approach	Rate of transmission	Rate of acquisition	Individual-level variables	CI 95%
Grooming	OADA	Best null model	75.365	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref	s'=0 Lower = 0 Upper = 21.06953

		Best social model	78.442	0.18	Additive	Irrelevant	NA	contactlatencynorm, optionpref	s'=0 Lower = 0 Upper = 21.06953
	TADA	Best null model	327.55	0.49	Multiplicative	Non-constant	Non-constant	contactlatencynorm, optionpref	s’=1.549390e-07 Lower = 0 Upper = 7642.548
		Best social model	327.43	0.51	Multiplicative	Constant	Non-constant	contactlatencynorm	s’=1.608572e+02 Lower = 7.613828 Upper = 624.5939
Proximity 1m	OADA	Best null model	75.365	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref	Lower = 0 Upper = 9.876998
		Best social model	78.442	0.18	Additive	Irrelevant	NA	contactlatencynorm, optionpref	Lower = 0 Upper = 9.876998
	TADA	Best null model	327.55	0.87	Multiplicative	Non-constant	Non-constant	contactlatencynorm, optionpref	Lower = 0 Upper = 2818.995
		Best social model	331.40	0.13	Multiplicative	Constant	Non-constant	contactlatencynorm	Lower = 0 Upper = 201.8482
Proximity 5m	OADA	Best null model	75.365	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref	s'=0 Upper = 0.8542514 Lower = 0
		Best social model	78.442	0.18	Additive	Irrelevant	NA	contactlatencynorm, optionpref	s'=0 Upper = 0.8542514 Lower = 0
	TADA	Best null model	328.53	0.84	Multiplicative	Irrelevant	Non-constant	contactlatencynorm	s’=1.0495606 Upper = 46.83233 Lower = 0
		Best social model	331.88	0.16	Multiplicative	Constant	Non-constant	contactlatencynorm	s’=1.0495606 Upper = 46.83233 Lower = 0
Affiliative (CSI)	OADA	Best null model	75.365	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref	s’=0 Upper = 0.01105721 Lower = 0
		Best social model	78.442	0.18	Additive	Irrelevant	NA	contactlatencynorm, optionpref	s’=0 Upper = 0.01105721 Lower = 0
	TADA	Best null model	327.55	0.75	Multiplicative	Irrelevant	Non-constant	contactlatencynorm, optionpref	s’=2.749416e-02 Upper = 0.4071213 Lower = 0
		Best social model	329.70	0.25	Multiplicative	Constant	Non-constant	contactlatencynorm	s’=8.318400e-02 Upper = 0.5917765 Lower = 0
Observation 1m	OADA	Best null model	75.365	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref	s'=0 Upper = 0.3178795 Lower = 0
		Best social model	78.442	0.18	Additive	Irrelevant	NA	contactlatencynorm, optionpref	s'=0 Upper = 0.3178795 Lower = 0
	TADA	Best null model	327.55	0.19	Multiplicative	Irrelevant	Non-constant	contactlatencynorm, optionpref	s'=1.808863e+02 Upper = 1292.208 Lower = 12.53251
		Best social model	324.64	0.81	Multiplicative	Non-constant	Non-constant	contactlatencynorm	s’=298.2299856 Upper = 1775.852 Lower = 27.12552
Observation 5m	OADA	Best null model	75.365	0.82	Additive	Irrelevant	NA	contactlatencynorm, optionpref	s’=0 Upper = 1.802274 Lower = 0
		Best social model	78.442	0.18	Additive	Irrelevant	NA	contactlatencynorm, optionpref	s’=0 Upper = 1.802274 Lower = 0
	TADA	Best null model	327.55	0.29	Multiplicative	Irrelevant	Non-constant	contactlatencynorm, optionpref	s’=1.164894e+00 Upper = 8.62119 Lower = 0.06368795
		Best social model	325.77	0.71	Multiplicative	Constant	Non-constant	contactlatencynorm	s’=2.012367e+00 Upper = 7.979102 Lower = 0.2349988

OADA: Order of acquisition diffusion analysis. TADA: Time of acquisition diffusion analysis. Irrelevant: The same result was obtained for constant and non-constant rates. NA: Not applicable = OADA is not sensitive to the baseline rate of acquisition, but TADA is, so this measure was only relevant for TADA (Hoppitt & Laland, 2011). Individual-level variables that better explained the models included contact latency normalized (contactlatencynorm) and preferred option (optionpref) (see ***Table 5.3*** in ***Chapter 5***).

For the blue/yellow task, confidence intervals of the s' parameter, either wide or narrow, always included a lower 95% limit equal to zero. Therefore, social networks were likely to provide little/weak or no evidence of social transmission at all in the blue/yellow task. These results match the conclusions drawn in Chapter 5 of no evidence of social learning for the blue/yellow task.

For the push/lift-up task, confidence intervals of the s' parameter, either wide or narrow, included a lower 95% limit equal to zero (indicating little/weak or no evidence of social transmission) except for the affiliative (CSI) network in TADA (indicating a small effect of social transmission) and for the 5m observation network in both OADA and TADA (indicating evidence of social transmission, with TADA providing a stronger effect in the social diffusion than OADA). These results match the conclusion drawn in Chapter 5 of some and strong evidence of social transmission in affiliative (CSI) and 5m observation networks, respectively.

For the rotating-door task, confidence intervals of the s' parameter, either wide or narrow, included a lower 95% limit equal to zero (indicating little/weak or no evidence of social transmission) except for TADA using grooming and both observation networks. Accordingly, the grooming and observation networks were likely to provide evidence of social transmission using TADA, although the evidence would be small in the 5m observation network, potentially strong in the grooming network and clearly strong in the 1m observation network. In Chapter 5, enough evidence of social transmission was only found for 1m observation networks. Evidence of social transmission was almost sufficient to be considered significant in 5m observation networks. This confirms the conclusion that being in close proximity was relevant to acquire detailed information necessary to solve this task, which hardly could be obtained by observing from a longer distance. The social learning model for the grooming network was better than the asocial learning model, but evidence of social transmission was far from being sufficient. Despite this, grooming, which is a coalitionary behaviour used in exchange of commodities such as privilege access to resources (Barrett et al., 1999, Henzi et al., 2003; Barelli et al., 2011; Schülke et al., 2020), may have had a small potential influence in social learning of this task. Other affiliative networks (e.g, proximity), including the combined network CSI that includes grooming, did not have much power to detect social transmission and the social learning model was never better than the asocial learning model in any case. Therefore, it is likely that, to some extent, only specific affiliative relations established via grooming played a role in determining who was tolerated in close proximity of the task to observe the specific manipulations required to solve it (see ***Chapter 5***).

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