Grooming Interactions and Cooperation in Wild Barbary Macaques (Macaca sylvanus)

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Abstract

The study of cooperation has been crucial to research on the evolution of social living in human and animal societies. Grooming interactions have been used as model to investigate the exchange of services in animals. Using both established and novel methodologies, this thesis examines grooming interactions and cooperation in two populations of wild Barbary macaques living in the Middle Atlas Mountains of Morocco. It is important to have a comprehensive idea of the costs and benefits of grooming interactions, and of the effect of grooming interactions on the anxiety of the grooming partners. This thesis showed that, contrary to previous studies, anxiety increased after grooming interactions in both the donor and recipient. This highlights the need to further investigate the link between grooming and emotions. Individuals may also affect the grooming interactions of other group members. This thesis showed that individuals benefit from disrupting grooming interactions of group members by gaining grooming opportunities for themselves and by stopping the group members from grooming each other, although grooming disruptions may be risky. Monkeys may affect others' grooming interactions to favour their own social and dominance positions. A key aspect of this thesis was also to assess whether grooming is reciprocated in the short-term and which type of reciprocity (i.e. direct, indirect and generalised) play a role in the exchanges of grooming. This study showed that direct but not indirect and generalised reciprocity play a role in the exchange of grooming. While there is a wide range of evidence that direct reciprocity plays a role in the exchange of services in animals, there is little evidence of indirect and generalised reciprocity. Additionally to exchanging grooming for grooming, animals also exchange grooming for other services such as tolerance around food resource and support during agonistic interactions. In this thesis, no evidence of short-term contingency between the exchange of grooming and food tolerance was found. The exchanges of services may be little affected by recent single events, and mechanisms involving an emotional mediation based on long-term social bonds between partners may play a more important role. The capacity to make effective choices among potential social partners is an important social skill, as choosing the best available partner improves the chances to establish successful cooperative interactions. This thesis highlighted, to some extents, the importance of factors such as tolerance and relationship quality between partners, in the performances of individuals and their choice of partners to solve a cooperative task. Tolerant relationships may have been a prerequisite for the evolution of cognitively complex cooperation. Testing a comprehensive framework of predictions, this thesis brings novel contributions to the understanding of grooming interactions and cooperation in wild Barbary macaques.

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A female Barbary macaque with her infant (picture by S. Molesti)

Preface

The results' Chapters of this thesis (i.e. Chapters 3 to 7) are presented in a format that makes them easier to be adapted and submitted to peer-reviewed international journals (each result's chapter in thus a paper in preparation). The results of Chapter 3 have been published in a peer-reviewed international journal (see the front page of the paper in the appendix), and most of the work of this thesis has been presented to national and international conferences and workshops:

Journal

Molesti, S. & Majolo, B. 2013. Grooming increases self-directed behaviour in wild Barbary macaques (*Macaca sylvanus*). *Animal Behaviour*, **86**, 169-175.

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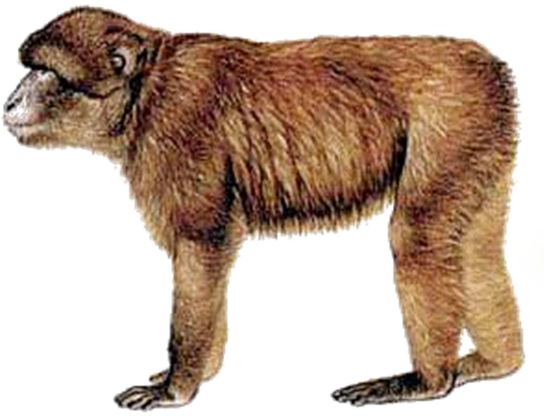

Drawing of a Barbary macaque.

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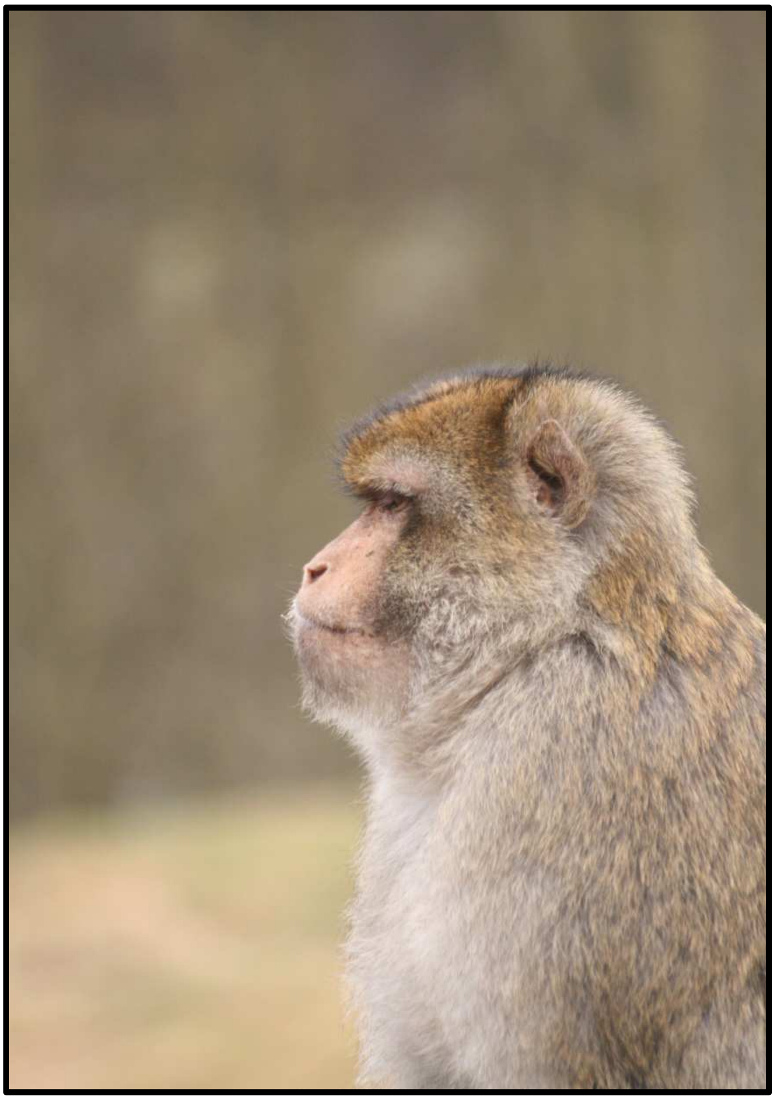
An infant Barbary macaque (picture by S. Molesti).

Chapter 1

General introduction



A male Barbary macaque (picture by S. Molesti).

This thesis investigates grooming interactions and cooperation in wild Barbary macaques. This chapter first describes the costs and benefits of group living and the advantages of social and dominance relationships in animals. It also introduces the use of grooming interactions as model to investigate the exchange of services in animals, particularly in non-human primates. Then, it discusses the evolution and mechanisms of exchanges of services in non-human primates, the use of cooperative tasks to investigate cooperation in animals, and the extent to which advanced cognitive capacities are required or not for cooperation. Finally, this Chapter lays out the aims of each study of this thesis.

1.1. GROUP LIVING AND SOCIAL RELATIONSHIPS

It is thought that living in a group is beneficial as it reduces the risk of predation (van Schaik & Hörstermann, 1994; Lima, 1995; Garay, 2009) and infanticide (van Schaik & Kappeler, 1997; van Schaik & Janson, 2000), and improves access to resources such as food and mating opportunities (Wrangham, 1980; van Schaik, 1989; Dunbar, 1995; Sterck et al, 1997; Dunbar, 2001; Johnson et al, 2002, Kappeler & van Schaik, 2002; Lindenfors et al, 2004). However, living in groups increases competition for resources between group members and increases the risk of disease and parasite transmission (Freeland, 1976; Janson, 1985; van Schaik, 1989; Møller et al, 1993; Cote & Poulin, 1995; Johnson et al, 2004; Nunn & Altizer, 2006). Because females devote more energy than males to the production and care of offspring (e.g. lactating, nurturing and protecting offspring), they compete principally over food and water resources (Trivers, 1972). Males invest relatively little energy in the production and care of offspring, and they compete principally over access to mating partners (Trivers, 1972).

The driving forces (e.g. resource distribution, competition, predation risk) behind the evolution of group living are still debated (Wrangham, 1980; Johnson et al, 2002; Kappeler & van Schaik, 2002; Lindenfors et al, 2004). The formation and maintenance of social relationships between group members is believed to mediate the risks associated with intra-group competition (e.g. being injured during a conflict for access to resources) (Wrangham, 1980).

Social relationships involve the exchange of friendly interactions, such as grooming, and agonistic interaction, such as aggression, between group members. Social relationships imply that the occurrence and outcome of interactions between two individuals affects the occurrence and outcome of their subsequent interactions (Hinde, 1976, 1979, 1983; Aureli et al, 2012). Thus individuals modify their behaviour according to the quality of their relationships with other group members. This may be mediated by emotion: the frequency and quality of previous interactions with group members may affect the emotional experience of an individual. Such emotional experience would be partner specific and affect the way the individual interact with group members (Aureli & Schaffner, 2002; Aureli & Whiten, 2003; Aureli & Schino, 2004; Schino & Aureli, 2009, 2010a; Aureli et al, 2012; Seyfarth & Cheney, 2012). Dyads exchanging friendly behaviours at high frequency are usually referred as having a strong relationship. Feeding at the same resource, mating opportunities, support during agonistic interaction (i.e. on individual intervenes on behalf of another in an agonistic interaction) and defence against predator are known benefits of social relationships in non-human primates (Palombit et al, 1997; Sapolsky et al, 1997, Sterck et al, 1997, Barrett et al, 1999; van Schaik & Aureli, 2000, Gumert 2007b; Silk, 2007; Clarke et al, 2010; Seyfarth & Cheney, 2012; Micheletta et al, 2012; Langergraber et al, 2013). Additionally, there is evidence that having strong social relationships within a group enhances reproductive success (Silk, 2007). For example, strong social integration was associated with higher rate of infant survival in female baboons (*Papio cynocephalus*; Silk et al, 2003, 2009) and horses (*Equus caballus*; Cameron et al, 2009), and higher rate of sired offspring in male Assamese macaques (*Macaca assamensis*; Schülke et al, 2010). Moreover, individuals who form stronger social bonds live longer (Silk et al, 2010b) and have better chance of survival following extreme environmental conditions (McFarland & Majolo, 2013). Because of the benefits associated with social bonds and the costs associated with aggression (e.g. injury, anxiety), animals may exchange friendly behaviours after a conflict to restore their relationship (i.e. post-conflict affiliations: Aureli & de Waal, 2000; Aureli et al, 2002). Post-conflict affiliation has been observed in several species such as dolphins (*Tursiops truncates*; Weaver, 2003), hyenas (*Corocuta crocuta*; Hofer & East, 2000), ravens (*Corvus corax*; Fraser & Bugnyar, 2011) and non-human primates (e.g. Aureli & van Schaik, 1991; Castles & Whiten, 1998). The quality of social relationships between group members is usually measured using the frequency of friendly behaviour exchanged such as grooming interaction and social proximity (Cord, 1997; Sapolsky et al, 1997, Silk, 2002; Silk et al, 2003, 2006, 2010a; Dunbar & Shultz, 2010).

Animals also establish dominance relationships within the group. The outcomes of aggressive interactions (i.e. who wins and who looses, the looser usually displaying submissive behaviour toward the winner) of an individual determine their dominance position within the group. A high rank position in the dominance hierarchy brings various benefits such as priority access to food resources and mating opportunities (Seyfarth, 1977, Packer, 1979, Cowlishaw & Dunbar, 1991, Isabell et al, 1999; Schino, 2001; Alberts et al, 2006). There is also evidence in non-human primates that dominant females live longer and have higher infant survival, and dominant males have higher fecundity and mating success (Bulger & Hamilton, 1987; Wasser et al, 2004; Silk, 2007; Rodriguez-Llanes et al, 2009; Silk et al, 2010b; Majolo et al, 2012a).

Animals have knowledge of other group members' dominance rank and social relationships (Cheney & Seyfarth, 1990; Cheney et al, 1995; Silk, 1999; Bergman et al, 2003; Perry et al, 2004; Kitchen et al, 2005; Schino et al, 2006; Shettleworth, 2010; Cheney, 2011; Borgeaud et al, 2013). Rank-reversal playback experiments showed that monkeys looked longer at speakers when listening a sequence of calls that mimicked a lower-ranking individual aggressing a higher-ranking individual (i.e. a situation inconsistent with the existing hierarchy), than when listening a sequence mimicking a higher-ranking individual aggressing a lower-ranking individual (i.e. a situation consistent with the existing hierarchy), presumably because the rank-reversal sequence transgressed the listener's expectations (Cheney et al, 1995; Bergman et al, 2003; Borgeaud et al, 2013). Moreover during conflicts, wild capuchin monkeys (*Cebus capucinus*) recruited allies which had a higher relationship quality with themselves than with their opponents, and which had a higher dominance rank than their opponents, increasing their chance to win the conflicts (Perry et al, 2004). Japanese macaques (*Macaca fuscata*) also recruited allies ranking higher than their opponents and they recruited allies that were not a kin of their opponents (Schino et al, 2006). In wild chimpanzees (*Pan troglodytes*), victims exaggerated their screams only when they were aggressed in the presence of potential allies of higher dominance rank than their aggressor (Slocombe & Zuberbühler, 2007).

The pattern of social and dominance relationships observed in a species is usually referred as the species dominance style (de Waal & Luttrell, 1989; Matsumura, 1999). For example, the different species of macaque show a great diversity of dominance style, ranging from species with a high social tolerance to species with strong nepotism and dominance hierarchy (Thierry et al, 2004). For instance, contrary to more tolerant species such as Tonkean and crested macaques (*Macaca tonkeana* and *Macaca nigra*), in less tolerant macaque species, such as Japanese and rhesus macaques (*Macaca fuscata* and *Macaca mulatta*), conflicts are unidirectional and of high intensity, reconciliation (i.e. post-conflict affiliation) is not frequent, and the distribution of affiliative behaviours is more kin-biased (Thierry, 2007).

It can be noted that the habitat (e.g. availability of resources and predation risk), social organization, mating system and social structure of the species studied has to be taken into account when analysing social interactions between individuals (e.g. Kappeler et al, 2013). For example, it has been proposed that reconciliation would occur mainly in species with individualized relationships, where conflicts can be resolved with aggression, and where conflicts disturb the valuable relationships of the opponents, particularly with a loss of the benefits associated with the relationships (Aureli et al, 2002). For instance, reconciliation occurs and functions to repair damaged social relationships in Japanese Macaques (*Macaca fuscata*; Koyama, 2001), whereas reconciliation is not observed in red-bellied tamarins (*Saguinus labiatus*) because their aggressive interactions do not disturb their relationships (Schaffner & Caine, 2000; Schaffner et al, 2005). Another example of variation across species is the fact that the distribution of grooming interactions may be affected by the tolerance level of the species studied. For instance, in more egalitarian social groups with high degree of social tolerance, it is expected that dominant individuals would not tend to restrict access to food resources. Therefore, grooming given to higher-ranking individuals would not be exchanged for food tolerance, but would rather be exchanged for grooming itself (e.g. Barrett et al, 1999). The distribution of grooming interactions within a group may also potentially vary depending on the size of the group, dispersal patterns and sex ratio (e.g. Lehmann et al, 2007; Majolo et al, 2008; Majolo et al, 2009; Sueur et al, 2011).

1.2. GROOMING

Allo-grooming (hereafter grooming) is a common friendly social behaviour of many animal societies (Spruijt et al, 1992). Grooming is defined as one individual using its hands and/or mouth to clean the fur and body of another individual (Figure 1.1 and 1.2; Schino, 1988; Hart, 1990). Grooming is observed in a number of mammals and birds, such as horses (*Equus caballus;* Kimura, 1998), antelopes (several species; Hart et al, 1992), meerkats (*Suricata suricatta*; Kutsukake & Clutton-Brock, 2006), vampire bats (*Desmodus rotundus*; Wilkinson, 1986), ravens (*Corvus corax*; Fraser & Bugnyar, 2010), green woodhoopoe (*Phoeniculus purpureus;* Radford et al, 2006), keas (*Nestor notabilis*; Diamond & Bond, 1999), non-human primates (several species; Dunbar, 1991), and humans (Nelson & Geher, 2007). Grooming has a hygienic function, as dirt and parasites are removed from parts of the body that animals cannot reach through self-grooming, improving physical health (Hutchins & Barash, 1976; Hart & Hart, 1992; Hart et al, 1992; Tanaka & Takefushi, 1993; Zamma, 2002; Radford & Du Plessis, 2006; Scantlebury et al, 2007; Akinyi et al, 2013). Grooming thus reduces the risk of parasite infection. Non-human primates groom group members more than necessary for a solely hygienic function, indicating that grooming has also a social function (Dunbar & Sharman, 1984; Dunbar, 1991). For example, baboons and macaques devote up to 20% of their time to groom with other group members (Dunbar, 1988). Grooming is indeed the main behaviour used to establish and maintain friendly relationships (Dunbar, 1991; Henzi & Barrett, 1999; Dunbar & Shultz, 2010).

Giving grooming is assumed to be a costly activity, as it reduces vigilance against predators and competitors (Maestripieri, 1993; Cords, 1995; Mooring & Hart, 1995), and the time available for other activities such as feeding and infant care (Dunbar & Sharman, 1984; Dunbar, 1992; Maestripieri, 1993; Tanaka & Takefushi, 1993; Scantlebury et al, 2007; Dunbar et al, 2009). Giving grooming may also increases the risk of parasite transmission (Johnson et al, 2004; Nunn & Alteizer, 2006). Conversely, receiving grooming has a positive effect on physical conditions as it reduces ectoparasites infection, and improves skin health (Hutchins & Barash, 1976; Hart et al, 1992; Tanaka & Takefushi, 1993; Zamma, 2002; Radford & Du Plessis, 2006; Scantlebury et al, 2007; Akinyi et al, 2013). It is also thought that grooming reduces anxiety in the recipient (Terry, 1970; Schino et al, 1988; Boccia et al, 1989; Feh & de Mazières, 1993; Aureli et al, 1999). There is notably evidence that the recipient of grooming experiences a reduced heart rate during grooming (Boccia et al, 1989; Feh & de Mazières, 1993; Aureli et al, 1999) and a release of endorphins in the blood (Keverne et al, 1989; Martel et al, 1995). However recent studies showed that grooming may also reduce anxiety in the donor (Aureli & Yates, 2010; Radford, 2012). It remains thus unclear whether grooming elicits a similar reduction of anxiety in the donor and recipient. This is important because a short-term change of anxiety following grooming may affect subsequent social interactions between animals as well as their choice of social partners. To answer this question, Chapter 3 of this thesis investigates the anxiety reduction effect of grooming in the donor and recipient in wild Barbary macaques (*Macaca sylvanus*).

Figure 1.1. Two Barbary macaque males grooming in the Middle Atlas Mountain of Morocco (picture by S. Molesti).

Figure 1.2. Precise removal of dirt and parasites with the hands during grooming (picture by S. Molesti).

1.3. COOPERATION AND RECIPROCITY

Cooperation generally refers to any behaviour benefitting another individual (e.g. West et al, 2007b). Acts of cooperation are seen every day in humans as our societies are based upon cooperation. Scientists have studied cooperation in humans and in non-human animals, in an attempt to give important insights on the origin of human cooperation. These studies showed that some basic human cooperative traits such as returning a favour, coordination of movements between partners, and division of rewards are not limited to humans (e.g. Clutton-Brock, 2009; Melis & Semmann, 2010; Cheney, 2011). Cooperation increases individual success as by cooperating together animals can obtain benefits that they could not attain alone, such as accessing food resources (e.g. West et al, 2007b; Clutton-Brock, 2009; de Waal & Suchak, 2010; Melis & Semmann, 2010). Group hunting, group defence, cooperative breeding, tolerance around food resource, grooming and agonistic support have been considered as examples of cooperative behaviours in animals (Boesch & Boesch, 1989; Dukatkin, 1997; Gazda et al, 2005; Clutton-Brock, 2009; Melis & Semmann, 2010). In this thesis, cooperative behaviours are considered to include altruistic behaviours (also called ‘services’) and mutual cooperation (also called mutualism: de Waal, 2000). It can be noted that the concepts of cooperation and altruism are still debated (e.g. West et al, 2011).

1.3.1. Exchange of services

Altruistic behaviours (or ‘services’) are defined as behaviours reducing the immediate payoff of the actor while benefitting the recipient (Trivers, 1971; Axelrod & Hamilton, 1981; Schino & Aureli, 2009; Brosnan & Bshary, 2010; Schino & Aureli, 2010a; see West et al, 2007a, 2007b for alternative definitions). Because giving grooming is mainly beneficial to the recipient and potentially costly for the donor, grooming can be referred as a service (Hutchins & Barash, 1976), and grooming distribution can be used as a model to investigate the mechanism and function of service exchanges in non-human primates. Other social behaviours that may be referred as services in non-human primates include, for example, tolerance over food resource and support during agonistic interaction.

Kin selection and reciprocity are among the many theories that have been proposed to explain the occurrence of altruistic behaviours (e.g. West et al, 2007a, 2011). For kin selection, inclusive fitness benefits (particularly indirect fitness effects) explain altruistic behaviours between genetic relatives (Hamilton, 1964). Individuals would bias the giving of benefits toward their genetic relatives, improving the propagation of their shared genes (Hamilton, 1964; Dawkins, 1976). Supporting this view, social relationships shared by kin tend to be stronger than those shared by non-kin (Silk et al, 2006, 2010a). For reciprocity (Alexander, 1974), individuals (independently of their genetic relatedness) act as the donor or the recipient of short-term (i.e. not lifetime) costly altruistic acts and can switch roles over time to balance the short-term benefits and costs of altruism (Trivers, 1971). Because short-term costs and benefits are balanced, reciprocity leads to long-term (i.e. lifetime) direct fitness benefits for the partners, and reciprocity becomes an evolutionarily stable strategy (Trivers, 1971; Axelrod & Hamilton, 1981). Trivers (1971) proposed that for the evolutionary stability of reciprocity, the reciprocated benefit should out-weigh the immediate cost. Reciprocity gives advantages, but it is costly and at risk of exploitation, as the returned benefit is not guaranteed because of the possible temporal decoupling between the costs and benefits for each individual.

Three main patterns of reciprocity have been proposed following a service given: direct, indirect and generalised reciprocity. In direct reciprocity, the recipient of an altruistic act is more likely to directly return the benefit to the former donor than to any other individual (Axelrod, 1984). For this, individuals interact repeatedly and recognise each other (Trivers, 1971). Indirect reciprocity assumes that giving an altruistic act increases the donor's reputation and so its chances to receive an altruistic act from bystanders are greater (Alexander, 1987; Nowak & Sigmund, 1998; Leimar & Hammerstein, 2001; Fehr & Fischbacher, 2003; Nowak & Sigmund, 2005; Sigmund, 2012). In generalised reciprocity, the recipient of an altruistic act experience a general benevolent mood which makes it more likely to give an altruistic act to anyone else (Hamilon & Taborsky, 2005). While indirect and generalised reciprocity play an important role in the exchange of altruistic behaviours in humans (Emmons & McCullough, 2004; Semmann et al, 2005; Bartlett & De Steno, 2006; Nowak, 2006; Sommerfeld et al, 2007; Sylwester & Roberts, 2010), their role in explaining the exchange of services in animals is unclear and evidences are scarce (Pinto et al, 2001; Bshary, 2002; Bshary & D'Souza, 2005; Bshary & Grutter, 2006; Rutte & Taborsky, 2007; Akcay et al, 2010; Majolo et al, 2012b). On the contrary, there is a wide range of evidence that direct reciprocity plays an important role in the exchange of services in humans as well as animals (Dawes, 1980; Schino & Aureli, 2008a; Rand et al, 2009; Melis & Semmann, 2010; Clutton-Brock, 2009; Majolo et al, 2012b). For example, the exchange of agonistic support in baboons (*Papio Anubis;* Packer, 1977), food sharing in vampire bats (*Desmodus rotundus;* Wilkinson, 1984; Carter & Wilkinson, 2013) and cooperative nest defence in red-winged blackbirds (*Agelaius phoeniceus*; Olendorf et al, 2004) are considered forms of direct reciprocity. Assessing the relative role of each type of reciprocity in explaining exchanges of services in non-human primates may thus bring important insight into which factors play a role in the evolution of altruism. Chapter 5 investigates the role of direct, indirect and generalised reciprocity in explaining the exchange of grooming.

Evaluating the exchange of services in social groups such as non-human primates is key to understand further the mechanisms and evolution of altruistic behaviours. In non-human primates, there is evidence that grooming is exchanged for itself (e.g. see Schino & Aureli, 2008a for a meta-analysis based on 22 species) and for other social services such as agonistic support (see Schino, 2007 for a meta-analysis), infant handling (Muroyama, 1994; Henzi & Barrett, 2002; Gumert, 2007a; Tiddi et al, 2010; Fruteau et al, 2011), food tolerance (de Waal, 1997; Ventura et al, 2006; Carne et al, 2011; Tiddi et al, 2011; Wei et al, 2012) and mating opportunities (Gumert, 2007b; Norscia et al, 2009; Clarke et al, 2010; Barelli et al, 2011). Moreover, the biological market approach predicts that the availability of a service and the capacity of each animal to retain resources (e.g. dominance status and fighting abilities) affect the exchange of services (Noé & Hammerstein, 1994; Barrett et al, 1999; Noë et al, 2001). Thus the biological market framework (Noë & Hammerstein, 1994; Noë et al, 2001) views animal social behaviour as resembling human economic markets where services that animals exchange (e.g. grooming or tolerance over food) can be compared to goods or services exchanged in human economic markets. The biological market theory assumes that supply and demand ratios determine the ‘value’ of services exchanged and that individuals compete over social partner based on the value and availability of services. For example, when food resources are scarce and can be monopolised, only high-ranking individuals have direct access to high-quality food resources, and low-ranking individuals may exchange a service given (e.g. grooming) for tolerance over food resources, which would result in grooming distribution being directed up the hierarchy (Seyfarth, 1977; Henzi & Barrett, 1999; Schino & Aureli, 2008b). High-ranking individuals may thus be considered as high value social partners because of the rank-related services that they can potentially provide to lower-ranking individuals (e.g. tolerance around food resource and support during agonistic interaction).

Due to the many potential benefits of grooming exchange and since time for grooming is limited, individuals compete over valuable grooming partners (Dunbar, 1992). Specifically, the disruption of grooming interactions among group members has been proposed as resulting from such competition over access to grooming partners (Cheney & Seyfarth, 1990). By disrupting on-going grooming interactions, individuals may gain access to grooming partners that would not be available otherwise. However, disruption may potentially be risky as the grooming partners disrupted may direct aggression toward the disrupter. Chapter 4 of this thesis investigates the benefits of grooming disruption for the disrupters in term of social relationships and grooming opportunities, as well as the risks (e.g. receiving aggression) associated with grooming disruption. Individuals differ also in their capacity to extort resources from other individuals. Indeed, dominant individuals may use direct aggression or threat in order to extort mating opportunities and grooming from lower-ranking individuals (Silk, 1982; Smuts & Smuts, 1993; Clutton-Brock & Parker, 1995a; Muller & Wrangham, 2009; McFarland & Majolo, 2011). The capacity of individuals to extort resources from other group members and/or to direct aggression toward group members who act against their interest, may also influence the exchange's pattern of social benefits such as grooming (Clutton-Brock & Parker, 1995b; Colmenares et al, 2002).

Two different ways in which direct reciprocal exchange of services can be manifested have been proposed in non-human primates (Bull & Rice, 1991; Noë, 2006; Schino & Aureli, 2009, 2010a; Tiddi et al, 2011). First of all, an animal can give a service to a partner depending on how the partner behaved toward it in the recent past.

This mechanism is usually tested by examining the temporal contingency between service given and received over short time period (i.e. minutes or hours; Schino et al, 2009; Cheney et al, 2010). This first process called ‘temporal relations between events’ (Tiddi et al, 2011; Campennì & Schino, 2014) is equivalent to the ‘partner-fidelity model’ described by Bull and Rice (1991) and to the ‘partner control model’ described by Noë (2006), and is essentially classical reciprocal altruism (Trivers, 1971). For example in chimpanzees, a temporal contingency was found between grooming received and food sharing (de Waal, 1997). Second, the partner choice mechanism assumes that individuals can overall give more services toward individuals from who they overall received more services, even if no temporal contingency is found between a service received and given over a short time period (Bull & Rice, 1991; Noë & Hammerstein, 1994; Noë, 2001; Silk, 2002, 2003; Noë, 2006; Schino & Aureli, 2009, 2010a; Campennì & Schino, 2014). For example, even when cases of immediate reciprocation were removed, monkeys still groomed more the partners that groomed them more (Schino & Pellegrini, 2009; Schino et al, 2009). These two mechanisms are both plausible and are not mutually exclusive. However, there is only little evidence of temporal contingency between services given and received in animals, and exchanges over longer time frames seem more balanced than exchanges over short time frames (Schino et al, 2007; Melis et al, 2008; Frank & Silk, 2009; Gomes et al, 2009; Schino et al, 2009; Cheney, 2011; Tiddi et al, 2011; Sabbatini et al, 2012; Jaeggi et al, 2013). Specifically, while there is evidence for long-term correlation between grooming and food tolerance in non-human primates, results for short-term contingency between these services are mixed (de Waal, 1997; Schino & Aureli, 2009; Tiddi et al, 2011). Despite this lack of evidence, short-term contingency between services given and received is traditionally used as the basic mechanism to explain and demonstrate reciprocity. There is thus a need to further investigate whether short-term contingencies can explain the exchanges of services in non-human primates. Increasing the number and range of species studied may help to understand the causes of these discrepancies. Chapter 6 of this thesis investigates the temporal contingency between grooming and food tolerance in wild Barbary macaques.

1.3.2. Mutual cooperation

Mutual cooperation is defined as cooperative interactions that yield benefit for the participants involved simultaneously (e.g. Noë, 2001, 2006; West et al, 2007b; Bshary & Bergmüller, 2008; Clutton-Brock, 2009; Melis & Semmann, 2010). Since mutual cooperation produces direct benefits for each partner, the resulting cooperative interaction is principally self-serving, even if it benefits other participants at the same time (de Waal & Suchak, 2010). The coordination of actions between partners has been proposed as a required mechanism of mutual cooperation. For example, during cooperative hunting in animals different levels of coordination can take place, ranging from simple synchronous actions to a division of labour among participants to reach the goal of catching the prey (e.g. Boesch & Boesch, 1989; Gazda et al, 2005). Because it is difficult to evaluate the coordination of behaviours of animals in the wild, studies in laboratory have investigated whether individuals are able to coordinate their action to reach a common goal in a cooperative setting (e.g. Crawford, 1937). For example, in the Crawford's paradigm (1937) two animals are faced with a cooperative task where they need to pull together a rope in a coordinated way, in order to bring a tray within arm reach and get a food reward. This experiment has been conducted on a variety of species including several species of non-human primates (Chalmeau et al, 1997a, 1997b; Mendres & de Waal, 2000; Visalberghi et al, 2000; Cronin et al, 2005; Hattori et al, 2005; Melis et al, 2006; Hare et al, 2007; Hirata & Fuwa, 2007), birds (Seed et al, 2008;

Scheid & Noë, 2010; Péron et al, 2011), hyenas (*Crocuta crocuta*; Drea & Carter, 2009), and Asian elephants (*Elephas maximus*; Plotnik et al, 2011).

Nevertheless, most of these studies have mainly focused on investigating the simultaneity of actions between two individuals and whether animals understand the role of their partner in solving the task. However, the choice of partner with whom to cooperate is key to initiate and maintain cooperative interactions and still need to be investigated in animals (Noë, 2006). Choosing the best available partner (e.g. in term of reliability or ability) improves the chances to establish a successful cooperative interaction (Noë, 2001, 2006), and unsatisfactory cooperative partners may be abandoned and replaced with other partners with greater benefits (Noë & Hammerstein, 1994; de Waal & Suchak, 2010). In most of the cooperative tasks conducted so far, animals were paired in dyads, with no or little opportunity to choose their partner to solve the task. However, group-living animals live in complex social groups and can choose their social partner to interact with among several individuals differing in aspects such as sex, age, abilities, dominance status, or relationship quality with the other group members. The capacity to make effective choices among potential social partners is thus an important social skill. Therefore, it is necessary to assess the mechanism underlying the choice of cooperative partners in a social context, that is, to assess which social and individual factors affect the choice of partner and performance in cooperative interactions. Chapter 7 of this thesis investigates the performance of wild Barbary macaques in a cooperative task, and the social and individual factors affecting their choice of partner and their performance.

1.3.3. Cognitive capacities and emotional mediations

The extent to which advanced cognitive capacities are required or not in the exchanges of services in non-human primates is still unclear and highly debated (Stevens & Hauser, 2004; Stevens et al, 2005; Puga-Gonzalez et al, 2009; Schino & Aureli, 2009; Brosnan et al, 2010; Schino & Aureli, 2010a). Some scientists argue that the exchange of services may require advanced cognitive abilities such as time estimation and quantifying of the services given and received (Stevens & Hauser, 2004; Stevens et al, 2005; Brosnan et al, 2010). For example, it has been proposed that because animals strongly discount future benefits, that is, they are less willing to cooperate for a progressively delayed benefit, this limits their ability to reciprocate over long time periods (Stevens & Hauser, 2004; Stevens et al, 2005). Consequently, it has been suggested that most animal species lack the cognitive abilities necessary for the exchange of services, which constrains the evolution of reciprocity (Stevens & Hauser, 2004; Stevens et al, 2005).

Other scientists argue that reciprocity would be cognitively demanding only if individuals are motivated by the expectation of receiving future benefit, that is, if individuals plan social interactions (e.g. giving grooming) in order to obtain future benefits (e.g. receiving food tolerance) (Schino & Aureli, 2009, 2010a). Studies suggest that these capacities may be beyond the cognitive capacities of most non-human primates species (Roberts, 2002; Suddendorf & Corballis, 2007; Schino & Pellegrini, 2011). For example in mandrills (*Mandrillus sphinx*), the alpha male (i.e. the most effective provider of support during agonistic interaction) was more likely to provide agonistic support after receiving grooming, but group members did not systematically groomed the alpha male before engaging in aggression. This suggests that mandrills do not plan their grooming interaction on the expectation of receiving agonistic support. Thus, although grooming appeared to promote agonistic support, agonistic support was not the motivational factor sustaining grooming (Schino & Pellegrini, 2011).

In contrast, exchange of services could be mediated by past service received, that is, the proximate motivation of individual may be past-based rather than future-oriented (Schino & Aureli, 2009, 2010a). Mechanisms involving partner-specific emotional bonds may allow the long-term tracking of exchanges of services with several partners, which could maintain reciprocity without the necessity of advanced cognitive abilities (Aureli & Schaffner, 2002; Silk, 2003; Schino & Aureli, 2009, 2010a). Emotional bonds would develop as a consequence of past services given and received between two individuals, and individuals would make their decision about with whom to cooperate on the basis of the emotional state associated with each possible partner (Schino & Aureli, 2009). Based on the establishment and maintenance of social bonds consequent to the exchange of services, emotionally based reciprocity could be within the cognitive capacities of non-human primates and widespread (Aureli & Schaffner, 2002; Schino & Aureli, 2009, 2010a). The emotional mediation of reciprocity would also favour the long-term exchange of services of different nature such as the exchange of grooming for food tolerance (Schino & Aureli, 2009). Indeed, the receipt of benefits of different nature may have similar emotional consequences, although the value of the different services may vary in relation to their availability depending on ecological conditions (e.g. availability of food resources) and biological market status (e.g. the number of infants currently available within the group) (Schino & Aureli, 2009). Supporting the emotional mediation hypothesis, neurotransmitters such as oxytocin underlie social bonding in humans and animals and may play a role in modulating altruistic behaviours (Insel & Shapiro, 1992; Insel & Young, 2001; Kosfeld et al, 2005; Schino & Aureli, 2009). In humans, emotions such as gratitude (i.e. the positive emotion one feels when receiving something of value from somebody; McCullough et al, 2001; McCullough & Tsang, 2004) also motivate the exchange of services (Bartlett & DeSteno, 2006; Tsang, 2006; McCullough et al, 2008).

1.4. THESIS AIMS

Grooming interactions are used as model to investigate cooperation and particularly the exchange of services in non-human primates. This thesis aims to bring novel contributions to our understanding of grooming interactions and cooperation in wild Barbary macaques in three major steps. Before to investigate the exchanges of grooming interactions, it is important to have a comprehensive idea of the costs and benefits of grooming interactions and of whether individuals influence grooming interactions of other group members. This is first covered by Chapter 3 and 4. Then, this thesis examines whether and how grooming is exchanged for itself and whether grooming is exchanged for another social service in Chapter 5 and 6. Finally, this thesis looks deeper into the importance of partner choice for cooperation by using an experimental approach in Chapter 7. More precisely, Chapters 3 to 7 of this thesis aim to investigate:

- **Chapter 3**: Post-grooming anxiety in the donor and recipient of grooming

Grooming has traditionally been viewed as a behaviour that is mainly beneficial, from a stress-releasing point of view, for the recipient than for the donor. Recent studies challenged this approach by showing that grooming may also reduce anxiety in the donor. This poses the question of whether grooming elicits a similar reduction in anxiety in the donor and recipient. This is important because a short-term post-grooming reduction in anxiety can affect subsequent social interactions between animals as well as their choice of social partners. This Chapter investigates the anxiety reduction mechanism of grooming by comparing post-grooming behavioural indicators of anxiety (i.e. self-directed behaviours) for the donor and recipient of the same grooming interactions.

- **Chapter 4**: Costs and benefits of grooming disruption

Grooming is the main behaviour used to establish and maintain social relationships in non-human primates, and can be exchanged with various services. However, individuals compete for valuable grooming partners, and individuals differ in the degree of control they have over services which play a role in the distribution of grooming. Grooming disruption has been proposed as a way to compete over access to grooming partners. This Chapter investigates what the benefits and costs of grooming disruption are for the disrupters, as an attempt to define the consequences of grooming disruptions.

- **Chapter 5**: Role of direct, indirect and generalised reciprocity in explaining grooming exchange

Three main patterns of reciprocity may follow the giving of grooming. Direct reciprocity is based on the assumption that the recipient of grooming is more likely to return the favour to the former donor. Indirect reciprocity is based on the assumption that giving grooming increases the donor’s reputation, and so it increases its chance to receive grooming from third parties. Generalised reciprocity assumes that individuals who have received grooming experience a general benevolent mood which makes them more likely to groom anyone else. Each of these forms of reciprocity may potentially play a role in the exchange of grooming. In animals, while direct reciprocity seems to play a role in the exchange of services, evidences for indirect and generalised reciprocity are scarce. This

Chapter investigates the role of direct, indirect and generalised reciprocity in explaining the exchange of grooming, by analysing the temporal contingency between giving and receiving grooming.

- **Chapter 6**: Short-term contingency between grooming and food tolerance

In non-human primates, individuals can exchanges several services such as grooming, food tolerance, infant handling and agonistic support. Exchanges can occur following a short-term contingency, or individuals can overall give more services toward individuals from who they received more services on a long-term basis. Despite the mixed evidence of short-term contingency between services given and received in animals, this approach is traditionally used as the basic mechanism to explain and demonstrate reciprocity. This Chapter investigates the exchanges of grooming for food tolerance, by analysing the short-term contingency between these events.

- **Chapter 7**: Introducing a cooperative task to a wild group of Barbary macaques: performance and partner choice

A key aspect of mutual cooperation is the choice of partners with whom to cooperate. However, in most of the experiments on cooperation conducted so far, subjects were given no opportunity to choose their cooperative partner, or the choice was reduced to two individuals. Non-human primates live in complex social group where the choice of the appropriate cooperative partner is an important social skill. This Chapter investigates whether wild Barbary macaques succeed to cooperate in an experimental task to get food, and which individual and social factors (i.e. sex, age, dominance status, tolerance, relationship quality and temperament) affect their choice of cooperative partner and their performances.

These questions are investigated in two groups of wild Barbary macaques (*Macaca sylvanus*), living in the Middle-Atlas Mountains of Morocco. The *Macaca* genus is closely related to humans, sharing a common ancestor around 25 million years ago (Kumar & Hedges, 1998; Stewart & Disotell, 1998). The Barbary macaque is a relatively tolerant macaque species, and their social relationships are less kin-biased than other macaque's species such as rhesus macaque (*Macaca mulatta:* Thierry & Aureli, 2006). However, in non-human primates reciprocity alone plays a larger role in explaining the exchange of grooming than kinship (Schino & Aureli, 2010b). Barbary macaques live in multi-male-multi-female groups where cooperative interactions such as grooming and food tolerance are frequent between all group members, and they individually recognise each other (e.g. Cheney & Seyfarth, 1982; Adachi & Hampton, 2011; Schell et al, 2011). The Barbary macaque is thus a suitable model to investigate grooming interactions and cooperative behaviours.

1.5. REFERENCES

Adachi, I. & Hampton, R. R. 2011. Rhesus monkeys see who they hear: spontaneous cross-modal memory for familiar conspecifics. *PLoS ONE*, **6**, e23345.

Akçay, A., Reed, V. A., Campbell, S. E., Templeton, C. N. & Beecher, M. D. 2010. Indirect reciprocity: song sparrows distrust aggressive neighbours based on eavesdropping. *Animal Behaviour*, **80**, 1041-1047.

Akinyi, M. Y., Tung, J., Jeneby, M., Patel, N. B., Altmann, J. & Alberts, S. C. 2013. Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behaviour*, **85**, 559-568.

Alberts, S. C., Buchan, J. C. & Altmann J. 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. *Animal Behaviour*, **72**, 1177-1196.

Alexander, R. D. 1974. The evolution of social behavior. *Annual Review of Ecological Systems*, **5**, 325-383.

Alexander, R. D. 1987. *The biology of moral systems*. New York: Aldine De Gruyter.

Aureli, F. & de Waal, F. B. M. 2000. *Natural conflict resolution*. California: University of California Press.

Aureli, F. & Schaffner, C. M. 2002. Relationship assessment through emotional mediation. *Behaviour*, **139**, 393-420.

Aureli, F. & Schino, G. 2004. The role of emotions in social relationships. In: *Macaque societies: a model for the study of social organization* (Ed. by B. Thierry, M. Singh & W. Kaumanns.), pp. 38-60. Cambridge: Cambridge University Press.

Aureli, F. & van Schaik, C. P. 1991. Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*). I. The social events. *Ethology,* **89**, 89-100.

Aureli, F. & Whiten, A. 2003. Emotions and behavioral flexibility. In: *Primate psychology: bridging the gap between the mind and behavior of human and nonhuman primates* (Ed. by D. Maestripieri), pp. 289-323. Cambridge: Harvard University Press.

Aureli, F. & Yates, K. 2010. Distress prevention by grooming others in crested black macaques. *Biology Letters,* **6**, 27-29.

Aureli, F., Cords, M. & van Schaik, C. P. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour,* **64**, 325-343.

Aureli, F., Fraser, O. N., Schaffner, C. M. & Schino, G. 2012. The regulation of social relationships. In: *The evolution of primate societies* (Ed. by J. Mitani, J. Call, P. Kappeler, R. Palombit & J. Silk), pp. 531-551. Chicago: University of Chicago Press.

Aureli, F., Preston, S. D. & de Waal, F. B. M. 1999. Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. *Journal of Comparative Psychology,* **113**, 59-65.

Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science,* **211**, 1390-1396.

Axelrod, R. 1984. *The evolution of cooperation*. New York: Basic Books.

Barelli, C., Reichard, U. H. & Mundry, R. 2011. Is grooming used as a commodity in wild white-handed gibbons, *Hylobates lar*? *Animal Behaviour*, **82**, 801-809.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999. Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B,* **266**, 665-670.

Bartlett, M. Y. & de Steno, D. 2006. Gratitude and prosocial behavior: helping when it costs you. *Psychological Science,* **17**, 319-325.

Bergman, T. J., Beehner, J. C, Cheney, D. L. & Seyfarth, R. M. 2003. Hierarchical classification by rank and kinship in baboons. *Science*, **302**, 1234-1236.

Boccia, M. L., Reite, M. & Laudenslager, M. 1989. On the physiology of grooming in a pigtail macaque. *Physiology & Behavior*, **45**, 667-670.

Boesch, C. & Boesch, H. 1989. Hunting behavior of wild chimpanzees in the Tai national park. *American Journal of Physical Anthropology*, **78**, 547-573.

Borgeaud, C., van de Waal, E. & Bshary, R. 2013. Third-party ranks knowledge in wild vervet monkeys (*Chlorocebus aethiops pygerythrus*). *PLoS ONE*, **8,** e58562.

Brosnan, S. F. & Bshary, R. 2010. Cooperation and deception: from evolution to mechanisms. *Philosophical Transactions of the Royal Society B*, **365**, 2593-2598.

Brosnan, S. F., Salwiczek, L. & Bshary, R. 2010. The interplay of cognition and cooperation. *Philosophical Transactions of the Royal Society B*, **365**, 2699-2710.

Bshary, R. & Bergmüller, R. 2008. Distinguishing four fundamental approaches to the volution of helping. *Journal of Evolutionary Biology*, **21**, 405-420.

Bshary, R. & D'Souza, A. 2005. Cooperation in communication networks: indirect reciprocity in interactions between cleaner fish and client reef fish. In: *Animal communication networks* (Ed. by P. K. McGregor), pp. 521-539. Cambridge: Cambridge University Press.

Bshary, R. & Grutter, A. S. 2006. Image scoring and cooperation in a cleaner fish mutualism. *Nature*, **441**, 975-978.

Bshary, R. 2002. Biting cleaner fish use altruism to deceive image scoring clients. *Proceedings of the Royal Society B*, **269**, 2087-2093.

Bulger, J. & Hamilton, W. J. 1987. Rank and density correlates of inclusive fitness measures in a natural chacma baboon (*Papio ursinus*) population. *International Journal of Primatology*, **8**, 635-650.

Bull, J. J. & Rice, W. R. 1991. Distinguishing mechanisms for the evolution of co-operation. *Journal of Theoretical Biology*, **149**, 63-74.

Cameron, E. Z., Setsaas, T. H. & Linklater, W. L. 2009. Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, **106**, 13850-13853.

Campennì, M. & Schino, G. 2014. Partner choice promotes cooperation: the two faces of testing with agent-based models. *Journal of Theoretical Biology*, **344**, 49-55.

Carne, C., Wiper, S. & Semple, S. 2011. Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology*, **73**, 1127-1133.

Carter, G. & Wilkinson, G. 2013. Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B*, **280**, 1753.

Castles, D. L. & Whiten, A. 1998. Post-conflict behaviour of wild olive baboons. II. Stress and self-directed behaviour. *Ethology*, **104**, 148-160.

Chalmeau, R., Lardeux, K., Brandibas, P. & Gallo, A. 1997a. Cooperative problem solving by orangutans (*Pongo pygmaeus*). *International Journal of Primatology*, **18**, 23-32.

Chalmeau, R., Visalberghi, E. & Gallo, A. 1997b. Capuchin monkeys, *Cebus apella*, fail to understand a cooperative task. *Animal Behaviour*, **54**, 1215-1225.

Cheney, D. L. & Seyfarth, R. M. 1982. Recognition of individuals within and between groups of free-ranging vervet monkeys. *American Zoologist*, **22**, 519-529.

Cheney, D. L. & Seyfarth, R. M. 1990. *How monkeys see the world: inside the mind of another species.* Chicago: University of Chicago Press.

Cheney, D. L. 2011. Extent and limits of cooperation in animals. *Proceedings of the National Academy of Sciences*, **108**, 10902-10909.

Cheney, D. L., Moscovice, L. R., Heesen, M., Mundry, R. & Seyfarth, R. M. 2010. Contingent cooperation between wild female baboons. *Proceedings of the National Academy of Sciences*, **107**, 9562-9566.

Cheney, D. L., Seyfarth, R. M. & Silk, J. B. 1995. The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: evidence for causal reasoning? *Journal of Comparative Psychology*, **109**, 134-141.

Clarke, P. M. R., Halliday, J. E. B., Barrett, L. & Henzi, S. P. 2010. Chacma baboon mating markets: competitor suppression mediates the potential for intersexual exchange. *Behavioral Ecology*, **21**, 1211-1220.

Clutton-Brock, T. 2009. Cooperation between non-kin in animal societies. *Science*, **462**, 51-57.

Clutton-Brock, T. H. & Parker, G. A. 1995a. Sexual coercion in animal societies. *Animal Behaviour*, **49**, 1345-1365.

Clutton-Brock, T. H. & Parker, G. A. 1995b. Punishment in animal societies. *Natur*e, **373**, 209-216.

Colmenares, F., Zaragoza, F. & Hernández-Lloreda, M. V. 2002. Grooming and coercion in one-male units of hamadryas baboons: market forces or relationship constraints? *Behaviour*, **139**, 1525-1553.

Cords, M. 1995. Predator vigilance costs of allogrooming in wild blue monkeys. *Behaviour*, **132**, 559-569.

Cords, M. 1997. Friendship, alliances, reciprocity and repair. In: *Machiavellian intelligence. II Extensions and evaluations* (Ed. by A. Whiten & R. W. Byrne), pp. 24-49. Cambridge: Cambridge University Press.

Cote, I. M. & Poulin, R. 1995. Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology*, **6**, 159-165.

Cowlishaw, G. & Dunbar, R. I. M. 1991. Dominance rank and mating success in male primates. *Animal Behaviour*, **41**, 1045-1056.

Crawford, M. P. 1937. The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs,* **14**, 1-88.

Cronin, K. A., Kurian, A. V. & Snowdon, C. T. 2005. Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). *Animal Behaviour,* **69**, 133-142.

Dawes, R. M. 1980. Social dilemmas. *Annual Review of Psychology*, **31**, 169-193.

Dawkins, R. 1976. *The selfish gene*. Oxford: Oxford University Press.

de Waal, F. B. M. & Luttrell, L. M. 1989. Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stumptail monkeys. *American Journal of Primatology,* **19**, 83-109.

de Waal, F. B. M. & Suchak, M. 2010. Prosocial primates: selfish and unselfish motivations. *Philosophical Transactions of the Royal Society B*, **365**, 2711-2722.

de Waal, F. B. M. 1997. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, **18**, 375-386.

de Waal, F. B. M. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, **60**, 253-261.

Diamond, J. & Bond, A. B. 1999. *Kea, bird of paradox: the evolution and behavior of a New Zealand parrot*. Berkeley, CA: University of California Press.

Drea, C. M. & Carter, A. N. 2009. Cooperative problem solving in a social carnivore. *Animal Behaviour,* **78**, 967-977.

Dugatkin, L. A. 1997. *Cooperation among animals: an evolutionary perspective*. Oxford: Oxford University Press.

Dunbar, R. I. M. & Sharman, M. 1984. Is social grooming altruistic? *Journal of comparative ethology,* **64**, 163-173.

Dunbar, R. I. M. & Shultz, S. 2010. Bondedness and sociality. *Behaviour,* **147**, 775-803.

Dunbar, R. I. M. 1988. *Primate social systems.* Comstock Publishing Associates, Cornell: Cornell University Press.

Dunbar, R. I. M. 1991. Functional significance of social grooming in primates. *Folia Primatologica*, **57**, 121-131.

Dunbar, R. I. M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, **3**, 35-49.

Dunbar, R. I. M. 1995. The mating system of callitrichid primates. I. Conditions for the coevolution of pair bonding and twinning. *Animal Behaviour*, **50**, 1057-1070.

Dunbar, R. I. M. 2001. Brains on two legs: group size and the evolution of intelligence. In: *Tree of origin: what primate behavior can tell us about human social evolution* (Ed. by F. B. M. de Waal), pp. 173-192. Cambridge: Harvard University Press.

Dunbar, R. I. M., Korstjens, A. H. & Lehmann, J. 2009. Time as an ecological constraint. *Biological Reviews*, **84**, 413-429.

Emmons, R. A. & McCullough, M. E. 2004. *The psychology of gratitude*. New York: Oxford University Press.

Feh, C. & de Mazières, J. 1993. Grooming at a preferred site reduces heart rate in horses. *Animal Behaviour*, **46**, 1191-1194.

Fehr, E. & Fischbacher, U. 2003. The nature of human altruism. *Nature*, **425**, 785-791.

Frank, R. E. & Silk, J. B. 2009. Impatient traders or contingent reciprocators? Evidence for the extended time course of grooming exchanges in baboons. *Behaviour*, **146**, 1123-1135.

Fraser, O. N & Bugnyar, T. 2010. The quality of social relationships in ravens. *Animal Behaviour*, **79**, 927-933.

Fraser, O. N & Bugnyar, T. 2011. Ravens reconcile after aggressive conflicts with valuable partners. *PLoS ONE*, **6**, e18118.

Freeland, W. J. 1976. Pathogens and the evolution of primate sociality. *Biotropica*, **8**, 12-24.

Fruteau, C., van de Waal, E., van Damme, E. & Noë, R. 2011. Infant access and handling in sooty mangabeys and vervet monkeys. *Animal Behaviour*, **81**, 153-161.

Garay, J. 2009. Cooperation in defence against a predator. *Journal of Theoretical Biology*, ***257***, 45-51.

Gazda, S. K., Connor, R. C., Edgar, R. K. & Cox, F. 2005. A division of labour with rule specialization in group hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society B*, **272**, 135-140.

Gomes, C. M., Mundry, R. & Boesch, C. 2009. Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B,* **276**, 699-706.

Gumert, M. 2007a. Grooming and infant handling interchange in *Macaca fascicularis*: the relationship between infant supply and grooming payment. *International Journal of Primatology*, **28**, 1059-1074.

Gumert, M. D. 2007b. Payment for sex in a macaque mating market. *Animal Behaviour,* **74**, 1655-1667.

Hamilton, I. M. & Taborsky, M. 2005. Contingent movement and cooperation evolve under generalised reciprocity. *Proceedings of the Royal Society B*, **272**, 2259-2267.

Hamilton, W. D. 1964. Genetical evolution of social behaviour. *The Journal of Theoretical Biology*, **7**, 17-52.

Hare, B., Melis, A. P., Woods, V., Hastings, S. & Wrangham, R. W. 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, **17**, 619-623.

Hart, B. L. & Hart, L. A. 1992. Reciprocal allogrooming in impala, *Aepyceros melampus*. *Animal Behaviour*, **44**, 1073-1083.

Hart, B. L. 1990. Behavioral adaptations to pathogens and parasites: five strategies. *Neuroscience & Biobehavioral Reviews,* ***14***, 273-294.

Hart, B. L., Hart, L. A., Mooring, M. S. & Olubayo, R. 1992. Biological basis of grooming behaviour in antelope: the body size, vigilance and habitat principles. *Animal Behaviour,* **44**, 615-631.

Hattori, Y., Kuroshima, H. & Fujita, K. 2005. Cooperative problem solving by tufted capuchin monkeys (*Cebus apella*): spontaneous division of labor, communication, and reciprocal altruism. *Journal of Comparative Psychology*, **119**, 335-342.

Henzi, S. P. & Barrett, L. 1999. The value of grooming to female primates. *Primates*, **40**, 47-59.

Henzi, S. P. & Barrett, L. 2002. Infants as a commodity in a baboon market. *Animal Behaviour*, **63**, 915-921.

Hinde, R. A. 1976. Interactions, relationships and social structure. *Man*, **11**, 1-17.

Hinde, R. A. 1979. *Towards understanding relationships*. London: Academic Press.

Hinde, R. A. 1983. A conceptual framework. In: *Primate social relationships: an integrated approach* (Ed. by R. A. Hinde), pp. 1-7. Oxford: Blackwell Scientific Publications.

Hirata, S. & Fuwa, K. 2007. Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates,* **48,** 13-21.

Hofer, H. & East, M. L. 2000. Conflict management in female-dominated spotted hyenas. In: *Natural conflict resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 232-234. Berkeley: University of California Press.

Hutchins, M. & Barash, D. P. 1976. Grooming in primates: implications for its utilitarian function. *Primates*, **17**, 145-150.

Insel, T. R. & Shapiro, L. E. 1992. Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. *Proceedings of the National Academy of Sciences*, **89**, 5981-5985.

Insel, T. R. & Young, L. J. 2001. The neurobiology of attachment. *Nature Review of Neuroscience*, **2**, 129-136.

Isbell, L. A., Pruetz, J. D., Lewis, M. & Young, T. P. 1999. Rank differences in ecological behavior: a comparative study of patas monkeys (*Erythrocebus patas*) and vervets (*Cercopithecus aethiops*). *International Journal of Primatology*, **20**, 257-272.

Jaeggi, A. V, de Groot, E., Stevens, J. M. G. & van Schaik, C. P. 2013. Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, **34**, 69-77.

Janson, C. 1985. Aggresive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, **18**, 125-138.

Johnson, D. D. P., Kays, R., Blackwell, P. G. & Macdonald, D. W. 2002. Does the resource dispersion hypothesis explain group living? *Trends in Ecology & Evolution,* **17**, 563-570.

Johnson, D. D. P., Stopka, P. & Macdonald, D. W. 2004. Ideal flea constraints on group living: unwanted public goods and the emergence of cooperation. *Behavioral Ecology,* **15**, 181-186.

Kappeler, P. M. & van Schaik, C. P. 2002. Evolution of primate social systems. *International Journal of Primatology,* **23**, 707-740.

Kappeler, P. M., Barrett, L., Blumstein, D. T. & Clutton-Brock, T. H. 2013. Constraints and flexibility in mammalian social behaviour: introduction and synthesis. *Philosophical Transactions of the Royal Society B,* **368**, 20120337.

Keverne, E. B., Martensz, N. D. & Tuite, B. 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology,* **14**, 155-161.

Kimura, R. 1998. Mutual grooming and preferred associate relationships in a band of free-ranging horses. *Applied Animal Behaviour Science*, **59**, 265-276.

Kitchen, D. M., Cheney, D. L. & Seyfarth, R. M. 2005. Male chacma baboons (*Papio hamadryas ursinus*) discriminate loud call contests between rivals of different relative ranks. *Animal Cognition*, **8**, 1-6.

Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U. & Fehr, E. 2005. Oxytocin increases trust in humans. *Nature*, **435**, 673-676.

Koyama, N. F. 2001. The long-term effects of reconciliation in Japanese macaques (*Macaca fuscata*). *Ethology,* **107**, 975-987.

Kumar, S. & Hedges, S. B. 1998. A molecular timescale for vertebrate evolution. *Nature*, **392**, 917-920.

Kutsukake, N. & Clutton-Brock, T. H. 2006. Social function of allogrooming in cooperatively breeding meerkats. *Animal Behaviour*, **72**, 1059-1068.

Langergraber, K., Mitani, J., Watts, D. & Vigilant, L. 2013. Male-female socio-spatial relationships and reproduction in wild chimpanzees. *Behavioral Ecology and Sociobiology*, **67**, 861-873.

Lehmann, J., Korstjens, A. H. & Dunbar, R. I. M. 2007. Group size, grooming and social cohesion in primates. *Animal Behaviour,* **74**, 1617-1629.

Leimar, O. & Hammerstein, P. 2001. Evolution of cooperation through indirect reciprocity. *Proceedings of the Royal Society B*, **268**, 745-753.

Lima, S. L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour,* **49**, 11-20.

Lindenfors, P., Fröberg, L. & Nunn, C. L. 2004. Females drive primate social evolution. *Proceedings of the Royal Society B*, **271**, S101-S103.

Maestripieri, D. 1993. Vigilance costs of allogrooming in macaque mothers. *The American Naturalist*, **141**, 744-753.

Majolo, B., de Bortoli Vizioli, A. & Schino, G. 2008. Costs and benefits of group living in primates: group size effects on behaviour and demography. *Animal Behaviour*, **76**, 1235-1247.

Majolo, B., Lehmann, J., de Baroli Vizioli, A. & Schino, G. 2012a. Fitness-related benefits of dominance in primates. *American Journal of Physical Anthropology,* **147,** 652-660.

Majolo, B., Schino, G. & Aureli, F. 2012b. The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges. *Animal Behaviour*, **83**, 763-771.

Majolo, B., Ventura, R., Koyama, N. F., Hardie, S. M., Jones, B. M., Knapp, L. A. & Schino, G. 2009. Analysing the effects of group size and food competition on Japanese macaque social relationships. *Behaviour,* **146**, 113-137.

Martel, F. L., Nevison, C. M., Simpson, M. J. A. & Keverne, E. B. 1995. Effects of opioid receptor blockade on the social behavior of rhesus monkeys living in large family groups. *Developmental Psychobiology,* **28**, 71-84.

Matsumura, S. 1999. The evolution of 'egalitarian' and 'despotic' social systems among macaques. *Primates,* **40**, 23-31.

McCullough, M. E. & Tsang, J. 2004. Parent of the virtues? The prosocial contours of gratitude. In: *The psychology of gratitude* (Ed. by R. A. Emmons & M. E. McCullough), pp. 123-141. New York: Oxford University Press.

McCullough, M. E., Kilpatrick, S. D., Emmons, R. A. & Larson, D. B. 2001. Is gratitude a moral affect? *Psychological Bulletin,* **127**, 249-266.

McCullough, M. E., Kimeldorf, M. B. & Cohen, A. D. 2008. An adaptation for altruism? The social causes, social effects, and social evolution of gratitude. *Current Directions in Psychological Science,* **17**, 81-285.

McFarland, R. & Majolo, B. 2011. Grooming coercion and the post-conflict trading of social services in wild Barbary macaques. *PLoS ONE,* **6**, e26893.

Mcfarland, R. & Majolo, B. 2013. Coping with the cold: predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biology Letters*, **9**, 20130428.

Melis, A. P. & Semmann, D. 2010. How is human cooperation different? *Philosophical Transactions of the Royal Society B,* **365**, 2663-2674.

Melis, A. P., Hare, B. & Tomasello, M. 2006. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Animal Behaviour,* **72,** 275-286.

Melis, A. P., Hare, B. & Tomasello, M. 2008. Do chimpanzees reciprocate received favours? *Animal Behaviour,* **76**, 951-962.

Mendres, K. A & de Waal, F. B. M. 2000. Capuchins do cooperate: the advantage of an intuitive task. *Animal Behaviour,* **60**, 523-529.

Micheletta, J., Waller, B. M., Panggur, M., Neumann, C., Duboscq, J. & Agil M. 2012. Social bonds affect anti-predator behaviour in a tolerant species of macaques, *Macaca nigra*. *Proceedings of the Royal Society B,* **279**, 4042-4050.

Møller, A. P., Dufva, R. & Allander, K. 1993. Parasites and the evolution of host social behaviour. *Advances in the Study of Behaviour,* **22**, 65-102.

Mooring, M. S. & Hart, B. L. 1995. Costs of allo-grooming in impala: distraction from vigilance. *Animal Behaviour,* **49**, 1414-1416.

Muller, M. N. & Wrangham, R. W. 2009. *Sexual coercion in primates: an evolutionary perspective on male aggression against females*. Cambridge: Harvard University Press.

Muroyama, Y. 1994. Exchange of grooming for allomothering in female patas monkeys. *Behaviour,* **128**, 103-119.

Nelson, H. & Geher, G. 2007. Mutual grooming in human dyadic relationships: an ethological perspective. *Current Psychology,* **26**, 121-140.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism, and mating. *Behavioral Ecology and Sociobiology*, **35**, 1-11.

Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of cooperation. In: *Economics in nature: social dilemmas, mate choice and biological markets* (Ed. by R. Noë, J. A. R. A. M van Hooff & P. Hammerstein), pp. 93-118. Cambridge: Cambridge University Press.

Noë, R. 2006. Cooperation experiments: coordination through communication versus acting apart together. *Animal Behaviour,* **71**, 1-18.

Noë, R., van Hooff, J. A. R. A. M. & Hammerstein, P. 2001. *Economics in nature: social dilemmas, mate choice and biological markets.* Cambridge: Cambridge University Press.

Norscia, I., Antonacci, D. & Palagi, E. 2009. Mating first, mating more: biological market fluctuation in a wild prosimian. *PLoS ONE,* **4**, e4679.

Nowak, M. A. & Sigmund, K. 1998. Evolution of indirect reciprocity by image scoring. *Nature,* **393**, 573-577.

Nowak, M. A. & Sigmund, K. 2005. Evolution of indirect reciprocity. *Nature,* **437**, 1291-1298.

Nowak, M. A. 2006. Five rules for the evolution of cooperation. *Science*, **314**, 1560-1563.

Nunn, C. L. & Altizer, S. M. 2006. *Infectious diseases in primates: behavior, ecology and evolution.* Oxford: Oxford University Press.

Olendorf, R., Getty, T. & Scribner, K. 2004. Cooperative nest defence in red-winged blackbirds: reciprocal altruism, kinship or by-product mutualism? *Proceedings of the Royal Society B,* **271**, 177-182.

Packer, C. 1977. Reciprocal altruism in *Papio anubis*. *Nature,* **265**, 441-443.

Packer, C. 1979. Male dominance and reproductive activity in *Papio anubis*. *Animal Behaviour,* **27**, 37-45.

Palombit, R. A., Seyfarth, R. M. & Cheney, D. L. 1997. The adaptive value of ‘friendship’ to female baboons: experimental and observational evidence. *Animal Behaviour,* **54**, 599-614.

Perry, S., Barrett, H. C. & Manson, J. 2004. White-faced capuchin monkeys show triadic awareness in their choice of allies. *Animal Behaviour*, **67**, 165-170.

Pinto, A., Oates, J., Grutter, A. & Bshary, R. 2011. Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Current Biology,* **21**, 1140-1144.

Plotnik, J. M., Lair, R., Suphachoksahakun, W. & de Waal, F. B. M. 2011. Elephants know when they need a helping trunk in a cooperative task. *Proceedings of the National Academy of Sciences,* **108**, 5116-5121.

Puga-Gonzalez, I., Hildenbrandt, H. & Hemelrijk, C. K. 2009. Emergent patterns of social affiliation in primates, a model. *PLOS Computational Biology*, **5**, e1000630.

Radford, A. N. & Du Plessis, M. A. 2006. Dual function of allopreening in the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*. *Behavioral Ecology and Sociobiology,* **61**, 221-230.

Radford, A. N. 2012. Post-allogrooming reductions in self-directed behaviour are affected by role and status in the green woodhoopoe. *Biology Letters,* **8**, 24-27.

Rand, D. G., Ohtsuki, H. & Nowak, M. A. 2009. Direct reciprocity with costly punishment: generous tit-for-tat prevails. *The Journal of Theoretical Biology,* **256**, 45-57.

Roberts, W. A. 2002. Are animals stuck in time? *Psychological Bulletin,* **128**, 437-489.

Rodriguez-Llanes, J. M., Verbeke, G. & Finlayson, C. 2009. Reproductive benefits of high social status in male macaques (*Macaca*). *Animal Behaviour,* **78**, 643-649.

Rutte, C. & Taborsky, M. 2007. Generalised reciprocity in rats. *PLoS Biology*, **5**, 1421-1425.

Sabbatini, G., De Bortoli Vizioli, A., Visalberghi, E. & Schino, G. 2012. Food transfers in capuchin monkeys: an experiment on partner choice. *Biology Letters*, **8**, 757-759.

Sapolsky, R. M., Alberts, S. C. & Altmann, J. 1997. Hypercortisolism associated with social subordinate or social isolation among wild baboons. *Archive of General Psychiatry,* **54**, 1137-1143.

Scantlebury, M., Waterman, J. M., Hillegass, M., Speakman, J. R. & Bennett, N. C. 2007. Energetic costs of parasitism in the Cape ground squirrel *Xerus inauris. Proceedings of the Royal Society B,* **274,** 2169-2177.

Schaffner, C. M. & Caine, N. G. 2000. The peacefulness of cooperatively breeding primates. In: *Natural conflict resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 155-169. California: University of California Press.

Schaffner, C. M., Aureli, F. & Caine, N. G. 2005. Following the rules: why small groups of tamarins do not reconcile conflicts. *Folia Primatologica*, **76**, 67-76.

Scheid, C. & Noë, R. 2010. The performance of rooks in a cooperative task depends on their temperament. *Animal Cognition*, **13**, 545-553.

Schell, A., Rieck, K., Schell, K., Hammerschmidt, K. & Fischer, J. 2011. Adult but not juvenile Barbary macaques spontaneously recognize group members from pictures. *Animal Cognition*, **14**, 503-509.

Schino, G. & Aureli, F. 2008a. Grooming reciprocation among female primates: a meta-analysis. *Biology Letters,* **4**, 9-11.

Schino, G. & Aureli, F. 2008b. Trade-offs in primate grooming reciprocation: testing behavioural flexibility and correlated evolution. *Biological Journal of the Linnean Society,* **95**, 439-446.

Schino, G. & Aureli, F. 2009. Reciprocal altruism in primates: partner choice, cognition and emotions. *Advances in the Study of Behavior*, **39**, 45-69.

Schino, G. & Aureli, F. 2010a. Primate reciprocity and its cognitive requirements. *Evolutionary Anthropology,* **19**, 130-135.

Schino, G. & Aureli, F. 2010b. The relative roles of kinship and reciprocity in explaining primate altruism. *Ecology Letters*, **13**, 45-50.

Schino, G. & Pellegrini, B. 2009. Grooming in mandrills and the time frame of reciprocal partner choice. *American Journal of Primatology*, **71**, 884-888.

Schino, G. & Pellegrini, B. 2011. Grooming and the expectation of reciprocation in mandrills (*Mandrillus sphinx*). *International Journal of Primatology*, **32**, 406-414.

Schino, G. 2001. Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, **62**, 265-271.

Schino, G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology,* **18**, 115-120.

Schino, G., di Giuseppe, F. & Visalberghi, E. 2009. The time frame of partner choice in the grooming reciprocation of *Cebus apella*. *Ethology,* **115**, 70-76.

Schino, G., Polizzi di Sorrentino, E. & Tiddi, B. 2007. Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame of reciprocation. *Journal of Comparative Psychology*, **121**, 181-188.

Schino, G., Scucchi, S., Maestipieri, D. & Turillazzi, P. G. 1988. Allogrooming as a tension-reduction mechanism: a behavioural approach. *American Journal of Primatology,* **16**, 43-50.

Schino, G., Tiddi, B. & Di Sorrentino, E. P. 2006. Simultaneous classification by rank and kinship in Japanese macaques. *Animal Behaviour*, **71**, 1069-1074.

Schülke, O., Bhagavatula, J., Vigilant, L. & Ostner, J. 2010. Social bonds enhance reproductive success in male macaques. *Current Biology*, **20**, 2207-2210.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2008. Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society B,* **275**, 1421-1429.

Semmann, D., Krambeck, H.-J. & Milinski, M. 2005. Reputation is valuable within and outside one's own social group. *Behavioral Ecology and Sociobiology*, **57**, 611-616.

Seyfarth, R. M. & Cheney D. L. 2012. The evolutionary origin of friendship. *Annual Review of Psychology,* **63**,153-77.

Seyfarth, R. M. 1977. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, **65**, 671-698.

Shettleworth, S. 2010. *Cognition, evolution, and behavior.* 2nd edn. New York: Oxford University Press.

Sigmund, K. 2012. Moral assessment in indirect reciprocity. *Journal of Theoretical Biology*, **299**, 25-30.

Silk, J. B. 1982. Altruism among female *Macaca radiata:* explanations and analysis of patterns of grooming and coalition-formation. *Behaviour*, **79,** 162-188.

Silk, J. B. 1999. Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour*, **58**, 45-51.

Silk, J. B. 2002. Using the ‘F’ word in primatology. *Behaviour*, **139**, 421-446.

Silk, J. B. 2003. Cooperation without counting: the puzzle of friendship. In: *The genetic and cultural evolution of cooperation* (Ed. by P. Hammerstein), pp. 37-54. Cambridge: The MIT Press.

Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B,* **362**, 539-559.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance infant survival. *Science,* **302**, 1231-1234.

Silk, J. B., Altmann, J. & Alberts S. 2006. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology,* **61**, 183-195.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B*, **276**, 3099-3104.

Silk, J. B., Beehner, J. C., Berman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2010a. Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, **61**, 197-204.

Silk, J. B., Beehner, J. C., Berman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2010b. Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, **20**, 1359-1361.

Slocombe, K. E. & Zuberbühler, K. 2007. Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences,* **104**, 17228-17233.

Smuts, B. B. & Smuts, R. W. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior,* **22**, 1-63.

Sommerfeld, R. D., Krambeck, H.-J., Semmann, D. & Milinski, M. 2007. Gossip as an alternative for direct observation in games of indirect reciprocity. *Proceedings of National Academy of Sciences*, **104**, 175435-175440.

Spruijt, B. M., van Hooff, J. A. R. A. M. & Gispen, W. H. 1992. Ethology and neurobiology of grooming behavior. *Physiological Reviews*, **72**, 825-852.

Sterck, E. H. M., Watts, D. P. & van Schaik, C. P. 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology,* **41**, 291-309.

Stevens, J. R. & Hauser, M. D. 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences,* **8**, 60-65.

Stevens, J. R., Cushman, F. A. & Hauser, M. D. 2005. Evolving the psychological mechanisms for cooperation. *Annual Review of Ecology, Evolution, and Systematics,* **36**, 499-518.

Stewart, C. B. & Disotell, T. R. 1998. Primate evolution-in and out of Africa. *Current Biology*, **8**, 582-588.

Suddendorf, T. & Corballis, M. C. 2007. The evolution of foresight: what is mental time travel, and is it unique to humans? *Behavioral and Brain Sciences*, **30**, 299-313.

Sueur, C., Deneubourg, J.-L., Petit, O. & Couzin, I. D. 2011. Group size, grooming and fission in primates: a modeling approach based on group structure. *Journal of Theoretical Biology*, **273**, 156-166.

Sylwester, K. & Roberts, G. 2010. Cooperators benefit through reputation-based partner choice in economic games. *Biology Letters*, **6**, 659-662.

Tanaka, I. & Takefushi, H. 1993. Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropological Science*, **101**, 187-193.

Terry, R. 1970. Primate grooming as a tension reduction mechanism. *Journal of Psychology*, **76**, 129-136.

Thierry, B. & Aureli, F. 2006. Barbary but not barbarian: social relations in a tolerant macaque. In: *The Barbary macaque: biology, management and conservation* (Ed. by J. K. Hodges & J. Cortes), pp. 29-45. Nottingham: Nottingham University press.

Thierry, B. 2007. Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology*, **16**, 224-238.

Thierry, B., Singh, M. & Kaumanns, W. 2004. *Macaque societies: a model for the study of social organization*. Cambridge: Cambridge University Press.

Tiddi, B., Aureli, F. & Schino, G. 2010. Grooming for infant handling in tufted capuchin monkeys: a reappraisal of the primate infant market. *Animal Behaviour*, **79**, 1115-1123.

Tiddi, B., Aureli, F., Polizzi di Sorrentino, E., Janson, C. H. & Schino, G. 2011. Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. *Behavioral Ecology*, **22**, 663-669.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *The Quarterly Review of Biology*, **46**, 35-57.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual selection and the descent of man* (Ed. by B. Campbell), pp. 136-79. Chicago: Aldine.

Tsang, J. 2006. Gratitude and prosocial behaviour: an experimental test of gratitude. *Cognition and Emotion*, **20**, 138-148.

van Schaik, C. P. & Aureli, F. 2000. The natural history of valuable relationships in primates. In: *Natural conflict resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 307-333. Berkeley: University of California Press.

van Schaik, C. P. & Hörstermann, M. 1994. Predation risk and the number of adult males in a primate group: a comparative test. *Behavioural Ecology and Sociobiology*, **35**, 261-272.

van Schaik, C. P. & Janson, C. H. 2000. *Infanticide by males and its implications*. Cambridge: Cambridge University Press.

van Schaik, C. P. & Kappeler, P. M. 1997. Infanticide risk and the evolution of male-female association in primates. *Proceedings of the Royal Society B*, **264**, 1687-1694.

van Schaik, C. P. 1989. The ecology of social relationships amongst female primates. In: *Comparative socioecology: the behavioural ecology of humans and other mammals* (Ed. by V. Standen), pp. 195-218. Oxford: Blackwell.

Ventura, R., Majolo, B., Koyama, N. F., Hardie, S. & Schino, G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology*, **68**, 1138-1149.

Visalberghi, E., Quarantotti, B. P. & Tranchida, F. 2000. Solving a cooperation task without taking into account the partner's behavior: the case of capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, **114**, 297-301.

Wasser, S. K., Norton, G. W., Kleindorfer, S. & Rhine, R. J. 2004. Population trend alters the effects of maternal dominance rank on lifetime reproductive success in yellow baboons. *Behavioral Ecology and Sociobiology*, **56**, 338-345.

Weaver, A. 2003. Conflict and reconciliation in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science*, **19**, 836-846.

Wei, W., Qi, X.-G., Guo, S.-T., Zhao, D.-P., Zhang, P., Huang, K. & Li, B.-G. 2012. Market powers predict reciprocal grooming in golden snub-nosed monkeys (*Rhinopithecus oxellana*). *PLoS ONE*, **7,** e36802.

West, S. A., El Mouden, C. & Gardner, A. 2011. Sixteen common misconceptions about the evolution of cooperation in humans. *Evolution and Human Behavior*, **32**, 231-262.

West, S. A., Griffin, A. S. & Gardner, A. 2007a. Evolutionary explanations for cooperation. *Current Biology*, **17**, 661-672.

West, S. A., Griffin, A. S. & Gardner, A. 2007b. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, **20**, 415-432.

Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bats. *Nature*, **308,** 181-184.

Wilkinson, G. S. 1986. Social grooming in the common vampire bat, *Desmodus rotundus*. *Animal Behaviour*, **34**, 1880-1889.

Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, ***75***, 262-300.

Zamma, K. 2002. Grooming site preferences determined by lice infection among Japanese macaques in Arashiyama. *Primates,* **43**, 41-49.

Chapter 2

General methods

Barbary macaques grooming after an experimental session (picture by S. Molesti).

2.1. STUDY SPECIES

The species studied in this thesis was the Barbary macaque (*Macaca sylvanus*). The genus *Macaca* belongs to the family of Cercopithecidae and it contains around 20 species (Thierry et al, 2004). The macaques are the most widespread non-human primate genus and the majority are found in South and East Asia. The Barbary macaque is the most primitive of the *Macaca* genus (Purvis, 1995; Morales & Melnick, 1998). The Barbary macaque is unique within the genus *Macaca* in several respects: it is the only macaque species that is found outside of Asia and that has a tail which is reduced to a boneless vestige or absent (Fooden, 2007). Natural populations of this species are distributed among several fragmented populations in Morocco and Algeria. In Morocco, Barbary macaques can be found in the Middle and High Atlas Mountains and the Rif Mountains (Figure 2.1). In Algeria, they are found in the Tellian Atlas (Fa, 1984c; Ménard & Vallet, 1993b; Scheffrahn et al, 1993). The current distribution of this species ranges from a latitude of around 31° 15’N to 36° 45’N and from a longitude of around 7° 45’W to 5° 35’E (Fooden, 2007). The total population size in the wild is estimated between 5,000 and 10,000 individuals (von Segesser et al, 1999; Camperio Ciani et al, 2005; van Lavieren & Wich, 2009). A non-native free-ranging population of around 250 macaques inhabits the Rock of Gibraltar outside Africa. Over the last decades the numbers of wild Barbary macaques have decreased rapidly in Morocco and Algeria, from a total population size estimated at around 21,000 individuals around 40 years ago (Taub, 1975, 1978; van Lavieren & Wich, 2009). In the Middle Atlas Mountains of Morocco, the average number of individuals estimated per km^2 decreased from 40-70 in the early 1970s (Deag, 1984) to 7 in 2005 (Camperio Ciani et al, 2005). The remaining populations in Morocco and Algeria are highly fragmented, with gaps up to round 700 km between populations (Fooden, 2007), which prevents migration of macaques between groups. The decline of the population is mainly due to the destruction of the habitat of the species (e.g. habitat fragmentation, competition over food and water sources between the macaques and humans and their livestock), and the illegal capturing of infants for the pet trade (e.g. Mehlman, 1989; Camperio Ciani & Mouna, 2007; van Lavieren, 2008; Majolo et al, 2013a). An estimated 300 infant macaques are smuggled into Europe annually (van Lavieren, 2008). The species is listed as endangered in the IUCN Red List (IUCN red list of threatened species, 2013). Semi-free ranging provisioned Barbary macaques can be found in several parks in France (La Montagne des Singes, Kintzheim and La Forêt des Singes, Rocamadour), Germany (Affenberg Salem, Salem), and England (Trentham Monkey Forest, Trentham).

The Barbary macaque inhabits the cedar-oak forests (*Cedrus atlantica* & *Quercus ilex*), deciduous oak forests (*Quercus faginea* & *Quercus afores*), scrubs, grasslands, fir forests and rocky ridges dominated by herbaceous vegetation (Fooden, 2007). This species experiences warm dry summers and cold wet winters with snow (Fooden, 2007). It is thus one of a few non-human primate species to live in a snowy environment for a big part of the year (at elevations above 1500m, snow accumulations can persist until mid-May: Fa, 1982; Mehlman, 1984). The elevation distribution of Barbary macaques is considered to lie between 400 and 2300m above sea level (Fooden, 2007). Barbary macaques are semi-terrestrial, they spend most of their time on the ground during daylight (Deag, 1985, Ménard & Vallet, 1997; Fooden, 2007), they flee into trees to escape danger (Deag, 1985), and they sleep in trees (Taub, 1977; Mehlman, 1989; Hammerschmidt et al, 1994) or in caves on rocky cliffs (Alvarez & Hiraldo, 1975; Fa et al, 1984; Mehlman, 1984). The diet of Barbary macaques is highly diverse and varies seasonally. It includes leaves, seeds, fruits, fungi, roots, lichens, saps, animal preys (e.g. scorpions, earthworms, beetles and birds), and bark (Fa, 1984b; Mehlman, 1984, 1988;

Ménard & Qarro, 1999; Ménard, 2002; Fooden, 2007; Young et al, 2012). The pelage of adult Barbary macaques is yellowish-brown to grey with a lighter underside, and their face is dark pink. The fur becomes thicker during winter months and moulting occurs during the spring and summer (Fooden, 2007). At birth, the pelage is blackish and it acquires the characteristic of adult pelage at around 145 days old (Fooden, 2007). The average adult body length varies between males and females (550-600mm for males, and around 450mm for females), as well as the average body weight (15.3-17kg for males, and 10.2-11kg for females) (Fa, 1989). Males have elongated canines which play an important role in dominance related behaviours. The greatest life span reported in captivity is 30 years for a female and 25 years for a male, but wild Barbary macaques are unlikely to live beyond 15-17 years (Fooden, 2007).

Barbary macaques live in multi-male-multi-female groups (Thierry et al, 2004) of average size of 27.1 monkeys, group size can ranges from 7 to 88 individuals and group composition varies widely too (Ménard, 2002; Fooden, 2007). Fission usually occurs in natural groups reaching a high number of individuals: a group of 88 members in Algeria divided into three groups of 50, 24 and 13 members, and 1 member disappeared (Ménard & Vallet, 1993a, 1993b; Lathuillière et al, 2004). Sex ratio can vary from 0.6 to 1.6 females per male (Ménard, 2002). Provisioned semi-free-ranging groups can become larger than natural groups (de Turckheim & Merz, 1984; Fooden, 2007). Females are philopatric (i.e. they remain in their natal group all their life), whereas males usually emigrate to another group when they reach sexual maturity (Ménard & Vallet, 1993a; Ménard & Vallet, 1996). Female philopatry leads to the constitution of matrilines and the coexistence of several generations within the same group (Thierry, 2007). The average home range area varies between groups and it is suggested to be around 18.4 ha in the Moroccan Moyen Atlas Mountains, 804.5 ha in the Moroccan Rif Mountains and 279.7

ha in Algeria (Fooden, 2007). The Barbary macaque is a seasonal breeder, with mating occurring between September and January. In the current study, data were collected across the mating and non-mating season, and the mating season was defined as lasting from the first to the last copulation observed in the group. Gestation lasts around 164.3 days and births occur between late March and June. Male emigration reduces the possibility of inbreeding to occur and increases the chance of finding viable mating partners (Paul & Kuester, 1985; Kuester & Paul, 1999; Lathuillière et al, 2004). Females reach their sexual maturity at around 4-5 years (i.e. capability of gestation) and males at around 5 years (i.e. capability of ejaculatory copulation) (Deag, 1980; Ménard et al, 1985; Ménard & Valley, 1996). Barbary macaques are sub-adults when aged 4 to 5 years (Ménard & Vallet, 1993b). During the mating season, females show a significant perineal swelling (de Turckheim & Merz, 1984; Fa, 1984a; Kuester & Paul, 1984; Dixson, 1998; Möhle et al, 2005).

According to the classification of Thierry and colleagues (2004) on the social tolerance of macaques' species, the Barbary macaque is a relatively tolerant species: it is classified as a grade 3, where grade 1 represents highly despotic macaque species such as rhesus and Japanese macaques (*Macaca mulatta* and *Macaca fuscata,* respectively) and grade 4 represents more egalitarian macaque species such as Tonkean and black crested macaques (*Macaca tonkeana* and *Macaca nigra,* respectively) (Thierry & Aureli, 2006; Thierry, 2007). More despotic macaque species are considered to be more kin-biased in their distribution of affiliation, notably grooming interaction, compared to more egalitarian species (Thierry, 2007; de Waal & Luttrell, 1989). Grooming is observed frequently in both same-sex and different-sex pairs in Barbary macaques. The Barbary macaque also shares some social features with more despotic macaque species such as low frequency of counter-aggression (Balasubramaniam et al, 2012), a steep dominance hierarchy (Kaburu et al, 2012), and grooming coercion (McFarland & Majolo, 2011). Each adult and sub-adult of a group can be ranked according to its relative dominance status to other group members, males being usually dominant over females (e.g. Lee & Oliver, 1979; Berard, 1999). In Barbary macaques, dominance is less pronounced among males than among females (Preuschoft et al, 1998). Adult males often interact with infants and use them as social buffers to facilitate approach and affiliation among males (Deag & Crook, 1971; Deag, 1980; Taub, 1985; Paul et al, 1992, 1996; Henkel et al 2010).

Because the tolerance level of Barbary macaques is intermediate among macaques' species, Barbary macaques are not always tolerant around food resources, so it may be expected that low-ranking individuals exchange grooming for tolerance over food. Moreover in captive Barbary macaques, there is evidence that, overall, grooming interactions are reciprocated and exchanged for tolerance while feeding (Carne et al, 2011). However, it is still unknown whether Barbary macaques exchange social services in the short-term. This would allow to investigate in the same species which mechanism plays a major role in the exchange of services. Additionally, because of the proximity with tourists of certain groups of wild Barbary macaques, both observational and experimental data collection can be conducted on wild individuals of the same species, in a more natural environment than in laboratories. This makes the Barbary macaque a particularly suitable species to investigate all the research questions of this thesis.

2.2. STUDY FIELD SITE

This study took place in the Ifrane National Park, in the Middle Atlas Mountains of Morocco, where the largest population of Barbary macaques can be found (Figure 2.1). The field site (Figure 2.2) was a deciduous cedar and oak forest (*Cedrus atlantica* & *Quercus ilex*) situated between 1600 and 2000m a.s.l., near the city of Azrou (33° 24’N - 005° 12’W). During the course of the study, the field site experienced a variation of temperature from -7°C to 38°C, with snow in the winter months (Figure 2.3). At the field site, daily rainfall ranged from 0 to 117 mm and relative humidity from to 0 to 100% (Majolo et al, 2013b). In addition to the Barbary macaques, the forest was also inhabited by Golden jackals (*Canis aureus*), red foxes (*Vulpes vulpes*), wild boars (*Sus scrofa*), genets (*Genetta genetta*), wild cats (*Felis silvestris*) and a number of small mammals (such as rabbits and hares), reptiles, birds (including birds of prey) and insects (‘Inventaire de la biodiversité du Parc National d’Ifrane’, 2007). Some caracals (*Caracal caracal*), otters (*Lutra lutra*) and mongooses (*Herpestes ichneumon*) are thought to appear in the Ifrane National Park but have not been observed at the field site (‘Inventaire de la biodiversité du Parc National d’Ifrane’, 2007).

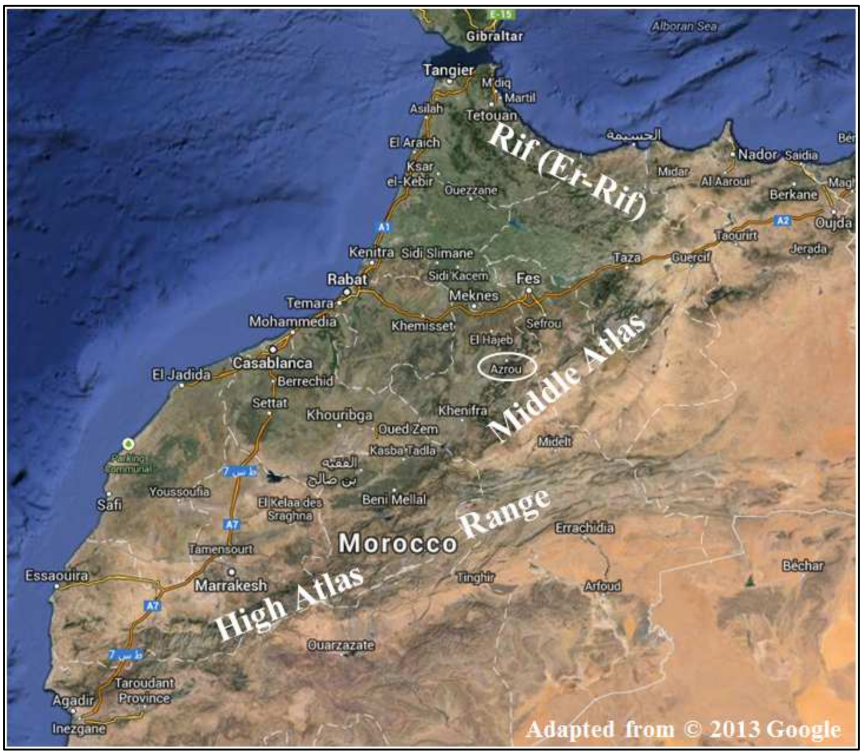


Figure 2.1. Map of the Middle-Atlas Mountains of Morocco. The city of Azrou is circled.

Figure 2.2. Map of the field site near the city of Azrou. The arrow represents the approximate location of the field site.

Figure 2.3. A male Barbary macaque during the winter months at the field site (picture by S. Molesti).

2.3. STUDY SUBJECTS

The subjects of this study belonged to two groups of wild Barbary macaques: the ‘Green group’ and the ‘Tourist group’. Both groups were representative of the species in terms of group size and composition (Ménard, 2002). All the individuals were recognisable from natural markings and were followed on foot from dawn to dusk on each day of observation. All subjects were already habituated to the presence of human observers before the beginning of the study. The study was mainly conducted on the adults and sub-adult monkeys of each group, and details on the number of subjects used in each specific study are provided in Chapters 3 to 7. Kinship data were not available for these groups.

The ‘Green group’ was a wild non-provisioned group of Barbary macaques composed at the beginning of the study of 16 adults and sub-adults (8 adult males, 7 adult females, and 1 sub-adult male; Table 2.1), 7 juveniles (4 males and 3 females; Table 2.2) and several infants. In 2011, 6 infants were born and all of them were still present at the end of the data collection period in January 2012. This group fed on a natural diet. During the course of the study, one adult male emigrated to another neighbouring group and one old adult female died of apparently natural causes. Besides the presence of researchers, the monkeys of this group only experienced occasional encounters with shepherds.

The ‘Tourist group’ was a wild, partially-provisioned group of Barbary macaques composed of 24 adult and sub-adult monkeys (9 adult males, 10 adult females, 2 sub-adult males and 3 sub-adult females; Table 2.3), 12 juveniles (7 males and 5 females; Table 2.4) and several infants. In 2011, 8 infants were born, 1 deceased and 7 were still present at the end of the data collection period in January 2012. Three juveniles (2 males and 1 female) died in 2011 during the study period and were not included in the analyses. The home-range of this group included a tourist site where tourists could come to visit the monkeys (Maréchal et al, 2011). In addition to their natural diet, this group also received a variety of food from tourists such as fruits, bread and peanuts (personal observations). Consequently, in addition to observational data collection, experimental data collection using food rewards could also be conducted on the monkeys of this group without disturbing their usual diet and health, and without the presence of the experimenters bothering them.

Table 2.1. ID, sex and ordinal dominance rank of each adult and sub-adult monkey of the 'Green group'. The rank 1 represents the highest dominance status in the group.

Subject	**Sex**	**Dominance rank**
Artemis	Male	1
Oz	Male	2
Ben	Male	3
Lewis	Male	4
Nick	Male	5
Noddy	Male	6
George	Male	7
Larsson	Male	8
Simon	Male	9
Anna	Female	10
Danni	Female	11
Joan	Female	12
Kerry	Female	13
Helen	Female	14
Neo	Female	15
Rebecca	Female	16

Table 2.2. ID and sex of the juveniles of the 'Green group'.

Subject	**Sex**
Abderrahim	Male
Karl	Male
Mac	Male
Rafiq	Male
Dakini	Female
Dakota	Female
Krissy	Female

Table 2.3. ID, sex and ordinal dominance rank of each adult and sub-adult monkey of the 'Tourist group'. The rank 1 represents the highest dominance status in the group.

Subject	**Sex**	**Dominance rank**
Kitkat	Male	1
Milkiway	Male	2
Twix	Male	3
Fingers	Male	4
Nutella	Male	5
Galack	Male	6
Donut	Male	7
Chocobon	Male	8
Eliotte	Male	9
Pepito	Male	10
Attila	Male	11
Luna	Female	12
Fidji	Female	13
Athena	Female	14
Clarisse	Female	15
Shannon	Female	16
Grace	Female	17
Venus	Female	18
Morticha	Female	19
Nelly	Female	20
Osiris	Female	21
Leila	Female	22
Windy	Female	23
Tamara	Female	24

Table 2.4. ID and sex of the juveniles of the 'Tourist group'. The asterisk indicates the juveniles who died in 2011.

Subject	**Sex**
Bart	Male
Caramello	Male
Felice	Male
Hassane	Male
Luca	Male
M&M's *	Male
Vegas *	Male
Elodie	Female
Gaëlle	Female
Neptune	Female
Opale *	Female
Saana	Female

2.4. DATA COLLECTION

Permission to conduct the research was granted by the 'Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification' of Morocco and the Ethics Committee of the University of Lincoln, U.K. This study adheres to Moroccan and U.K. legislation regarding the ethical use of animals in research.

Data were collected by Sandra Molesti and three research assistants, fully trained by Sandra Molesti. Inter-observer reliability was checked weekly and was always above 95% throughout the study. Each week, the observers collected data simultaneously on a randomly chosen monkey and data were compared to ensure inter-observer agreement. The data analysed in this study were collected daily between 6am and 7pm, from

November 2010 to January 2012. The days of data collection were split between the ‘Green group’ and the ‘Tourist group’. A large amount of data was collected and only part of the data have been analysed and included in this thesis. The data collection was both observational and experimental, and a Pocket PC loaded with Pendragon Forms v5.1 (Pendragon Software Corporation, 2010) was used to record the data. Scan, ad libitum, and focal sampling methods were used to collect the data (Altmann, 1974). The post-event-control method (de Waal & Yoshihara, 1983) was used to analyse the aftermath of events such as grooming. Ambient temperature and relative humidity were measured using a Kestrel 3500 pocket weather meter. Rainfall (mm) was recorded daily using a pluviometer. Specific details of data collection are described in Chapters 3 to 7. Tables 2.5 to 2.9 define the self-directed, aggressive, submissive, sexual, and affiliative behaviours recorded. For these behaviours, either their frequency and/or duration was recorded. More specifically, the duration of behavioural states (i.e. behaviours with a measurable duration such as grooming) was recorded, and the frequency of behavioural events (i.e. behaviours too short to be able to measure a duration such as slapping) was recorded.

Table 2.5. Self-directed behaviours collected in the current study.

Behaviour	Description	Type
Self-Scratching	The monkey scratches its own body, usually for no more than 2-3 seconds.	Event
Self-Grooming	The monkey starts to groom its own body, i.e. goes through its fur with its fingers and mouth, removing particles such as dirt and/or parasites.	State

Table 2.6. Aggressive behaviours collected in the current study.

Behaviour	Description	Type
Lunge	The monkey makes a sudden intense movement toward another monkey. It does not move over a large distance. Sometimes only the upper body is moved.	Event
Charge	The monkey chases another monkey for less than 5 metres.	Event
Chase	The monkey chases another monkey at high speed for over 5 metres.	Event
Slap	The monkey hits another monkey with an opened hand.	Event
Grab	The monkey forcefully grabs another monkey with its hands and/or legs.	Event
Push and Pull	The monkey grabs hold of another monkey’s fur and skin, and makes a brief ‘shaking’ movement.	Event
Jump On	The monkey jumps onto another monkey.	Event
Bite	The monkey bites another monkey.	Event
Ground Slap	The monkey stare at another monkey and slaps the ground with an opened hand in short, intense movements.	Event
Open mouth	The monkey’s mouth is opened, the jaws are tensed, and the lips cover the teeth. The eyes are wide open and the monkey stares at the other monkey. The head is often lowered and stuck forward.	Event
Stare	The body of the monkey is tense, usually the head is lowered and stuck forward. The eyes are wide open and the monkey stares at the other monkey. The ears are held out away from the head, sometimes the eyebrows are lifted.	Event

Table 2.7. Submissive behaviours collected in the current study.

Behaviour	Description	Type
Make room	The monkey makes the beginning of a movement away from another monkey. Quite often, only the upper body is moved, the monkey never moves over a large distance.	Event
Give ground	The monkey creates a distance between itself and another monkey, by moving away from it, but not at full speed.	Event
Flee	The monkey flees at full speed, away from another monkey.	Event
Crouch	The monkey presses itself to the ground, trying to make itself as small as possible, by tucking its arms, legs and head under its body.	Event
Present Submission	Monkey presents its hindquarters to a more dominant individual as an indication of submission.	Event
Teeth Chatter	The monkey pulls up its eyebrows and scalp, and flattens its ears against the head. The monkey pulls up its lips and shows its teeth and usually also its gums. The monkey opens and closes its mouth rapidly, sometimes with the tongue sticking out. Teeth chatter was considered as submissive when it occurred between adults/sub-adults in response to an aggressive behaviour received.	Event

Table 2.8. Sexual behaviours collected in the current study.

Behaviour	Description	Type
Copulation	The male monkey copulates with a female monkey.	State
Sexual interaction	The monkey sniffs, touch or look the hind quarter of another monkey, usually a female.	Event

Table 2.9. Affiliative behaviours collected in the current study.

Behaviour	**Description**	**Type**
Proximity	The monkey approaches another monkey within at least 1.5m.	State
Groom Present	The monkey 'presents' a body part to be groomed to another monkey.	Event
Grooming	The monkey starts to groom another monkey, i.e. goes through the fur of another monkey with its fingers and mouth, removing particles such as dirt and/or parasites.	State
Role Reverse	Swapping of roles between groomer and groomee during grooming.	Event
Body Contact	The monkey comes so close to another monkey that parts of their bodies touch. No other social activity between the two monkeys is observed (e.g. no grooming, embracing, sandwich interaction, or physical contact during fighting). All individuals can simultaneously be involved in other activities (e.g. feeding, resting).	State
Embrace	Two monkeys are facing each other and grab each other by the arms. Sometimes, they also grab each other by the legs with their feet. It is often accompanied by teeth chatter.	Event
Play	The monkey starts to play with another monkey. During play, the monkey shows the play face: the scalp and eyebrows are pulled backwards, the eyes are half-closed and the mouth is open and relaxed, usually the teeth show.	State
Sandwich interaction	An infant is used as a social 'buffer' between two monkeys. Sometimes the monkeys embrace. Very often it is accompanied by teeth chatter.	State

Ad libitum data (Altmann, 1974) were collected opportunistically to determine the dominance hierarchy of the monkeys for each group. Each time a dyadic conflict not involving third parties and with a clear-cut result (i.e. one opponent displayed aggressive behaviour and the other opponent displayed submissive behaviour) was observed, data were collected on the ID of the winner and loser of the conflict. In a dyadic conflict, the winner was defined as the monkey who displayed aggressive behaviour, and the loser was defined as the monkey who displayed submissive behaviour. The aggressive and submissive behaviours used to assess hierarchy are described in the Table 2.6 and 2.7 above.

For each group, scan samples (Altmann, 1974) were collected every hour on the activity of all visible monkeys within 10 minutes of the beginning of the scan. The activity of each group member was not sampled more than once in a single scan. Data were collected on the activity of the adult and sub-adult monkeys (i.e. travelling, resting, feeding, groom given, groom received, self-grooming, play, sandwich interaction, and copulation), their ≤ 1.5m proximity or body contact to other study subjects, and on the identity of their social partners. The activity, distance, and social partner ID (if adult or sub-adult) of the nearest juvenile was also recorded for each subject.

The experimental data collection consisted in food tests and cooperative tasks with food reward (Crawford, 1937), and was only conducted on the 'Tourist group'. Because the group members of the 'Tourist group' received regularly food from tourists, their usual diet and health was not affected by the use of food reward. A description of the food rewards used for each study is given in Chapters 6 and 7. The cooperative apparatus was designed and constructed prior to the data collection by Sandra Molesti. Pilot experiments using a simpler version of the cooperative apparatus were done at the Trentham Monkey Forest park (Trentham, U.K.) where two groups of Barbary macaques roam freely in a 60 acre forest, to check if Barbary macaques would be interested in manipulating the apparatus. The experimental data collection of each study is described in Chapters 6 and 7.

2.5. DATA ANALYSIS

2.5.1. Dominance hierarchy

Based on the dyadic conflicts collected, a winner-loser socio-metric dominance matrix was constructed for each group. Matman 1.1 (Noldus Information Technology, 2003; de Vries et al, 1993) was used to assign an ordinal dominance rank to each study monkey for each group (see Table 2.1 and 2.3 above), according to the number of group members each monkey dominated (i.e. the more group members a subject dominates, the higher its rank). Because the study was conducted on adults and sub-adults, and because dominance status between juveniles is unstable and not properly defined, only dominance relationships between adults and sub-adults were assessed.

2.5.2. Relationship quality

For each group, scan sample data were used to assess the relationship quality between the monkeys (Hinde, 1979). Affiliative behaviours and time spent in close proximity are commonly used as a measure of relationship quality between individuals (e.g. Silk et al 2003; Silk, 2007; Fraser et al, 2008; Majolo et al, 2010; Silk et al, 2010). In this study, a ‘composite sociality index’ (hereafter CSI) was used to measure the relationship quality between group members, using several variables (Sapolsky et al, 1997; Silk et al 2003, 2006b). The frequency of hourly scans in which two monkeys were observed grooming, in proximity or in body contact were used as behavioural measures of relationship quality and entered into the index accordingly (Table 2.10). For each dyad of monkeys, their CSI was calculated based on the formula (Sapolsky et al, 1997; Silk et al, 2003, 2006b, 2010):

$$\frac{\sum_{i=1}^{n} \frac{x_i}{m_i}}{n}$$

n = total number of behavioural measures entered into the index (e.g. n = 3 if grooming, proximity and body contact were all entered into the index).

x_i = dyad's value for each of the behavioural measures (e.g. the proportion of hourly scans in which two monkeys of a dyad were grooming divided by the total number of hourly scans in which the general activity of the two animals was recorded).

m_i = group's median (e.g. Sapolsky et al, 1997) or group's mean (e.g. Silk et al, 2006b) value for each of the behavioural measures (e.g. group's median value for the proportion of hourly scans spent grooming by the whole group).

CSI values can range from 0 to infinite, and a high CSI indicates a high quality relationship between two monkeys of a dyad. The formula used to calculate the CSI of group members was adapted for each study, depending on the distribution of the available data. The specific behavioural measures entered into the formula (i.e. among the three behavioural measures grooming, proximity and body contact; Table 2.10) and the use of the group's mean or group's median value are specifically described for each study in Chapters 3 to 7. For the 'Tourist group', 929 hourly scans were collected (mean number of adult and sub-adult monkeys per scan ± SE = 10 ± 0.1). For the 'Green group', 724 hourly scans were collected (mean number of adult and sub-adult monkeys per scan ± SE = 8.9 ± 0.1). Additionally for the 'Green group', 1,999 hourly scans collected from October 2009 to January 2011 by Chris Young and his research assistants (personal communication) were available to be used in the calculations of CSI (so a total of 2,723 hourly scans were available for the 'Green group'). Calculating the CSI over a period of several years may allow a more stable measure of relationship quality, lowering the potential variations across years and seasons (Barrett & Henzi, 2002; Silk et al, 2006a). For the ‘Green group’, there was a significant and positive correlation between CSI values of dyads calculated from the 724 hourly scans and CSI values of dyads calculated from the total 2,723 hourly scans (matrix correlation (Mantel test): r = 0.91, P = 0.0001, N = 105), indicating that the different time windows did not significantly change the CSI values of the study animals. For each study, the number of hourly scans used for the calculation of CSI is described in Chapters 3 to 7.

Table 2.10. Behavioural measures entered into the composite sociality index.

Behavioural Measures	**Description**
Grooming	The proportion of hourly scans in which two individuals were grooming, divided by the total number of hourly scans in which the general activity of the two animals was recorded.
Body contact	The proportion of hourly scans in which two individuals were in body contact but not grooming, divided by the total number of hourly scans in which the general activity of the two animals was recorded.
Proximity	The proportion of hourly scans in which two individuals were within ≤ 1.5m but not in body contact, divided by the total number of hourly scans in which the general activity of the two animals was recorded.

2.5.3. Statistics

In this thesis, data were analysed using a series of generalised linear mixed models (hereafter GLMMs), survival analyses and non-parametric tests. GLMMs are advanced statistics tests that allow analysing the effect of a series of independent variables (i.e. test and control factors) on a continuous or categorical dependent variable (Pinheiro & Bates, 2000; Rabe-Hesketh & Skrondal, 2008). GLMMs are particularly advantageous in the case of clustered data (e.g. group, sex) and when repeated measures are taken on the same individuals. GLMMs allow to use single observations (e.g. when repeated observations are collected on the same individuals or dyads) as a single data point. The risk of sample inflation using this procedure is controlled by adding random factors to the models (Pinheiro & Bates, 2000; Rabe-Hesketh & Skrondal, 2008). Random factors take into account the clustering of data due, for example, to multiple observations being collected on the same animal (a method commonly used in the data collection on wild animals and used in the current study), so that biases in the distribution and clustering of data (e.g. one animal having more observations than another) are controlled for (Pinheiro & Bates, 2000; Rabe-Hesketh & Skrondal, 2008). Moreover, random factors are advantageous when comparing post-event-matched-control data as the ID of the matching pairs can be entered as random factor. Additionally, entering the ID of the monkeys as random factors when analysing dyadic data is very useful as a monkey A may behave in a certain way with a partner B, but in a totally different way with a partner C. The random factors may be entered into a GLMM as crossed or nested random factors. For crossed random factors, each level of each factor may occur with each level of each other factor (e.g. the ID of two monkeys involved in social interactions). For nested random factors, levels of one factor occur within levels of another factor (e.g. the ID of the monkeys involved in grooming and the ID of the post-grooming-matched control pairs). The random factors (e.g. ID of the study subjects) and control factors (e.g. CSI values and dominance rank) entered into the GLMMs are described for each study in Chapters 3 to 7. For the sake of brevity, the results of the control variables were included in the tables but were not discussed. Common GLMMs include linear regression, logistic regression, and Poisson regression. When data did not met the assumption of normality, and/or when a behaviour was observed at a low frequency, and/or for count data (e.g. the occurrences of self-scratching), GLMM with a Poisson regression was used. When the dependent variable was binary (i.e. whether an event occurred or not), data were analysed using a GLMM with a logistic regression. The type of GLMMs used for each study is described in Chapters 3 to 7.

Survival analyses (Cox proportional hazards model) were used (Cleves et al, 2008) to assess the effect of a factor (e.g. grooming) on the latency to occur of an event (e.g. reciprocity). Survival analyses allow to take into account cases where the event did not occur (e.g. when subjects did not reciprocated grooming at the end of the focal observation). Basically, survival analyses deal with events (e.g. reciprocation) that occurred or not in a particular time window (e.g. post-grooming or control sessions). If the event did not occur during the time window, it could potentially have occurred outside this time window. In the survival analyses, when the end of the time window is reached without the event having occurred, the observation is considered as censored. When the event occurred during the time window, this time window is considered as uncensored (i.e. failure event). Survival analyses are thus powerful and informative to analyses the latency of event to occur in a time window (e.g. for an applications of this method to animal behaviour, see Schino et al, 2009; Schino & Pellegrini, 2011; Majolo et al, 2012). The ‘shared frailty’ is an option of survival models in STATA v12.1 software (StataCorp., 2011) which is similar to the use of random factors in GLMMs to control for sample inflation. While several variables can be entered as random factors in GLMMs, only one variable can be entered using the ‘shared frailty’ option. Details of the survival analyses used are given in Chapter 5.

GLMM analysis is an advanced statistical procedure which could potentially be affected by small sample sizes. When sample sizes were considered small (e.g. < 70 data points), non-parametric tests were used. Wilcoxon signed rank tests for paired samples and Mann-Whitney U test were used to analyse individual scores (minimum 6 individuals). Correlations between two variables were assessed using the Pearson correlation test if the data met the assumption of normality, and the Spearman correlation test if the data did not meet the assumption of normality. Correlations between matrices of data were assessed using the Mantel test and the partial Kendall rowwise matrix correlation (both with tests for significance based on 10,000 permutations). Kolmogorov-Smirnov test was used to assess whether the set of data followed a normal distribution. GLMMs and survival analyses were conducted using STATA v12.1 software (StataCorp., 2011), and non-parametric tests and correlations were conducted using IBM SPSS statistics v19 software (IBM Corp., 2010). Matrix correlations were conducted using Matman 1.1 (Noldus Information Technology, 2003). In the current thesis, the sample size ‘N’ represented the number of data points for GLMMs and survival analyses, while ‘N’ represented the number of individuals for non-parametric tests. All tests were two-tailed and the significance level was set at < 0.05. Each analysis is described in Chapters 3 to 7.

2.6. REFERENCES

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227-267.

Alvarez, F. & Hiraldo, F. 1975. Distribution and habitat of the Barbary macaque (*Macaca sylvana*) in North Morocco. *Doñana-Acta Vertebrata*, **2**, 253-259.

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B., Ogawa, H., Schino, G., Thierry, B. & de Waal, F. B. M. 2012. Hierarchical steepness, counter-aggression, and macaque social style scale. *American Journal of Primatology*, **74**, 915-925.

Barrett, L. & Henzi, S. P. 2002. Constraints of relationship formation among female primates. *Behaviour*, **139**, 263-289.

Berard, J. 1999. A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*). *Primates,* **40**, 159-175.

Camperio Ciani, A. & Mouna, M. 2007. Human and environmental causes of the rapid decline of the Barbary macaque in the Middle Atlas of Morocco. In: *The Barbary macaque: biology, management & conservation* (Ed. by J. K. Hodges & J. Cortes), pp. 257-273. Nottingham: Nottingham University Press.

Camperio Ciani, A., Palentini, L., Arahou, M., Martinoli, L., Capi Luppi, C. & Mouna, M. 2005. Population decline of *Macaca sylvanus* in the Middle Atlas of Morocco. *Biological Conservation,* **121**, 635-641.

Cleves, M., Gould, W. W., Gutierrez, R. G. & Marchenko, Y. U. 2008. *An introduction to survival analysis using Stata*. 2nd edn. College Station: Stata Press.

Crawford, M. P. 1937. The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs*, **14**, 1-88.

de Turckheim, G. & Merz, E. 1984. Breeding Barbary macaques in outdoor open enclosures. In: *The Barbary macaque: a case study in conservation* (Ed. by J. E. Fa), pp. 241-261. New York: Plenum Press.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour,* **125**, 157-175.

de Waal, F. B. M. & Luttrell, L. M. 1989. Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stumptail monkeys. *American Journal of Primatology*, **19**, 83-109.

de Waal, F. B. M. & Yoshihara, D. 1983. Reconciliation and redirected affection in rhesus monkeys. *Behaviour,* **85**, 224-241.

Deag, J. M. & Crook, J. H. 1971. Social behaviour and ‘agonistic buffering’ in the wild Barbary macaque *Macaca sylvana* L. *Folia Primatologica,* **15,** 183-200.

Deag, J. M. 1980. Interactions between males and un-weaned Barbary macaques: testing the agonistic buffering hypothesis. *Behaviour,* **75**, 54-81.

Deag, J. M. 1984. Demography of the Barbary macaque at Ain Kahla in the Moroccan Moyen Atlas. In: *The Barbary macaque: a case study in conservation* (Ed. by J. E. Fa), pp. 113-133. New York: Plenum Press.

Deag, J. M. 1985. The diurnal patterns of behaviour of the wild Barbary macaque *Macaca sylvanus*. *Journal of Zoology,* **206**, 403-413.

Dixson, A. F. 1998. *Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings*. Oxford: Oxford University Press.

Fa, J. E. 1982. A survey of population and habitat of the Barbary macaque *Macaca sylvanus* L. in North Morocco. *Biological Conservation*, **24**, 45-66.

Fa, J. E. 1984a. Appendix I. Definition of age-sex classes for the Barbary macaque. In: *The Barbary macaque: a case study in conservation* (Ed. by J. E. Fa), pp. 347-355. New York: Plenum Press.

Fa, J. E. 1984b. Appendix II. Diet of the Barbary macaque in the wild. In: *The Barbary macaque: a case study in conservation* (Ed. by J. E. Fa), pp. 347-355. New York: Plenum Press.

Fa, J. E. 1984c. The Barbary macaque. In: *The Barbary macaque: a case study in conservation* (Ed. by J. E. Fa), pp. 3-15. New York: Plenum Press.

Fa, J. E. 1989. The genus *Macaca*: a review of taxonomy and evolution. *Mammal Review*, **19**, 45-81.

Fa, J. E., Taub, D. M., Ménard, N. & Stewart, P. J. 1984. The distribution and current status of the Barbary macaque in North Africa. In: *The Barbary macaque: a case study in conservation* (Ed. by J. E. Fa), pp. 79-111. New York: Plenum Press.

Fooden, J. 2007. Systematic review of the Barbary macaque, *Macaca sylvanus* (Linnaeus, 1758). *Fieldiana Zoology*, **113**, 1-60.

Fraser, O. N., Schino, G. & Aureli, F. 2008. Components of relationship quality in chimpanzees. *Ethology*, **114**, 834-843.

Hammerschmidt, K., Ansorge, V., Fischer, J. & Todt, D. 1994. Dusk calling in Barbary macaques (*Macaca sylvanus*): demand for social shelter. *American Journal of Primatology*, **32**, 277-289.

Henkel, S., Heistermann, M. & Fischer, J. 2010. Infants as costly social tools in male Barbary macaque networks. *Animal Behaviour*, ***79***, 1199-1204.

Hinde, R. A. 1979. *Towards understanding relationships*. London: Academic Press.

IBM Corp. 2010. *IBM SPSS statistics for Windows, version 19.0.* Armonk: IBM Corp.

Inventaire de la biodiversité, Parc National d'Ifrane. 2007. Projet d'aménagement et de protection des massifs forestiers de la province d'Ifrane. <ma.chm-cbd.net>. Downloaded on 25 July 2013.

IUCN. 2013. IUCN red list of threatened species. Version 2013.1. <www.iucnredlist.org>. Downloaded on 23 July 2013.

Kaburu, S. S. K., MacLarnon, A., Majolo, B., Qarro, M. & Semple, S. 2012. Dominance rank and self-scratching among wild female Barbary macaques (*Macaca sylvanus*). *African Zoology*, **47,** 74-79.

Kuester, J. & Paul, A. 1984. Female reproductive characteristics in semifree-ranging Barbary macaques (*Macaca sylvanus* L. 1758). *Folia Primatologica*, **43**, 69-83.

Kuester, J. & Paul, A. 1999. Male migration in Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *International Journal of Primatology*, **20,** 85-106.

Lathuillière, M., Crouau-Roy, B., Petit, E., Sheffrahn, W. & Ménard, N. 2004. Influence of group fission on gene dispersion in the Barbary macaque (*Macaca sylvanus*). *Folia Primatologica*, **75**, 175-176.

Lee, P. C. & Oliver, J. I. 1979. Competition, dominance, and the acquisition of rank in juvenile yellow baboons (*Papio eynocephalus*). *Animal Behaviour*, **27**, 576-585.

Majolo, B., Lavieren, E., Maréchal, L., MacLarnon, A., Marvin, G., Qarro, M. & Semple, S. 2013a. Out of Asia: the singular case of the Barbary macaque. In: *The macaque connection* (Ed. by S. Radhakrishna, M. A. Huffman & A. Sinha), pp. 167-183. New York: Springer.

Majolo, B., McFarland, R., Young, C. & Qarro, M. 2013b. The Effect of climatic factors on the activity budgets of the Barbary macaque (*Macaca sylvanus*). *International Journal of Primatology*, **34**, 500-514.

Majolo, B., Schino, G. & Aureli, F**.** 2012. The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges. *Animal Behaviour*, **83**, 763-771.

Majolo, B., Ventura, R. & Schino, G. 2010. Asymmetry and dimensions of relationship quality in the Japanese macaque (*Macaca fuscata yakui*). *International Journal of Primatology*, **31**, 736-750.

Maréchal, L., Semple, S., Majolo, B., Qarro, M., Heistermann, M. & MacLarnon, A. 2011. Impacts of tourism on anxiety and physiological stress levels in wild male Barbary macaques. *Biological Conservation*, **144**, 2188-2193.

McFarland, R. & Majolo, B. 2011. Grooming coercion and the post-conflict trading of social services in wild Barbary macaques. *PLoS ONE*, **6**, e26893.

Mehlman, P. T. 1984. Aspects of the ecology and conservation of the Barbary macaque in the fir forest habitat of the Moroccan Rif Mountains. In: *The Barbary macaque: a case study in conservation* (Ed. by J. E. Fa), pp. 165-199. New York: Plenum Press.

Mehlman, P. T. 1988. Food resources of the wild Barbary macaque (*Macaca sylvanus*) in high-altitude fir forest, Ghomaran Rif, Morocco. *Journal of Zoology*, **214**, 469-490.

Mehlman, P. T. 1989. Comparative density, demography, and ranging behavior of Barbary macaques (*Macaca sylvanus*) in marginal and prime conifer habitat. *International Journal of Primatology*, **10**, 269-292.

Ménard, N. & Qarro, M. 1999. Bark stripping and water availability: a comparative study between Moroccan and Algerian Barbary macaques (*Macaca sylvanus*). *Revue d'Ecologie*, **54**, 123-132.

Ménard, N. & Vallet, D. 1993a. Dynamics of fission in a wild Barbary macaque group (*Macaca sylvanus*). *International Journal of Primatology*, **14**, 479-500.

Ménard, N. & Vallet, D. 1993b. Population dynamics of *Macaca sylvanus* in Algeria: an 8-year study. *American Journal of Primatology*, **30**, 101-118.

Ménard, N. & Vallet, D. 1996. Demography and ecology of Barbary macaques (*Macaca sylvanus*) in two different habitats. In: *Evolution and ecology of macaque societies* (Ed. by J. E. Fa & D. G. Lindburg), pp. 106-131. Cambridge: Cambridge University Press.

Ménard, N. & Vallet, D. 1997. Behavioral responses of Barbary macaques (*Macaca sylvanus*) to variations in environmental conditions in Algeria. *American Journal of Primatology*, **43**, 285-304.

Ménard, N. 2002. Ecological plasticity of Barbary macaques (*Macaca sylvanus*). *Evolutionary Anthropology*, **11**, 95-100.

Ménard, N., Vallet, D. & Gautier-Hion, A. 1985. Démographie et reproduction de *Macaca sylvanus* dans différents habitats en Algerie. *Folia Primatologica*, **44**, 65-81.

Möhle, U., Heistermann, M., Dittami, J., Reinberg, V. & Hodges, J. K. 2005. Patterns of anogenital swelling size and their endocrine correlates during ovulatory cycles and early pregnancy in freeranging Barbary macaques (*Macaca sylvanus*) of Gibraltar. *American Journal of Primatology*, **66**, 351-368.

Morales, J. C. & Melnick, D. J. 1998. Phylogenetic relationships of the macaques (Cercopithecidae: *Macaca*), as revealed by high resolution restriction site mapping of mitochondrial ribosomal genes. *Journal of Human Evolution*, **34**, 1-23.

Noldus Information Technology. 2003. *Matman, software for matrix manipulation and analysis, version 1.1.* Wageningen, The Netherlands.

Paul, A. & Kuester, J. 1985. Intergroup transfer and incest avoidance in semifree-ranging Barbary macaques (*Macaca sylvanus*) at Salem (FRG). *American Journal of Primatology*, **8**, 317-322.

Paul, A., Kuester, J. & Arnemann, J. 1992. DNA fingerprinting reveals that infant care by male Barbary macaques (*Macaca sylvanus*) is not paternal investment. *Folia Primatologica*, **58**, 93-98.

Paul, A., Kuester, J. & Arnemann, J. 1996. The sociobiology of male-infant interactions in Barbary macaques (*Macaca sylvanus*). *Animal Behaviour*, **51**, 155-170.

Pendragon Software Corporation. 2010. *Pendragon forms, version 5.1*. Libertyville: Pendragron Sofware Corporation.

Pinheiro, J. C. & Bates, D. M. 2000. *Mixed effects models in S and S-PLUS*. 1st edn. New York: Springer-Verlag.

Preuschoft, S., Paul, A. & Kuester, J. 1998. Dominance styles of female and male Barbary macaques. *Behaviour*, **135**, 731-755.

Purvis, A. 1995. A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society B*, **348**, 405-421.

Rabe-Hesketh, S. & Skrondal, A. 2008. *Multilevel and longitudinal modeling using Stata*. 2nd edn. College Station, Texas: Stata Press.

Sapolsky, R. M., Alberts, S. C. & Altmann, J. 1997. Hypercortisolism associated with social subordinate or social isolation among wild baboons. *Archive of General Psychiatry*, **54**, 1137-1143.

Scheffrahn, W., Menard, N., Vallet, D. & Gaci, B. 1993. Ecology, demography, and population genetics of Barbary macaques in Algeria. *Primates*, **34**, 381-394.

Schino, G. & Pellegrini, B. 2011. Grooming and the expectation of reciprocation in mandrills (*Mandrillus sphinx*). *International Journal of Primatology*, **32**, 406-414.

Schino, G., di Giuseppe, F. & Visalberghi, E. 2009. The time frame of partner choice in the grooming reciprocation of *Cebus apella*. *Ethology*, **115**, 70-76.

Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B*, **362**, 539-559.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance infant survival. *Science*, **302**, 1231-1234.

Silk, J. B., Alberts, S. C. & Altmann, J. 2006a. Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, **61**, 197-204.

Silk, J. B., Altmann, J. & Alberts S. C. 2006b. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, **61**, 183-195.

Silk, J. B., Beehner, J. C., Berman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2010. Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, **61**, 197-204.

StataCorp. 2011. *Stata statistical software: release 12*. College Station, Texas: StataCorp LP.

Taub, D. M. 1975. Notes and news. *Oryx*, **13**, 229.

Taub, D. M. 1977. Geographic distribution and habitat diversity of the Barbary macaque (*Macaca sylvanus* L.). *Folia Primatologica*, **27**, 108-133.

Taub, D. M. 1978. The Barbary macaques in North Africa. *Oryx*, **14**, 245-253.

Taub, D. M. 1985. Male-infant interactions in baboons and macaques: a critique and reevaluation. *American Zoologist*, **25**, 861-871.

Thierry, B. & Aureli, F. 2006. Barbary but not barbarian: social relations in a tolerant macaque. In: *The Barbary macaque: biology, management and conservation* (Ed. by J. K. Hodges & J. Cortes), pp. 29-45. Nottingham: Nottingham University press.

Thierry, B. 2007. Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology*, **16**, 224-238.

Thierry, B., Singh, M. & Kaumanns, W. 2004. *Macaque societies: a model for the study of social organization*. Cambridge: Cambridge University Press.

van Lavieren, E. & Wich, S. A. 2009. Decline of the endangered Barbary macaque *Macaca sylvanus* in the cedar forest of the Middle Atlas Mountains, Morocco. *Oryx*, **44**, 133-138.

van Lavieren, E. 2008. The illegal trade in Barbary macaques from Morocco and its impact on the wild population. *Traffic Bulletin*, **21**, 123-130.

von Segesser, F., Ménard, N., Gaci, B. & Martin, D. 1999. Genetic differentiation within and between isolated Algerian subpopulations of Barbary macaques (*Macaca sylvanus*): evidence from microsatellites. *Molecular Ecology*, **8**, 433-442.

Young, C., Schülke, O., Ostner, J. & Majolo, B. 2012. Consumption of unusual prey items in the Barbary macaque (*Macaca sylvanus*). *African Primates*, **7**, 224-229.

Chapter 3

Post-grooming anxiety in the donor and recipient of grooming

Chapter 3 investigates the anxiety reduction mechanism of grooming in wild Barbary macaques by analysing post-grooming anxiety for the donor and recipient of the same grooming interactions.

The results of this Chapter have been published in a peer-reviewed journal (see the front page of the paper in the Appendix):

Molesti, S. & Majolo, B. 2013. Grooming increases self-directed behaviour in wild Barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, **86**, 169-175.

3.1. INTRODUCTION

In many mammals and birds, grooming has a hygienic function, as animals exchange this behaviour to remove dirt and parasites from parts of the body that they cannot reach through self-grooming (Hutchins & Barash, 1976; Hart & Hart, 1992; Tanaka & Takefushi, 1993; Zamma, 2002; Radford & Du Plessis, 2006; Scantlebury et al, 2007; Akinyi et al, 2013). Grooming also has a social function, because it plays an important role in the establishment and maintenance of social bonds (e.g. Dunbar, 1991; Henzi & Barrett, 1999). The giving of grooming is assumed to be a costly activity, as it reduces vigilance against predators and/or competitors and the time available for other activities (e.g. feeding; Dunbar & Sharman, 1984; Maestripieri, 1993; Scantlebury et al, 2007), whereas receiving grooming has a positive effect on physical conditions (e.g. Terry, 1970; Zamma, 2002; Scantlebury et al, 2007). For these reasons, grooming can be exchanged for itself (e.g. Schino & Aureli, 2008; Majolo et al, 2012), or for other social services, such as support in aggression or tolerance over food (Noë & Hammerstein, 1994; Henzi & Barrett, 1999; Schino, 2007).

Grooming is also thought to have an anxiety-reduction benefit (Terry, 1970). However, the studies on the anxiety-reduction function of grooming are limited and mostly restricted to captive animals (for a notable exception see: Radford, 2012). These studies showed that the recipient of grooming (i.e. groomee) experiences a reduced heart rate during grooming (Boccia et al, 1989; Feh & de Mazières, 1993; Aureli et al, 1999), a release of opioids in the blood (Keverne et al, 1989; Martel et al, 1995), and a lower concentration of stress hormones (i.e. serum cortisol; Gust et al, 1993). Moreover, in the first few minutes after grooming, the groomee displays a lower frequency of self-directed behaviours (hereafter SDBs) such as self-scratching and self-grooming (Schino et al, 1988; Radford, 2012). Self-grooming is defined as picking through and/or slow brushing aside one’s own fur with one or both hand, and self-scratching is defined as movement of the hand or foot during which fingertips are drawn across the individual’s fur (Schino et al, 1988; Chapter 2).

SDBs are behaviours apparently irrelevant to the situation in which they appear (Maestripieri et al, 1992; McFarland, 1966; Troisi, 2002). They are common in situation of motivational conflict to perform several incompatible activities simultaneously, or when animals are prevented from performing goal-directed behaviour, leading to frustration (McFarland, 1966; Maestripieri et al, 1992; Troisi, 2002). Self-scratching, self-grooming, and body-shaking constitute common SDBs. There is evidence that SDBs are linked to anxiety in animals (Maestripieri et al, 1992; Schino et al, 1996; Troisi, 2002). First, physiological changes related to anxiety are accompanied by changes in the occurrence of SDBs. For example, the increase of heart rate was accompanied by a concomitant increase of the frequency of self-scratching after conflict in macaques (Boccia et al, 1989; Aureli et al, 1989). In Greylag geese (*Anser anser*), the heart rate recorded during conflict positively predicted the increase of post-conflict SDBs (Washer et al, 2010). Second, drugs that are effective in increasing and decreasing anxiety (i.e. anxiogenics and anxiolytics, respectively) produce a similar effect on SDBs. Female long-tailed macaques (*Macaca fascicularis*) displayed a lower frequency of self-scratching following the administration of lorazepam, an anxiolytic drug (Schino et al, 1991). Similarly, infant rhesus macaques (*Macaca mulatta*) showed a higher frequency of self-scratching following the administration of the anxiogenic beta-CCE, and a lower frequency following the administration of the anxiolytic drug midazolam (Maestripieri et al, 1992). In marmosets (*Callithrix penicillata*), the administration of the anxiolytic diazepam induced a reduction of self-scratching, when the animals were exposed to a taxidermized predator (Barros et al, 2000) or paired with an unfamiliar animal (Cilia & Piper, 1997). Moreover, the occurrence of self-scratching, self-grooming, and body-shaking decreased with the anxiolytic drug lorazepam and increase with the anxiogenic compound FG 7142 in male long-tailed macaques in a dose-dependent manner (Schino et al, 1996).

There is also evidence that SDBs increase during, or in the first few minutes after events known to increase anxiety. These events are often related to the uncertainty about other group members' behaviour such as the probability to receive aggression from group members. Baker and Aureli (1997) showed that self-scratching rate was higher when chimpanzees (*Pan troglodytes*) were exposed to neighbour vocalisation, that is, in situations at risk of intra-group aggression. Also, self-scratching and self-grooming rates increased when unfamiliar females long-tailed macaques were paired together, resulting in an unresolved establishment of the dominance hierarchy between the two animals of the pair (Schino et al, 1990). The SDBs rate were lower when the pairing was done between familiar animals (i.e. their social status was already established), and between unfamiliar animals when a rapid establishment of the dominance hierarchy between the two animals occurred (Schino et al, 1990). Furthermore, SDB rates increased when individuals are in close proximity to higher-ranking animals, as this situation increases the probability of receiving aggression (Troisi & Schino, 1987; Pavani et al, 1991; Castles et al, 1999). Heart rate has been shown to increase, indicating physiological anxiety, in the same kind of situations (Aureli et al, 1999). Agonistic interactions also result in an elevation of SDB rates (Aureli et al, 1989; Aureli & van Schaik, 1991; Aureli, 1992; Aureli, 1997; Castles & Whiten, 1998; Kutsukate & Castles, 2001; Aureli et al, 2002; Cooper et al, 2006; Koshi et al, 2007; Schino et al, 2007), which decrease after reconciliation (i.e. the exchange of friendly behaviour between opponents in the minutes following a conflict; Aureli & de Waal, 2000) takes place (Aureli et al, 1989; Aureli & van Schaik, 1991; Castles & Whiten, 1998; Das et al, 1998; Arnold & Whiten, 2001; Kutsukate & Castles, 2001; Cooper et al, 2006; Fraser et al, 2010; Mcfarland & Majolo, 2011). Mother rhesus monkeys expressed more SDBs when their infant was at risk of receiving aggression (Maestripieri, 1993). Monkeys also showed a higher frequency of SDBs in high density housing conditions (Aureli & de Waal, 1997). In rats, the most anxious animals were also the ones who self-groomed the most (Estanislau, 2012; Nunes et al, 2012). Therefore, SDBs are often used as non-invasive, reliable behavioural manifestation of anxiety in animals (Maestripieri et al, 1992; Schino et al, 1996; Troisi, 2002) and as such, they are a particularly precious tool to assess anxiety in wild animals where physiological data collection is difficult or not possible.

Although the anxiety-reduction function of grooming was originally proposed for the groomee (Terry, 1970), recent studies show that grooming may also reduce anxiety in the donor (i.e. groomer; Shutt et al, 2007; Aureli & Yates, 2010; Radford, 2012). The groomer displayed fewer SDBs in the post-grooming periods than in control conditions in captive crested black macaques (*Macaca nigra*; Aureli & Yates, 2010). Similarly, the frequency of SDBs was lower in the post-preening period than in control conditions in the green woodhoopoe (*Phoeniculus purpureus*) for the groomer and the groomee from different preening interactions (Radford, 2012). Shutt et al (2007) showed that the amount of grooming given was negatively related to the level of stress hormones (i.e. cortisol) in Barbary macaques (*Macaca sylvanus*). However, contrary to the other studies on the short-term anxiety-reduction effect of grooming, Shutt et al (2007) tested the long-term relationship between grooming and anxiety.

Taken together, these studies pose the question of whether grooming elicits a similar reduction in anxiety in the groomer and the groomee. This is important because a short-term post-grooming reduction in anxiety can affect subsequent social interactions between animals as well as their choice of social partners. For example, emotional responses to grooming interactions are thought to be important for the establishment of social bonds between two animals (Schino & Aureli, 2009). If two animals experienced a reduction in anxiety after they groomed one another, irrespective of their social role (i.e. groomer or groomee), they should be more likely to friendly interact again in the future, such as grooming again and/or tolerate each other near food resources. Therefore, studies on the proximate effect of grooming on anxiety can help us understand partner choice and the social benefits of this behaviour.

With this background in mind, post-grooming anxiety was analysed in wild Barbary macaques (*Macaca sylvanus*). A well-established methodology based on post-grooming and matched-control observations was used (Aureli & Yates, 2010; Radford, 2012). The first aim of this Chapter was to compare anxiety in post-grooming sessions (hereafter PG) with anxiety in matched-control sessions (hereafter MC) as a test of the short-term anxiety-reduction mechanism of grooming. To my knowledge, this is the first study to analyse the anxiety-reduction function of grooming in a wild primate species. The second aim of this Chapter was to directly compare PG anxiety between the groomer and groomee of the same grooming interactions. This novel, within-grooming/dyad approach can effectively analyse whether grooming has similar or different effects on PG anxiety in the two grooming partners. In line with previous studies testing the anxiety-reduction function of grooming, SDBs were used as behavioural measures of anxiety

(Maestripieri et al, 1992; Schino et al, 1996; Troisi, 2002). The predictions tested in this Chapter were as follow:

(1) If monkeys experience a reduction of SDBs after grooming, the frequency of self-scratching and the time spent self-grooming would be lower in PG than MC sessions.

(2) If the groomees experience a higher reduction of SDBs after grooming than the groomers, the frequency of self-scratching and the time spent self-grooming in PGs would be lower for the groomees than groomers.

3.2. METHODS

3.2.1. Study subjects

Subjects of this study were the 16 adult and sub-adult monkeys of the ‘Green group’ (which during the study consisted of 8 adult males, 7 adult females, 1 sub-adult male, 7 juveniles and several infants) living in the Middle Atlas Mountains of Morocco (33° 24’N - 005° 12’W). The group lived in the deciduous cedar and oak forest of the Ifrane National Park, between 1600 and 2000m a.s.l. See Chapter 2 for details on the study animals and field site.

3.2.2. Data collection

Data were collected from May 2011 to January 2012. A similar data collection protocol as in Aureli and Yates (2010) was used, but data were collected simultaneously on the groomer and groomee of each grooming interaction. PG data were collected after grooming sessions observed from the start and that lasted more than 30 seconds. As soon as a grooming session was terminated (i.e. no grooming was observed for ≥ 30s), two observers ran two simultaneous 10-minutes PG focal sessions on the former groomer and groomee. Inter-observer reliability was checked weekly and was always above 95% throughout the study. On the next possible day (within two weeks from the matched PG session), two MC focal sessions were run on the same two animals of the matched PG. The MC sessions were postponed if the focal individuals were involved in a grooming interaction or aggression (see Chapter 2 for details on the aggressive and submissive behaviours used in this study) within 10 minutes prior to the planned MCs.

During the PG and MC sessions all the occurrences of self-scratching and the time spent self-grooming by the focal animal were recorded. Two occurrences of self-scratching had to be separated by a minimum of 5 seconds to be considered two separate events (Majolo et al, 2009). In the PGs and MCs, any social interaction (i.e. grooming, aggression, submission, physical contact, social play, sexual behaviour and ≤ 1.5m approaches; see Chapter 2) involving the focal animal was also recorded.

At the start of each PG-MC session, data were collected on ambient temperature and relative humidity as these climatic variables can affect the occurrence of SDBs (Pavani et al, 1991; Ventura et al, 2005). These climatic variables were matched within each PG-MC pair; a maximum difference of 5ºC for ambient temperature and 10% for relative humidity was allowed. If these criteria were not met within two weeks from a given PG, the PG session was discarded.

Scan sampling (Altmann, 1974) was used to collect data on the relationship quality between the study animals. Scan samples were collected every hour during the study. During these hourly scans and for each visible study animal, their proximity (i.e. two or more animals being within 1.5m but not grooming) or grooming with the other adult or sub-adults in the group was recorded, as well as the identity of their social partner. Ad libitum data (Altmann, 1974) were used to determine the dominance hierarchy of the study animals. Ad libitum data were collected opportunistically on any observed dyadic conflicts not involving third parties and with a clear-cut result (i.e. one opponent displayed aggressive behaviour and the other opponent displayed submissive behaviour; see Chapter 2 for details on aggressive and submissive behaviours used).

3.2.3. Data analysis

A composite sociality index (hereafter CSI) was calculated to measure the relationship quality between two individuals, based on the data collected during 724 hourly scans. For each dyad of monkeys, their CSI was calculated based on the formula (Sapolsky et al, 1997; Silk et al, 2003):

$$\frac{\sum_{i=1}^{2} \frac{x_i}{m_i}}{2}$$

x_i = dyad's value for each of the two behavioural measures (i.e. the proportion of hourly scans in which two monkeys of a dyad were grooming or in proximity, divided by the total number of hourly scans in which the general activity of the two animals was recorded).

m_i = group's median value for the proportion of hourly scans spent grooming, or in proximity, by the whole group.

A high CSI indicates a high quality relationship between two monkeys of a dyad. The CSI values ranged from 0 to 6.4 (mean CSI value ± SE = 1.27 ± 0.1). Moreover, based on the dyadic conflicts collected ad libitum, a winner-loser socio-metric dominance matrix was constructed. Matman 1.1. (Noldus Information Technology, 2003; de Vries et al, 1993) was used to assign an ordinal dominance rank to each study monkey.

Analyses on the anxiety reduction mechanism of grooming were based on 115 PG-MC pairs. All of the 16 study monkeys were represented in the dataset (mean number of PG-MC sessions ± SE per monkey = 7.67 ± 1.42 for the groomer and 7.67 ± 1.42 for the groomee; 15 monkeys per role). The frequency of self-scratching was positively correlated to the duration of self-grooming in the study group (Pearson correlation test on individual scores: $r_{14} = 0.55$, $p = 0.03$). However, the analyses presented below were run separately on the two SDBs to give a comprehensive test of PG anxiety and because the two behaviours have different behavioural/temporal constrains. For example, an animal can self-scratch while being engaged in another activity (e.g. grooming) but cannot self-groom whilst grooming another monkey.

Two methodological approaches were used to analyse PG anxiety. First, the analyses were run while controlling for any social interaction (i.e. grooming, aggression, submission, physical contact, social play, sexual behaviour, and ≤ 1.5m approaches; see Chapter 2) the focal animal had in PG or MC sessions. To do this, if a social interaction occurred before the end of a 10-minutes PG session, only SDBs occurring between the start of the PG session and the start of the first social interaction involving the focal animal were considered in the analyses. When the time window of a PG session was shortened, the same time window was used for the matched MC session. For example, if a PG was stopped after 120 seconds, because the focal animal was engaged in a social interaction, only the first 120 seconds of the matched MC was used, providing no social interaction or approaches occurred. Moreover, if in the MC a social interaction occurred before the 120 seconds necessary to match the duration of the PG session (as in the example above), the MC session was discarded and a new MC session was collected at another suitable time. If MC data could not be collected within two weeks from the matched PG session (for the same duration of the PG and a similar lack of social interactions, based on the criteria described above), the PG session was discarded from the analyses. This method (hereafter 'short PG' method) allowed to analyse the anxiety-reduction mechanism of grooming while controlling for the confounding effect that social interactions during PGs-MCs could have on SDBs (e.g. Troisi & Schino, 1987; Pavani et al, 1991; Castles et al, 1999; Aureli, 1997; Koski et al, 2007; Schino et al, 2007).

The 'short PG' method, however, reduced the time window that could be considered in the analyses to less than three minutes, as the focal animal was often engaged in social interactions in PGs (mean duration of the PGs-MCs ± SE following this method = 169 ± 15 seconds). This short time window could give a partial picture of PG anxiety as, for example, SDBs may peak in the first few seconds after a grooming interaction is over (e.g. Schino et al, 1988). Therefore, a second approach was used to control for this possibility and to have comparable data with studies that have used 10-minutes PG sessions (Aureli & Yates, 2010; Radford, 2012). For this second method (hereafter '10-minutes PG'), the whole 10-minutes of the PGs was considered to calculate the occurrence of SDBs. However, PG-MC sessions in which the focal animal was engaged in a grooming interaction were excluded from the analyses. The '10-minutes PG' method gave 68 PG-MC pairs to be used for the analyses.

Data did not meet the assumption of normality. Therefore, PG-MC data were analysed running a series of generalised linear mixed models (GLMM) with a Poisson distribution and a log link. It can be noted that the time spent self-grooming would have been better analysed with a Poisson regression with robust standard errors. However, the option of robust standard errors was not available for mixed-effects Poisson regression in STATA v12.1 software (StataCorp., 2011b). Therefore p values concerning these analyses have to be interpreted with caution. In the GLMMs each session (i.e. PG or MC) per focal animal (i.e. groomer or groomee) was treated as a single data point, that is, for each PG-MC pair there were four data points (i.e. one PG and MC session for both the groomer and groomee). The risk of sample inflation using this procedure was controlled for, in GLMMs, by adding random factors to the models (Pinheiro & Bates, 2000; Rabe-Hesketh & Skrondal, 2008). The PG-MC pair ID, nested into the ID of the focal animal, were entered in the GLMMs as random factors. The number of self-scratching events, or the time spent self-grooming in each focal session, were the two dependent variables. The total duration of the PG-MC session was entered as the exposure variable (Rabe-Hesketh & Skrondal, 2008). ‘PG vs. MC’ was the categorical test variable for the GLMMs run to test the anxiety-reduction mechanism of grooming whereas ‘groomer vs. groomee’ was the categorical test variable used to analyse the difference in PG anxiety between the groomer and groomee. In summary, for each of the two SDBs considered (i.e. self-scratching or self-grooming) three GLMMs were run: two GLMMs comparing SDBs between PGs and MCs, respectively in the groomer and groomee, and one GLMM comparing SDB in the PGs between groomer and groomee.

In all the GLMMs, the following control variables were also entered: ‘sex of the dyad’ (categorical: male-male, male-female, or female-female), ‘% of time spent in proximity in PGs or MCs’ between the groomer and the groomee (continuous: the time in seconds spent in proximity), ‘role of the higher-ranking animal’ (categorical: whether the higher-ranking monkey within each grooming dyad was the groomee or groomer), and ‘CSI of the dyad’ (continuous: the composite sociality index of the dyad). These variables were entered in the GLMMs to control for their effect on PG anxiety (e.g. Aureli & Yates, 2010; Radford, 2012). Given that the effect of the control variables was similar when using the ‘short PG’ and ‘10-minutes PG’ methods, for brevity, only the results of the control variables for the analyses run using the ‘short PG’ method were presented below.

Additional analyses were run to assess whether differences in SDBs in PGs and MCs were due to an increased risk of aggression received in the PG sessions (Schino et al, 2005) and in relation to the role of the focal animal (i.e. groomer or groomee). The frequency of aggression received by the focal animal was calculated using the ‘10-minutes PG’ method and three GLMMs were run. The frequency of aggression received by the focal monkey was compared between, respectively, PGs and MCs for the groomer and the groomee, and between PGs collected on the groomer and PGs collected on the groomee. In these GLMMs, the same random and control factors used for the analyses on SDBs above were entered. None of the control variables had a significant effect on the frequency of aggression, and for the sake of brevity, the results of the control variables for these two GLMMs are not presented below.

3.3. RESULTS

In the analyses run using the ‘short PG’ method, the frequency of self-scratching and the time spent self-grooming were significantly higher in PG than in MC sessions for the groomer and groomee (Table 3.1 and 3.2; Figure 3.1 and 3.2). In the analyses run using the ‘10-minutes PG’ method, the percentage of time spent self-grooming was higher in PGs than in MCs for the groomer (GLMM, $z = -13.15$, $p = 0.001$) and the groomee (GLMM, $z = -17.49$, $p = 0.001$). Similarly, the frequency of self-scratching was also higher in PGs than MCs for the groomee (GLMM, $z = -3.78$, $p = 0.001$). However, no significant difference was found for self-scratching for the groomer when comparing PGs and MCs (GLMM, $z = -1.68$, $p = 0.09$).

Table 3.1. Coefficients and significance of the test and control variables entered in the GLMMs to compare self-scratching between PG and MC conditions, for the groomer and groomee, using the 'short PG' method (N = 230). MM = male-male, MF = male-female, FF = female-female dyads.

Focal role	Variables	Coefficient ± SE	Z	P	95% CIs	Significance
Groomer	PG vs. MC	-0.42 ± 0.19	-2.19	0.03	-0.8 – -0.04	✓
	Sex of the dyad:					
	MM vs. MF	-1.01 ± 0.32	-3.15	0.002	-1.63 – -0.38	✓
	MM vs. FF	-1.35 ± 0.38	-3.6	0.001	-2.09 – -0.62	✓
	MF vs. FF	-0.35 ± 0.31	-1.1	0.27	-0.96 – 0.27	✗
	Role of the higher-ranking animal	0.42 ± 0.26	1.59	0.11	-0.1 – 0.94	✗
	% of time spent in proximity in PGs or MCs	-0.002 ± 0.004	-0.5	0.61	-0.01 – 0.01	✗
	CSI of the dyad	0.19 ± 0.1	1.95	0.05	-0.001 – 0.37	✗
Groomee	PG vs. MC	-1.02 ± 0.18	-5.57	0.001	-1.38 – -0.66	✓
	Sex of the dyad:					
	MM vs. MF	-0.29 ± 0.24	-1.18	0.24	-0.77 – 0.19	✗
	MM vs. FF	-0.82 ± 0.3	-2.73	0.01	-1.41 – -0.23	✓
	MF vs. FF	-0.53 ± 0.26	-2.05	0.04	-1.05 – -0.02	✓
	Role of the higher-ranking animal	-0.49 ± 0.21	-2.35	0.02	-0.9 – -0.08	✓
	% of time spent in proximity in PGs or MCs	-0.02 ± 0.004	-3.35	0.001	-0.02 – -0.01	✓
	CSI of the dyad	0.1 ± 0.08	1.2	0.23	-0.06 – 0.26	✗

Table 3.2. Coefficients and significance of the test and control variables entered in the GLMMs to compare self-grooming between PG and MC conditions, for the groomer and groomee, using the 'short PG' method (N = 230). MM = male-male, MF = male-female, FF = female-female dyads.

Focal role	Variables	Coefficient ± SE	Z	P	95% CIs	Significance
Groomer	PG vs. MC	-0.43 ± 0.1	-4.52	0.001	-0.62 – -0.24	✓
	Sex of the dyad:					
	MM vs. MF	-2.1 ± 2.6	-0.81	0.42	-7.17 – 2.97	✗
	MM vs. FF	-2.17 ± 2.96	-0.73	0.46	-7.98 – 3.63	✗
	MF vs. FF	-0.08 ± 1.8	-0.04	0.97	-3.6 – 3.46	✗
	Role of the higher-ranking animal	-0.58 ± 1.84	-0.32	0.75	-4.19 – 3.01	✗
	% of time spent in proximity in PGs or MCs	0.04 ± 0.005	8.59	0.001	0.03 – 0.05	✓
	CSI of the dyad	0.18 ± 0.64	0.28	0.78	-1.08 – 1.44	✗
Groomee	PG vs. MC	-3.63 ± 0.13	-27.65	0.001	-3.89 – -3.37	✓
	Sex of the dyad:					
	MM vs. MF	-0.41 ± 1.59	-0.26	0.8	-3.52 – 2.71	✗
	MM vs. FF	-0.23 ± 1.81	-0.13	0.9	-3.77 – 3.31	✗
	MF vs. FF	0.18 ± 1.19	0.15	0.88	-2.16 – 2.52	✗
	Role of the higher-ranking animal	0.93 ± 1.14	0.82	0.41	-1.3 – 3.17	✗
	% of time spent in proximity in PGs or MCs	-0.03 ± 0.002	-13.62	0.001	-0.03 – -0.02	✓
	CSI of the dyad	0.17 ± 0.43	0.4	0.69	-0.68 – 1.02	✗

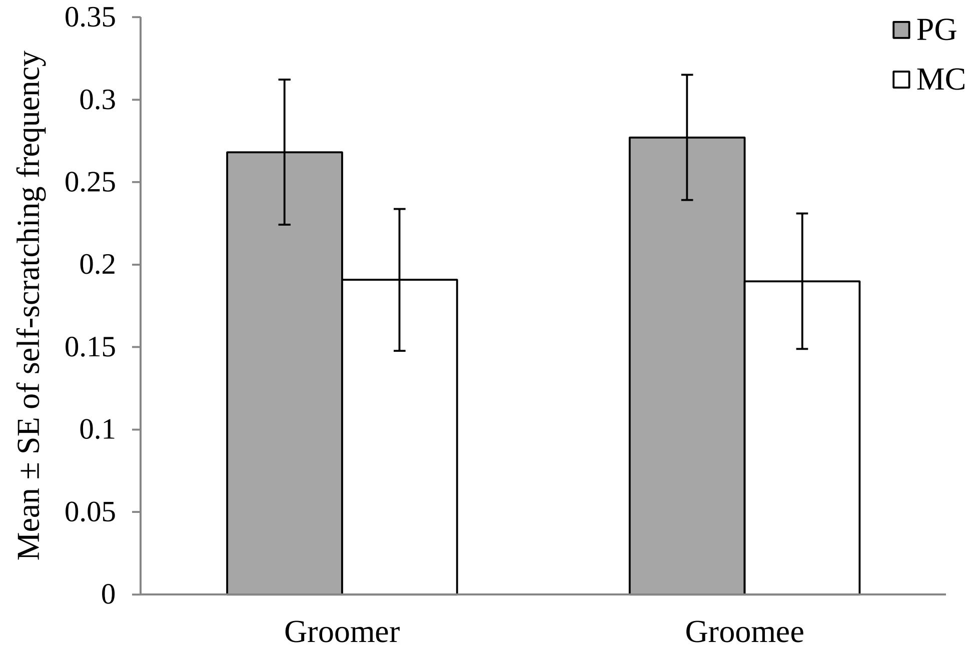


Figure 3.1. Mean frequency (number of occurrences per minute) of self-scratching ± SE in the post-grooming (PG) and matched-control (MC) sessions for the groomer and groomee, for the 'short PG' method.

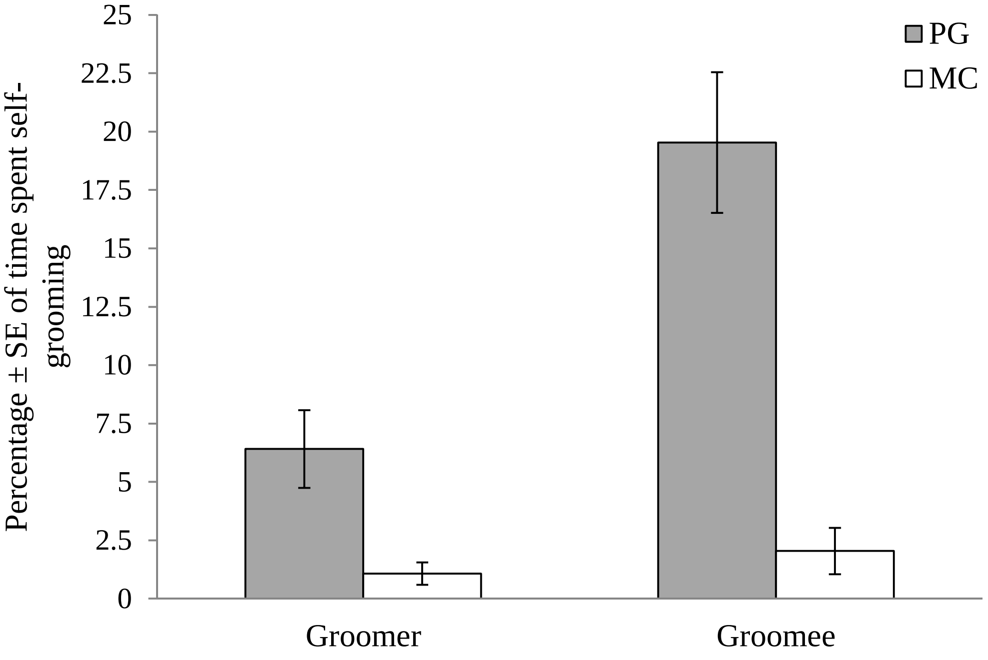


Figure 3.2. Percentage of time spent self-grooming (in seconds) during the sessions ± SE in the post-grooming (PG) and matched-control (MC) sessions for the groomer and groomee, for the 'short PG' method.

In the analyses run using the ‘short PG’ method, the frequency of PG self-scratching was not significantly different between the groomee and the groomer (Figure 3.1; Table 3.3). However, the percentage of time spent self-grooming (Figure 3.2) in the PG sessions was significantly higher for the groomee than for the groomer (Table 3.3). Similar results were obtained for the analyses run using the ‘10-minutes PG’ method. The frequency of self-scratching was not significantly different between the groomer and the groomee (GLMM, $z = 1.76$, $p = 0.08$) whereas the percentage of time spent self-grooming in the PG sessions was significantly higher for the groomee than for the groomer (GLMM, $z = 5.58$, $p = 0.001$).

No significant difference was found between the frequency of aggression received by the groomer (GLMM, $z = 1.08$, $p = 0.28$) or the groomee (GLMM, $z = -0.53$, $p = 0.59$) in PG sessions versus MCs, using the ‘10-minutes PG’ method’ (Figure 3.3). Moreover, no significant difference was found between the frequency of PG aggression received by the groomer and the groomee (GLMM, $z = -0.01$, $p = 0.99$).

Table 3.3. Coefficients and significance of the test and control variables entered in the GLMMs to compare self-scratching and self-grooming in the PG sessions between the groomer and groomee, using the ‘short PG’ method (N = 230). MM = male-male, MF = male-female, FF = female-female dyads.

Behaviour	**Variables**	**Coefficient ± SE**	**Z**	**P**	**95% CIs**	**Significance**
Self-scratching	Groomer vs. groomee	0.22 ± 0.14	1.58	0.11	-0.05 – 0.49	✗
	Sex of the dyad :					
	MM vs. MF	-0.44 ± 0.23	-1.93	0.05	-0.88 – 0.01	✗
	MM vs. FF	-0.73 ± 0.28	-2.65	0.01	-1.27 – -0.19	✓
	MF vs. FF	-0.29 ± 0.24	-1.21	0.23	-0.76 – 0.18	✗
	Role of the higher-ranking animal	0.04 ± 0.18	0.21	0.83	-0.32 – 0.4	✗
	% of time spent in proximity in PGs or MCs	-0.01 ± 0.003	-3.07	0.002	-0.02 – -0.004	✓
	CSI of the dyad	0.05 ± 0.07	0.65	0.52	-0.1 – 0.19	✗
Self-grooming	Groomer vs. groomee	0.98 ± 0.04	26.96	0.001	0.91 – 1.05	✓
	Sex of the dyad:					
	MM vs. MF	-0.43 ± 1.54	-0.28	0.78	-3.45 – 2.59	✗
	MM vs. FF	-0.69 ± 1.72	-0.4	0.69	-4.06 – 2.68	✗
	MF vs. FF	-0.26 ± 1.24	-0.21	0.83	-2.69 – 2.17	✗
	Role of the higher-ranking animal	0.48 ± 1.03	0.46	0.64	-1.54 – 2.5	✗
	% of time spent in proximity in PGs or MCs	0.004 ± 0.01	0.32	0.75	-0.02 – 0.03	✗
	CSI of the dyad	0.36 ± 0.43	0.84	0.4	-0.48 – 1.21	✗

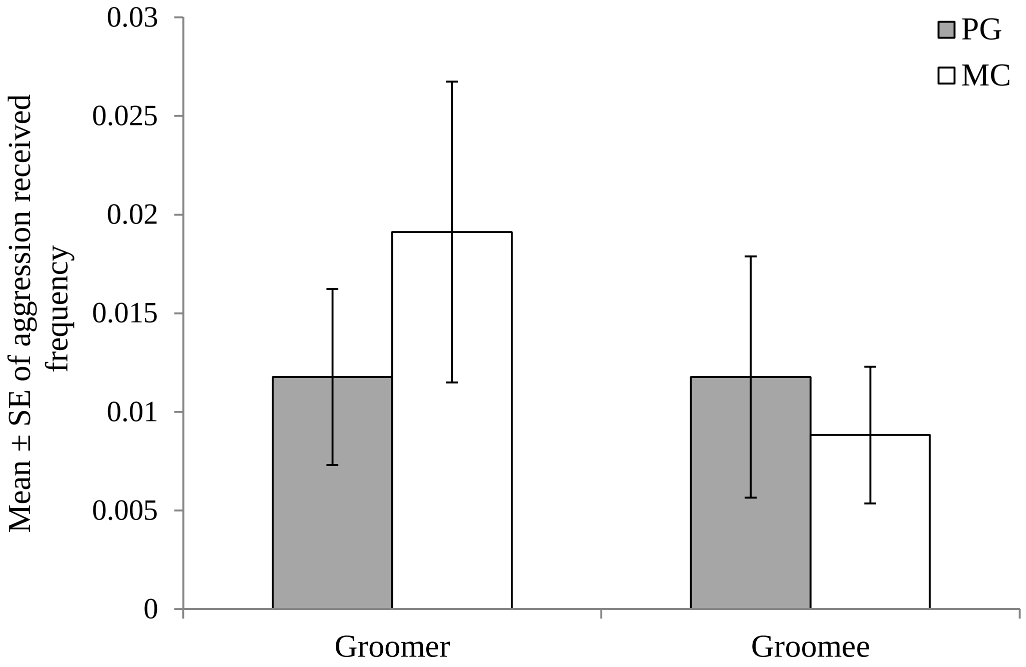


Figure 3.3. Mean frequency (number of occurrences per minute) of aggression received ± SE in the post-grooming (PG) and matched-control (MC) sessions for the groomer and groomee, for the ’10-minutes PG’ method.

3.4. DISCUSSION

To my knowledge, this is the first study to analyse post-grooming anxiety in a wild primate species and simultaneously on the groomer and groomee of the same grooming interactions. This study showed that a short-term increase of self-directed behaviours, which are behavioural indicators of anxiety, follows the termination of grooming interaction in wild Barbary macaques. This study used an established methodology to analyse post-grooming SDBs (Schino et al, 1988; Aureli & Yates, 2010; Radford, 2012) but, unlike previous studies, no support for the anxiety-reduction mechanism of grooming was found. However, the results are similar to a recent study that showed an increase of self-scratching after grooming in captive female Barbary macaques (Semple et al, 2013). The anxiety-reduction effect of grooming is a proximate mechanism that has been proposed to affect grooming interactions and the establishment or maintenance of social bonds (e.g. Schino & Aureli, 2009). These findings highlight the importance of conducting further research to investigate the link between grooming and anxiety, in order to better understand how emotions modulate social relationships.

The link between grooming and anxiety may be more complex than what expected by solely looking at the short-term anxiety-reduction function of grooming. Three factors that can potentially modulate post-grooming anxiety are proposed and discussed below: the risk of post-grooming aggression, the emotional consequences of behavioural transitions and the frustration due to the termination of grooming.

The social pressure of exchanging grooming with valuable partners (e.g. high-ranking individuals; Schino et al, 2005), to receive rank-related benefits such as tolerance and agonistic support (Seyfarth, 1977; Dunbar, 1991), may conflict with the risk of approaching high-ranking individuals. This could explain, for example, the positive correlation found between the frequency of self-scratching and the grooming given to adult males by Barbary macaque females (Kaburu et al, 2012). In a study on captive Japanese macaques (*Macaca fuscata*; Schino et al, 2005) aggression was found to be positively correlated with the amount of grooming. Barbary macaques use aggression to coerce grooming from subordinates (McFarland & Majolo, 2011). Such coercion of grooming and the short inter-individual distance required for grooming to occur could increase the risk of post-grooming aggression and anxiety (Schino et al, 2005; Carne et al, 2011; McFarland & Majolo, 2011). To test this hypothesis, post-grooming frequency of aggression received by the focal animal was compared to control conditions and no difference was found in the risk of aggression for both partners. Therefore, the higher frequency of post-grooming SDBs cannot be explained by a greater risk of receiving aggression by the groomer or groomee.

The frequency of SDBs peaks during or around behavioural transitions from one activity to another (e.g. from grooming to moving; Diezinger & Anderson, 1986). SDBs may also increase after grooming due to the frustration caused by the termination of grooming (Schino et al, 1988). Buckley and Semple (2012) found that the frequency of self-scratching was significantly higher before and after changes of activity in ring-tailed lemurs (*Lemur catta*). In captive female Barbary macaques, the rate of self-scratching was greater soon after a grooming interaction was terminated than before its start or than the overall mean rate of self-scratching (Semple et al, 2013). Moreover, in wild white-faced capuchins (*Cebus capucinus*) SDBs were higher before and after grooming (Manson & Perry, 2000). Finally, in male long-tailed macaques (*Macaca fascicularis*), the groomee engaged in more self-scratching in the first 10 seconds following grooming (Schino et al, 1988). Therefore, anxiety may decrease during grooming interactions (Boccia et al, 1989; Aureli et al, 1999) but not so or, in fact, increase when grooming is terminated. The hypotheses that SDBs increase either around behavioural transitions or because of the frustration caused by the termination of grooming are not mutually exclusive and they could both play a role in explaining the findings of this Chapter. However, comprehensive analyses on the occurrence of SDBs during various activities (e.g. grooming or feeding) and around behavioural transitions are necessary to fully understand whether these hypotheses can explain the findings of this study. Moreover, the possible frustration effect for the termination of grooming has so far received little attention (Schino et al, 1988) and this study highlights the need to explore this hypothesis further.

The results indicate that the short-term post-grooming increase in anxiety is more evident for the groomee than for the groomer when focusing on self-grooming, but not so for self-scratching. Moreover, PG anxiety lasted longer for the groomee than for the groomer, as for the groomer the frequency of self-scratching was higher in PGs than MCs when using the ‘short PG’ method but not with the ‘10-minutes PG’ method. The difference in PG self-grooming between the groomer and groomee might be due to frustration at the termination of grooming (Schino et al, 1988) being more evident in the recipient of grooming. It is also possible that the difference found in the PG self-grooming between the two grooming partners is due to the need, for the groomee, to fulfil the hygienic benefits of grooming through self-grooming. The analyses thus indicate that both the donor and recipient of grooming experience a short-term increase in anxiety after grooming, but that the increase lasts longer for the groomee than for the groomer.

In conclusion, this study showed that in wild Barbary macaques both grooming partners show a short-term increase of SDBs after grooming, but more significantly so in the groomee. Therefore, the social and hygienic benefits of grooming may out-weigh its short-term cost in terms of anxiety. This increase in SDBs may be the result of the emotional response to the change in activity (e.g. from grooming to travelling) and/or to the frustration caused by the termination of grooming. The findings highlight the need to further investigate the link between emotions and grooming. Understanding the proximate mechanisms of grooming is essential to shed light on what factors affect the choice of social partners and exchange of services in animals.

3.5. REFERENCES

Akinyi, M. Y., Tung, J., Jeneby, M., Patel, N. B., Altmann, J. & Alberts, S. C. 2013. Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behaviour,* **85**, 559-568.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour,* **49**, 227-267.

Arnold, K. & Whiten, A. 2001. Post-conflict behaviour of wild chimpanzees (*Pan troglodytes*) in the Budongo forest, Uganda. *Behaviour,* **138**, 649-690.

Aureli, F. & de Waal, F. B. M. 1997. Inhibition of social behavior in chimpanzees under high-density conditions. *American Journal of Primatology,* **41**, 213-228.

Aureli, F. & de Waal, F. B. M. 2000. *Natural conflict resolution*. California: University of California Press.

Aureli, F. & van Schaik, C. P. 1991. Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*). II. Coping with the uncertainty. *Ethology*, **89**, 101-114.

Aureli, F. & Yates, K. 2010. Distress prevention by grooming others in crested black macaques. *Biology Letters,* **6**, 27-29.

Aureli, F. 1992. Post-conflict behaviour among wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology,* **31**, 329-337.

Aureli, F. 1997. Post-conflict anxiety in nonhuman primates: the mediating role of emotion in conflict resolution. *Aggressive Behavior*, **23**, 315-328.

Aureli, F., Cords, M. & van Schaik, C. P. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour,* **64**, 325-343.

Aureli, F., Preston, S. D. & de Waal, F. B. M. 1999. Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. *Journal of Comparative Psychology,* **113**, 59-65.

Aureli, F., van Schaik, C. P. & van Hooff, J. A. R. A. M. 1989. Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology,* **19**, 39-51.

Baker, K. C. & Aureli, F. 1997. Behavioural indicators of anxiety: an empirical test in chimpanzees. *Behaviour,* **134**, 1031-1050.

Barros, M., Boere, V., Huston, J. P. & Tomaz, C. 2000. Measuring fear and anxiety in the marmoset (*Callithrix penicillata*) with a novel predator confrontation model: effects of diazepam. *Behavioural Brain Research*, **108**, 205-211.

Boccia, M. L., Reite, M. & Laudenslager, M. 1989. On the physiology of grooming in a pigtail macaque. *Physiology & Behavior,* **45**, 667-670.

Buckley, V. & Semple, S. 2012. Evidence that displacement activities facilitate behavioural transitions in ring-tailed lemurs. *Behavioural Processes,* **90**, 433-435.

Carne, C., Wiper, S. & Semple, S. 2011. Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology,* **73**, 1127-1133.

Castles, D. L. & Whiten, A. 1998. Post-conflict behaviour of wild olive baboons. I. Reconciliation, redirection and consolation. *Ethology,* **104**, 126-147.

Castles, D. L., Whiten, A. & Aureli, F. 1999. Social anxiety, relationships and self-directed behaviour among wild female olive baboons. *Animal Behaviour*, **58**, 1207-1215.

Cilia, J. & Piper, D. C. 1997. Marmoset conspecific confrontation: and ethologically-based model of anxiety. *Pharmacology Biochemistry and Behavior*, **58**, 85-91.

Cooper, M. A., Aureli, F. & Singh, M. 2006. Sex difference in reconciliation and post-conflict anxiety in Bonnet macaque. *Ethology,* **113**, 26-38.

Das, M., Penke, Z. & van Hooff, J. A. 1998. Postconflict affiliation and stress-related behavior of long-tailed macaque aggressors. *International Journal of Primatology,* **19**, 53-71.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour,* **125**, 157-175.

Diezinger, F. & Anderson, J. R. 1986. Starting from scratch: a first look at a ‘displacement activity’ in group-living rhesus monkeys. *American Journal of Primatology,* **11**, 117-124.

Dunbar, R. I. M. & Sharman, M. 1984. Is social grooming altruistic? *Journal of comparative ethology*, **64**, 163-173.

Dunbar, R. I. M. 1991. Functional significance of social grooming in primates. *Folia Primatologica,* **57**, 121-131.

Estanislau, C. 2012. Cues to the usefulness of grooming behaviour in the evaluation of anxiety in the elevated plus-maze. *Psychology & neurosciences,* **5**, 105-112.

Feh, C. & de Mazières, J. 1993. Grooming at a preferred site reduces heart rate in horses. *Animal Behaviour*, **46**, 1191-1194.

Fraser, O. N., Stahl, D. & Aureli, F. 2010. The function and determinants of reconciliation in *Pan troglodytes*. *International Journal of Primatology,* **31**, 39-57.

Gust, D. A., Gordon, T. P., Hambright, M. K. & Wilson, M. E. 1993. Relationship between social factors and pituitary: adrenocortical activity in female rhesus monkeys (*Macaca mulatta*). *Hormones and Behavior,* **27**, 318-331.

Hart, B. L. & Hart, L. A. 1992. Reciprocal allogrooming in impala, *Aepyceros melampus*. *Animal Behaviour,* **44**, 1073-1083.

Henzi, S. P. & Barrett, L. 1999. The value of grooming to female primates. *Primates,* **40**, 47-59.

Hutchins, M. & Barash, D. P. 1976. Grooming in primates: implications for its utilitarian function. *Primates,* **17**, 145-150.

Kaburu, S. S. K., MacLarnon, A., Majolo, B., Qarro, M. & Semple, S. 2012. Dominance rank and self-scratching among wild female Barbary macaques (*Macaca sylvanus*). *African Zoology,* **47,** 74-79.

Keverne, E. B., Martensz, N. D. & Tuite, B. 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology,* **14**, 155-161.

Koski, S. E., Koops, K. & Sterck, E. H. M. 2007. Reconciliation, relationship quality, and post-conflict anxiety: testing the integrated hypothesis in captive chimpanzees. *American Journal of Primatology,* **69**, 158-172.

Kutsukake, N. & Castles, D. L. 2001. Reconciliation and variation in post-conflict stress in Japanese macaques (*Macaca fuscata fuscata*): testing the integrated hypothesis. *Animal Cognition,* **4**, 259-268.

Maestripieri, D. 1993. Vigilance costs of allogrooming in macaque mothers. *The American Naturalist*, **141**, 744-753.

Maestripieri, D., Schino, G., Aureli, F. & Troisi, A. 1992. A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour,* **44**, 967-979.

Majolo, B., Schino, G. & Aureli F. 2012. The relative prevalence of direct, indirect and generalised reciprocity in macaque grooming exchanges. *Animal Behaviour*, **83**, 763-771.

Majolo, B., Ventura, R. & Koyama, N. F. 2009. Anxiety level predicts post-conflict behaviour in wild Japanese macaques (*Macaca fuscata yakui*). *Ethology,* **115**, 986-995.

Manson, J. H. & Perry, S. 2000. Correlates of self-directed behaviour in wild white-faced capuchins. *Ethology,* **106**, 301-317.

Martel, F. L., Nevison, C. M., Simpson, M. J. A. & Keverne, E. B. 1995. Effects of opioid receptor blockade on the social behavior of rhesus monkeys living in large family groups. *Developmental Psychobiology,* **28**, 71-84.

McFarland, D. J. 1966. On the causal and functional significance of displacement activities. *Zeitschrift für Tierpsychologie*, **23**, 217-235.

McFarland, R. & Majolo, B. 2011. Grooming coercion and the post-conflict trading of social services in wild Barbary macaques. *PLoS ONE,* **6**, e26893.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology,* **35**, 1-11.

Noldus Information Technology. 2003. *Matman, software for matrix manipulation and analysis, version 1.1.* Wageningen, The Netherlands.

Nunes, H. C., Pezzato, F. A. & Hoshino, K. 2012. Self-grooming, experimental anxiety and paradoxical sleep deprivation in rats. *Sleep Science,* **5**, 19-23.

Pavani, S., Maestripieri, D., Schino, G. & Turillazzi, P. G. 1991. Factors influencing scratching behaviour in long-tailed macaques (*Macaca fascicularis*). *Folia Primatologica,* **57**, 34-38.

Pinheiro, J. C. & Bates, D. M. 2000. *Mixed effects models in S and S-PLUS*, 1st edn. New York: Springer-Verlag.

Rabe-Hesketh, S. & Skrondal, A. 2008. *Multilevel and longitudinal modeling using Stata*. 2nd edn. College Station, Texas: Stata Press.

Radford, A. N. & Du Plessis, M. A. 2006. Dual function of allopreening in the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*. *Behavioral Ecology and Sociobiology,* **61**, 221-230.

Radford, A. N. 2012. Post-allogrooming reductions in self-directed behaviour are affected by role and status in the green woodhoopoe. *Biology Letters*, **8**, 24-27.

Sapolsky, R. M., Alberts, S. C. & Altmann, J. 1997. Hypercortisolism associated with social subordinate or social isolation among wild baboons. *Archive of General Psychiatry*, **54**, 1137-1143.

Scantlebury, M., Waterman, J. M., Hillegass, M., Speakman, J. R. & Bennett, N. C. 2007. Energetic costs of parasitism in the Cape ground squirrel *Xerus inauris. Proceedings of the Royal Society B,* **274,** 2169-2177.

Schino G. & Aureli F. 2008. Grooming reciprocation among female primates: a meta-analysis. *Biology Letters,* **4**, 9-11.

Schino, G. & Aureli, F. 2009. Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behavior*, **39**, 45-69.

Schino, G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, **18**, 115-120.

Schino, G., Maestripieri, D., Scucchi, S. & Turillazzi, P. G. 1990. Social tension in familiar and unfamiliar pairs of long-tailed macaques. *Behaviour*, **113**, 264-272.

Schino, G., Perretta, G., Taglioni, A. M., Monaco, V. & Troisi, A. 1996. Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety*, **2**, 186-191.

Schino, G., Rosati, L., Geminiani, S. & Aureli, F. 2007. Post-conflict anxiety in Japanese macaques (*Macaca fuscata*): aggressor's and victim's perspectives. *Ethology*, **113**, 1081-1088.

Schino, G., Scucchi, S., Maestipieri, D. & Turillazzi, P. G. 1988. Allogrooming as a tension-reduction mechanism: a behavioural approach. *American Journal of Primatology*, **16**, 43-50.

Schino, G., Troisi, A., Perretta, G. & Monaco, V. 1991. Measuring anxiety in nonhuman primates: effect of lorazepam on macaque scratching. *Pharmacology Biochemistry and Behavior*, **38**, 889-891.

Schino, G., Ventura, R. & Troisi, A. 2005. Grooming and aggression in captive Japanese macaques. *Primates*, **46**, 207-209.

Semple, S., Harrison, C. & Lehmann, J. 2013. Grooming and anxiety in Barbary macaques. *Ethology*, **119**, 779-785.

Seyfarth, R. M. 1977. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, **65**, 671-698.

Shutt, K., MacLarnon, A., Heistermann, M. & Semple, S. 2007. Grooming in Barbary macaques: better to give than to receive? *Biology Letters*, **3**, 231-233.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance infant survival. *Science*, **302**, 1231-1234.

Tanaka, I. & Takefushi, H. 1993. Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropological Science*, **101**, 187-193.

Terry, R. 1970. Primate grooming as a tension reduction mechanism. *Journal of Psychology*, **76**, 129-136.

Troisi, A. & Schino, G. 1987. Environmental and social influences on autogrooming behaviour in a captive group of Java monkeys. *Behaviour*, **100**, 292-302.

Troisi, A. 2002. Displacement activities as behavioural measures of stress in non-human primates and human subjects. *Stress*, **5**, 42-54.

Ventura, R., Majolo, B., Schino, G. & Hardie, S. 2005. Differential effects of ambient temperature and humidity on allogrooming, selfgrooming, and scratching in wild Japanese macaques. *American Journal of Physical Anthropology*, **126**, 453-457.

Wascher, C. A. F., Fraser, O. N. & Kotrschal, K. 2010. Heart rate during conflicts predicts post-conflict stress-related behavior in Greylag geese. *PLoS ONE*, **5**, e15751.

Wiper, S. & Semple, S. 2007. The function of teeth-chattering in the Barbary macaque (*Macaca sylvanus*). *American Journal of Primatology*, **69**, 1179-1188.

Zamma, K. 2002. Grooming site preferences determined by lice infection among Japanese macaques in Arashiyama. *Primates*, **43**, 41-49.

Chapter 4

Divide and rule: costs and benefits of grooming disruption

Chapter 3 investigated the anxiety reduction mechanism of grooming in wild Barbary macaque by comparing post-grooming anxiety for the donor and recipient of the same grooming interactions. The results showed that anxiety was higher in post-grooming than control sessions for the donor and recipient. The release of anxiety may not be a key benefit of grooming in Barbary macaques. In this species, higher-ranking monkeys sometime disrupt grooming interactions of other group members. This Chapter investigates what the benefits and costs of grooming disruption are for the disrupters, as an attempt to define the consequences of grooming disruptions in Barbary macaques.

4.1. INTRODUCTION

Grooming is observed in many animal societies (e.g. Spruijt et al, 1992). Receiving grooming reduces parasite infection and removes dirt from part of the fur animals cannot reach through self-grooming, improving physical health (Hutchins & Barash, 1976; Hart et al, 1992; Tanaka & Takefushi, 1993; Zamma, 2002; Radford & Du Plessis, 2006; Scantlebury et al, 2007; Akinyi et al, 2013). Giving grooming is costly as it reduces vigilance against predators and competitors (Maestripieri, 1993; Cords, 1995) and the time available for other activities such as infant care, feeding or self-grooming (Dunbar & Sharman, 1984; Dunbar, 1992). It also increases the risk of parasite transmission (Johnson et al, 2004; Nunn & Alteizer, 2006). Chapter 3 showed that anxiety may also be a cost of grooming for the donor and the recipient in Barbary macaques.

Altruism refers to any behaviour giving costs to donors and benefits to recipients (Trivers, 1971; Axelrod & Hamilton, 1981). Grooming is thus a naturally occurring altruistic behaviour in primates and can be easily quantified. Non-human primates groom group members more than necessary for a solely hygienic function, indicating that grooming has also a social function (Dunbar & Sharman, 1984). Grooming is indeed the main behaviour used to establish and maintain friendly relationships (Dunbar, 1991). Due to its costs and benefits, grooming is exchanged for grooming or for other social services such as support during agonistic interaction, tolerance, access to infant and preferential access to resources such as food and mating partners (e.g. de Waal, 1997; Barrett & Henzi, 2001, 2006; Ventura et al, 2006; Carne et al, 2011). The biological market approach (an extension of the reciprocal altruism approach: Schino & Aureli, 2010) predicts that the availability of a commodity and the capacity of each animal to retain resources affect the exchange of commodities (Noé & Hammerstein, 1994; Barrett et al, 1999; Noë et al, 2001). The model predicts for example that when competition for resources is weak, grooming is traded for grooming, but when competition is strong, grooming may be traded for rank-related commodities, which result in a rank related asymmetric grooming distribution (i.e. grooming is directed up the hierarchy; Schino & Aureli, 2008). For example, when food is scarce only high-ranking individuals have direct access to high-quality food sources whereas low-ranking individuals may exchange a service given (e.g. grooming) for tolerance over food. Consequently, the asymmetry in grooming between higher-ranking and lower-ranking is strongest when resources are scarce and can be monopolized by a single animal.

There is evidence that non-human primates exchange grooming for other rank-related commodities. First of all, grooming up the hierarchy increases the probability of lower-ranking individuals to be tolerated in the proximity of higher-ranking individuals, and so increases tolerance over food (Silk, 1982; de Waal, 1997; Ventura et al, 2006; Carne et al, 2011; Tiddi et al, 2011; Aureli & Yates, 2010; Wei et al, 2012). For example, wild tufted capuchin monkeys (*Cebus apella nigritus;* Tiddi et al, 2011) and females Barbary macaques (*Macaca sylvanus*; Carne et al, 2011) exchange grooming for tolerance over food resources. Moreover, Fruteau and colleagues (2009) set up an experiment where two low-ranking vervet monkeys (*Chlorocebus pygerythrus*) were allowed to repeatedly provide food to their group members by triggering the opening of a food dispenser. The authors showed that food providers received more grooming, relative to the amount of grooming they provided themselves, in exchange of the food they made available to the other monkeys. In addition, in line with the predictions of biological market theory, the benefit (in term of grooming received) that food providers received from the other group members was reduced when more than one monkey was able to operate the food dispenser.

Another market effect is related to the number of infant in a group: when fewer infants are present in non-human primates group, infants are the desired commodity, mothers control the access to their infants, and other females can exchange grooming with the mothers to gain access to their infants (Muroyama, 1994; Henzi & Barrett, 2002; Schaffner & Aureli, 2005; Gumert, 2007a; Slater et al, 2007; Tiddi et al, 2010; Fruteau et al, 2011). Females' attraction to infants seems to be a by-product of selection for appropriate maternal care, that is, females strongly attracted to infants make better mothers (Silk, 1999). In chacma baboons (*Papio cynocephalus ursinus*) for example, grooming was interchanged with infant handling, and gromming duration was inversely related to the number of infants present in the group (Henzi & Barrett, 2002). Moreover, the more the mother was higher-ranking than the potential handlers, the more the potential handlers had to groom the mother to gain access to the infant. Similarly in long-tailed macaques (*Macaca fascicularis*), grooming promoted exchanges with infant handling and the supply of available infants was related to how long females groomed mothers (Gumert, 2007a).

Non-human primates also exchange grooming for access to mating partners (Gumert, 2007b; Norscia et al, 2009; Barelli et al, 2011; Clarke et al, 2010; Koyama et al, 2012). In long-tailed macaques, male to female grooming was associated with an increase of sexual activities with the female (Gumert, 2007b). Following the biological market prediction, the amount of grooming a male give to a female in exchange of mating, was related to the current availably of females around the interaction. Moreover in chimpanzees, females received more grooming from males when swollen (i.e. in oestrus) than when not swollen, and males groomed swollen females less as the number of available swollen females increased in the group (Koyama et al, 2012). In chacma baboons, females grooming with males was positively associated with the probability that females would successfully initiate mating (Clarke et al, 2010).

Finally, non-human primates exchange grooming for support during coalitions (see Schino, 2007 for a meta-analysis). Coalitions are coordinated agonistic interactions by at least two individuals against one or more targets (van Schaik et al, 2004). Winning coalitions may either only increase the access to limiting resources (e.g. food or mating partner), without changing the dominance rank of the participants, or may additionally improve the dominance rank of the participants. All-up coalitions include participants with dominance ranks inferior to the dominance ranks of the targets, whereas bridging coalitions include targets with dominance rank in-between participants' ranks (van Schaik et al, 2004). By grooming higher-ranking individuals, lower-ranking individuals can establish or maintain strong social relationships with them, and strong relationships increase the probability that the individuals would form alliances together against other group members. In wild female Japanese macaques (*Macaca fuscata yakui*), grooming was directed up the hierarchy and was positively related to agonistic support given against adult males (Ventura et al, 2006; but see also on the same species Schino et al, 2007). An interchange of grooming given and support received has also been found in females Barbary macaques (Carne et al, 2011), chimpanzees (*Pan troglodyte*; Hemelrijk & Ek, 1991; Watts, 2002; Koyama et al, 2006; Mitani, 2006), bonobos (*Pan paniscus*; Vervaecke et al, 2000), vervet monkeys (*Chlorocebus aethiops*; Seyfarth & Cheney, 1984), long-tailed macaques (Hemelrijk, 1994), and bonnet macaques (*Macaca radiata*; Silk, 1982, 1992). In male Barbary macaques, coalition formation during the mating season was predicted by social affiliation such as close proximity and grooming in the non-mating season (Berghänel et al, 2011).

Due to the many potential benefits of grooming exchanges and since time for grooming is limited, individuals compete over valuable grooming partners (Dunbar, 1992). However, individuals differ also in their capacity to out-compete other group members and extort resources such as grooming from other individuals. A positive correlation between grooming given and aggression received (i.e. individuals harass more often group members who groom them most) has been found in female bonnet macaques (*Macaca radiata*; Silk, 1982), female Japanese macaques (*Macaca fuscata*; Schino et al, 2005), male stump-tailed macaques (*Macaca arctoides*; Richter et al, 2009) and Barbary macaques (Carne et al, 2011). This finding suggests that dominant individuals (i.e. individuals who have usually higher fighting abilities) may use direct aggression or threat in order to extort grooming from lower-ranking individuals (Silk, 1982). For this, dominant individuals may aggress lower-ranking individuals until they receive grooming from them (e.g. McFarland & Majolo, 2011). Consequently, the capacity of individuals to extort services from other group members and/or to aggress other group members who transgress their interest, may influence the exchanges of social services such as grooming (Clutton-Brock & Parker, 1995b; Colmenares et al, 2002). While sexual coercion by males on females (i.e. the use of threat or force in a sexual context; Smuts & Smuts, 1993; Clutton-Brock & Parker, 1995a) is well documented (e.g. bottlenose dolphins, *Tursiops sp*: Scott et al, 2005; chimpanzees: Muller et al, 2007; Stumpf & Boesch, 2010; Japanese macaques: Enomoto, 1981; rhesus macaques: Manson, 1994; or see for a review: Smuts & Smuts, 1993 and Muller & Wrangham, 2009), data on grooming coercion (i.e. the use of threat or aggression toward an individual to extort grooming) are limited (Kutsukake & Clutton-Brock, 2006; McFarland & Majolo, 2011). Wild Barbary macaques renewed aggression toward the victims in the aftermath of conflicts, if the victims failed to give grooming to the aggressors soon after the conflict (McFarland & Majolo, 2011). However, giving grooming to the aggressor in the aftermath of a conflict has the benefit to reduce the risk of renewed aggression for the victim and to repair the relationship with the aggressor.

Occasionally, animals approach (generally aggressively) a grooming interaction between group members, until one or both grooming partners stop the grooming interaction. This grooming disruption behaviour has been reported in wild vervet monkeys (*Chlorocebus pygerythrus*; Cheney & Seyfarth, 1990), wild baboons (*Papio hamadryas ursinus*; Henzi et al, 2003), wild meerkats (*Suricata suricatta*; Kutsukake & Clutton-Brock, 2006), wild long-tailed macaques (*Macaca fascicularis*; Wheatley, 1999) and wild Japanese macaques (Oki & Maeda, 1973). Cheney and Seyfarth defined “competitive interaction over access to a grooming partner, as occurring whenever a vervet female approached two grooming partners, supplanted one of them, and then groomed the other” (1990, p 38). In this definition, grooming disruption is presented as resulting from competition for grooming partners. All the female vervets were involved in these competitive interactions, and the most attractive partners were high-ranking monkeys (Cheney & Seyfarth, 1990). Seyfarth’s model of social grooming among female monkeys (1977) proposes that (1) there is an optimized ratio of grooming received and given, according to the hygienic and social function of grooming and to the limited time available for grooming, and (2) higher-ranking females are more attractive as grooming partner because of their value as coalition partner. Consequently, when resources are scarce and contest competition is advantageous for the winner, the value of higher-ranking females as grooming partners increases and females compete for valuable grooming partner (Seyfarth, 1977; for test of the model see Schino, 2001 and Henzi et al, 2003). Following this model, Henzi and colleagues (2003) tested the assumption that grooming disruption, through the displacement of subordinates, will increase when competition for resources increases, and the dominance rank of the disruptive monkey will be between that of the grooming partners. They showed that in periods of intense resource competition female-female baboons grooming was disrupted at 2.3%, and at 3.04% in period of low resource competition. Among the few grooming disrupted, less than half involved higher-ranking females. There was thus no increase of grooming disruption when resource competition increased (Henzi et al, 2003). Another example of grooming disruption comes from meerkats, a cooperatively breeding species where related individuals form a family group and one dominant female produces at least 80% of the youngs (Griffin et al, 2004). In this species, the breeding female and the dominant male more frequently disrupted grooming interactions involving one of them with a subordinate group member (Kutsukake & Clutton-Brock, 2006). Moreover, in most of the cases the dominant pair groomed each other after the disruptions. The authors suggested that grooming in meerkats functions to maintain and reinforce the sexual bond between dominant animals. Moreover, there is evidence in captive stump-tailed macaques (*Macaca arctoides*) that individuals disrupt affiliative interactions (e.g. grooming, contact sitting and play) involving other group members (Mondragón-Ceballos, 2001). The disruptions of affiliative behaviours were sometimes aggressive, and the interruptions inhibited the renewal of the behaviours. The author suggested that such interferences may function to sabotage the formation and/or maintenance of others' affiliative interactions.

To my knowledge, no study has directly assessed what the costs (e.g. aggression received) and benefits of grooming disruptions are for the disrupters. Dominance provides a number of fitness-related benefits in primates, such as preferential access to food, mating partners and infant survival (Majolo et al, 2012). By increasing grooming opportunities, grooming disruption may increase the fitness of the disrupters through the hygienic benefits of grooming, but also through the social benefits of grooming, such as the establishment or maintenance of strong bonds with higher-ranking monkeys which may support the individual during conflict. The functions of grooming disruption may be to coerce grooming from lower-ranking individuals, and/or to increase grooming opportunities by increasing the availability of high-value grooming partners. For example (Figure 4.1), if we consider a grooming interaction where monkey C grooms monkey A, A being higher-ranking than C. Monkey B disrupts the grooming interaction by displacing monkey C when approaching, B's rank being in-between the rank of A and C. B may disrupt the grooming between A and C as an attempt to access the high valuable grooming partner A, or to extort grooming from C. A may be considered as a high value grooming partner for B and C, as socializing with higher-ranking individuals bring benefits such as support in agonistic interactions (e.g. Schino, 2007). Moreover, monkey B may also disrupt the grooming between A and C as an attempt to avoid C establishing a strong relationship with A. By successfully disrupting grooming interactions, individuals may prevent group members from assessing the various benefits of grooming interactions. In the example above (Figure 4.1), by disrupting the grooming between monkeys A and C, B may prevent C from socializing with A. By doing this, B may prevent C from building or maintaining a strong relationship with A, and so may prevent C from having A as potential agonistic support against B (i.e. bridging coalition). Consequently, grooming disruption may be a social tool to sustain dominance and social relationships (Clutton-Brock & Parker, 1995b) and generate continuous uncertainty in subordinates (Silk, 2002). However, approaching higher-ranking group members to disrupt their grooming may conflict with the risk of receiving aggression from them (e.g. Troisi & Schino, 1987; Pavani et al, 1991; Castle et al, 1999; Kaburu et al, 2012). Consequently, grooming disruption may be costly for the disrupters too.

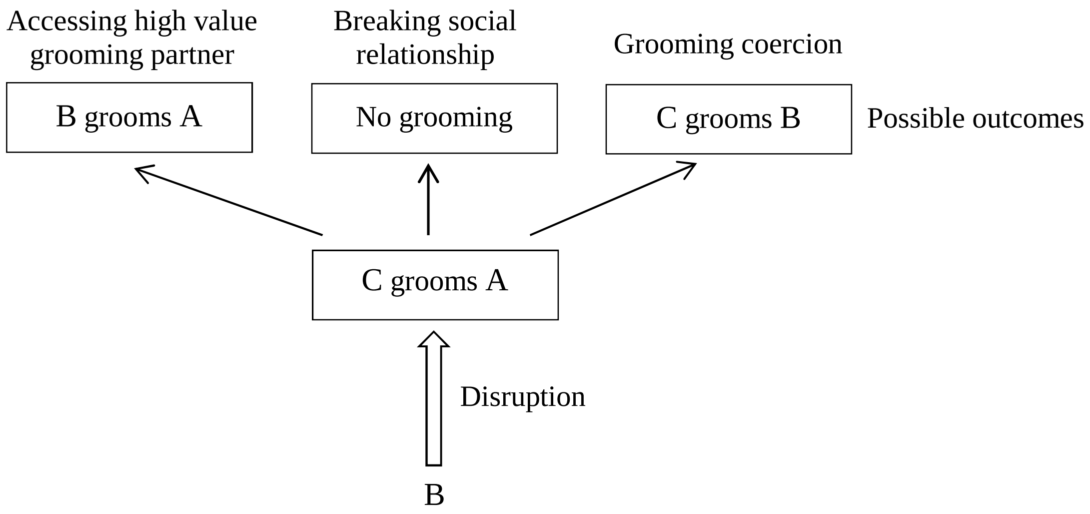


Figure 4.1. Illustration of some examples of outcomes that may occur after the disruption of a grooming interaction between the monkeys A and C, by a monkey B. The dominance status of the monkeys from higher-ranking to lower-ranking is A > B > C.

The aim of this Chapter was to investigate the potential costs and benefits of the disruption for the disrupter, as an attempt to define the consequences of grooming disruptions in Barbary macaques. Grooming disruption was defined as whenever a monkey approached two grooming partners at a minimum distance of 1.5 meters, interrupting the grooming interaction for at least five seconds. This definition differs from the “competitive interaction over access to a grooming partner” defined by Cheney and Seyfarth (1990, p 38), in that it considers any grooming disruption, including those not followed by grooming between the disrupter and the animals disrupted. This approach allows to investigate more comprehensively grooming disruption, by assessing what the disrupter gains from the disruption and what the risks are. Grooming disruptions may give direct benefits to the disrupters such as grooming opportunities and/or indirect benefits by affecting the social relationships of other group members, but this behaviour may be potentially risky. Consequently, two potential benefits of the disruption for the disrupter were considered in this study: (1) grooming opportunities, that is, any post-disruption grooming between the disrupter and the former grooming partners, and (2) the success of the disruption in stopping the two former grooming partners from grooming during the post-disruption period. Post-disruption aggressions received by the disrupter from the grooming partners disrupted were considered as costs of the disruption for the disrupter. The predictions tested in this Chapter were as follow:

(1) If grooming disruption gives to the disrupters grooming opportunities with the former grooming partners, the disrupters would exchange more grooming with the former grooming partners after disruption than in control condition.

(2) If grooming disruption puts the disrupters at risk of receiving aggression from the former grooming partners, the disrupters would receive more aggression from the former grooming partners after disruption than in control condition.

(3) If disrupters are successful at stopping the two former grooming partners from grooming, the grooming partners would less resume grooming each other after disruption than in control condition.

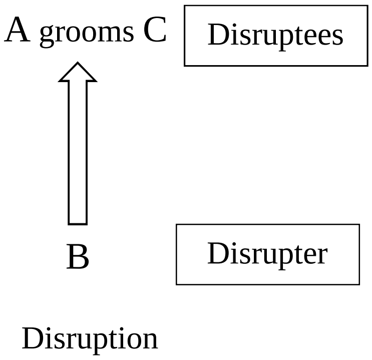
4.2. METHODS

4.2.1. Study subjects

Data were collected on the 15 adults and sub-adults monkeys of the ‘Green group’ (which at the beginning of this study consisted of 7 adult males, 7 adult females, 1 sub-adult male, 7 juveniles and several infants) living in the Middle Atlas Mountains of Morocco (33° 24’N - 005° 12’W). The group lived in the deciduous cedar and oak forest of the Ifrane National Park, between 1600 and 2000m a.s.l. See Chapter 2 for details on the study animal and field site.

4.2.2. Data collection

Data were collected daily between 6am and 7pm from April 2011 to January 2012 (4.5 months of non-mating season and 4 months of mating season). A well-established post-event-control methodology, used for example to assess post-conflict (de Waal & Yoshihara, 1983) and post-grooming (Aureli & Yates, 2010; Chapter 3) behaviours, was followed in this study. This methodology was used to collect post-disruption (hereafter PD) and control focal sessions. As soon as a monkey approached two grooming partners at a minimum distance of 1.5m and stopped the grooming interaction for at least 5 seconds, a 10-minutes PD focal session were collected on the disrupting monkey. The approach by the disrupter was usually aggressive, and the grooming interactions stopped because one of the grooming partners displayed a submissive behaviour toward the disrupter (see Chapter 2 for a description of the aggressive and submissive behaviours recorded). ‘The disrupter’ was defined as the animal who disrupted the grooming interaction, and ‘the disruptees’ as the animals whose grooming interaction was disrupted (Figure 4.2). Moreover in this Chapter, the terminology usually used to define the three different types of coalitions (i.e. ‘all-up’, ‘all-down’ and ‘bridging’; Chapais, 1995; Kuester & Paul, 1992; van Schaik et al, 2004; Bissonnette et al, 2009) was adapted to define the three different types of disruption according to the dominance status of the disrupter and the disruptees (Figure 4.2). ‘All-down disruptions’ referred to disruptions where the disrupter was higher-ranking than both disruptees. ‘All-up disruptions’ referred to disruptions where the disrupter was lower-ranking than both disruptees. ‘Bridging disruptions’ referred to disruptions where the dominance rank of the disrupter was in-between the ones of the disruptees.



Type of disruption	Dominance status
All-down disruption	B > A and C
Bridging disruption	A > B > C
All-up disruption	B < A and C

Figure 4.2. Illustration of the terminology used for the three types of grooming disruptions.

During the PDs, data were recorded on the first grooming interaction and the first aggression (see Chapter 2 for details on the aggressive behaviours recorded) involving the disrupter, as well as on the ID of the partners and direction of the behaviour (i.e. given or received). Consequently, only the first grooming and aggression involving the disrupters were collected, even if the behaviour did not involve the disruptees. This method was more conservative as it looked at the direct cause-effect between the disruption and the first grooming or aggression occurring, avoiding potential bias that other grooming or aggression occurring in-between may play. Consider for example a situation where monkey B disrupted a grooming between monkeys A and C. If during the PD period, B was first groomed by another monkey D, and then B groomed A, it is unclear whether the grooming B gave to A was a result of the previous disruption, or of the grooming B had previously received from D. Barbary macaques display a steep dominance hierarchy (Kaburu et al, 2012) and a low frequency of counter-aggression in agonistic interactions (defined as lower-ranking monkey directing aggression toward higher-ranking monkey during a conflict; Balasubramaniam et al, 2012). Consequently after being disrupted, only disruptees who were higher-ranking than the disrupters could direct aggression toward the disrupters. Data were also recorded on the sex and dominance status of the disrupter and disruptees, and on whether the disruptees resumed grooming or switched their groomer/groomee role within 10 minutes from the disruption.

Two kinds of control were collected: one on the disrupter and one on the disruptees. First, on the next possible day a 10-minutes control focal session was collected on the disrupter and using the same data collection than the method used in the PD sessions. Control sessions were not started on focal animals already involved in a grooming or aggressive interaction. Thus for each PD session, a control session was collected on the disrupter. This allowed to compare the grooming and aggressive behaviours involving the disrupters and disruptees between PD and control sessions. Second, another control was collected to assess whether the disruptions were successful at preventing the two disruptees from grooming each other within 10 minutes after the disruption. For each PD session, a control session was collected on the disruptees. So for each disruption of a monkey A grooming a monkey B, a 10-minutes control focal session was collected following the end of a grooming interaction (observed from start) where the monkey A groomed the monkey B, without being disrupted by a third individual. The end of the grooming interaction was defined as when the monkeys stopped grooming for at least 5 seconds. Data were collected on whether the grooming partners resumed grooming or switched their groomer/groomee role within 10 minutes from the end of their grooming interaction.

Ad libitum data (Altmann, 1974) were used to determine the dominance hierarchy of the monkeys. Ad libitum data were collected opportunistically on any observed dyadic conflicts not involving third parties and with a clear-cut result (i.e. one opponent displayed aggressive behaviour and the other opponent displayed submissive behaviour; see Chapter 2 for details on the aggressive and submissive behaviours recorded).

4.2.3. Data analysis

Based on the dyadic conflicts collected ad libitum, a winner-loser socio-metric dominance matrix was constructed. Matman 1.1. (Noldus Information Technology, 2003; de Vries et al, 1993) was used to assign an ordinal dominance rank to each study monkey. Analyses of the costs and benefits of grooming disruptions were based on 160 PD-control pairs. The two lowest-ranking females were never observed to be disrupters. Thus all but the two lowest-ranking adult females were represented as disrupters (mean number of PD-control sessions ± SE per monkey = 12.31 ± 3.95; N = 13). Three generalised linear mixed models (GLMM) with a logistic distribution were run to compare, (1) grooming involving the disrupters between PD and control sessions, (2) aggression received by the disrupters between PD and control sessions, and (3) the success of the disruptions in preventing the disruptees from grooming each other in PD compare to control sessions. In the three GLMMs, each PD or control session was treated as a single data point. The risk of sample inflation using this procedure was controlled for, in GLMMs, by adding random factors to the models (Pinheiro & Bates, 2000). Random factors take into account the clustering of data due, for example, to multiple observations being collected on the same animal, so that biases in the distribution and clustering of data (e.g. one animal having more observations than another) are controlled for. For the first two GLMMs, the PG-control pair ID, nested into the ID of the disrupter were entered in the GLMMs as random factors. For the third GLMM, the ID of the disrupter and the ID of the disruptees' dyad were entered as crossed random factors, both nested into the PG-control pair ID.

In the first GLMM run to assess grooming opportunities, the binary dependent variable was whether the disrupter was involved in a grooming interaction with any of the disruptees in PD or control, or not. In the second GLMM run to assess the risk of receiving aggression, the binary dependent variable was whether the disrupter received aggression from any of the disruptees in PD or control, or not. Because lower-ranking disruptees would not direct aggression toward higher-ranking disrupters, this second GLMM was only run on PD-control sessions following bridging disruptions (all-up disruption never occurred, see the section 4.3.1), that is, in situation where aggressive behaviour directed from one disruptee to the disrupter was possible. 'PD vs. MC' was the categorical test variable for these two GLMMs. In these two GLMMs, the control variables 'season' (categorical: non-mating or mating season) and 'sex combination' (categorical: whether the triad disrupter–disruptee/disruptee were of same-sex, i.e. female–female/female and male–male/male, or of different-sex, i.e. male–male/female, male–female/female, female–male/female and female–male/male), were entered in the models because these variables may affect the occurrence of grooming (e.g. Mitchell & Tokunaga, 1976; Seyfarth, 1977; Soltis, 1999; Lehmann & Boesch, 2008; Schino & Aureli, 2008), and aggression (e.g. Brockman et al, 1998; Matsubara & Sprague, 2004). The interaction between the variables 'season' and 'sex combination' was also entered as control variable, as these two factors may be closely linked. For example, the effect of season may be more obvious with different-sex than same-sex triads as monkeys compete for mating partners during the mating season. Additionally, in the first GLMM aimed to assess grooming opportunities, the control variable 'dominance combination' (categorical: whether the disruption was all-down, bridging, or all-up) was also added to the model because dominance status affects grooming exchanges (e.g. Schino & Aureli, 2008). This control variable was not entered in the second GLMM aimed to assess the risk of receiving aggression, as this GLMM was only run on PD-control sessions following bridging disruptions.

In the third GLMM run to assess the success of the disruptions, the binary dependent variable was whether the disruption was successful (i.e. the grooming partners did not resume grooming or switched their groomer/groomee role within the session) or unsuccessful. ‘PD vs. MC’ was the categorical test variable. The control variables ‘dominance combination’, ‘season’, ‘sex combination’, as well as the interaction between ‘season’ and ‘sex combination’ were also entered in the GLMM. The model was run twice; first included all PD sessions (i.e. including sessions where the disrupters were engaged in grooming with a disruptee), and second excluding PD sessions (and their matched controls) where the disrupters became involved in a grooming interaction with the disruptees. This allowed to assess whether the act of disruption was enough to stop the former grooming partners from grooming, or whether the fact that one disruptee was engaged in grooming with the disrupter, and so not available for resuming grooming with the other disruptee, was key to the success of the disruption.

Finally, individual scores were calculated to investigate in more details the PD grooming interactions between the disrupters and the disruptees. First, focusing only on PD sessions where grooming between the disrupters and the disruptees occurred, the proportion of grooming given to or received from the disruptees was calculated for each disrupter. Second, individual scores were calculated only from PD sessions resulting from bridging disruptions and where the disrupters engaged in grooming with the disruptees, in order to assess whether the disrupters based their choice of PD grooming partner on the dominance status of the disruptees. For each disrupter, the proportion of grooming exchanged with the higher-ranking or the lower-ranking disruptee was calculated, as well as the proportion of grooming given and received.

Paired samples Wilcoxon signed rank tests were used to analyse the individual scores in this study. For each box plot presented below, the bottom and top sides of the boxes represent respectively the first and third quartiles of the data, the band inside the boxes represents the median, and the bottom and top ends of the whiskers represent respectively the minimum and maximum scores of the data set.

4.3. RESULTS

4.3.1. Description of the PD sessions collected

The details of the number of PD sessions collected as well as the number of individuals involved are shown in the Table 4.1. The number of PD sessions collected opportunistically differed depending on the sex combination of the individuals, the season, and the dominance status of the disrupters and disruptees. First of all, all the disrupters were higher-ranking than at least one of the disruptees, that is, all-up disruptions were never observed. Consequently, as all males were dominant over females (see Chapter 2 for details on the dominance hierarchy of the group), no female disrupted grooming interactions between two males. Half of the PD sessions were collected following all-down disruptions and half were collected following bridging disruptions. The aggressive behaviours directed by the disrupter toward the disruptees during the disruption included lunge, charge, chase, grab, open mouth, and stare (see Chapter 2 for further details on these behaviours).

The disruptions were directed toward subordinate monkeys grooming dominant monkeys at 61.9%, and the disruptions were directed toward dominant monkeys grooming subordinate monkeys at 38.1%. When considering only all-down disruptions, the percentages were 75% and 25% respectively, and 51.25% and 48.75% respectively when considering only bridging disruptions. In bridging disruptions, the percentages of PD sessions collected during the non-mating and mating seasons were both 50%. In all-down disruptions, 65% of the PD sessions were collected during the mating season, and 35% during the non-mating season. The percentages of PD sessions collected on different-sex triads were 66.4% in the mating season and 33.6% in the non-mating season. Conversely, the percentages of PD sessions collected on same-sex triads were 65.9% in the non-mating season and 34.1% in the mating season. Only three PD sessions were collected on male disrupting male/male grooming. Grooming interactions involving male-female and female-female grooming partners were disrupted by females at 64.97% and by males at 35.03%. Moreover, males disrupted these grooming interactions involving at least one female at 80% during the mating season and at 20% during the non-mating season, whereas females disrupted these grooming interactions at 47.1% in the mating season and at 52.9% in the non-mating season.

Table 4.1. Details of the number of PD sessions collected and number of monkeys involved (i.e. disrupters), depending on sex combination, season, and dominance status.

				Number of PD sessions			**Number of individuals**	
	Disrupter	**Disruptee**	**Disruptee**	**Non-mating season**	**Mating season**	***Total both seasons***	**Non-mating season**	**Mating season**
Sex combinations	Male	Male	Male	3	0	*3*	2	0
	Female	Female	Female	26	15	*41*	5	4
	Total same-sex triads			*29*	*15*	*44*	*7*	*4*
	Male	Male	Female	3	14	*17*	2	6
	Male	Female	Female	8	30	*38*	5	6
	Female	Male	Male	0	0	*0*	0	0
	Female	Male	Female	28	33	*61*	4	4
	Total different-sex triads			*39*	*77*	*116*	*11*	*11*
	Total all sex combinations			*68*	*92*	*160*	*13*	*12*
All-up disruption	Low-ranking	High-ranking	High-ranking	0	0	*0*	0	0
Bridging disruption	High-ranking	High-ranking	Low-ranking	40	40	*80*	8	7
All-down disruption	High-ranking	Low-ranking	Low-ranking	28	52	*80*	10	8

4.3.2. Costs and benefits of grooming disruption

The disrupters significantly exchanged more grooming with the disruptees in PD than control sessions (Table 4.2; Figure 4.3). Three disrupters (2 males and 1 female) were never involved in grooming with the disruptees in PD sessions. For bridging disruptions, the disrupters were significantly at greater risk of receiving aggression from the disruptees in PD than control sessions (Table 4.3; Figure 4.4).

Table 4.2. Coefficients and significance of the test and control variables entered in the GLMM to compare grooming between the disrupters and the disruptees in PD and control sessions (N = 320).

Variable	Coefficient ± SE	Z	P	95% CIs	Significance
PD vs. MC	-2.92 ± 0.46	-6.36	0.001	-3.82 – -2.02	✓
Season	0.05 ± 0.64	0.09	0.93	1.2 – 1.31	×
Sex combination	0.11 ± 0.5	0.23	0.82	0.86 – 1.08	×
Season * Sex combination	-0.66 ± 0.75	-0.89	0.38	2.13 – 0.8	×
Dominance combination	1.27 ± 0.35	3.65	0.001	0.59 – 1.95	✓

Table 4.3. Coefficients and significance of the test and control variables entered in the GLMM to compare aggression received by the disrupters from the disruptees, between PD and control conditions (N = 160).

Variable	Coefficient ± SE	Z	P	95% CIs	Significance
PD vs. MC	-3.18 ± 1.02	-3.11	0.002	5.18 – -1.18	✓
Season	1.49 ± 1.49	1	0.32	1.43 – 4.41	×
Sex combination	0.93 ± 1.03	0.91	0.36	1.08 – 2.95	×
Season * Sex combination	-1.68 ± 1.62	-1.03	0.3	4.86 – 1.51	×

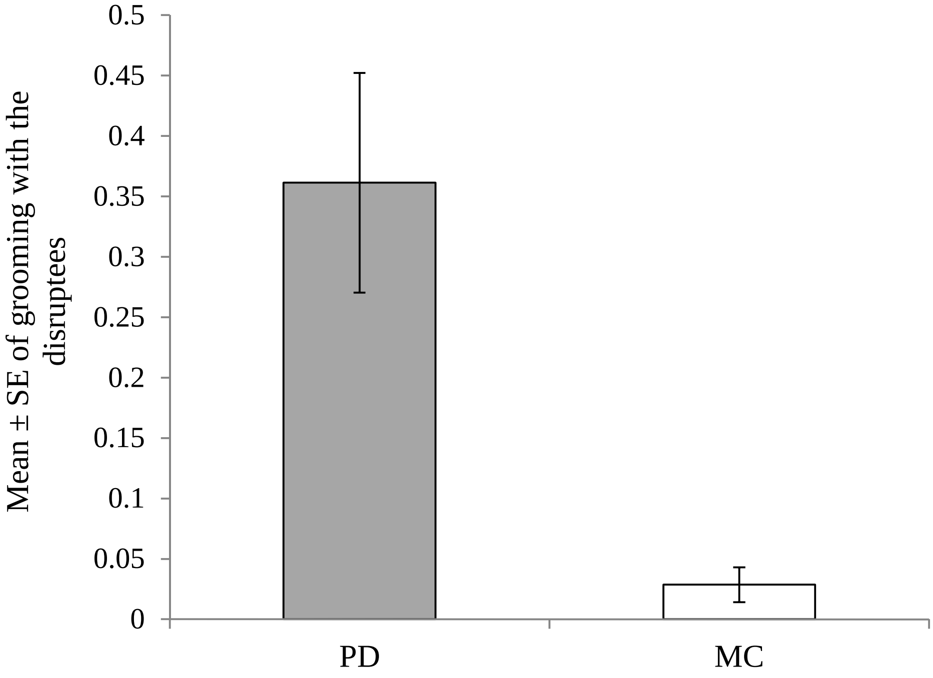


Figure 4.3. Mean ± SE of occurrence of grooming (i.e. whether it occurred at least once or not per session) between the disrupters and the disruptees, in PD and control sessions.

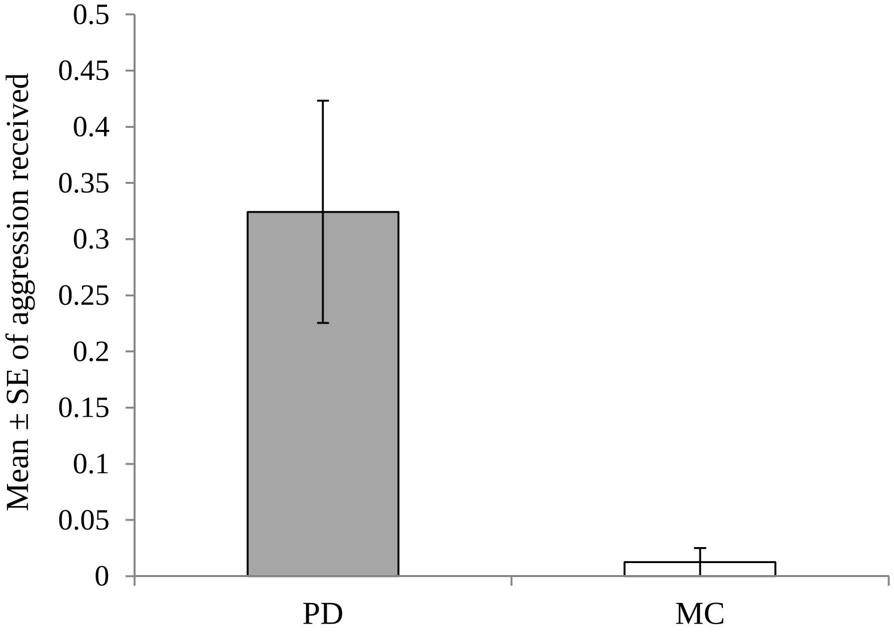


Figure 4.4. Mean ± SE of occurrence of aggression (i.e. whether it occurred at least once or not per session) received by the disrupters from the disruptees in PD and control sessions, for bridging disruptions.

The disruptions were successful at preventing the two former grooming partners from grooming each other, as the grooming partners significantly resumed grooming or switched their groomer/groomee role less often after disruption than in control condition (Table 4.4; Figure 4.5). The disruptions remained successful when the disrupters were not engaged in grooming with the disruptees following the disruptions (Table 4.5; Figure 4.5).

Table 4.4. Coefficients and significance of the test and control variables entered in the GLMM to assess the success of the disruptions among all data (N = 320).

Variable	Coefficient ± SE	Z	P	95% CIs	Significance
PD vs. MC	-1.65 ± 0.28	-5.84	0.001	-2.21 – -1.1	✓
Season	0.22 ± 0.54	0.41	0.68	-0.83 – 1.27	×
Sex combination	-0.33 ± 0.39	-0.83	0.41	-1.1 – 0.44	×
Season * Sex combination	-0.01 ± 0.62	-0.01	0.99	-1.22 – 1.2	×
Dominance combination	0.21 ± 0.26	0.82	0.42	-0.3 – 0.73	×

Table 4.5. Coefficients and significance of the test and control variables entered in the GLMM to assess the success of the disruptions when the disrupters were not involved in grooming with the disruptees (N = 198).

Variable	Coefficient ± SE	Z	P	95% CIs	Significance
PD vs. MC	-1.01 ± 0.31	-3.21	0.001	-1.62 – -0.39	✓
Season	0.13 ± 0.65	0.2	0.84	-1.14 – 1.4	×
Sex combination	-0.06 ± 0.48	-0.13	0.9	-1.004 – 0.88	×
Season * Sex combination	0.03 ± 0.76	0.04	0.97	-1.46 – 1.52	×
Dominance combination	0.17 ± 0.33	0.52	0.6	-0.47 – 0.82	×

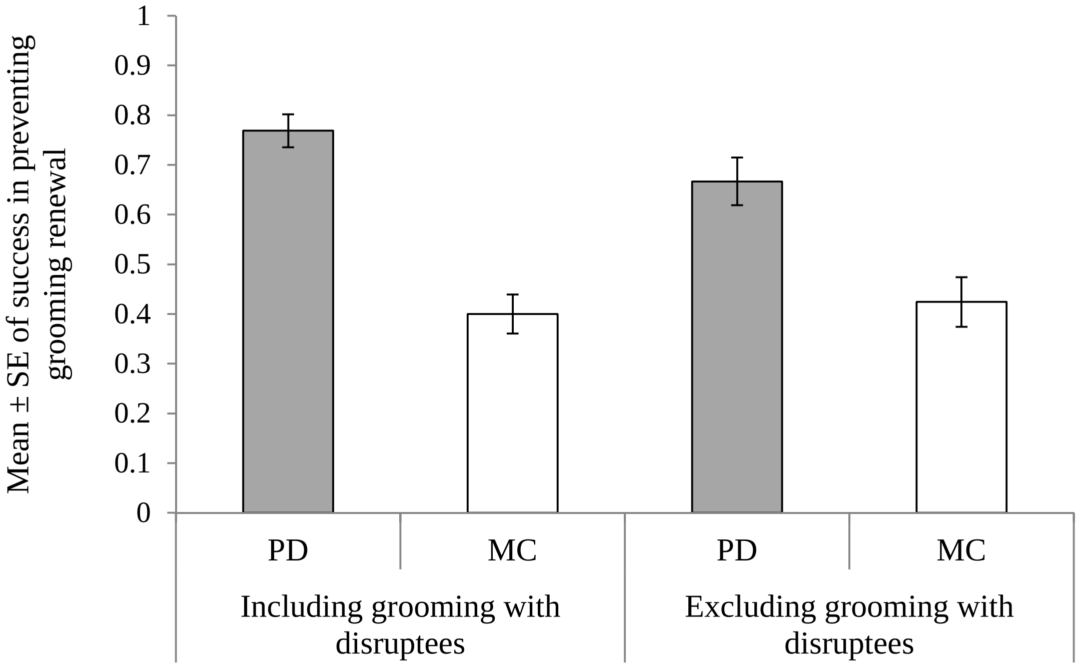


Figure 4.5. Mean ± SE of success in preventing grooming renewal in PD compare to control (i.e. whether the grooming partners did not resume grooming or switched their groomer/groomee role during the session). Including grooming with disruptees: all the PD sessions and their controls, i.e. including PDs where the disrupters were involved in grooming with the disruptees. Excluding grooming with disruptees: excluding PD sessions (and their controls) where the disrupters were involved in a grooming interaction with the disruptees.

4.3.3. Details of the PD grooming interactions between the disrupters and the disruptees

When the disrupters were involved in a grooming interaction in PD sessions with the disruptees, they significantly received more grooming from, than gave grooming to the disruptees (z = -2, p = 0.046, N = 10; Figure 4.6). Finally, for bridging disruptions where the disrupters were involved in grooming with the disruptees, there was no significant difference between grooming involving the higher- or lower-ranking disruptee (z = -0.41, p = 0.75, N = 6), and between grooming given or received (z = -0.74, p = 0.53, N = 6).

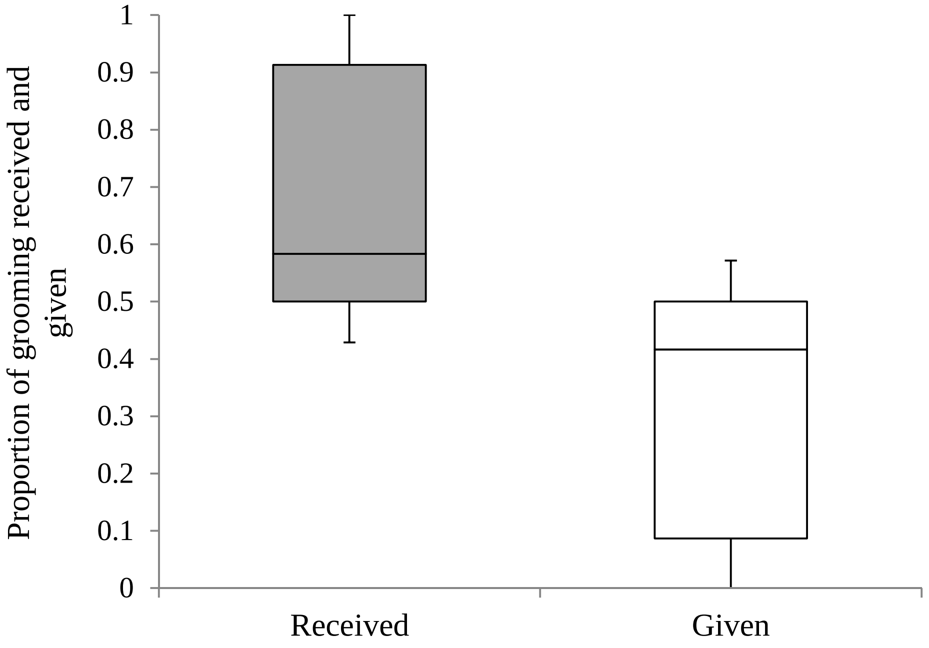


Figure 4.6. Proportion of grooming received and given between the disrupters and the disruptees in PD.

4.4. DISCUSSION

This study showed that in wild Barbary macaques, although grooming disruption may be costly as it increases the risk of receiving aggression, the disrupters gain direct grooming opportunities with the disruptees and are successful at stopping the disruptees from grooming each other. In this study, the disrupters were always higher-ranking than at least one of the disruptees. Submissive behaviours displayed by at least one disruptee toward the disrupter following its approach triggered the interruption of the grooming interactions. Because of the steep dominance hierarchy of the species (Kaburu et al, 2012), an approach by a lower-ranking monkey toward two higher-ranking grooming partners may be too risky. The low rate of male disrupting males grooming in this study may be due to the low frequency of male-male grooming interactions in Barbary macaques (Thierry et al, 2004). Bridging coalitions were costly as the disrupters received aggression from the higher-ranking disruptees. When post-disruption grooming is exchanged with the higher-ranking disruptee, it may reduce the risk of aggressive behaviour like in post-conflict conditions (McFarland & Majolo, 2011). The various benefits of grooming disruption for the disrupters may out-weight its direct cost.

First, gaining grooming opportunities may increase the health of the disrupters by decreasing their ectoparasite load (Hutchins & Barash, 1976; Hart et al, 1992; Tanaka & Takefushi, 1993; Zamma, 2002; Radford & Du Plessis, 2006; Scantlebury et al, 2007; Akinyi et al, 2013). Indeed, the disrupters received more grooming from than gave grooming to the disruptees. Disrupters may thus increase the opportunity to have their fur and skin cleaned by disrupting on-going grooming interactions between group members. While this may be achieved by disrupting grooming partners regardless of their dominance status, disrupters may target the disruption of lower-ranking monkeys to extort grooming from them (e.g. McFarland & Majolo, 2011).

Second, gaining grooming opportunities may also increase the social benefits the disrupters gain from grooming exchanges. Grooming exchanges play an important role in the establishment and maintenance of friendly relationships with group members (Dunbar, 1991), and grooming with high-value partners may be beneficial in term of increasing tolerance over food, coalition support, and the access to mating partner and infant (e.g. Barrett & Henzi, 2001, 2006; Ventura et al, 2006; Gumert, 2007b; Barelli et al, 2011; Carne et al, 2011). Disrupters may thus disrupt grooming interaction to access high value grooming partners, and so to obtain the social benefits associated with exchanging grooming with them. For example, males may disrupt grooming involving females to gain mating opportunities (e.g. Gumert, 2007b; Norscia et al, 2009; Clarke et al, 2010; Barelli et al, 2011). The number of disruptions collected opportunistically on different-sex triads was higher during the mating than non-mating season. This may reflect the higher rate of competition for grooming, mating and coalition partners in the mating season (Eaton et al, 1981; Small, 1990; Kuester & Paul, 1992, 1996; Ostner et al, 2011). Moreover, by competing to gain access to grooming with high-ranking monkeys, low-ranking monkeys may increase their opportunities to form a strong relationship with them and so to potentially have high-ranking allies when a conflict arise with other group members. This is similar to what is found in wild vervet monkeys, as females disrupt grooming interaction to then preferentially groom with the higher-ranking females, as higher-ranking females are more attractive as grooming partners because of their value as coalition partner (Cheney & Seyfarth, 1990). However like in baboons (Henzi et al, 2003), only half of the disruptions recorded involved a higher-ranking monkey in this study. Grooming disruption in Barbary macaques may thus not solely result from direct competition to gain access to high-ranking grooming partners.

In bridging disruption, disrupters may have the choice to exchange grooming either with the lower- or higher-ranking disruptee. Choosing to receive grooming from lower-ranking disruptees may be a sign of grooming coercion, whereas choosing to groom with higher-ranking disruptees may be a sign of competition for high-value grooming partners (e.g. Cheney & Seyfarth, 1990). No difference was found between the proportion of grooming involving the lower-ranking or higher-ranking disruptee, and between the proportion of grooming given or received. This may suggest that both of these mechanisms may play a role in bridging grooming disruptions, and/or that other mechanisms may be involved in the choice of grooming partners after disruption, such as the relationship quality and/or sex between the disrupter and disruptees. However, the non-significance of the results may also be due to the relative small sample size used in these analyses. Further studies analysing the choice of grooming partners following disruption according to the sex, dominance status and relationship quality of the individuals would help to further understand the mechanisms underlying post-disruption grooming.

Finally, by stopping grooming interactions the disrupters may prevent other group members from accessing the hygienic and social benefits of grooming. As such, the disrupters may maintain their social and dominant positions in the group by controlling the social relationships of other group members, notably by controlling their grooming exchanges. By stopping grooming interactions, disrupters may prevent the disruptees from accessing the various benefits associated with grooming interactions such as ectoparasites removal, tolerance over food, access to mating partner or infant, and support during agonistic interaction. For example, grooming disruption may prevent lower-ranking monkeys from grooming with higher-ranking monkeys, that is, high value grooming partners, and exchange theses grooming interactions for other social services. Grooming disruptions may prevent the establishment or maintenance of friendly relationships between the grooming partners, relationships that may favour the formation of an agonistic alliance between the grooming partners against the disrupters (Carne et al, 2001; Berghänel et al, 2011). The disrupters may thus prevent relationships that could be detrimental for their dominant position and their privileged access to resources. For instance, all-down disruptions may prevent all-up coalitions, and bridging disruptions may prevent bridging coalitions. Consequently, grooming disruption in Barbary macaques may increase the benefits associated with grooming exchanges for the disrupters, while decreasing those benefits for the disruptees. This is similar to wild meerkats (Kutsukake & Clutton-Brock, 2006) where grooming disruption preserves the sexual bond of the breeding couple, and so their privileges (e.g. privileged access to mating and food resource), while preventing other group members from bonding with them. By generating continuous uncertainty about the risk of being disrupted while grooming, the fear of grooming disruptions may increase grooming-related anxiety (see Chapter 3). Thus grooming disruption in Barbary macaques seems to play a role in establishing and/or reinforcing own social relationships while preventing others. Grooming disruption may allow individuals to influence the social relationships of other group members at their own advantage.

In conclusion, grooming disruption can be costly for the disrupter as it increases aggression risk, but it gives direct grooming benefits and may help maintening social and dominance status. Grooming disruptions seems thus to be an efficient strategy for monkeys to sustain their social and/or dominance position in a group. Such strategy may be related to the 'divide et impera' maxim (i.e. divide and rule) that has been successfully employed in political, military and economic contexts in human history. This strategy consists in breaking up existing power structures and preventing smaller power groups from linking up. Although the strategies employed by humans under this maxim may be cognitively demanding, it is unlikely than animals plan grooming disruption to gain benefits (Schino & Pellegrini, 2011). Less cognitively demanding mechanisms such as mechanisms based on emotion may play a role in grooming disruption in animals. More studies are necessary to investigate the mechanism underlying grooming disruption in animals. Particularly, further studies would need to assess which characteristics of the grooming interactions and disrupters (e.g. in term of age, sex, oestrous cycle stage, dominance status, and relationship quality between the individuals involved) affect grooming disruptions, that is, which kind of grooming interaction is more likely to be disrupted, and which animal is more likely to be a disrupter. Moreover, it could be useful to assess the long-term consequences of grooming disruptions, that is, whether grooming disruptions affect social behaviours such as coalitions, and relationship quality between individuals. Studying the patterns of grooming disruptions depending on the availability of resources such as grooming partner, food or mating partner may also help to find the evolutionary explanation of this behaviour.

4.5. REFERENCES

Akinyi, M. Y., Tung, J., Jeneby, M., Patel, N. B., Altmann, J. & Alberts, S. C. 2013. Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behaviour*, **85**, 559-568.

Aureli, F. & Yates, K. 2010. Distress prevention by grooming others in crested black macaques. *Biology Letters*, **3**, 231-233.

Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science*, **211**, 1390-1396.

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B., Ogawa, H., Schino, G., Thierry, B. & de Waal, F. B. M. 2012. Hierarchical steepness, counter-aggression, and macaque social style scale. *American Journal of Primatology*, **74**, 915-925.

Barelli, C., Reichard, U. H. & Mundry, R. 2011. Is grooming used as a commodity in wild white-handed gibbons, *Hylobates lar*? *Animal Behaviour*, **82**, 801-809.

Barrett, L. & Henzi, S. P. 2001. The utility of grooming in baboon troops. In: *Economics in nature: social dilemmas, mate choice and biological markets* (Ed. by R. Noë, J. A. R. A. M van Hooff & P. Hammerstein), pp. 119-145. Cambridge: Cambridge University Press.

Barrett, L. & Henzi, S. P. 2006. Monkeys, markets and minds: biological markets and primate sociality. In: *Cooperation in primates and humans: mechanisms and evolution* (Ed. by P. M. Kappeler & C. P. van Schaik,), pp. 209-232. New-York: Springer.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999. Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B*, **266**, 665-670.

Berghänel, A., Ostner, J., Schröder, U. & Schülke, O. 2011. Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, **81**, 1109-1116.

Brockman, D. K., Whitten, P. L., Richard, A. F. & Schneider, A. 1998. Reproduction in free-ranging male *Propithecus verreaxi*: the hormonal correlates of mating and aggression. *American Journal of Physical Anthropology*, **105**, 137-151.

Carne, C., Wiper, S. & Semple, S. 2011. Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology*, **73**, 1127-1133.

Castles, D. L., Whiten, A. & Aureli, F. 1999. Social anxiety, relationships and self-directed behaviour among wild female olive baboons. *Animal Behaviour*, **58**, 1207-1215.

Chapais, B. 1995. Alliances as a means of competition in primates: evolutionary, developmental, and cognitive aspects. *American Journal of Physical Anthropology*, **38**, 115-136.

Cheney, D. L. & Seyfarth, R. M. 1990. *How monkeys see the world: inside the mind of another species*. Chicago: University of Chicago Press.

Clarke, P. M. R., Halliday, J. E. B., Barrett, L. & Henzi, S. P. 2010. Chacma baboon mating markets: competitor suppression mediates the potential for intersexual exchange. *Behavioral Ecology*, **21**, 1211-1220.

Clutton-Brock, T. H. & Parker, G. A. 1995a. Sexual coercion in animal societies. *Animal Behaviour*, **49**, 1345-1365.

Clutton-Brock, T. H. & Parker, G. A. 1995b. Punishment in animal societies. *Natur*e, **373**, 209-216.

Colmenares, F., Zaragoza, F. & Hernández-Lloreda, M. V. 2002. Grooming and coercion in one-male units of hamadryas baboons: market forces or relationship constraints? *Behaviour*, **139**, 1525-1553.

Cords, M. 1995. Predator vigilance costs of allogrooming in wild blue monkeys. *Behaviour*, **132**, 559-569.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, **125**, 157-175.

de Waal, F. B. M. & Yoshihara, D. 1983. Reconciliation and redirected affection in rhesus monkeys. *Behaviour*, **85**, 224-241.

de Waal, F. B. M. 1997. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, **18**, 375-386.

Dunbar, R. I. M. & Sharman, M. 1984. Is social grooming altruistic? *Journal of comparative ethology*, **64**, 163-173.

Dunbar, R. I. M. 1991. Functional significance of social grooming in primates. *Folia Primatologica*, **57**, 121-131.

Dunbar, R. I. M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, **31**, 35-49.

Eaton, G. G., Modahl, K. B. & Johnson, D. F. 1981. Aggressive behavior in a confined troop of Japanese macaques: effects of density, season, and gender. *Aggressive Behavior*, **7**, 145-164.

Enomoto, T. 1981. Male aggression and the sexual behavior of Japanese monkeys. *Primates*, **22**, 15-23.

Fruteau, C., van de Waal, E., van Damme, E. & Noë, R. 2011. Infant access and handling in sooty mangabeys and vervet monkeys. *Animal Behaviour*, **81**, 153-161.

Fruteau, C., Voelkl, B., van Damme, E. & Noë, R. 2009. Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences*, **106**, 12007-12012.

Griffin, A. S., Pemberton, J. M., Brotherton, P. N. M., McIlrath, G. M., Gaynor, D., Kansky, R. & Clutton-Brock, T. H. 2004. A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behavioral Ecology*, **14**, 472-480.

Gumert, M. 2007a. Grooming and infant handling interchange in *Macaca fascicularis*: the relationship between infant supply and grooming payment. *International Journal of Primatology*, **28**, 1059-1074.

Gumert, M. D. 2007b. Payment for sex in a macaque mating market. *Animal Behaviour*, **74**, 1655-1667.

Hart, B. L. & Hart, L. A. 1992. Reciprocal allogrooming in impala, *Aepyceros melampus*. *Animal Behaviour*, **44**, 1073-1083.

Hemelrijk, C. K. & Ek, A. 1991. Reciprocity and interchange of grooming and support in captive chimpanzees. *Animal Behaviour*, **41**, 923-935.

Hemelrijk, C. K. 1994. Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, **48**, 479-481.

Henzi, S. P. & Barrett, L. 2002. Infants as a commodity in a baboon market. *Animal Behaviour*, **63**, 915-921.

Henzi, S. P., Barrett, L., Gaynor, D., Greefe, J., Weingrill, T. & Hill, R. A. 2003. Effect of resource competition on the long-term allocation of grooming by female baboons: evaluating Seyfarth's model. *Animal Behaviour*, **66**, 931-938.

Hutchins, M. & Barash, D. P. 1976. Grooming in primates: implications for its utilitarian function. *Primates*, **17**, 145-150.

Johnson, D. D. P., Stopka, P. & Macdonald, D. W. 2004. Ideal flea constraints on group living: unwanted public goods and the emergence of cooperation. *Behavioral Ecology*, **15**, 181-186.

Kaburu, S. S. K., MacLarnon, A., Majolo, B., Qarro, M. & Semple, S. 2012. Dominance rank and self-scratching among wild female Barbary macaques (*Macaca sylvanus*). *African Zoology*, **47,** 74-79.

Koyama, N. F, Caws, C. & Aureli, F. 2006. Interchange of grooming and agonistic support in chimpanzees. *International Journal of Primatology*, **27**, 1293-1309.

Koyama, N. F., Caws, C. & Aureli, F. 2012. Supply and demand predict male grooming of swollen females in captive chimpanzees, *Pan troglodytes*. *Animal Behaviour*, **84**, 1419-1425.

Kuester, J. & Paul, A. 1992. Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca sylvanus*). *Behaviour,* **120**, 192-217.

Kuester, J. & Paul, A. 1996. Female-female competition and male mate choice in Barbary macaques (*Macaca sylvanus*). *Behaviour,* **133**, 763-790.

Kutsukake, N. & Clutton-Brock, T. H. 2006. Social function of allogrooming in cooperatively breeding meerkats. *Animal Behaviour*, **72**, 1059-1068.

Lehmann, J. & Boesch, C. 2008. Sex differences in sociality. *International Journal of Primatology*, **29**, 65-81.

Maestripieri, D. 1993. Vigilance costs of allogrooming in macaque mothers. *The American Naturalist*, **141**, 744-753.

Majolo, B., Lehmann, J., de Baroli Vizioli, A. & Schino, G. 2012. Fitness-related benefits of dominance in primates. *American Journal of Physical Anthropology*, **147,** 652-660.

Manson, J. H. 1994. Male aggression: a cost of female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour*, **48**, 473-475.

Matsubara, M. & Sprague, D. 2004. Mating tactics in response to costs incurred by mating with multiple males in wild female Japanese macaques. *International Journal of Primatology*, **25**, 901-917.

McFarland, R. & Majolo, B. 2011. Grooming coercion and the post-conflict trading of social services in wild Barbary macaques. *PLoS ONE*, **6**, e26893.

Mitani, J. C. 2006. Reciprocal exchange in chimpanzees and other primates. In: *Cooperation in primates and humans: mechanisms and evolution* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 107-119. New-York: Springer.

Mitchell, G. & Tokunaga, D. H. 1976. Sex differences in nonhuman primate grooming. *Behavioural Processes*, **4**, 335-345.

Mondragón-Ceballos, R. 2001. Interfering in affiliations: sabotaging by stumptailed macaques, *Macaca arctoides*. *Animal Behaviour*, **62**, 1179-1187.

Muller, M. N. & Wrangham, R. W. 2009. *Sexual coercion in primates: an evolutionary perspective on male aggression against females*. Cambridge: Harvard University Press.

Muller, M. N., Kahlenberg, S. K., Emery Thompson, M. & Wrangham, R. W. 2007. Male coercion and the costs of promiscuous mating in chimpanzees. *Proceedings of the Royal Society B*, **274**, 1009-1014.

Muroyama, Y. 1994. Exchange of grooming for allomothering in female patas monkeys. *Behaviour*, **128**, 103-119.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, **35**, 1-11.

Noë, R., van Hooff, J. A. R. A. M. & Hammerstein, P. 2001. *Economics in nature: social dilemmas, mate choice and biological markets.* Cambridge: Cambridge University Press.

Noldus Information Technology. 2003. *Matman, software for matrix manipulation and analysis, version 1.1.* Wageningen, The Netherlands.

Norscia, I., Antonacci, D. & Palagi, E. 2009. Mating first, mating more: biological market fluctuation in a wild prosimian. *PLoS ONE*, **4**, e4679.

Nunn, C. L. & Altizer, S. M. 2006. *Infectious diseases in primates: behavior, ecology and evolution*. Oxford: Oxford University Press.

Oki, J. & Maeda, Y. 1973. Grooming as a regulator of behaviour in Japanese macaques. In: *Behavioral regulators of behaviour in primates* (Ed. by C. R. Carpenter), pp. 149-163. Lewisburg: Bucknell University Press.

Ostner, J., Heistermann, M. & Schülke, O. 2011. Male competition and its hormonal correlates in wild Assamese macaques (*Macaca assamensis*). *Hormones & Behavior*, **59**, 105-113.

Pavani, S., Maestripieri, D., Schino, G. & Turillazzi, P. G. 1991. Factors influencing scratching behaviour in long-tailed macaques (*Macaca fascicularis*). *Folia Primatologica*, **57**, 34-38.

Pinheiro, J. C. & Bates, D. M. 2000. *Mixed effects models in S and S-PLUS*. 1st edn. New York: Springer-Verlag.

Radford, A. N. & Du Plessis, M. A. 2006. Dual function of allopreening in the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*. *Behavioral Ecology and Sociobiology*, **61**, 221-230.

Richter, C., Mevis, L., Malaivijitnond, S., Schülke, O. & Ostner, J. 2009. Social relationships in free-ranging male *Macaca arctoides*. *International Journal of Primatology*, **30**, 625-642.

Scantlebury, M., Waterman, J. M., Hillegass, M., Speakman, J. R. & Bennett, N. C. 2007. Energetic costs of parasitism in the Cape ground squirrel *Xerus inauris*. *Proceedings of the Royal Society B*, **274**, 2169-2177.

Schaffner, C. & Aureli, F. 2005. Embraces and grooming in captive spider monkeys. *International Journal of Primatology*, **26**, 1093-1106.

Schino, G. & Aureli, F. 2008. Trade-offs in primate grooming reciprocation: testing behavioural flexibility and correlated evolution. *Biological Journal of the Linnean Society*, **95**, 439-446.

Schino, G. & Aureli, F. 2010. The relative roles of kinship and reciprocity in explaining primate altruism. *Ecology Letters*, **13**, 45-50.

Schino, G. & Pellegrini, B. 2011. Grooming and the expectation of reciprocation in mandrills (*Mandrillus sphinx*). *International Journal of Primatology*, **32**, 406-414.

Schino, G. 2001. Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, **62**, 265-271.

Schino, G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, **18,** 115-120.

Schino, G., di Sorrentino, E. P. & Tiddi, B. 2007. Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame of reciprocation. *Journal of Comparative Psychology*, **121**, 181-188.

Schino, G., Ventura, R. & Troisi, A. 2005. Grooming and aggression in captive Japanese macaques. *Primates*, **46**, 207-209.

Scott, E. M., Mann, J., Watson-Capps, J. J., Sargeant, B. L. & Connor, R. C. 2005. Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour*, **142**, 21-44.

Seyfarth, R. M. & Cheney, D. L. 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, **308**, 541-543.

Seyfarth, R. M. 1977. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, **65**, 671-698.

Silk, J. B. 1982. Altruism among female *Macaca radiate:* explanations and analysis of patterns of grooming and coalition-formation. *Behaviour*, **79,** 162-188.

Silk, J. B. 1992. The patterning of intervention among male bonnet macaques: reciprocity, revenge, and loyalty. *Current Anthropology*, **33**, 318-325.

Silk, J. B. 1999. Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour,* **57**, 1021-1032.

Silk, J. B. 2002. Practice random acts of aggression and senseless acts of intimidation: the logic of status contests in social groups. *Evolutionary Anthropology*, **11**, 221-225.

Slater, K. Y., Schaffner, C. M. & Aureli, F. 2007. Embraces for infant handling in spider monkeys: evidence for a biological market? *Animal Behaviour,* **74**, 455-461.

Small, M. F. 1990. Promiscuity in Barbary macaques (*Macaca sylvanus*). *American Journal of Primatology,* **20**, 267-282.

Smuts, B. B. & Smuts, R. W. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior,* **22**, 1-63.

Soltis, J. 1999. Measuring male-female relationships during the mating season in wild Japanese macaques. *Primates,* **40,** 453-467.

Spruijt, B. M., van Hooff, J. & Gispen, W. H. 1992. Ethology and neurobiology of grooming behavior. *Physiological Reviews*, **72**, 825-852.

Stumpf, R. M. & Boesch, C. 2010. Male aggression and sexual coercion in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour,* **79**, 333-342.

Tanaka, I. & Takefushi, H. 1993. Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropological Science,* **101**, 187-193.

Thierry, B., Singh M. & Kaumanns, W. 2004. *Macaque societies: a model for the study of social organization*. Cambridge: Cambridge University Press

Tiddi, B., Aureli, F. & Schino, G. 2010. Grooming for infant handling in tufted capuchin monkeys: a reappraisal of the primate infant market. *Animal Behaviour*, **79**, 1115-1123.

Tiddi, B., Aureli, F., Polizzi di Sorrentino, E., Janson, C. H. & Schino, G. 2011. Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. *Behavioral Ecology*, **22**, 663-669.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *The Quarterly Review of Biology*, **46**, 35-57.

Troisi, A. & Schino, G. 1987. Environmental and social influences on autogrooming behaviour in a captive group of Java monkeys. *Behaviour,* **100**, 292-302.

van Schaik, C. P., Pandit, S. A. & Vogel, E. R. 2004. A model for within-group coalitionary aggression among males. *Behavioral Ecology and Sociobiology,* **57**, 101-109.

Ventura, R., Majolo, B., Koyama, N. F., Hardie, S. & Schino, G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology*, **68**, 1138-1149.

Vervaecke, H., De Vries, H. & van Elsacker, L. 2000. The pivotal role of rank in grooming and support behavior in a captive group of bonobos (*Pan paniscus*). *Behaviour,* **137**, 1463-1485.

Watts, D. P. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour,* **139**, 343-370.

Wei, W., Qi, X.-G., Guo, S.-T., Zhao, D.-P., Zhang, P., Huang, K. & Li, B.-G. 2012. Market powers predict reciprocal grooming in golden snub-nosed monkeys (*Rhinopithecus oxellana*). *PLoS ONE,* **7,** e36802.

Wheatley, B. P. 1999. *The sacred monkeys of Bali.* Waveland Press.

Zamma, K. 2002. Grooming site preferences determined by lice infection among Japanese macaques in Arashiyama. *Primates,* **43**, 41-49.

Chapter 5

The role of direct, indirect and generalised reciprocity in explaining grooming exchanges

Barbary macaques sometime disrupt grooming interactions of other group members. Chapter 4 investigated the potential costs and benefits of the disruption for the disrupters. The results showed that grooming disruption can be costly for the disrupters as it increases aggression risk, but it also gives direct grooming benefits and it is successful at stopping the disruptees from grooming each other. Grooming disruptions seems thus to be an efficient strategy for monkeys to maintain their social and dominance positions in a group. The current Chapter investigates the role of direct, indirect and generalised reciprocity in explaining grooming exchanges of wild Barbary macaques, by analysing the temporal contingency between giving and receiving grooming.

5.1. INTRODUCTION

Behaviours reducing the immediate payoff of the actor while benefitting the recipient are usually referred to as altruistic (e.g. Schino & Aureli, 2009; Brosnan & Bshary, 2010; Schino & Aureli, 2010; see West et al, 2007a, 2007b for alternative definitions). Kin selection and reciprocity are among the many theories that have been proposed to explain the occurrence of altruistic behaviours (e.g. West et al, 2007a, 2011). For kin selection, inclusive fitness benefits (particularly indirect fitness effects) explain altruism between genetic relatives (Hamilton, 1964). For reciprocity (Alexander, 1974), individuals (independently of their genetic relatedness) act as the donor or the recipient of short-term (i.e. not lifetime) costly altruistic acts and can switch roles over time to balance the short-term benefits and costs of altruism (Trivers, 1971). Because short-term costs and benefits are balanced, reciprocity leads to long-term (i.e. lifetime) direct fitness benefits for the partners, and reciprocity becomes an evolutionarily stable strategy (Trivers, 1971; Axelrod & Hamilton, 1981). Three main patterns of reciprocity have been proposed: direct, indirect and generalised reciprocity.

First, direct reciprocity is based on a tit-for-tat exchange where the recipient of an altruistic act is more likely to return the benefit to the former donor (Axelrod, 1984). There is a wide range of evidences that direct reciprocity plays an important role in humans. Indeed, humans directly reciprocate their partner’s altruistic act and establish successful cooperative relationships (Dawes, 1980; Rand et al, 2009; Melis & Semmann, 2010). One model to study direct reciprocity in humans is the repeated Prisoner’s Dilemma game (Luce & Raiffa, 1957). In each round of the simplest version of this game, individuals have the choice to either cooperate or not cooperate. For each single round, although both players gain a high pay-off when both cooperate, a higher individual pay-off is gained by the player who does not cooperate when the partner cooperates. The player who cooperates while the other does not, experiences the lowest pay-off of the game. One strategy to maintain cooperation when the game is played for several rounds is tit-for-tat, where the players first start to cooperate and then copy the partner's previous decision, that is, cooperate if the partner cooperates, and do not cooperate if the partner does not cooperate (Axelrod & Hamilton, 1981). The iterated Prisoners's Dilemma has been well studied and various mechanisms have been proposed to test the maintenance of cooperative behaviour through this game in humans (e.g. Dawes, 1980; Nowak, 2006; Rand et al, 2009).

In animals, evidence of direct reciprocation of benefits received comes from various species (Schino, 2007; Clutton-Brock, 2009; Schino & Aureli, 2009, 2010; Jaeggi & van Schaik, 2011). For example, the exchange of coalition support in baboons (*Papio anubis*; Packer, 1977), food sharing in vampire bats (*Desmodus rotundus;* Wilkinson, 1984; Carter & Wilkinson, 2013) and cooperative nest defence in red-winged blackbirds (*Agelaius phoeniceus*; Olendorf et al, 2004) are forms of direct reciprocity. More specifically in non-human primates, the giving of grooming is reciprocated (e.g. see Schino & Aureli, 2008a for a meta-analysis based on 22 species) or exchanged for other services such as support during agonistic interactions, tolerance, access to infant and preferential access to resources such as food and mating partners (e.g. de Waal & Berger, 2000; Barrett & Henzi, 2001; Watts, 2002; Ventura et al, 2006; Barrett et al, 2009; Carne et al, 2011).

Two decision-making processes have been proposed as mechanisms of direct reciprocity in animals (Bull & Rice, 1991; Noë, 2001). First, an animal can give benefits to a partner in relation to how the partner behaved toward it in the recent past (i.e. altruistically or not), regardless of the behaviour of other potential partners (e.g. Tiddi et al, 2011). Thus, an animal A can give a benefit to an animal B in relation to what B had previously given to A, each dyad being isolated from each other. This mechanism is usually tested by examining the within-dyad temporal relation between events over short time period (i.e. minutes or hours; Schino et al, 2009; Cheney et al, 2010). For example in chimpanzees (*Pan troglodytes*), a temporal contingency was found between grooming received and food sharing (de Waal, 1997), and between grooming received and agonistic support (Koyama et al, 2006). Pied flycatchers (*Ficedula hypoleuca*) helped mobbing a predator those neighbours who helped them before, but not the ones who did not help before (Krams et al, 2008). Moreover, some studies showed that animals time-matched the amount of grooming they have just received, supporting the view of a temporal contingency between the amount of grooming given and received (Hart & Hart, 1992; Barrett et al, 1999; Manson et al, 2004; Chancellor & Isbell, 2009).

The second mechanism is based on partner choice and assumes that animals behave altruistically toward specific partners but not others, by comparing how each partner behaved toward them over longer time frames (Noë, 2001; Schino & Aureli, 2009, 2010). Individuals would make their decision about which partner to cooperate with based on the emotional states associated with each potential partner (Silk, 2002, 2003; Schino & Aureli, 2009, 2010). Consequently, individuals overall give more benefits toward individuals from who they received more benefits, even if no temporal contingency is found between benefits received and given over short time frames. For example, even when cases of immediate reciprocation were removed, monkeys still groomed more the partners that groomed them more (Schino et al, 2009; Schino & Pellegrini, 2009). There was a strong positive correlation between grooming given and grooming or agonistic support received in Japanese macaques (*Macaca fuscata*), even without short-term contingency between events (Schino et al, 2003, 2007). A positive correlation was also found between the overall grooming given and received in hamadryas baboons (*Papio hamadryas hamadryas*; Leinfelder et al, 2001), Tibetan macaques (*Macaca thibetana*; Xia et al, 2012), blue monkeys (*Cercopithecus mitis stuhlmanni*; Rowel et al, 1991), and captive Barbary macaques (Carne et al, 2011). These two mechanisms are both plausible and are not mutually exclusive. However, exchanges of services over long time frames might be more balanced than exchanges over short time frames in animals (Schino et al, 2007, 2009; Melis et al, 2008; Frank & Silk, 2009; Gomes et al, 2009; Cheney, 2011; Tiddi et al, 2011; Sabbatini et al, 2012; Jaeggi et al, 2013).

Direct reciprocity assumes repeated encounter opportunities between partners and individual recognition. While direct reciprocity might require elaborated cognitive skills such as memory, time estimation and numerical discrimination (e.g. keeping track of the amount of benefits exchanged) (Stevens & Hauser, 2004; Stevens et al, 2005; Brosnan et al, 2010), other mechanisms involving emotional bookkeeping, that is, the formation of emotional bond between partners, might be less cognitively demanding (Aureli & Schaffner, 2002a, 2002b; Silk, 2003; Schino & Aureli, 2009, 2010; Raihani & Bshary, 2011).

Second, indirect reciprocity is based on reputation effects (Alexander, 1987; Nowak & Sigmund, 1998; Leimar & Hammerstein, 2001; Fehr & Fischbacher, 2003; Nowak & Sigmund, 2005; Sigmund, 2012) and assumes that the former donor of an altruistic act is more likely to receive benefit from another individual who was not involved in the former altruistic exchange. Indirect reciprocity is based on the assumption that giving an altruistic act increases the donor's reputation, and so its chances to receive an altruistic act from bystanders are greater (McGregor, 2005; Bshary

& Grutter, 2006). Image-scoring involves collecting information on interactions between third parties, for example by observing others' social interactions or learning from gossip in humans (McGregor, 2005). Indirect reciprocity assumes, first, that bystanders gain information via eavesdropping on potential cooperative partners and, second, that the donor of an altruistic act benefit from reputation by accessing bystanders as cooperative partners (Nowak & Sigmund, 1998, 2005). Consequently, individuals may be more cooperative in the presence of image-scoring potential partners as this would increase their probability to receive cooperation from them. This phenomenon is part of the audience effect where individuals modify their behaviour according to the presence of an audience (e.g. McGregor, 2005; Slocombe & Zuberbuhler, 2007). Two mechanisms have been proposed to explain the formation of reputation. First, reputation may be built through 'image-scoring' (Nowak & Sigmund, 1998), that is, the reputation increases and decreases respectively with every altruistic acts and defections given. Second, reputation may be built through 'standing' (Leimar & Hammerstein, 2001; Milinski et al, 2001) where defections given to defectors increase the reputation of the individuals instead of decreasing it. However, this last mechanism is still debated (Leimar & Hammerstein, 2001; Milinski et al, 2001; Panchanathan & Boyd, 2004).

Various studies confirm the important role of indirect reciprocity in humans. People use information gathered through observation of others' interactions or through gossips to choose with whom to cooperate, and they invest in their own reputation to be preferably chosen as cooperative partners (e.g. Semmann et al, 2005; Nowak, 2006; Sommerfeld et al, 2007; Sylwester & Roberts, 2010). For example, cues of being watched (e.g. image of a pair of eyes) increased the level of cooperation (Haley & Fessler, 2005; Bateson et al, 2006). When the history of previous interactions and donations were available, people donated more to individuals who previously donated to others (Wedekind & Milinski, 2000; Milinski et al, 2001; Seinena & Schram, 2006; Sylwester & Roberts, 2010). Reputation thus promotes cooperation in humans (Nowak & Sigmund, 1998; Wedekind & Milinski, 2000; Milinski et al 2002; Nowak & Sigmund, 2005; Semmann, 2012; Rand & Nowak, 2013).

Evidence of indirect reciprocity in animals is restricted to studies on cleaning mutualism involving cleaner wrasse (*Labroides dimidiatus*) and on song sparrows (*Melospiza melodia*). During cleaning behaviour, cleaner fishes remove and eat ectoparasites and dead tissues from other reef fish species called clients (Côté, 2000). Cleaner fishes have usually small territories, called cleaning stations, and clients visit those places when they need dead tissues or ectoparasites removal. During cleaning of a client, cleaners either cooperate, that is, remove ectoparasites from clients, or cheat, that is, feed on client's protective mucus which they prefer (Grutter, 1997; Grutter & Bshary, 2003). However, if their mucus (energetically costly to produce) is eaten, clients either swim away to another cleaning station/cleaner fish (Bshary & Schäffer, 2002), or chase the biting cleaner fish away (Bshary & Grutter, 2002). It has been experimentally shown that such client behaviours result in cleaner fishes being more cooperative (Bshary & Grutter, 2005). There is both observational and experimental evidence that indirect reciprocity plays a role in this cleaning mutualism. Field observations showed that cleaners were more cooperative in the presence of bystanders than alone (Bshary & D'Souza, 2005), and clients invited more for inspection cleaners they have witnessed as cooperative (i.e. the last cleaner's inspection ended without conflict) than non-cooperative (i.e. the last cleaner's inspection ended with a conflict; Bshary, 2002). In experimental studies, clients spent more time close to cleaners they witnessed as cooperative compared to cleaners of unknown cooperative propensity (Bshary & Grutter, 2006) or cheaters (Pinto et al, 2001). In a foraging task, cleaners learned to feed more cooperatively when their non-cooperative behaviour resulted in negative effects on their feeding (Bshary & Grutter, 2006). Cleaners also immediately increased their level of cooperation in presence of bystanders (Pinto et al, 2001). It should be noted that indirect reciprocity based on image-scoring clients requires probably only simple cognitive processes as clients react immediately to what they have just observed, and thus do not need to remember several third parties interactions (Bshary & Grutter, 2006).

Indirect reciprocity may also play a role in territory defence in birds. The ‘dear enemy effect’ states that animals restrain their aggression toward neighbours of their territory once the territory boundaries have been established (Fisher, 1954; Temeles, 1994). In this situation, animals either cooperate by mutually restraining their aggression, or defect by intruding into their neighbour’s territory. Akcay and colleagues (2010) found that after song sparrows witnessed simulated intrusion of their neighbour into a third bird territory (i.e. defection), they displayed more aggression toward the playback song of their neighbour, indicating the end of the mutual restrain of aggression. Moreover, a previous study showed that following a simulated intrusion by a neighbour, song sparrows responded more strongly to playback of this neighbour than to playback of a neutral neighbour (Akcay et al, 2009). The authors suggest that both direct and indirect reciprocity help to maintain the mutual restrain of aggression between neighbours.

Finally, generalised reciprocity (also called upstream indirect reciprocity; Nowak & Roch, 2007) assumes that individuals who have received the benefits of an altruistic act are more likely to act altruistically toward other individuals (Hamilton & Taborsky, 2005). As such, generalised reciprocity includes case of direct reciprocity in its original definition (Hamilon & Taborsky, 2005). Contrary to direct and indirect reciprocity, generalised reciprocity does not require individual recognition and specific social memory, as individuals can base their decision solely on the outcome of the last interaction they experienced with anonymous partners (Boyd & Richerson, 1989; Pfeiffer et al, 2005; Rankin & Taborsky, 2009; Barta et al, 2011). Generalised reciprocity is thus less cognitively demanding than direct or indirect reciprocity (Stevens & Hauser, 2004), and can occur in contexts where multiple encounters with the same partners are rare.

There is evidence in humans that people who received an altruistic act are more willing to be helpful toward others (e.g. Berkowitz & Daniels, 1964; Bartlett & De Steno, 2006). The ‘good mood hypothesis’ states that receiving an altruistic act affects the social attitude of the individuals toward all possible partners, that is, the recipients experience a general benevolent mood which makes them more willing to help (Emmons & McCullough, 2004). Gratitude (i.e. the positive emotion individuals feel after they have received something valuable) and other positive emotions such as the willingness to help others, foster altruistic behaviours and may favour generalised reciprocity in humans (Emmons & McCullough, 2004; Nowak & Roch, 2007).

Evidence of generalised reciprocity in animals is very scarce, and its occurrence has been observed experimentally only in rats (*Rattus norvegicus;* Rutte & Taborsky, 2007). Rats were trained to produce food for a partner by pulling a stick fixed to a baited tray. The authors showed that rats were more helpful toward a new partner, irrespective of the partner’s identity, after they previously experienced receiving help (i.e. by receiving food thanks to a partner) than after they did not previously received help (Rutte & Taborsky, 2007). No evidence of generalised reciprocity has been found in the exchanges of services such as grooming and food tolerance in long-tailed macaques (*Macaca fascicularis*; Majolo et al, 2012) and chimpanzees (de Waal, 1997; de Waal & Brosnan, 2006).

Direct, indirect and generalised reciprocity are not mutually exclusive and can potentially all occur in real biological systems. Evaluating the occurrence of the three types of reciprocity in social groups such as non-human primates is thus key to understand further the mechanisms and evolution of altruistic behaviours. Schino and Aureli (2009) stated that while in terms of ultimate function altruistic behaviors are selected because of their future benefits, in terms of proximate causation what motivates animals to act altruistically are the past benefits they received. The authors added that 'this proximate mechanism is favoured by natural selection because past behaviour is generally predictive of future behaviour' (Schino & Aureli, 2009, p 54). Understanding how altruistic acts are exchanged (i.e. proximate mechanism) is thus necessary to understand how these behaviours have evolved in social groups.

Studies that assessed more than one type of reciprocity at the same time in non-human primates are not common. For example, receiving grooming increased food sharing with the donor of grooming but not with any other group members in chimpanzees (de Waal, 1997; de Waal & Brosnan, 2006), suggesting a role of direct but not generalised reciprocity in the exchange of grooming for food sharing. Similarly, rats directly reciprocated help toward partners that helped them before compared to partners that did not help them before (Rutte & Taborsky, 2008). Moreover, after receiving help, rats were more helpful toward known partners that helped them before compared to unknown partners (Rutte & Taborsky, 2008). The authors concluded that in rats, direct reciprocity generate a higher cooperative propensity than generalised reciprocity. Recently, Majolo and colleagues (2012) assessed for the first time the relative role of direct, indirect and generalised reciprocity in explaining the grooming exchanges of captive long-tailed macaques (*Macaca fascicularis*). They found a strong evidence for direct reciprocity, limited support for indirect reciprocity, and no evidence for generalised reciprocity. They suggested that direct reciprocity is an important factor driving the evolution of altruism while the role of indirect and generalised reciprocity requires further research in animals. Assessing the relative role of each type of reciprocity in explaining exchanges of services in animals may thus bring important insight into which factors play a role in the evolution of altruism.

Following the study of Majolo and colleagues (2012), the aim of this chapter was to assess the role of direct, indirect and generalised reciprocity in the grooming exchanges of wild Barbary macaques (*Macaca sylvanus*). The giving of grooming is assumed to be a costly activity, as it reduces vigilance against predators and competitors (Maestripieri, 1993; Cords, 1995; Mooring & Hart, 1995), and the time available for other activities (e.g. feeding; Dunbar & Sharman, 1984; Maestripieri, 1993; Tanaka & Takefushi, 1993; Scantlebury et al, 2007). Conversely, receiving grooming has a positive effect on physical conditions as it reduces ectoparasites infection (Hutchins & Barash, 1976; Hart et al, 1992; Tanaka & Takefushi, 1993; Zamma, 2002; Radford & Du Plessis, 2006; Scantlebury et al, 2007; Akinyi et al, 2013). Grooming is thus a behaviour being costly for the donor and benefitting the recipient, and can be easily quantified. As such, grooming can be referred as altruistic behaviour in non-human primates (Hutchins & Barash, 1976). Barbary macaques live in multi-male-multi-female groups where social interactions, such as grooming, are frequent between group members, and they individually recognise group members (e.g. Thierry et al, 2004; Schell et al, 2011). Consequently, all the conditions are met to allow the three types of reciprocity to potentially play a role in grooming exchanges of Barbary macaques.

In order to assess the proximate mechanism of the three types of reciprocity, the aim of this Chapter was to test the temporal contingency of giving and receiving grooming in a naturalistic context, that is, where monkeys can freely choose their social partner. The predictions tested in this Chapter were as follow:

(1) If direct reciprocity plays a role in grooming exchanges, the occurrence and duration of the grooming A gave to B would be a predictor of the occurrence, latency and duration of the grooming B gave to A.

(2) If indirect reciprocity plays a role in grooming exchanges, the occurrence and duration of the grooming A gave to B would be a predictor of the occurrence, latency and duration of the grooming A received from a third individual C.

(3) If generalised reciprocity plays a role in grooming exchanges, the occurrence and duration of the grooming A gave to B would be a predictor of the occurrence, latency and duration of the grooming B gave to C. Two different cases of generalised reciprocity were considered. First, C can be a different individual than A (hereafter called cases of generalised reciprocation), and second, C can include A, that is, include cases of direct reciprocation (hereafter called cases of ‘broad generalised reciprocation’).

More specifically, for each type of reciprocity: (1) reciprocated grooming would occur more often after grooming than in control condition (i.e. following two monkeys being in proximity but not grooming); (2) it would occur earlier after grooming than in control condition; (3) it would occur earlier after grooming of longer duration; (4) the duration of reciprocated grooming would be longer after grooming of longer duration.

5.2. METHODS

5.2.1. Study subjects

Subjects of this study were the 16 adults and sub-adults Barbary macaques of the ‘Green group’ (consisting of 8 adult males, 7 adult females, 1 sub-adult male), living in the Middle Atlas Mountains of Morocco (33° 24’N - 005° 12’W). The group lived in the deciduous cedar and oak forest of the Ifrane National Park, between 1600 and 2000m a.s.l. Individuals were recognizable from natural markings and were followed on foot from dawn to dusk on each day of observation. See Chapter 2 for more details on the study animals and field site.

5.2.2. Data collection

Data were collected from May 2011 to January 2012. Grooming was defined as a monkey going through the fur of another monkey with its fingers and mouth, removing particles such as dirt and parasites (see Chapter 2). While ‘reciprocity’ refers to the evolutionary strategies explaining altruistic behaviours, the term ‘reciprocation’ is used in this Chapter to refer to events of reciprocated altruistic acts, that is, reciprocated grooming (see Figure 5.1). As soon as a grooming interaction between two monkeys (e.g. A grooms B) was observed from its start, data were collected on the ID of the grooming partners, their roles (i.e. groomer or groomee), and on the duration of the grooming interaction. Grooming interactions that lasted less than 30 seconds were not considered in this study. As soon as the grooming interaction was terminated, two simultaneous 60-minutes post-grooming (hereafter PG) focal sessions were run by two observers on the former groomer and groomee. Inter-observer reliability was checked weekly and was always above 95% throughout the course of the study. The grooming interaction was considered terminated when no grooming was exchanged for ≥ 30 seconds or when the grooming partners reversed their role (i.e. the groomer became the groomee and vice-versa). During PG sessions, the observers recorded the occurrence, latency (i.e. from the start of the PG session to the start of the grooming interaction), and duration of grooming interactions that followed the definition of direct, indirect and generalised reciprocity (Figure 5.1). The ‘former grooming’ was defined as the initial grooming A gave to B, its termination defining the start of the PG session (Figure 5.1). The ‘former groomee’ was defined as the recipient of the former grooming, that is B, and the ‘former groomer’ was defined as the donor of the former grooming, that is A. During each PG session, the first (i.e. in chronological order) grooming where B groomed A was defined as case of direct reciprocation (Figure 5.1). The first PG grooming where A received grooming from a third individual C was defined as case of indirect reciprocation. The first PG grooming where B groomed a third individual C (where C is another monkey than A) was defined as case of generalised reciprocation. Consequently all forms of reciprocation could potentially occur altogether in PG sessions. For each type of reciprocity respectively, if the type of grooming reciprocation was not observed in PG, the former grooming event was considered as not reciprocated. Cases of broad generalised reciprocation were defined as the sum of cases of direct and generalised reciprocation. If both direct and generalised reciprocation occurred in the same PG session, only the case of reciprocation which had the shortest latency for that session (i.e. occurred earlier) was considered. For example, if a case of direct reciprocation occurred in a PG session followed later by a case of generalised reciprocation, only the case of direct reciprocation was considered as a case of broad generalised reciprocation for that session.

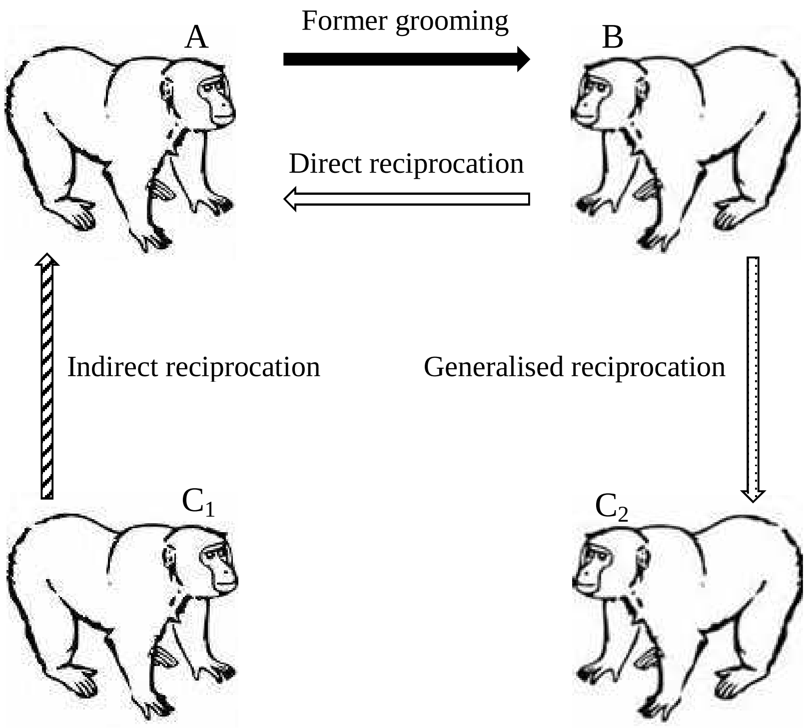


Figure 5.1. Illustration of the definition of the three types of reciprocation. Arrows represent direction of grooming interactions (from the donor to the recipient). The black arrow represents the former grooming interaction A gave to B. The white arrow represents grooming interactions part of direct reciprocation (i.e. B groomed A). The hatched arrow represents grooming interactions part of indirect reciprocation (i.e. C1 groomed A). The dotted arrow represents grooming interactions part of generalised reciprocation (i.e. B groomed C2). C1 and C2 may be either two different monkeys or the same monkey.

Consequently, the method used by Majolo and colleagues (2012) has been improved in this study in two different ways to more efficiently test the prevalence of the three types of reciprocity. First, the previous study collected data on either the groomer or the groomee of each grooming interaction (Majolo et al, 2012). By doing so, indirect reciprocation could only be assessed when data were collected on the groomer, generalised reciprocation could only be assessed when data were collected on the groomee, and direct reciprocation could be assessed from data on the groomer and groomee. The sample size for assessing direct reciprocation was thus double the samples used to assess indirect or generalised reciprocation. Conversely, the method used in this Chapter did not generate difference of sample size because data on the groomer and groomee of each grooming interaction were simultaneously collected. In this way, direct, indirect and generalised reciprocation could potentially be observed during each PG session without any bias due to the methodological procedure employed. Second, Majolo and colleagues (2012) stopped the focal sessions after the first case of reciprocated grooming occurred. However, this might bias data in favour of direct reciprocation simply because of the closer distance between the two former grooming partners rather than because indirect or generalised reciprocation may be less likely to occur. The focal sessions were not stopped after the first reciprocated grooming occurred, thus the three types of reciprocation could potentially occur after each former grooming interaction.

Independently of the PG sessions, control sessions were collected. As soon as two monkeys were observed in proximity (defined as two animals being within 1.5m) for a minimum of one minute without being involved in a grooming interaction, two simultaneous control sessions were run by two observers, on the two monkeys. During control sessions, the observers recorded the occurrence, latency (i.e. from the start of the control session to the start of the grooming interaction), and duration of grooming interactions involving the focal animals (i.e. the monkeys A and B being in proximity; Figure 5.2). The first grooming interaction involving the focal monkeys together was defined as control form of direct reciprocation (i.e. A groomed B or B groomed A). The first grooming where one of the focal monkey received grooming from a third individual was defined as control form of indirect reciprocation (i.e. C groomed A or B). The first grooming where one of the focal monkey gave grooming to a third individual was defined as control form of generalised reciprocation (i.e. A or B groomed C).

Consequently all forms of control reciprocation could potentially occur altogether in control sessions. For each type of reciprocity respectively, the former proximity event was considered as being not followed by control form of grooming reciprocation in the same way as the former grooming event was considered as not reciprocated in PG. Control cases of broad generalised reciprocation were defined as the sum of control forms of direct and generalised reciprocation, in the same way as case of broad generalised reciprocation were defined in PG sessions.

The control sessions were postponed if the focal individuals were involved in a grooming interaction or aggression, within 10 minutes prior to the start of the control sessions. PG sessions were not collected following former grooming interactions where the focal individuals were involved in another grooming interaction or aggression, within 10 minutes prior to the start of the former grooming. If a grooming interaction recorded during PG or control sessions was not terminated at the end of the session (i.e. at 60 minutes), the observers carried on the data collection until the end of the grooming interaction in order to record its duration. At the start of PG and control sessions, as well as at the beginning of the former grooming session in PG and then every 5min during the former grooming interaction, the number of other group members (i.e. excluding the focal animals) being within 10m of the grooming or proximity partners were also recorded. Those data were collected in order to analyse the effect of audience on grooming interactions.

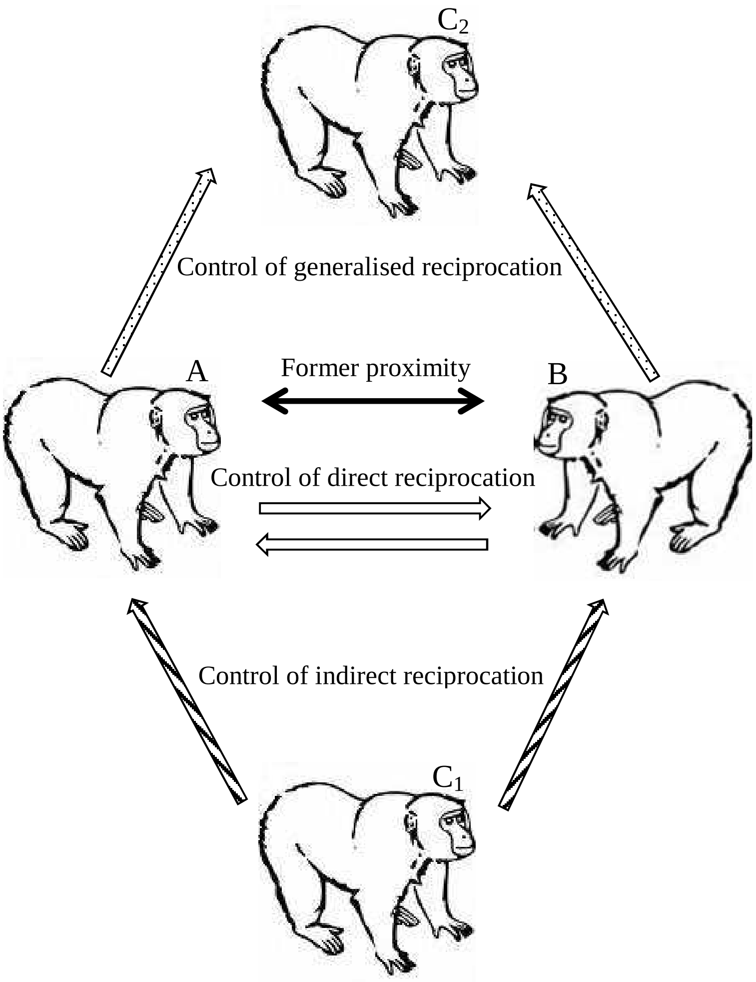


Figure 5.2. Illustration of the definition of the three control forms of reciprocation. The thin arrow represents the former proximity between the focal monkeys. Thick arrows represent direction of grooming interactions (from the donor to the recipient). The white arrow represents grooming interactions part of the control form of direct reciprocation (i.e. B groomed A or A groomed B). The hatched arrow represents grooming interactions part of the control form of indirect reciprocation (i.e. C1 groomed A or B). The dotted arrow represents grooming interactions part of the control form of generalised reciprocation (i.e. B or A groomed C2). C1 and C2 may be either two different monkeys or the same monkey.

Scan samples (Altmann, 1974) were collected every hour on the activity of all visible monkeys (see Chapter 2 for details on the activities recorded). Scan sample data were used to assess the relationship quality between the study animals. For each visible study animal, their proximity (defined as two or more animals being within 1.5m, excluding body contact and not exchanging grooming), body contact (defined as two or more animals being in body contact but not exchanging grooming) or grooming exchanged with the other adults or sub-adults in the group were recorded, as well as the identity of their social partner. Ad libitum data (Altmann, 1974) were used to determine the dominance hierarchy of the monkeys. Ad libitum data were collected opportunistically on any observed dyadic conflicts not involving third parties and with a clear-cut result (i.e. one opponent displayed aggressive behaviour and the other opponent displayed submissive behaviour). See Chapter 2 for details on aggressive and submissive behaviours used.

5.2.3. Data analysis

A composite sociality index (hereafter CSI) was calculated to measure the relationship quality between individuals, based on the data collected during 2,723 hourly scans. For each dyad of monkeys, their CSI was calculated based on the formula (Sapolsky et al, 1997; Silk et al, 2003):

$$\frac{\sum_{i=1}^{3} \frac{x_i}{m_i}}{3}$$

x_i = dyad's mean value for each of the three behavioural measures, that is, the average proportion of hourly scans in which two monkeys of a dyad were grooming, in proximity or in body contact.

m_i = group's median value for each of the three behavioural measures (i.e. grooming, proximity and body contact).

A high CSI indicates a high quality relationship between two monkeys of a dyad. The CSI values ranged from 0 to 5.5 (mean CSI value ± SE = 1.36 ± 0.1). Based on the dyadic conflicts collected ad libitum, a winner-loser socio-metric dominance matrix was constructed. Matman 1.1. (Noldus Information Technology, 2003; de Vries et al, 1993) was used to assign an ordinal dominance rank to each study monkey.

Analyses of the three types of reciprocation were based on 284 former grooming interactions and 63 control sessions (mean number of PG sessions ± SE per monkey = 18.93 ± 2.31, N = 15 for the groomer and 17.75 ± 3.54, N = 16 for the groomee; mean number of control sessions ± SE per monkey = 8.4 ± 0.98, N = 15). Four sets of analyses were conducted to test whether the occurrence and duration of the former grooming interaction were temporally linked to the different cases of reciprocation. In all the analyses, each former grooming interaction and control event was treated as a single data point. For each analyses, the following control variables were also entered: 'sex of the dyad' (categorical: male-male, male-female, or female-female), 'rank difference' (ordinal: the rank status of the groomer minus the rank status of the groomee; monkeys were randomly assigned the role of groomer or groomee for the control condition), 'CSI of the dyad' (continuous: the composite sociality index of the dyad), and 'audience' (continuous: total number of group members being in 10m of the focal subjects). These variables were entered in the GLMMs to control for their effect on grooming reciprocation (e.g. Mitchell & Tokunaga, 1976; Seyfarth, 1977; McGregor, 2005; Lehmann & Boesch, 2008; Schino & Aureli, 2008b; Radford, 2012). Each analysis was independently run to assess each type of reciprocation (i.e. direct, indirect, and generalised). Moreover, analyses testing generalised reciprocity were run twice, that is, excluding cases of direct reciprocations or including them (i.e. broad generalised reciprocation). IDs of the monkeys were used as random factors to control for non-independence of the data as multiple observations were collected on the same individuals (Pinheiro & Bates, 2000; Tabachnick & Fidell, 2007). The details of the random factors used are given below for each model. For the sake of brevity, the coefficients and significance of the control variables for analyses testing broad generalised reciprocation were not presented below and not discussed.

5.2.3.1. (1) For each type of reciprocity, reciprocated grooming would occur more often after grooming than in control condition

Four generalised linear mixed models (GLMMs) with a logistic distribution were run to assess whether each type of reciprocation was more likely to occur in PG than control sessions. The binary dependent variable was whether, respectively, direct, indirect, generalised or broad generalised reciprocation occurred in PGs or controls or not. 'PG vs. Control' was the categorical test variable for the four GLMMs. IDs of the two former monkeys were entered as two crossed random factors.

5.2.3.2. For each type of reciprocity, reciprocated grooming (2) would occur earlier after grooming than in control condition, and (3) it would occur earlier after grooming of longer duration

Two sets of four survival analyses (Cox proportional hazards model) were used (Cleves et al, 2008). Survival analyses allow to assess the effect of a factor (e.g. a treatment) on the latency to occur of an event (e.g. death). Survival analyses allow to take into account cases where the event did not occur (e.g. when subjects were still alive at the end of the trial). Basically, survival analyses deal with event (here reciprocation) that occurred or not in particular time windows (here PG or control sessions). If the event did not occur during the time window, it could potentially have occurred outside this time window. In the survival analyses, when the end of the time window is reached without the event having occurred, the observation is considered as censored. When the event occurred during the time window, this time window is considered as uncensored (i.e. failure event). Survival analyses are thus powerful and informative to analyses the latency of event to occur in a time window (e.g. for an applications of this method to animal behaviour, see Schino et al, 2009; Schino & Pellegrini, 2011; Majolo et al, 2012). In this Chapter, survival analyses are thus particularly effective in testing the predictions.

The first set of survival analyses tested respectively whether direct, indirect, generalised or broad generalised reciprocation occurred earlier in PG than control sessions. The second set tested respectively whether the duration of the former grooming affected the latency of direct, indirect, generalised and broad generalised reciprocation (i.e. control observations were excluded). For the two sets of analyses, a binary variable stating when case of reciprocation occurred and when reciprocation did not occur was used respectively as uncensored and censored event in the survival model. The latency for reciprocation to occur (i.e. from the start of the PG or control sessions, to the start of the reciprocated grooming) was entered as the continuous dependent variable for the two sets of analyses. ‘PG vs. Control’ was the categorical test variable for the first set of four survival analyses, and ‘grooming duration’ (i.e. the duration of the former grooming) was the continuous test variable for the second set of four survival analyses. The ‘shared frailty’ is an option of survival models in STATA v12.1 software (StataCorp., 2011b) which is similar to the use of random factors to control for sample inflation (StataCorp., 2011a). While several variables can be entered as random factors in GLMMs, only one variable can be entered using the ‘shared frailty’ option. ‘Groomer ID’ was entered for analyses testing indirect reciprocation, ‘Groomee ID’ was entered for analyses testing generalised and broad generalised reciprocation, and ‘dyad ID’ was entered for analyses testing direct reciprocation.

5.2.3.3. (4) For each type of reciprocity and when reciprocation does occur, the duration of reciprocated grooming would be longer after grooming of longer duration

Although a linear regression with robust standard errors may have been better to analyse the duration of reciprocated grooming, it was not possible to add the option of robust standard errors on mixed-effects linear regressions with two crossed random factors. Therefore mixed-effects Poisson regressions were used, and the p values may need to be interpreted with caution. Four generalised linear mixed models (GLMMs) with a Poisson distribution were run on PG sessions where reciprocated grooming occurred. When respectively, direct, indirect, generalised or broad generalised reciprocation occurred, these GLMMs assessed whether the duration of the former grooming interaction affected the duration of the reciprocated grooming interaction. The duration of the reciprocated grooming was used as the continuous dependent variable. The duration of the former grooming interaction was entered as the continuous test variable. ‘Groomer ID’ and ‘Groomee ID’ were entered in all the GLMMs as crossed random factors.

5.3. RESULTS

The mean duration (± SE) of the 284 former grooming collected was 7.31 ± 0.55 minutes. Among the 284 PG sessions collected, direct, indirect and generalised reciprocation occurred respectively in 38.73%, 33.8%, and 32.39% of the sessions.

Among the 63 control sessions collected, the control form of direct, indirect and generalised reciprocation occurred respectively in 11.1%, 55.55% and 49.21% of the sessions. Case and control form of broad generalised reciprocation occurred in 60.92% of the PG sessions and in 55.55% of the control sessions. Table 5.1 describes the number of PG sessions where direct, indirect and generalised reciprocation occurred, as well as their chronological order of occurrence. For example, 'direct, generalised, indirect' means that direct reciprocated grooming was the first to be observed in the PG session, followed by generalised reciprocated grooming and indirect reciprocated grooming. 'Direct' means that only directly reciprocated grooming occurred in the PG session. Among the 96 indirectly reciprocated grooming, 31 partners were part of the audience (i.e. 32.29% of indirectly reciprocated grooming). Table 5.2 describes the mean latency and duration for each type of reciprocated grooming.

Table 5.1. Percentage of PG sessions where the different types of reciprocation occurred, and their chronological order.

Order of reciprocation	Percentages of PG sessions (N = 284)
Direct	18.31
Indirect	11.62
Generalised	14.79
Direct, indirect	9.51
Direct, generalised	5.28
Indirect, direct	0.7
Indirect, generalised	2.82
Generalised, direct	0.35
Generalised, indirect	4.58
Direct, indirect, generalised	1.76
Direct, generalised, indirect	2.46
Indirect, generalised, direct	0.35
No reciprocation	27.46

Table 5.2. Mean ± SE of latency and duration (minutes) for each type of reciprocation across PG and control sessions.

	PG sessions		**Control sessions**	
Type of reciprocation	**Latency**	**Duration**	**Latency**	**Duration**
Direct reciprocation	4.93 ± 1.08	4.72 ± 0.62	17.95 ± 4.99	1.63 ± 0.32
Indirect reciprocation	25.92 ± 1.74	3.68 ± 0.54	25.22 ± 2.81	4.49 ± 0.83
Generalised reciprocation	28.67 ± 1.76	4.35 ± 0.72	25.52 ± 2.54	3.71 ± 0.78

5.3.1. (1) For each type of reciprocity, reciprocated grooming would occur more often after grooming than in control condition

Direct reciprocation was more likely to occur in PG than control sessions (Table 5.3 (a); Figure 5.3). Conversely, indirect and generalised reciprocation were more likely to occur in control than PG sessions (Table 5.3 (b) and (c); Figure 5.3). The occurrence of the former grooming interaction did not significantly affect the occurrence of broad generalised reciprocation (GLMM, z = -0.83, p = 0.41).

Table 5.3. Coefficients and significance of the test and control variables entered in the GLMMs with a logistic distribution to compare the occurrences of (a) direct reciprocation, (b) indirect reciprocation, and (c) generalised reciprocation between PG and control conditions (N = 347). MM = male-male, MF = male-female, FF = female-female dyads.

(a) Direct reciprocation

Variables	**Coefficient ± SE**	**Z**	**P**	**95% CIs**	**Significance**
PG vs. Control	-1.66 ± 0.43	-3.88	0.001	-2.5 – -0.82	✓
Sex of the dyad :					
MM vs. MF	0.39 ± 0.44	0.88	0.38	-0.48 – 1.25	✗
MM vs. FF	0.06 ± 0.47	0.12	0.91	-0.87 – 0.98	✗
MF vs. FF	-0.33 ± 0.32	-1.04	0.3	-0.96 – 0.29	✗
Rank difference	-0.03 ± 0.02	-1.72	0.09	-0.07 – 0.005	✗
CSI of the dyad	0.12 ± 0.1	1.2	0.23	-0.08 – 0.33	✗
Audience	-0.03 ± 0.06	-0.45	0.65	-0.13 – 0.08	✗

(b) Indirect reciprocation

Variables	**Coefficient ± SE**	**Z**	**P**	**95% CIs**	**Significance**
PG vs. Control	1.01 ± 0.31	3.28	0.001	0.41 – 1.61	✓
Sex of the dyad :					
MM vs. MF	1.55 ± 0.48	3.19	0.001	0.6 – 2.5	✓
MM vs. FF	1.72 ± 0.5	3.44	0.001	0.74 – 2.7	✓
MF vs. FF	0.17 ± 0.3	0.59	0.55	-0.41 – 0.76	✗
Rank difference	0.04 ± 0.02	2.04	0.04	0.002 – 0.08	✓
CSI of the dyad	-0.24 ± 0.1	-2.39	0.02	-0.44 – -0.04	✓
Audience	0.09 ± 0.06	1.58	0.12	-0.02 – 0.2	✗

(c) Generalised reciprocation

Variables	Coefficient ± SE	Z	P	95% CIs	Significance
PG vs. Control	0.79 ± 0.3	2.64	0.01	0.2 – 1.38	✓
Sex of the dyad :					
MM vs. MF	0.12 ± 0.42	0.28	0.78	-0.7 – 0.93	×
MM vs. FF	0.7 ± 0.46	1.52	0.13	-0.2 – 1.6	×
MF vs. FF	0.58 ± 0.31	1.87	0.06	-0.03 – 1.2	×
Rank difference	-0.01 ± 0.02	-0.54	0.59	-0.05 – 0.03	×
CSI of the dyad	-0.1 ± 0.1	-0.98	0.33	-0.3 – 0.1	×
Audience	-0.02 ± 0.06	-0.33	0.74	-0.13 – 0.09	×

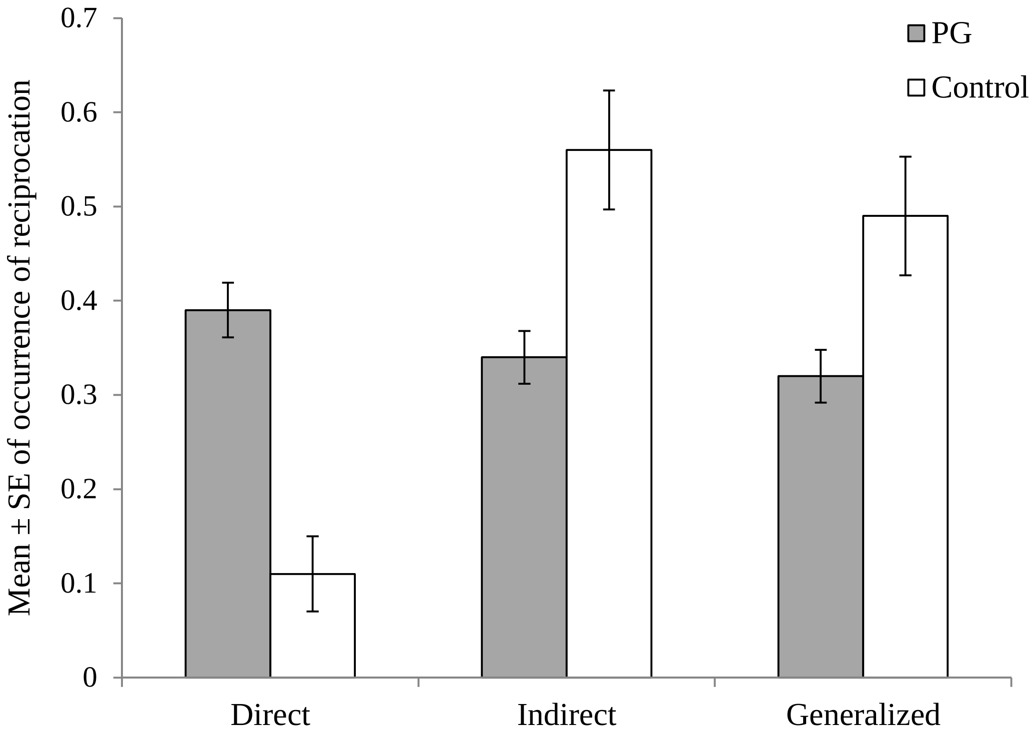


Figure 5.3. Mean ± SE of the occurrence of direct, indirect and generalised reciprocation in PG and control sessions (i.e. whether it occurred or not for each session).

5.3.2. (2) For each type of reciprocity, reciprocated grooming would occur earlier after grooming than in control condition

Directly reciprocated grooming occurred earlier in PG than control sessions (Table 5.4 (a)). Conversely, indirect and generalised reciprocation occurred earlier in control than PG sessions (Table 5.4 (b) and (c)). No significant difference was found between the latency of broad generalised reciprocity to occur in PGs or controls (GLMM, z = -1.79, p = 0.07).

Table 5.4. Coefficients and significance of the test and control variables entered in the survival analyses to test whether (a) direct reciprocation, (b) indirect reciprocation, and (c) generalised reciprocation occurred earlier in PG than control conditions (N = 347). MM = male-male, MF = male-female, FF = female-female dyads.

(a) Direct reciprocation

Variables	Hazards ratio ± SE	Z	P	95% CIs	Significance
PG vs. Control	0.24 ± 0.09	-3.67	0.001	0.11 – 0.51	✓
Sex of the dyad :					
MM vs. MF	1.26 ± 0.45	0.65	0.52	0.63 – 2.53	×
MM vs. FF	0.97 ± 0.36	-0.08	0.94	0.47 – 2.01	×
MF vs. FF	0.77 ± 0.19	-1.07	0.28	0.48 – 1.24	×
Rank difference	0.97 ± 0.01	-1.98	0.048	0.94 – 1	✓
CSI of the dyad	1.07 ± 0.09	0.87	0.39	0.92 – 1.24	×
Audience	0.98 ± 0.04	-0.46	0.65	0.9 – 1.07	×

(b) Indirect reciprocation

Variables	Hazards ratio ± SE	Z	P	95% CIs	Significance
PG vs. Control	1.98 ± 0.4	3.35	0.001	1.33 – 2.95	✓
Sex of the dyad :					
MM vs. MF	3.51 ± 1.39	3.16	0.002	1.6 – 7.64	✓
MM vs. FF	3.65 ± 1.49	3.16	0.002	1.64 – 8.14	✓
MF vs. FF	1.04 ± 0.23	0.18	0.86	0.67 – 1.61	✗
Rank difference	1.03 ± 0.01	2.02	0.04	1 – 1.06	✓
CSI of the dyad	0.84 ± 0.06	-2.3	0.02	0.72 – 0.97	✓
Audience	1.08 ± 0.04	1.86	0.06	1 – 1.17	✗

(c) Generalised reciprocation

Variables	Hazards ratio ± SE	Z	P	95% CIs	Significance
PG vs. Control	1.85 ± 0.4	2.85	0.004	1.21 – 2.82	✓
Sex of the dyad :					
MM vs. MF	1.08 ± 0.37	0.21	0.83	0.55 – 2.1	✗
MM vs. FF	1.6 ± 0.61	1.25	0.21	0.77 – 3.36	✗
MF vs. FF	1.49 ± 0.36	1.65	0.1	0.93 – 2.4	✗
Rank difference	0.99 ± 0.02	-0.34	0.73	0.96 – 1.03	✗
CSI of the dyad	0.91 ± 0.07	-1.18	0.24	0.79 – 1.06	✗
Audience	0.98 ± 0.04	-0.48	0.63	0.9 – 1.07	✗

5.3.3. (3) For each type of reciprocity, reciprocated grooming would occur earlier after grooming of longer duration

The latency of direct reciprocation to occur in PG sessions was faster for shorter former grooming interactions (Table 5.5 (a)). The duration of the former grooming interactions did not significantly affect the latency of PG indirect and generalised reciprocation (Table 5.5 (b) and (c)). STATA software (StataCorp., 2011b; v12.1) could not produce an output for the model assessing broad generalised reciprocation when the ID of the groomee was entered using the ‘shared frailty’ option to control for sample inflation (the error message stated that a maximum-likelihood model was estimated, and STATA's maximization procedure failed to converge to a solution). Consequently, the model was run by entering the ID of the groomee using the ‘strata’ option which is similar to the ‘shared frailty’ option to control for sample inflation in STATA. The duration of the former grooming interactions did not affect the latency of broad generalised reciprocation (GLMM, z = -1.63, p = 0.1).

Table 5.5. Coefficients and significance of the test and control variables entered in the survival analyses to test whether the duration of the former grooming event affects the latency of (a) direct reciprocation, (b) indirect reciprocation, and (c) generalised reciprocation (N = 284). MM = male-male, MF = male-female, FF = female-female dyads.

(a) Direct reciprocation

Variables	**Hazards ratio ± SE**	**Z**	**P**	**95% CIs**	**Significance**
Grooming duration	0.96 ± 0.02	-2.14	0.03	0.93 – 1	✓
Sex of the dyad :					
MM vs. MF	1.11 ± 0.43	0.28	0.78	0.52 – 2.36	×
MM vs. FF	0.74 ± 0.3	-0.74	0.46	0.34 – 1.63	×
MF vs. FF	0.67 ± 0.19	-1.46	0.15	0.39 – 1.15	×
Rank difference	0.96 ± 0.02	-2.27	0.02	0.94 – 1	✓
CSI of the dyad	1.07 ± 0.09	0.75	0.45	0.9 – 1.27	×
Audience	1.01 ± 0.05	0.16	0.88	0.92 – 1.11	×

(b) Indirect reciprocation

Variables	**Hazards ratio ± SE**	**Z**	**P**	**95% CIs**	**Significance**
Grooming duration	0.99 ± 0.14	-0.62	0.54	0.96 – 1.02	✗
Sex of the dyad :					
MM vs. MF	3.12 ± 1.59	2.23	0.03	1.15 – 8.49	✓
MM vs. FF	4.24 ± 2.16	2.83	0.01	1.56 – 11.5	✓
MF vs. FF	1.36 ± 0.36	1.16	0.25	0.81 – 2.28	✗
Rank difference	1.04 ± 0.02	2.39	0.02	1.01 – 1.08	✓
CSI of the dyad	0.81 ± 0.07	-2.45	0.01	0.68 – 0.96	✓
Audience	1.06 ± 0.05	1.33	0.19	0.97 – 1.17	✗

(c) Generalised reciprocation

Variables	**Hazards ratio ± SE**	**Z**	**P**	**95% CIs**	**Significance**
Grooming duration	1 ± 0.01	0.05	0.96	0.98 – 1.02	✗
Sex of the dyad :					
MM vs. MF	0.67 ± 0.27	-0.98	0.33	0.3 – 1.49	✗
MM vs. FF	1.26 ± 0.52	0.56	0.57	0.56 – 2.82	✗
MF vs. FF	1.88 ± 0.53	2.23	0.03	1.08 – 3.28	✓
Rank difference	0.99 ± 0.02	-0.72	0.47	0.95 – 1.03	✗
CSI of the dyad	0.97 ± 0.08	-0.31	0.76	0.83 – 1.15	✗
Audience	0.99 ± 0.48	-0.19	0.85	0.9 – 1.09	✗

5.3.4. (4) For each type of reciprocity and when reciprocation does occur, the duration of reciprocated grooming would be longer after grooming of longer duration

When reciprocation occurred in PG sessions, the duration of the former grooming interaction did not significantly affect the duration of direct, indirect, and generalised reciprocation (Tables 5.6 (a), (b), and (c)), as well as broad generalised reciprocation (GLMM, z = 1.62, p = 0.11).

Table 5.6. Coefficients and significance of the test and control variables entered in the GLMMs with a Poisson distribution to test whether the duration of the former grooming event affects the duration of (a) direct reciprocation, (b) indirect reciprocation, and (c) generalised reciprocation. MM = male-male, MF = male-female, FF = female-female dyads.

(a) Direct reciprocation (N = 110)

Variables	Coefficient ± SE	Z	P	95% CIs	Significance
Grooming duration	0.005 ± 0.01	0.63	0.53	-0.01 – 0.02	✗
Sex of the dyad :					
MM vs. MF	-0.26 ± 0.24	-1.1	0.27	-0.73 – 0.21	✗
MM vs. FF	-0.44 ± 0.36	-1.21	0.23	-1.15 – 0.27	✗
MF vs. FF	-0.18 ± 0.22	-0.82	0.41	-0.6 – 0.25	✗
Rank difference	0.03 ± 0.02	1.7	0.09	-0.004 – 0.06	✗
CSI of the dyad	-0.2 ± 0.05	-3.86	0.001	-0.3 – -0.1	✓
Audience	0.08 ± 0.03	3.08	0.002	0.03 – 0.14	✓

(b) Indirect reciprocation (N = 96)

Variables	**Coefficient ± SE**	**Z**	**P**	**95% CIs**	**Significance**
Grooming duration	-0.01 ± 0.01	-0.81	0.42	-0.03 – 0.01	✗
Sex of the dyad:					
MM vs. MF	-1.67 ± 0.33	-5.04	0.001	-2.23 – -1.02	✓
MM vs. FF	-1.53 ± 0.4	-3.87	0.001	-2.31 – -0.76	✓
MF vs. FF	0.14 ± 0.24	0.6	0.55	-0.32 – 0.6	✗
Rank difference	0.05 ± 0.02	2.48	0.01	0.01 – 0.09	✓
CSI of the dyad	0.05 ± 0.07	0.66	0.51	-0.09 – 0.18	✗
Audience	-0.13 ± 0.03	-3.95	0.001	-0.19 – -0.06	✓

(c) Generalised reciprocation (N = 92)

Variables	**Coefficient ± SE**	**Z**	**P**	**95% CIs**	**Significance**
Grooming duration	-0.001 ± 0.01	-0.08	0.93	-0.02 – 0.02	✗
Sex of the dyad :					
MM vs. MF	2.26 ± 0.51	4.48	0.001	1.27 – 3.26	✓
MM vs. FF	0.6 ± 0.78	0.77	0.44	-0.92 – 2.13	✗
MF vs. FF	-1.66 ± 0.4	-4.19	0.001	-2.44 – -0.88	✓
Rank difference	0.08 ± 0.04	2.1	0.04	0.005 – 0.16	✓
CSI of the dyad	-0.11 ± 0.07	-1.58	0.12	-0.24 – 0.03	✗
Audience	0.11 ± 0.03	3.58	0.001	0.05 – 0.17	✓

5.4. DISCUSSION

The results revealed a temporal contingency of grooming interactions exchanged in Barbary macaques, according to direct reciprocity but not according to indirect or generalised reciprocity (Table 5.7). To my knowledge, this is the first assessment of the three types of reciprocity altogether without methodological bias in grooming exchanges of a wild non-human primates' population. These results are notably consistent with a study that revealed strong support for direct reciprocity and limited or no support for indirect and generalised reciprocity for the temporal contingency of grooming exchanges in long-tailed macaques (Majolo et al, 2012). Evidence of direct but not generalised reciprocity was also found for the exchange of grooming for food sharing in chimpanzees (de Waal, 1997; de Waal & Brosnan, 2006).

Table 5.7. Summary of the results obtained for each prediction and each type of reciprocation.

Predictions	**Direct reciprocation**	**Indirect reciprocation**	**Generalised reciprocation**	**Broad generalised reciprocation**
(1) Reciprocated grooming would occur more often after grooming than in control condition	✓	✗	✗	✗
(2) Reciprocated grooming would occur earlier after grooming than in control condition	✓	✗	✗	✗
(3) Reciprocated grooming would occur earlier after grooming of longer duration	✗	✗	✗	✗
(4) The duration of reciprocated grooming would be longer after grooming of longer duration	✗	✗	✗	✗

First of all, the occurrence of the former grooming interaction was a predictor of the occurrence and latency of directly reciprocated grooming. These results provide strong evidence that direct reciprocation occurred and is related to the benefit received (i.e. grooming). Indeed, directly reciprocated grooming was related to previous grooming received and not to the fact that individual may be more likely to groom the closet available monkey, which, after a grooming interaction, is often the former grooming partner. Direct reciprocity occurred soon after the grooming end in this species (in approximately 5 minutes).

The duration of the former grooming interaction was a predictor of the latency of directly reciprocated grooming. However, while a shorter latency between bigger investment (i.e. longer grooming duration) and direct reciprocation may be expected to avoid cheating (i.e. the probability to receive direct reciprocation may decrease over time), the results showed that longer grooming were reciprocated later. However, the cost of a single non-reciprocated grooming (i.e. cheating) may be relatively low (Schino et al, 2003), and selection may have favoured the maximization of returned benefits more than the minimization of immediate costs due to no reciprocation (Schino & Aureli, 2009).

The duration of the former grooming interaction was not a predictor of the duration of directly reciprocated grooming. This indicates that while monkeys reciprocated the act of giving grooming, they did not match the quantity of grooming given with the quantity of grooming received in the short-term. This is consistent with other studies showing no short-term time-matching of grooming in non-human primates (e.g. Payne et al, 2003; Schino et al, 2003; Gumert & Ho, 2008; Port et al, 2009; Newton-Fisher & Lee, 2011; Majolo et al, 2012). First, this may be due to the different value of monkeys as social partners according to their dominance status, sex and relationship quality. Higher-ranking monkeys may be of higher social value because of the additional services such as tolerance over food or agonistic support that they can provide to lower ranking group members. Consequently within grooming dyads, the higher-ranking monkey may groom less and receive back a higher amount of grooming while the lower-ranking monkey may have to give a higher amount of grooming to receive back a smaller amount (Henzi et al, 2003). For example in chacma baboons (*Papio cynocephalus ursinus*), the more the mother of the infant was higher-ranking than the potential handlers, the more the potential handlers had to groom the mother to gain access to the infants (Henzi & Barrett, 2002). Similar difference may exist related to sex and relationship quality between monkeys, and may affect the amount of grooming exchanged. Indeed, dominance status, sex and relationship quality are factors known to affect grooming exchanges in non-human primates (e.g. Mitchell & Tokunaga, 1976; Seyfarth, 1977; Watt, 2000; Lehmann & Boesch, 2008; Silk et al, 2010), and it is important to control for these confounding variables when assessing grooming reciprocation. Another explanation could be that while the act of giving grooming may be significant and reciprocated, matching the quantity given to the quantity received may be irrelevant for monkeys or too cognitively demanding as it would require time estimation and good memory of amount received (e.g. Stevens & Hauser, 2004; Stevens et al, 2005). In Barbary macaques, direct contingent reciprocation of grooming may thus follows a ‘rule of thumb’, that is, the relevant aspect of short-term contingency may be the act to receive grooming, not the amount received.

Finally, while there is no evidence of short-term contingency between the amount of grooming given and received, grooming exchanges may be more balanced when looking at the overall dyadic grooming given and received irrespective of the time frames. For example, exchanges of amount of grooming given were balanced over longer time frames, without or with a weak contingency over short-time frames in chimpanzees

(*Pan troglodytes verus*; Gomes et al, 2009), white faced capuchins (*Cebus capucinus*; Manson et al, 1999, 2004), tufted capuchin monkeys (*Cebus apella*; Schino et al, 2009), olive baboons (*Papio anubis*; Frank & Silk, 2009), long-tailed macaques (Majolo et al, 2012), Japanese macaques (*Macaca fuscata*; Schino et al, 2003), and captive Barbary macaques (Carne et al, 2011). Comparing the overall amount of grooming given and received across dyads, irrespective of the time frames, would allow to test whether wild Barbary macaques overall balanced the duration of their grooming interactions, even if no short-term contingency have been found between the quantity of grooming exchanged.

This Chapter revealed that while non-human primates balance their grooming exchanges in the long-term (Schino & Aureli, 2009), the temporal contingency between grooming given and received may also play a role in the reciprocity of grooming in animals. Direct reciprocity is thus occurring in grooming exchanges and may be proximately driven by partner-specific emotional bookkeeping based on the emotional bond that develops as a consequence of past services received, which does not require complex cognitive capacities (Stevens & Hauser, 2004; Schino & Aureli, 2009). Supporting this view, neurotransmitters such as oxytocin underlie social bonding in humans and animals and may play a role in modulating altruistic behaviours (Insel & Shapiro, 1992; Insel & Young, 2001; Kosfeld et al, 2005; Schino & Aureli, 2009).

No evidence was found that Barbary macaques exchanged grooming interactions according to indirect or generalised reciprocity. Reciprocated grooming following the definitions of indirect or generalised reciprocity were actually less likely to occur and to occur faster after a grooming interaction than in control condition. The duration of the former grooming interaction was not a predictor of the latency and duration of generalised and indirect reciprocated grooming. Moreover, the occurrence and duration of the former grooming was not a predictor of the occurrence, latency and duration of generalised reciprocated grooming when including cases of directly reciprocated grooming.

Indirect reciprocity requires first the bookkeeping of past grooming interactions of other group members, and second that groomer benefits from the audience as potential partners to receive grooming. Grooming is a conspicuous behaviour, so monkeys of this study had the opportunity to observe grooming interactions between group members, and they were sometimes in proximity of grooming partners. Thus the conditions for indirect reciprocity to potentially occur were met. However, only 32.3% of the indirectly reciprocated grooming partners were part of the audience. Assessing the reputation of others through indirect experience may play a more important role as direct encounters between potential partners are infrequent or potentially risky such as assessing the fighting abilities of others (Sommerfeld et al, 2007; Herrmann et al, 2013). This is the case in humans where people often interact with unknown potential partners, invest in their own reputation, and the reputation they form from others strongly influence their future choice of partners (Nowak & Sigmund, 1998; Wedekind & Milinski, 2000; Milinski et al, 2001; Panchanathan & Boyd, 2004; Nowak & Sigmund, 2005; Sylwester & Roberts, 2010; Tennie et al, 2010). Gaining the cooperative propensity of potentials partners through eavesdropping is thus an important factors in humans and possibly in animals where the same conditions of encounter between partners are met (e.g. Bshary, 2002; Bshary & D’Souza, 2005). For example, there is mixed evidence that non-human primates are able to use the knowledge they gained through the observation of third parties interactions to make decision about with which new partners to cooperate with (Russel et al, 2008; Subiaul et al, 2008; Herrmann et al, 2013). Barbary macaques live in relatively small social groups (average size of 27.1 monkeys; Ménard, 2002; Fooden, 2007), and the group studied was composed of 16 adults and sub-adults. It is possible that each macaque may have had the opportunity to gain information on the cooperative propensity (i.e. the tendency to give grooming or not) of each potential partner by direct interaction (Dunbar, 1991, 1992), and gaining these information through observing third parties may, if present, play a less important role in this species. Moreover, if individuals chose their grooming partners in relation to the indirect information they gathered on them, they may do so in relation to the general (i.e. long-term) cooperative propensity observed rather than to the cooperative propensity inferred from a single grooming interaction. However, in long-tailed macaques the total time a monkey spent grooming another monkey was not related to the total time it received grooming by the rest of the group (Majolo et al, 2012). Furthermore, as there is no evidence that indirect reciprocity may be mediated by emotion, mechanisms such as image-scoring to gather information of every grooming interaction observed in the group may require too cognitively demanding capacities for animals (Stevens & Hauser, 2004; Stevens et al, 2005).

Generalised reciprocity does not play a role in the short-term grooming exchanges of Barbary macaques. Within a group, monkeys recognise each of their group members (e.g. Cheney & Seyfarth, 1982; Adachi & Hampton, 2011; Schell et al, 2011), and their potential partners are thus not unknown. Mechanisms involving partner-specific choice of cooperative partners play a more important role in the exchanges of benefits in animals, than the random choice of partners based on benefits just received. Mechanisms such as those involving partner-specific emotional experiences through friendly relationships may drive the exchange of services through direct reciprocity, but not generalised reciprocity. This explanation is consistent with findings in rats that showed that when individuals had the possibility to choose their partners for cooperation, they preferably chose known cooperative partners over unknown individuals (Rutte & Taborsky, 2008). Consequently, if mechanisms of reciprocity are affected by change in emotional state, this must be partner-specific and not generalisable to unknown individuals. In humans, generalised reciprocity may be a by-product of emotional mechanisms that initially evolved to facilitate direct reciprocity (Nowak & Roch, 2007).

In conclusion, this Chapter provides strong evidence that direct reciprocity plays an important role in the exchange of grooming in macaques, but not indirect and generalised reciprocity. The strong partner specificity required for direct reciprocity may explain the lack of evidence for generalised reciprocity. For indirect reciprocity, there is little evidence that non-human primates use information gathered through observation of third-parties interactions to regulate their cooperative interactions. Emotions may modulate the establishment of social bonds and the occurrence of direct reciprocity in animals. Notably, the exchanges may become more balanced over longer time frames. This study supports the hypothesis that direct reciprocity but not indirect and generalised reciprocity, plays an important role in contingent reciprocation in animals. Mechanisms involving partner-specific social bonds may be a low cognitively demanding mechanism of direct reciprocity (Schino & Aureli, 2009).

5.5. REFERENCES

Adachi, I. & Hampton, R. R. 2011. Rhesus monkeys see who they hear: spontaneous cross-modal memory for familiar conspecifics. *PLoS ONE*, **6**, e23345.

Akçay, A., Reed, V. A., Campbell, S. E., Templeton, C. N. & Beecher, M. D. 2010. Indirect reciprocity: song sparrows distrust aggressive neighbours based on eavesdropping. *Animal Behaviour*, **80**, 1041-1047.

Akçay, Ç., Wood, W. E., Searcy, W. A., Templeton, C. N., Campbell, S. E. & Beecher, M. D. 2009. Good neighbour, bad neighbour: song sparrows retaliate against aggressive rivals. *Animal Behaviour*, **78**, 97-102.

Akinyi, M. Y., Tung, J., Jeneby, M., Patel, N. B., Altmann, J. & Alberts, S. C. 2013. Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behaviour*, **85**, 559-568.

Alexander, R. D. 1974. The evolution of social behavior. *Annual Review of Ecological Systems*, **5**, 325-383.

Alexander, R. D. 1987. *The biology of moral systems*. New York: Aldine De Gruyter.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227-267.

Aureli, F. & Schaffner, C. M. 2002a. Empathy as a special case of emotional mediation of social behavior. *Behavioural and Brain Sciences*, **25**, 23-24.

Aureli, F. & Schaffner, C. M. 2002b. Relationship assessment through emotional mediation. *Behaviour*, **139**, 393-420.

Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science*, **211**, 1390-1396.

Axelrod, R. 1984. *The evolution of cooperation*. New York: Basic Books.

Barrett, L. & Henzi, S. P. 2001. The utility of grooming in baboon troops. In: *Economics in nature: social dilemmas, mate choice and biological markets* (Ed. by R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein), pp. 119-145. Cambridge: Cambridge University Press.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999. Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B*, **266**, 665-670.

Barta, Z., McNamara, J. M., Huszár, D. B. & Taborsky, M. 2011. Cooperation among non-relatives evolves by state-dependent generalized reciprocity. *Proceedings of the Royal Society B*, **278**, 843-848.

Bartlett, M. Y. & de Steno, D. 2006. Gratitude and prosocial behavior: helping when it costs you. *Psychological Science*, **17**, 319-325.

Bateson, M., Nettle, D. & Roberts, G. 2006. Cues of being watched enhance cooperation in a real-world setting. *Biology Letter*s, **2**, 412-414.

Berkowitz, L. & Daniels, L. R. 1964. Affecting the salience of the social responsibility norm: effects of past help on the response to dependency relationships. *Journal of Abnormal and Social Psychology*, **68**, 275-281.

Boyd, R. & Richerson, P. J. 1989. The evolution of indirect reciprocity. *Social Networks*, **11**, 213-238.

Brosnan, S. F. & Bshary, R. 2010. Cooperation and deception: from evolution to mechanisms. *Philosophical Transactions of the Royal Society B*, **365**, 2593-2598.

Brosnan, S. F., Salwiczek, L. & Bshary, R. 2010. The interplay of cognition and cooperation. *Philosophical Transactions of the Royal Society B*, **365**, 2699-2710.

Bshary, R. & D’Souza, A. 2005. Cooperation in communication networks: indirect reciprocity in interactions between cleaner fish and client reef fish. In: *Animal communication networks* (Ed. by P. K. McGregor), pp. 521-539. Cambridge: Cambridge University Press.

Bshary, R. & Grutter, A. S. 2002. Asymmetric cheating opportunities and partner control in the cleaner fish mutualism. *Animal Behaviour*, **63**, 547-555.

Bshary, R. & Grutter, A. S. 2005. Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biology Letters*, **1**, 396-399.

Bshary, R. & Grutter, A. S. 2006. Image scoring and cooperation in a cleaner fish mutualism. *Nature*, **441**, 975-978.

Bshary, R. & Schäffer, D. 2002. Choosy reef fish select cleaner fish that provide high service quality. *Animal Behaviour,* **63**, 557-564.

Bshary, R. 2002. Biting cleaner fish use altruism to deceive image scoring clients. *Proceedings of the Royal Society B*, **269**, 2087-2093.

Bull, J. J. & Rice, W. R. 1991. Distinguishing mechanisms for the evolution of co-operation. *Journal of Theoretical Biology*, **149**, 63-74.

Carne, C., Wiper, S. & Semple, S. 2011. Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology*, **73**, 1127-1133.

Carter, G. & Wilkinson, G. 2013. Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B*, **280**, 1753.

Chancellor, R. L. & Isbell, L. A. 2009. Female grooming markets in a population of gray-cheeked mangabeys (*Lophocebus albigena*). *Behavioral Ecology*, **20**, 79-86.

Cheney, D. L. & Seyfarth, R. M. 1982. Recognition of individuals within and between groups of free-ranging vervet monkeys. *American Zoologist*, **22**, 519-529.

Cheney, D. L. 2011. Extent and limits of cooperation in animals. *Proceedings of the National Academy of Sciences*, **108**, 10902-10909.

Cheney, D. L., Moscovice, L. R., Heesen, M., Mundry, R. & Seyfarth, R. M. 2010. Contingent cooperation between wild female baboons. *Proceedings of the National Academy of Sciences*, **107**, 9562-9566.

Cleves, M., Gould, W. W., Gutierrez, R. G. & Marchenko, Y. U. 2008. *An introduction to survival analysis using Stata*. 2nd edn. College Station: Stata Press.

Clutton-Brock, T. 2009. Cooperation between non-kin in animal societies. *Science*, **462**, 51-57.

Cords, M. 1995. Predator vigilance costs of allogrooming in wild blue monkeys. *Behaviour*, **132**, 559-569.

Côté, I. M. 2000. Evolution and ecology of cleaning symbioses in the sea. *Oceanography and marine biology, an annual review*, **38**, 311-355.

Dawes, R. M. 1980. Social dilemmas. *Annual Review of Psychology*, **31**, 169-193.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, **125**, 157-175.

de Waal, F. B. M. & Berger, M. L. 2000. Payment for labour in monkeys. *Nature*, **404**, 563.

de Waal, F. B. M. & Brosnan, S. F. 2006. Simple and complex social reciprocity in monkeys and apes. In: *Cooperation in primates and humans: mechanisms and evolution* (Ed. by P. Kappeler & C. van Schaik), pp. 79-99. New-York: Springer.

de Waal, F. B. M. 1997. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, **18**, 375-386.

Dunbar, R. I. M. 1991. Functional significance of social grooming in primates. *Folia Primatologica*, **57**, 121-131.

Dunbar, R. I. M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, **3**, 35-49.

Emmons, R. A. & McCullough, M. E. 2004. *The psychology of gratitude*. New York: Oxford University Press.

Fehr, E. & Fischbacher, U. 2003. The nature of human altruism. *Nature*, **425**, 785-791.

Fisher, J. 1954. Evolution and bird sociality. In: *Evolution as a process* (Ed. by J. Huxley, A. Hardy & E. Ford), pp. 71-83. London: Allen & Unwin.

Fooden, J. 2007. Systematic review of the Barbary macaque, *Macaca sylvanus* (Linnaeus, 1758). *Fieldiana Zoology*, **113**, 1-60.

Frank, R. E. & Silk, J. B. 2009. Impatient traders or contingent reciprocators? Evidence for the extended time course of grooming exchanges in baboons. *Behaviour*, **146**, 1123-1135.

Gomes, C. M., Mundry, R. & Boesch, C. 2009. Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B*, **276**, 699-706.

Grutter, A. S. & Bshary, R. 2003. Cleaner wrasse prefer client mucus: support for partner control mechanisms in cleaning interactions. *Proceedings of the Royal Society B*, **270**, 242-244.

Grutter, A. S. 1997. Spatio-temporal variation and feeding selectivity in the diet of the cleaner fish *Labroides dimidiatus*. *Copeia*, **2**, 346-355.

Gumert, M. & Ho, M. 2008. The trade balance of grooming and its coordination of reciprocation and tolerance in Indonesian long-tailed macaques (*Macaca fascicularis*). *Primates*, **49**, 176-185.

Haley, K. J. & Fessler, D. M. T. 2005. Nobody’s watching? Subtle cues affect generosity in an anonymous economic game. *Evolution and Human Behavior*, **26**, 245-256.

Hamilton, I. M. & Taborsky, M. 2005. Contingent movement and cooperation evolve under generalised reciprocity. *Proceedings of the Royal Society B*, **272**, 2259-2267.

Hamilton, W. D. 1964. Genetical evolution of social behaviour. *The Journal of Theoretical Biology*, **7**, 17-52.

Hart, B. L. & Hart, L. A. 1992. Reciprocal allogrooming in impala, *Aepyceros melampus*. *Animal Behaviour*, **44**, 1073-83.

Henzi, S. P. & Barrett, L. 2002. Infants as a commodity in a baboon market. *Animal Behaviour*, **63**, 915-921.

Henzi, S. P., Barrett, L., Gaynor, D., Greefe, J., Weingrill, T. & Hill, R. A. 2003. Effect of resource competition on the long-term allocation of grooming by female baboons: evaluating Seyfarth’s model. *Animal Behaviour*, **66**, 931-938.

Herrmann, E., Keupp, S., Hare, B., Vaish, A. & Tomasello, M. 2013. Direct and indirect reputation formation in nonhuman great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, **127**, 63-75.

Hutchins, M. & Barash, D. P. 1976. Grooming in primates: implications for its utilitarian function. *Primates,* **17**, 145-150.

Insel, T. R. & Shapiro, L. E. 1992. Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. *Proceedings of the National Academy of Sciences,* **89**, 5981-5985.

Insel, T. R. & Young, L. J. 2001. The neurobiology of attachment. *Nature Review of Neuroscience*, **2**, 129-136.

Jaeggi, A. V, de Groot, E., Stevens, J. M. G. & van Schaik, C. P. 2013. Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, **34**, 69-77.

Jaeggi, A. V. & van Schaik, C. P. 2011. The evolution of food sharing in primates. *Behavioral Ecology & Sociobiology*, **65**, 2125-2140.

Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U. & Fehr, E. 2005. Oxytocin increases trust in humans. *Nature*, **435**, 673-676.

Koyama, N. F, Caws, C. & Aureli, F. 2006. Interchange of grooming and agonistic support in chimpanzees. *International Journal of Primatology*, **27**, 1293-1309.

Krams, I., Krama, T., Igaune, K. & Mand, R. 2008. Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology,* **62**, 599-605.

Lehmann, J. & Boesch, C. 2008. Sex differences in sociality. *International Journal of Primatology,* **29**, 65-81.

Leimar, O. & Hammerstein, P. 2001. Evolution of cooperation through indirect reciprocity. *Proceedings of the Royal Society B*, **268**, 745-753.

Leinfelder, I., de Vries, H., Deleu, R. & Nelissen, M. 2001. Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. *American Journal of Primatology,* **55,** 25-42.

Luce, R. D. & Raiffa, H. 1957. *Games and decisions*. New York: Wiley.

Majolo, B., Schino, G. & Aureli, F. 2012. The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges. *Animal Behaviour,* **83**, 763-771.

Manson, J. H., Navarrete, C. D., Silk, J. B. & Perry, S. 2004. Time matched grooming in female primates? New analyses from two species. *Animal Behaviour,* **67**, 493-500.

Manson, J. H., Rose, L. M., Perry, S. & Gros-Louis, J. 1999. Dynamics of female-female relationships in wild *Cebus capucinus*: data from two Costa Rican sites. *International Journal of Primatology,* **20**, 679-706.

McGregor, P. K. 2005. *Animal communication networks*. Cambridge: Cambridge University Press.

Melis, A. P. & Semmann, D. 2010. How is human cooperation different? *Philosophical Transactions of the Royal Society B*, **365**, 2663-2674.

Melis, A. P., Hare, B. & Tomasello, M., 2008. Do chimpanzees reciprocate received favours? *Animal Behaviour,* **76**, 951-962.

Ménard, N. 2002. Ecological plasticity of Barbary macaques (*Macaca sylvanus*). *Evolutionary Anthropology*, **11,** 95-100.

Milinski, M., Semmann, D. & Krambeck, H. -J. 2002. Reputation helps solve the 'tragedy of the commons'. *Nature*, **415**, 424-426.

Milinski, M., Semmann, D., Bakker, T. C. M. & Krambeck, H. 2001. Cooperation through indirect reciprocity: image scoring or standing strategy? *Proceedings of the Royal Society B*, **268**, 2495-2501.

Mitchell, G. & Tokunaga, D. H. 1976. Sex differences in nonhuman primate grooming. *Behavioural Processes*, **4**, 335-345.

Mooring, M. S. & Hart, B. L. 1995. Costs of allo-grooming in impala: distraction from vigilance. *Animal Behaviour*, **49**, 1414-1416.

Newton-Fisher, N. E. & Lee, P. C. 2011. Grooming reciprocity in wild male chimpanzees. *Animal Behaviour*, **81**, 439-446.

Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of cooperation. In: *Economics in nature: social dilemmas, mate choice and biological markets* (Ed. by R. Noë, J. A. R. A. M van Hooff & P. Hammerstein), pp. 93-118. Cambridge: Cambridge University Press.

Noldus Information Technology. 2003. *Matman, software for matrix manipulation and analysis, version 1.1.* Wageningen, The Netherlands.

Nowak, M. A. & Roch, S. 2007. Upstream reciprocity and the evolution of gratitude. *Proceedings of the Royal Society B*, **274**, 605-610.

Nowak, M. A. & Sigmund, K. 1998. Evolution of indirect reciprocity by image scoring. *Nature*, **393**, 573-577.

Nowak, M. A. & Sigmund, K. 2005. Evolution of indirect reciprocity. *Nature*, **437**, 1291-1298.

Nowak, M. A. 2006. Five rules for the evolution of cooperation. *Science*, **314**, 1560-1563.

Olendorf, R., Getty, T. & Scribner, K. 2004. Cooperative nest defence in red-winged blackbirds: reciprocal altruism, kinship or by-product mutualism? *Proceedings of the Royal Society B*, **271**, 177-182.

Packer, C. 1977. Reciprocal altruism in *Papio anubis*. *Nature,* **265**, 441-443.

Panchanathan, K. & Boyd, R. 2004. Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature,* **432**, 499-502.

Payne, H. F. P., Lawes, M. J. & Henzi, S. P. 2003. Competition and the exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). *Behaviour*, **140**, 453-471.

Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M. & Bonhoeffer, S. 2005. Evolution of cooperation through generalised reciprocity. *Proceedings of the Royal Society B,* **272**, 1115-1120.

Pinheiro, J. C. & Bates, D. M. 2000. *Mixed effects models in S and S-PLUS*. 1st edn. New York: Springer-Verlag.

Pinto, A., Oates, J., Grutter, A. & Bshary, R. 2011. Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Current Biology,* **21**, 1140-1144.

Port, M., Clough, D. & Kappeler, P. M. 2009. Market effects offset the reciprocation of grooming in free ranging redfronted lemurs, *Eulemur fulvus rufus*. *Animal Behaviour,* **77**, 29-36.

Radford, A. N. 2012. Post-allogrooming reductions in self-directed behaviour are affected by role and status in the green woodhoopoe. *Biology Letters,* **8**, 24-27.

Raihani, N. J. & Bshary, R. 2011. Resolving the iterated Prisoner's Dilemma: theory and reality. *Journal of Evolutionary Biology,* **24**, 1628-1639.

Rand, D. G. & Nowak, M. A. 2013. Human cooperation. *Trends in Cognitive Sciences,* **17,** 413-425.

Rand, D. G., Ohtsuki, H. & Nowak, M. A. 2009. Direct reciprocity with costly punishment: generous tit-for-tat prevails. *The Journal of Theoretical Biology,* **256**, 45-57.

Rankin, D. & Taborsky, M. 2009. Assortment and the evolution of generalized reciprocity. *Evolution,* **63**, 1913-1922.

Rowell, T. E., Wilson, C. & Cords, M. 1991. Reciprocity and partner preference in grooming of female blue monkeys. *International Journal of Primatology,* **12**, 319-336.

Russell, Y. I., Call, J. & Dunbar, R. I. M. 2008. Image scoring in great apes. *Behavioural Processes*, **78**, 108 -111.

Rutte, C. & Taborsky, M. 2007. Generalised reciprocity in rats. *PLoS Biology*, **5**, 1421-1425.

Rutte, C. & Taborsky, M. 2008. The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): direct vs. generalised reciprocity. *Behavioral Ecology and Sociobiology*, **62**, 499-505.

Sabbatini, G., De Bortoli Vizioli, A., Visalberghi, E. & Schino, G. 2012. Food transfers in capuchin monkeys: an experiment on partner choice. *Biology Letters*, **8**, 757-759.

Sapolsky, R. M., Alberts, S. C. & Altmann, J. 1997. Hypercortisolism associated with social subordinate or social isolation among wild baboons. *Archive of General Psychiatry*, **54**, 1137-1143.

Schell, A., Rieck, K., Schell, K., Hammerschmidt, K. & Fischer, J. 2011. Adult but not juvenile Barbary macaques spontaneously recognize group members from pictures. *Animal Cognition*, **14**, 503-509.

Schino, G. & Aureli, F. 2008a. Grooming reciprocation among female primates: a meta-analysis. *Biology Letters*, **4**, 9-11.

Schino, G. & Aureli, F. 2008b. Trade-offs in primate grooming reciprocation: testing behavioural flexibility and correlated evolution. *Biological Journal of the Linnean Society*, **95**, 439-446.

Schino, G. & Aureli, F. 2009. Reciprocal altruism in primates: partner choice, cognition and emotions. *Advances in the Study of Behavior*, **39**, 45-69.

Schino, G. & Aureli, F. 2010. Primate reciprocity and its cognitive requirements. *Evolutionary Anthropology*, **19**, 130-135.

Schino, G. & Pellegrini, B. 2009. Grooming in mandrills and the time frame of reciprocal partner choice. *American Journal of Primatology*, **71**, 884-888.

Schino, G. & Pellegrini, B. 2011. Grooming and the expectation of reciprocation in mandrills (*Mandrillus sphinx*). *International Journal of Primatology*, **32**, 406-414.

Schino, G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, **18**, 115-120.

Schino, G., di Giuseppe, F. & Visalberghi, E. 2009. The time frame of partner choice in the grooming reciprocation of *Cebus apella*. *Ethology*, **115**, 70-76.

Schino, G., Polizzi di Sorrentino, E. & Tiddi, B. 2007. Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame of reciprocation. *Journal of Comparative Psychology*, **121**, 181-188.

Schino, G., Ventura, R. & Troisi, A. 2003. Grooming among female Japanese macaques: distinguishing between reciprocation and interchange. *Behavioral Ecology,* **14**, 887-891.

Seinena, I. & Schram, A. 2006. Social status and group norms: indirect reciprocity in a repeated helping experiment. *European Economic Review*, **50**, 581-602.

Semmann, D. 2012. Conditional cooperation can hinder network reciprocity. *Proceedings of the National Academy of Sciences*, **109**, 12846-12847.

Semmann, D., Krambeck, H.-J. & Milinski, M. 2005. Reputation is valuable within and outside one's own social group. *Behavioral Ecology and Sociobiology,* **57**, 611-616.

Seyfarth, R. M. 1977. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, **65**, 671-698.

Sigmund, K. 2012. Moral assessment in indirect reciprocity. *Journal of Theoretical Biology*, **299**, 25-30.

Silk, J. B. 2002. Using the ‘F’ word in primatology. *Behaviour*, **139**, 421-446.

Silk, J. B. 2003. Cooperation without counting: the puzzle of friendship. In: *The Genetic and cultural evolution of cooperation* (Ed. by P. Hammerstein), pp. 37-54. Cambridge: The MIT Press.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance infant survival. *Science*, **302**, 1231-1234.

Silk, J. B., Beehner, J. C., Berman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2010. Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, **61**, 197-204.

Slocombe, K. E. & Zuberbuhler, K. 2007. Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences,* **104**, 17228-17233.

Sommerfeld, R. D., Krambeck, H. -J., Semmann, D. & Milinski, M. 2007. Gossip as an alternative for direct observation in games of indirect reciprocity. *Proceedings of the National Academy of Sciences*, **104**, 175435-175440.

StataCorp. 2011a. *Stata 12 base reference manual*. College Station, Texas: Stata Press.

StataCorp. 2011b. *Stata statistical software: release 12*. College Station, Texas: StataCorp LP.

Stevens, J. R. & Hauser, M. D. 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences*, **8**, 60-65.

Stevens, J. R., Cushman, F. A. & Hauser, M. D. 2005. Evolving the psychological mechanisms for cooperation. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 499-518.

Subiaul, F., Vonk, J., Okamoto-Barth, S. & Barth, J. 2008. Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. *Animal Cognition*, **11**, 611-623.

Sylwester, K. & Roberts, G. 2010. Cooperators benefit through reputation-based partner choice in economic games. *Biology Letters*, **6**, 659-662.

Tabachnick, B. G. & Fidell, L. S. 2007. *Using multivariate statistics*. 5th edn. Pearson Int.

Temeles, E. J. 1994. The role of neighbours in territorial systems: when are they ‘dear enemies’? *Animal Behaviour*, **47**, 339-350.

Tennie, C., Frith, U. & Frith, C. D. 2010. Reputation management in the age of the world-wide web. *Trends in Cognitive Sciences*, **14**, 482-488.

Thierry, B., Singh, M. & Kaumanns, W. 2004. *Macaque societies: a model for the study of social organization*. Cambridge: Cambridge University Press.

Tiddi, B., Aureli, F., Polizzi di Sorrentino, E., Janson, C. H. & Schino, G. 2011. Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. *Behavioral Ecology*, **22**, 663-669.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *The Quarterly Review of Biology*, **46**, 35-57.

Ventura, R., Majolo, B., Koyama, N., Hardie, S. & Schino G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology*, **68**, 1138-1149.

Watts, D. 2000. Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. *International Journal of Primatology*, **21**, 211-238.

Watts, D. P. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, **139**, 343-370.

Wedekind, C. & Milinski, M. 2000. Cooperation through image scoring in humans. *Science*, **288**, 850-852.

West, S. A., El Mouden, C. & Gardner, A. 2011. Sixteen common misconceptions about the evolution of cooperation in humans. *Evolution and Human Behavior*, **32**, 231-262.

West, S. A., Griffin, A. S. & Gardner, A. 2007a. Evolutionary explanations for cooperation. *Current Biology*, **17**, 661-672.

West, S. A., Griffin, A. S. & Gardner, A. 2007b. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, **20**, 415-432.

Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bats. *Nature*, **308,** 181-184.

Xia, D., Li, J., Garber, P. A., Sun, L., Zhu, Y. & Sun, B. 2012. Grooming reciprocity in female Tibetan macaques *macaca thibetana*. *American journal of primatology*, **74**, 569-579.

Chapter 6

Short-term contingency between grooming and food tolerance

Chapter 5 investigated the role of direct, indirect and generalised reciprocity in explaining grooming exchanges of wild Barbary macaques, by analysing the temporal contingency between giving and receiving grooming. The results revealed a temporal contingency of grooming interactions exchanged according to direct reciprocity but not according to indirect or generalised reciprocity. The importance of partner specificity may explain the lack of evidence for generalised reciprocity. Indirect reciprocity requires the bookkeeping of past grooming interactions of other group members, and such mechanisms may be too cognitively demanding to occur in macaques. Emotions may modulate the establishment of social bonds and the occurrence of direct reciprocity in animals. The current Chapter investigates the exchange of grooming for food tolerance in a wild partially-provisioned group of Barbary macaques, by analysing the short-term contingency between these events.

6.1. INTRODUCTION

Food tolerance (also called ‘food sharing’ and ‘cofeeding’) mainly consists of one individual relinquishing a part of defendable food to another individual (Feistner & McGrew, 1989; Stevens & Gilby, 2004; Jaeggi & Schaik, 2011). Food tolerance benefits the recipient in term of nutrition by gaining access to food resources, while reducing the food available for the donor (e.g. de Waal, 1997b; Gilby, 2006). Food tolerance has been observed in a variety of non-human animals (Stevens & Gilby, 2004), including insects (e.g. Bolten et al, 1983), birds (e.g. Bugnyar & Kotrschal, 2002; de Kort et al, 2003, 2006), cetaceans (e.g. Johnson, 1982), bats (e.g. Wilkinson, 1984; Carter & Wilkinson, 2013), and non-human primates (e.g. Feistner & McGrew, 1989; Jaeggi & van Schaik, 2011). In non-human primates the majority of food sharing behaviours are passive, that is, individuals selectively allow other group members to remove food from their hand or mouth and/or to feed in their proximity (de Waal, 1989; Feistner & McGrew, 1989; Jaeggi et al, 2010a; Jaeggi & Schaik, 2011; Tiddi et al, 2011; Sabbatini et al, 2012). A classic example is the sharing of meat after hunting among wild chimpanzees, where beggars gather around food owners (*Pan troglodytes*; Mitani & Watts, 2001).

While food tolerance from adults to offspring can be explained by kin selection (Hamilton, 1964), two main hypotheses have been proposed to explain food tolerance among unrelated adults: harassment and reciprocal exchange (Feistner & McGrew, 1989; Brown et al, 2004). These two hypotheses are not mutually exclusive and may both take place in non-human primates. The benefits of sharing under the pressure of harassment for the food owner would be the direct reduction of the costs associated with harassment (e.g. receiving aggression). The benefits of reciprocal exchange of food sharing would be delayed until the recipient returns the favour (Stevens & Gilby, 2004; Gilby, 2006).

In the harassment hypothesis (also called ‘tolerated-theft’ hypothesis, Blurton-Jones, 1987), non-food owners interfere with the feeding of food owners by, for example, screaming, grabbing and stealing the food, which makes food defence less advantageous for food owners (Moor, 1984; Westergaard et al, 1998; Stevens & Stevens, 2002). In that case, food owners may relinquish a part of the food to avoid or reduce the immediate costs associated with beggar harassment such as reduced consumption rate, increased energy expenditure (e.g. by avoiding or chasing beggars), or being injured by the beggars (Blurton Jones, 1984, 1987; Stevens & Stevens, 2002). Observations in natural conditions indicated that harassment increases food tolerance in chimpanzees sharing colobus monkey meat, where the costs of harassment are relatively high such as aggression received from the individuals requesting food (i.e. beggars; Goodall, 1986; Boesch & Boesch, 1989; Gilby, 2006). A theoretical model also showed that harassment influences food tolerance (Stevens & Stevens, 2002). These theoretical and observational results were confirmed by controlled experiments, where a high level of harassment was associated with a high level of sharing in chimpanzees (Stevens, 2004; Silk et al, 2013), squirrel monkeys (*Saimiri boliviensis*; Stevens, 2004), and jackdaws (*Corvus monedula*; de Kort et al, 2006). Similarly in rhesus macaques (*Macaca mulatta*), monkeys received less aggression and consume more food if they recruited and shared with group members than if they did not (Hauser, 1992).

In species where food possessors are mainly dominant individuals, the costs of defending food are very small, and harassment may not explain food tolerance by higher-ranking toward lower-ranking individuals. In this case, food tolerance is defined as a higher-ranking individual (i.e. the donor) relinquishing a part of defendable food to a lower-ranking individual (i.e. the recipient). Reciprocal altruism (Trivers, 1971) presupposes that individuals exchange over time services that are costly for the donor and beneficial for the recipient. Food tolerance benefits the recipient in term of nutrition by gaining access to food resources, while reducing the food available for the donor (e.g. de Waal, 1997b; Gilby, 2006), and can thus be considered as a social service. There is evidence of reciprocal exchanges of food sharing in vampire bats (*Desmodus rotundus*; Wilkinson, 1984; Denault & McFarlane, 1995; Carter & Wilkinson, 2013.), birds (de Kort et al, 2006), capuchin monkeys (*Cebus apella*; de Waal, 1997a; Westergaard & Suomi, 1997; de Waal, 2000; Sabbatini et al, 2012), chimpanzees (Hemelrijk & Ek, 1991; Mitani & Watts, 2001; Mitani, 2006; Jaeggi et al, 2010b), cotton-top tamarins (*Saguinus Oedipus*; Hauser et al, 2003), and Sichuan snub-nosed monkeys (*Rhinopithecus roxellana;* Xue & Su, 2011). A recent meta-analysis showed evidence of reciprocity of food tolerance in humans and non-human primates (Jaeggi & Gurven, 2013). There is also evidence that food tolerance can be traded for other services such as mating opportunities (e.g. Tutin, 1979; Stanford et al, 1994; Jaeggi & van Schaik, 2011), coalition support (e.g. Nishida et al, 1992; Stanford et al, 1994; Mitani & Watts, 2001; Jaeggi & van Schaik, 2011), and grooming (e.g. Tiddi et al, 2011).

In baboons (*Papio anubis*) and orangutans (*Pongo abelii* and *Pongo pygmaeus wurmbii*) for example, the few instances of sharing occurred between male-female dyads, and more often between consort partners or within pairs of stronger relationship quality (Strum, 1981; van Noordwijk & van Schaik, 2009). Similar results have been found in chimpanzees, where males were more likely to share meat with their frequent female grooming partners (Gilby, 2006), and fruits from raids of plantation with females (Hockings et al, 2007). This suggests that sharing with females may increase the reproductive success of males by increasing mating opportunities (Tutin, 1979; van Noordwijk & van Schaik, 2009; Jaeggi & van Schaik, 2011; Dubuc et al, 2012). In that case, animals would share food not to avoid immediate costs inflicted by harassment, but to gain social benefits such as mating partner (Schino & Aureli, 2009; Jaeggi & van Schaik, 2011). While further evidence of short-term contingent exchanges of food sharing for mating is missing (Mitani & Watts, 2001; Watts & Mitani, 2002; Gilby, 2006; Gilby et al, 2010), long-term food tolerance has been correlated with higher mating success (Gomes & Boesch, 2009; van Noordwijk & van Schaik, 2009).

In many mammal species and birds, grooming plays an important role in the establishment and maintenance of social bonds (Dunbar, 1991). Grooming is also assumed to be costly for the donor as it reduces vigilance against predators and competitors (Maestripieri, 1993; Cords, 1995), and the time available for other activities (e.g. feeding; Dunbar & Sharman, 1984; Maestripieri, 1993), while benefitting the recipient by reducing ectoparasite infection (Hutchins & Barash, 1976; Tanaka & Takefushi, 1993; Zamma, 2002; Radford & Du Plessis, 2006; Scantlebury et al, 2007; Akinyi et al, 2013). Hence like food sharing, grooming can be considered as a service that benefits the recipient while giving some costs to the donor, and thus can be potentially reciprocated or traded for other services. There is evidence in non-human primates that the giving of grooming is reciprocated (e.g. see Schino & Aureli, 2008 for a meta-analysis based on 22 species) or exchanged for other services such as support during agonistic interaction, tolerance, access to infant and preferential access to resources such as food and mating partners (e.g. Hemelrijk & Ek, 1991; Hemelrijk, 1994; de Waal & Berger, 2000; Barrett & Henzi, 2001; Watts, 2002; Ventura et al, 2006; Barelli et al, 2011; Carne et al, 2011).

Two proximate mechanisms have been proposed to explain the exchanges of services in animals (Bull & Rice, 1991; Noë, 2001). First of all, an animal can give a benefit to a partner depending on how the partner behaved toward it in the recent past

(Tiddi et al, 2011). This mechanism is usually tested by examining the within-dyad temporal relation between events given and received over short time periods (i.e. minutes or hours; Schino et al, 2009; Cheney et al, 2010). Secondly, the partner choice mechanism assumes that animals give favours toward specific partners but not others, by comparing how each partner behaved toward them over longer time frames (Noë, 2001; Silk, 2002, 2003; Schino & Aureli, 2009, 2010), mainly through emotional bookkeeping of known partners. Consequently, individuals overall reciprocate more toward social partners from who they received more, even if no temporal contingency is found between benefits received and given over short time frames. Both of these mechanisms may potentially explain the reciprocation and exchanges of grooming and food tolerance in non-human primates. Overall, long-term exchanges are usually more balanced than short-term exchanges, which suggests that partner choice mechanisms may play a more important role in the exchange of services in animals than short-term reciprocation (Schino, 2007; Schino & Aureli, 2009).

There is evidence that grooming increases food tolerance in a variety of non-human primates. Grooming positively correlated with food tolerance in chimpanzees (e.g. Mitani, 2006), spider monkeys (*Ateles geoffroyi*; Pastor-Nieto, 2001), rhesus macaques (*Macaca mulatta*; Kapsalis & Berman, 1996) and Japanese macaques (*Macaca fuscata*; Ventura et al, 2006). Dominant capuchin monkeys tolerated during feeding more often subordinates that groomed them most (Tiddi et al, 2012). In a study on wild tufted capuchin monkeys (*Cebus apella nigritus*), Tiddi and colleagues (2011) assessed the temporal relation between grooming and tolerance over contestable food, both in natural contexts and during feeding on provisioning platforms. More specifically, they analysed whether grooming received from subordinates within two hours affected tolerance over food given by dominants. Tiddi and colleagues (2011) found no evidence that tolerance during experimental feeding increased after grooming received. However, they found a positive relation between overall grooming received and food tolerance given for both feeding conditions, suggesting than the exchange of grooming for food tolerance may be more balanced over longer time frames (Tiddi et al, 2011). In addition, food tests were conducted on captive chimpanzees to compare whether tolerance over food between two individuals was higher in the two hours following their grooming (de Waal, 1997b). Food tests consisted of freshly cut branches of different plant species, tied together into large monopolisable bundles, and thrown in the enclosure of the study animals. This study found that grooming increased the subsequent food sharing by the recipient but not the donor of grooming (de Waal, 1989, 1997b). Moreover, the effect of grooming on food tolerance was stronger for dyads of individuals who rarely groomed each other (de Waal, 1997b). In another study conducted on chimpanzees and bonobos (*Pan paniscus*), the short-term effect of grooming received on food tolerance disappeared when controlling for social factors such as relationship quality, sex and dominance rank (Jaeggi et al, 2013). Moreover, there was no evidence that aggressive behaviours during food requests decreased when grooming occurred before feeding. Thus, the likelihood of providing food tolerance was dependent on the relationship history of the individuals and not strongly related to the contingency of recent single events (Jaeggi et al, 2013). Also, Fruteau and colleagues (2009) set up an experiment where two low-ranking vervet monkeys (*Chlorocebus pygerythrus*) were allowed to repeatedly provide food to their group members by triggering the opening of a food dispenser. This study showed that providers overall received more grooming than they gave, as a consequence of the food they made available to their group members. Similar results were found in long-tailed macaques (*Macaca fascicularis*) in a similar experiment (Stammbach, 1988). Finally, overall grooming is exchanged with tolerance while feeding in captive Barbary macaques (*Macaca sylvanus*; Carne et al, 2011).

While there is evidence for long-term correlation between grooming and food tolerance, results for short-term contingencies of the exchange of these services are mixed (Schino & Aureli, 2009; Tiddi et al, 2011). Despite this lack of evidence, especially in captive animals, short-term contingency between services given and received is often used as the basic mechanism to explain reciprocal altruism and social exchanges. Understanding the causes of these variations is important to our understanding of the evolution of exchange of services. Chapter 5 showed that wild Barbary macaques do not match the amount of grooming given and received in the short-term. This may suggest that grooming is perhaps also exchanged for other services in the short-term, such as tolerance over food. The aim of this chapter was to assess the short-term contingency of grooming on food tolerance in wild Barbary macaques. This species is characterised by a steep dominance hierarchy (Kaburu et al, 2012), so lower-ranking monkeys rarely interfere with the feeding of higher-ranking monkeys (see Chapter 2). In this chapter, food tolerance was thus defined as lower-ranking monkeys feeding in the proximity (i.e. within 1.5 meters) of higher-ranking monkeys (e.g. Tiddi et al, 2012). More precisely, the first aim was to assess whether food tolerance between monkeys A and B was higher immediately after A and B groomed than if they had not done so, and whether the role of the grooming partners (i.e. groomer or groomee) affected tolerance. Second, grooming would decrease aggressive response to food taken, facilitating contingent exchanges (de Waal, 1997b; Jaeggi et al, 2013). Therefore, it was also assessed whether aggression around food resources between the monkeys A and B was lower immediately after A and B groomed together than if they had not done so, and whether the role of the grooming partners affected aggression. Furthermore, in order to give a more comprehensive picture of aggression and tolerance occurring around food resources, it was tested whether higher-ranking individuals were more aggressive toward lower-ranking monkeys when they were feeding in their proximity or not. This would allow to distinguish between feeding interactions resulting from dominant monkeys selectively allowing subordinate monkeys to feed in their proximity (and so not aggressing them), from feeding interactions resulting from subordinate monkeys stealing food in front of dominant monkeys, and risking aggression. Finally, food tolerance may depend on the type of food available, that is, on whether the resource is shareable or not (Elgar, 1986; Stevens, 2004). For example, house sparrows (*Passer domesticus*) gave more food recruitment calls for shareable than non-shareable food (Elgar, 1986). In macaques, the increase of the food size increased aggression, while the food dispersion affected the ability of the monkeys to monopolize the foods (Mathy & Isbell, 2001). Chimpanzees gave more food calls when feeding on a divided than intact food resource (Hause et al, 1993). Consequently, it was also assessed whether the shareability of the food resource affected food tolerance and aggression. In detail, the predictions tested in this chapter were as follow:

(1) Tolerance over food would be higher after grooming than in control condition, and more importantly so for shareable than non-shareable food.

(2) Post-grooming tolerance (i.e. from dominant to subordinate monkeys) would occur more often when the lower-ranking monkey was the groomer than the groomee, and more importantly so for shareable than non-shareable food.

(3) Aggression over food would occur less often after grooming than in control condition, and more importantly so for shareable than non-shareable food.

(4) Post-grooming aggression would occur less often when the lower-ranking monkey was the groomer than the groomee, and more importantly so for shareable than non-shareable food.

(5) If dominant monkeys selectively allowed subordinate monkeys around food resources, there would be no difference between aggression received when the lower-ranking monkey got the food or not.

6.2. METHODS

6.2.1. Study subjects

Subjects of this study were the 24 adult and sub-adult monkeys of the ‘Tourist group’ (consisting of 9 adult males, 10 adult females, 2 sub-adult males, 3 sub-adult females, 12 juveniles and several infants) living in the Middle Atlas Mountains of Morocco. The group lived in the deciduous cedar and oak forest of the Ifrane National Park, between 1600 and 1860m a.s.l. The study animals were often close to tourists, especially in the middle hours of the day (e.g. from 11:00 to 14:00), who fed them with a variety of food, such as fruits, bread and peanuts (personal observations). Consequently, food tests could be conducted on the monkeys of this group without disturbing their usual diet and health, and without the presence of the experimenters disturbing them. See Chapter 2 for more details on the study animals and field site.

6.2.2. Data collection

Food tests were conducted from June 2011 to January 2012. In order to assess whether tolerance over food of higher-ranking monkeys toward lower-ranking monkeys increased after grooming, food tests were conducted in two different conditions: immediately following a grooming interaction (hereafter ‘PG’) and in control conditions where two monkeys were in proximity but not grooming.

6.2.2.1. Food tests

Food tests consisted of a food reward placed on the ground at equal distance between two monkeys, 1 meter in front of them. Just before to place the reward on the ground, the experimenter showed the food reward to the monkeys in order to ensure that both monkeys had seen it. Once the reward was placed on the ground, the experimenter moved away from the monkeys to a distance of minimum 3 meters. For each test, the ID of the monkey who obtained the reward was recorded as well as the occurrence of any aggressive interaction between the two individuals (see Chapter 2 for a description of aggressive behaviours recorded). Tolerance was defined as the lower-ranking monkey getting a part or all of the reward, while still in proximity (i.e. within 1.5m) with the higher-ranking monkey. No tolerance was recorded if only the higher-ranking monkey got the reward or if the lower-ranking monkey got the reward while not being in proximity of the higher-ranking monkey (e.g. when the higher-ranking monkey ate a part of the reward and then left). For each food test, data collection was stopped when all the food was eaten (an aggressive behaviour occurring within 5 seconds of the consumption of the last item of food was still recorded) or when the monkeys moved away from the food for more than 1.5 meters.

PG food tests were collected opportunistically after grooming interactions observed from start to end. As soon as a grooming interaction started, the ID of the monkeys, their role (i.e. groomer or groomee), the duration of the grooming, as well as whether the partners switched their groomer/groomee role during the grooming interaction were recorded. Food tests were conducted on the two grooming partners as soon as the grooming interaction stopped (i.e. the monkeys were not observed grooming for 5 seconds). If one monkey or both left immediately after the grooming ended, no food test was conducted.

As control conditions, food tests were conducted opportunistically on two monkeys being in proximity (i.e. within 1.5m) but not exchanging grooming for a minimum of 10 seconds. The tests were postponed if the monkeys had been observed grooming in the 10 minutes prior to the test. The same data collection procedure as the one used for PG conditions was followed for control conditions.

Two food-sharing conditions were used for the tests. The first condition called ‘non-shareable’ consisted of food that could not be shared, that is, food that could be grabbed and eaten by only one monkey. One item of food (average dimensions of 2.5 x 1.5 cm) was placed on the ground at 1 meter in front of the two monkeys, and at equal distance between them. The items used for the non-shareable condition were a piece of fruit (i.e. orange, apple or mandarin), vegetable (i.e. carrot, courgette or tomato), bread or peanut in shell. Food preference tests were conducted before the PG-control experiments and showed that each item of food was always grabbed whole and eaten in just one bite, preventing any possibility of sharing. Because the monkeys also received these items from tourists, regularly varying the items of food used allowed to keep the monkeys motivated for the tests. Tolerance was defined to occur in tests where the lower-ranking monkey of the pair grabbed and ate the reward. No tolerance was recorded if the higher-ranking monkey got the reward.

The second food-sharing condition called ‘shareable’, consisted of food that could potentially be shared by the monkeys. For that, small items of food were dispersed on the ground to allow two monkeys seating or standing in proximity (i.e. ≤ 1.5m) to both eat part of the reward at the same time. For this condition, a handful of wheat (i.e. around 25 grams) was dispersed on the ground, at 1 meter in front of the two monkeys, and at equal distance between them. The reward was dispersed in a disk of 50cm of diameter to potentially allow two individuals to eat in proximity at the same time. The reward used for the shareable condition was always wheat as this food was eaten by the monkeys and easily dispersible on the ground. Wheat was never observed to be given to the monkeys by tourists, consequently this item was new and motivating for the monkeys (i.e. always eaten by the monkeys when given to them), and the use of other items was not needed. Food preference tests were conducted before the experimentation and showed that each monkey liked to eat wheat, and that two monkeys could be in proximity eating wheat together. Tolerance was defined to occur in tests where the lower-ranking monkey ate a part of the reward while still in proximity with the higher-ranking monkey. No tolerance was recorded if only the higher-ranking monkey ate the reward.

Only one kind of reward was used per test, and the shareable and non-shareable food conditions were balanced across PG and control tests. For each test, the time of the day was also recorded to control for satiety effects on tolerance over food (Perry & Rose, 1994; Hattori et al, 2012). The time of the day was divided in three categories, each lasting 4 hours: ‘morning’ (i.e. tests conducted from 6am to 10am), ‘noon’ (i.e. tests conducted from 10am to 2pm), and ‘afternoon’ (i.e. tests conducted from 2pm to 6pm).

6.2.2.2. Relationship quality and hierarchy

Scan samples (Altmann, 1974) were collected every hour on the activity of all visible monkeys (see Chapter 2 for details on the activities recorded). For this Chapter, scan sample data were used to assess the relationship quality between the study animals. For each visible monkey, their proximity (i.e. ≤ 1.5m but not grooming) or grooming with the other adults or sub-adults in the group were recorded, as well as the identity of their social partner (see Chapter 2 for further details).

Ad libitum data (Altmann, 1974) were used to determine the dominance hierarchy of the study animals. Ad libitum data were collected opportunistically on any observed dyadic conflicts not involving third parties and with a clear-cut result (i.e. one opponent displayed aggressive behaviour and the other opponent displayed submissive behaviour; see Chapter 2 for details on the aggressive and submissive behaviours recorded).

6.2.3. Data analysis

A composite sociality index (hereafter CSI) was calculated to measure the relationship quality between two individuals, based on the data collected during 929 hourly scans. For each dyad of monkeys, their CSI was calculated based on the formula (Sapolsky et al, 1997):

$$\frac{\sum_{i=1}^{2} \frac{x_i}{m_i}}{2}$$

x_i = dyad’s value for each of the two behavioural measures (i.e. the proportion of hourly scans in which two monkeys of a dyad were grooming, or in proximity, divided by the total number of scans in which the activity of the two animals was recorded).

m_i = group’s median value for the proportion of hourly scans spent grooming, or in proximity, by the whole group.

A high CSI indicates a high quality relationship between two monkeys of a dyad. The CSI values ranged from 0 to 12.4 (mean CSI value ± SE = 1.7 ± 0.1).

Based on the dyadic conflicts collected ad libitum, a winner-loser socio-metric dominance matrix was constructed. Matman 1.1 (Noldus Information Technology, 2003; de Vries et al, 1993) was used to assign an ordinal dominance rank to each study monkey. See Chapter 2 for details on the hierarchy of this group.

Among the 426 tests collected on adults and sub-adults (217 post-grooming tests and 209 control tests), 40 were removed from the analyses because none of the focal subjects obtained the food (i.e. 24 tests where no monkey took the food, and 16 tests where only a third monkey took the food). Thus there were 386 tests used for the analyses. Among these tests, 29 were conducted after grooming interactions where the partners switched their groomer/groomee role at least once (17 with non-shareable food and 12 with shareable food). The mean ± SE number of tests per monkey was 15.8 ± 2.2 (N = 24) for the PGs and 16.4 ± 1.6 (N = 24) for the controls. Table 6.1 shows the number of tests collected for each PG or control condition and non-shareable or shareable reward.

Table 6.1. Number of food tests collected for PG or control condition and for non-shareable or shareable food.

Number of food tests	PG	Control	Total
Non-shareable	97	95	192
Shareable	92	102	194
Total	189	197	386

A series of generalised linear mixed models (GLMMs) with a logistic distribution were run to test each prediction. For each GLMM, each food test was treated as a single data point. The risk of sample inflation using this procedure was controlled for by adding to the models the ID of the two focal monkeys as two crossed random factors (Pinheiro & Bates, 2000). For each model, the test variables ‘CSI of the dyad’ (continuous: the CSI value of the dyads) and ‘sex of the dyad’ (categorical: different-sex or same-sex pairs) were also included in the model to assess whether tolerance was higher and aggression lower in dyads having a higher relationship quality, and whether the sex of the partners affected food tolerance and aggression (e.g. de Waal, 1997b; Soltis, 2004; Gilby, 2006; Lehmann & Boesch, 2008; van Noordwijk & van Schaik, 2009; Tiddi et al, 2011; Jaeggi et al, 2013). Details of each model run are described below.

6.2.3.1. (1) Tolerance over food would be higher after grooming than in control condition, and more importantly so for shareable than non-shareable food.

Two GLMMs with a logistic distribution were run to assess whether tolerance occurred more often in PG than control conditions. The first GLMM was run on all the data, and the second GLMM was run on controls and PG sessions where a subordinate monkey groomed a dominant monkey (and so excluding PG food tests where the partners switched their groomer/groomee role). For the two GLMMs, the binary dependent variable was whether tolerance occurred in PGs or controls, or not. ‘PG vs. Control’, ‘shareability’ (categorical: whether the food was non-shareable or shareable), and the interaction between ‘PG vs. Control’ and ‘shareability’ were the test variables for the two GLMMs. The control variables ‘rank difference’ (ordinal: the rank status of the groomer minus the rank status of the groomee; monkeys were randomly assigned the role of groomer or groomee for the control condition), ‘time of the day’ (categorical: morning, noon, or afternoon), and ‘grooming duration’ (continuous: the duration in seconds of the grooming interaction) were also entered in the models to control for their potential effect on tolerance over food. The control variable ‘role reverse’ (categorical: whether the grooming partners switched their groomer/groomee role or not) was also entered in the first GLMM as the occurrence of grooming turn taking may influence the tolerance over food of grooming partners.

6.2.3.2. (2) Post-grooming tolerance (i.e. from dominant to subordinate monkeys) would occur more often when the lower-ranking monkey was the groomer than the groomee, and more importantly so for shareable than non-shareable food.

One GLMM with a logistic distribution was run to assess whether lower-ranking monkey received more tolerance in PG when they were the groomer than the groomee. The GLMM was run only on PG data, excluding tests where the grooming partners switched their groomer/groomee role. The binary dependent variable was whether tolerance occurred in PGs or not. ‘Groomer vs. Groomee’, ‘shareability’, and the interaction between ‘Groomer vs. Groomee’ and ‘shareability’ were the categorical test variables. The control variables ‘rank difference’, ‘time of the day’ and ‘grooming duration’ were also entered in the GLMM.

6.2.3.3. (3) Aggression over food would occur less often after grooming than in control condition, and more importantly so for shareable than non-shareable food.

Two GLMMs with a logistic distribution were run to assess whether aggression occurred less often in PG than control conditions. The first GLMM was run on all the data, and the second GLMM was run on controls and PG sessions where a subordinate monkey groomed a dominant monkey (and so excluding PG food tests where the partners switched their groomer/groomee role). For the two GLMMs, the binary dependent variable was whether aggression occurred in PGs or controls, or not. ‘PG vs. Control’, ‘shareability’, and the interaction between ‘PG vs. Control’ and ‘shareability’ were the test variables for the two GLMMs. The control variables ‘rank difference’, ‘time of the day’, and ‘grooming duration’ were also entered in the models to control for their potential effects on aggression. The control variable ‘role reverse’ (categorical: whether the grooming partners switched their groomer/groomee role or not) was also entered in the first GLMM as the occurrence of grooming turn taking may influence aggression between partners.

6.2.3.4. (4) Post-grooming aggression would occur less often when the lower-ranking monkey was the groomer than the groomee, and more importantly so for shareable than non-shareable food.

One GLMM with a logistic distribution was run to assess whether lower-ranking monkey received less aggression in PG when they were the groomer than the groomee. The GLMM was run only on PG data, excluding tests where the grooming partners switched their groomer/groomee role. The binary dependent variable was whether aggression occurred in PGs or not. ‘Groomer vs. Groomee’, ‘shareability’, and the interaction between ‘Groomer vs. Groomee’ and ‘shareability’ were the categorical test variables. The control variables ‘rank difference’, ‘time of the day’ and ‘grooming duration’ were also entered in the GLMM.

6.2.3.5. (5) If dominant monkeys selectively allow subordinate monkeys around food resources, there would be no difference between aggression received when the lower-ranking monkey gets the food or not.

One GLMM with a logistic distribution was run to assess whether aggression was higher when only the lower-ranking monkey got the food than when only the higher-ranking monkey got the food. The binary dependent variable was whether aggression occurred or not. The categorical test variable ‘rank of who got the food’ was whether only the lower-ranking monkey or the higher-ranking monkey got the food. The control variables ‘rank difference’, ‘time of the day’, ‘role reverse’, ‘grooming duration’, and ‘food item’ (categorical: fruit, vegetable, bread, peanut and wheat) were entered in the model.

6.3. RESULTS

6.3.1. (1) Tolerance over food would be higher after grooming than in control condition, and more importantly so for shareable than non-shareable food

When analysing all the data set, tolerance was not significantly different in PG than control conditions, but tolerance was higher for shareable than non-shareable food (Table 6.2; Figure 6.1). There was no significant effect of the interaction between PG and control conditions and shareability of food on tolerance (Table 6.2). There was a no significant tendency showing a higher level of tolerance between dyads of higher CSI values (Table 6.2). Tolerance was significantly higher for different-sex than same-sex dyads (Table 6.2).

Similar results were found when focusing on data where a subordinate monkey groomed a dominant monkey. Tolerance was not significantly different in PG than control conditions, and tolerance was higher for shareable than non-shareable food (Table 6.3). There was no significant effect of the interaction between PG and control conditions and shareability of food on tolerance (Table 6.3). CSI values had no significant effect on tolerance, and tolerance was significantly higher for different-sex than same-sex dyads (Table 6.3).

Table 6.2. Coefficients and significance of the test and control variables entered in the GLMM to compare tolerance between PG and control conditions for all data (N = 386).

Variables	Coefficient ± SE	Z	P	95% CIs	Significance
PG vs. Control	0.15 ± 0.6	0.25	0.8	-1.03 – 1.33	✗
Shareability	1.81 ± 0.48	3.75	0.001	0.86 – 2.76	✓
PG vs. Control * Shareability	-0.21 ± 0.64	-0.32	0.75	-1.47 – 1.05	✗
CSI of the dyad	0.09 ± 0.05	1.91	0.056	-0.002 – 0.19	✗
Sex of the dyad	-1.16 ± 0.4	-2.89	0.004	-1.95 – -0.37	✓
Rank difference	0.02 ± 0.01	1.25	0.21	-0.01 – 0.04	✗
Time of the day: Morning vs. Noon	0.5 ± 0.35	1.45	0.15	-0.18 – 1.18	✗
Morning vs. Afternoon	0.42 ± 0.36	1.19	0.24	-0.28 – 1.13	✗
Noon vs. Afternoon	-0.08 ± 0.35	-0.21	0.83	-0.77 – 0.62	✗
Role reverse	-0.7 ± 0.68	-1.02	0.31	-2.04 – 0.64	✗
Grooming duration	0.0003 ± 0.005	0.61	0.54	-0.001 – 0.001	✗

Table 6.3. Coefficients and significance of the test and control variables entered in the GLMM to compare tolerance between PG and control conditions, for data when a subordinate monkey groomed a dominant monkey (N = 290).

Variables	Coefficient ± SE	Z	P	95% CIs	Significance
PG vs. Control	0.64 ± 0.95	0.67	0.5	-1.23 – 2.5	✗
Shareability	2.53 ± 0.83	3.03	0.002	0.9 – 4.17	✓
PG vs. Control * Shareability	-0.91 ± 0.94	-0.96	0.34	-2.75 – 0.94	✗
CSI of the dyad	0.07 ± 0.07	1.12	0.27	-0.06 – 0.2	✗
Sex of the dyad	-1.18 ± 0.53	-2.21	0.03	-2.22 – -0.13	✓
Rank difference	0.03 ± 0.02	1.53	0.13	-0.01 – 0.06	✗
Time of the day:					
Morning vs. Noon	1.27 ± 0.44	2.91	0.004	0.41 – 2.13	✓
Morning vs. Afternoon	1.11 ± 0.44	2.53	0.01	0.25 – 1.97	✓
Noon vs. Afternoon	-0.16 ± 0.4	-0.4	0.69	-0.95 – 0.63	✗
Grooming duration	-0.001 ± 0.001	-0.36	0.72	-0.003 – 0.002	✗

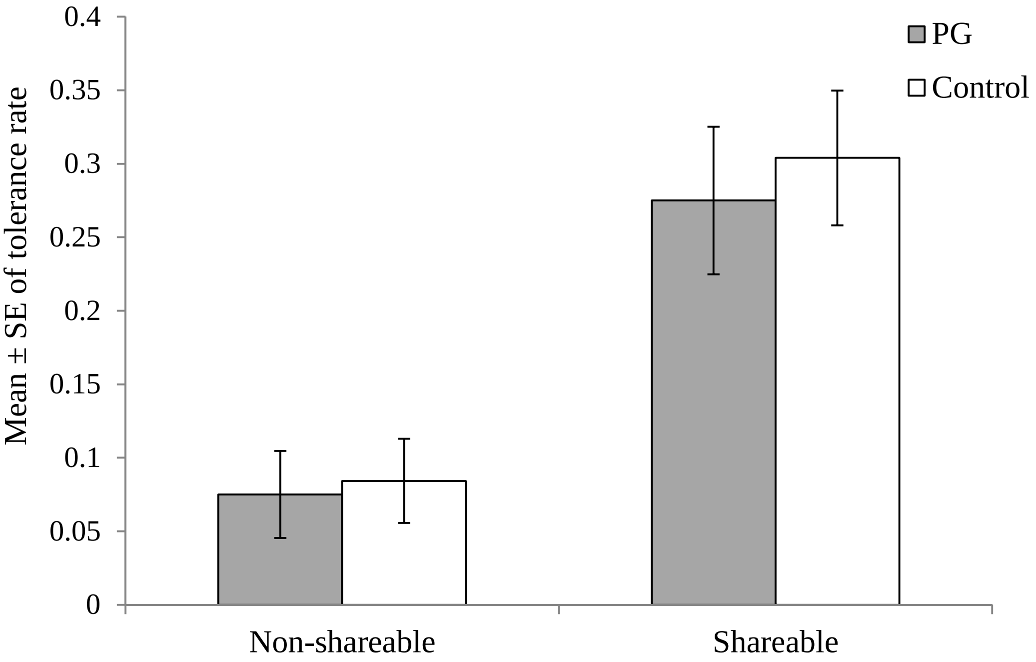


Figure 6.1. Mean ± SE of tolerance rate (i.e. whether tolerance occurred or not for each session) in post-grooming (PG) and control conditions, for non-shareable and shareable food, including all data.

6.3.2. (2) Post-grooming tolerance (i.e. from dominant to subordinate monkeys) would occur more often when the lower-ranking monkey was the groomer than the groomee, and more importantly so for shareable than non-shareable food.

The lower-ranking monkeys did not obtain the reward in PG more often when they were the groomer than the groomee (Table 6.4). PG tolerance was higher for shareable than non-shareable food (Table 6.4). There was no effect of the interaction between the role of the lower-ranking monkey and shareability of food (Table 6.4). PG tolerance was not affected by the CSI values of the dyads, but was higher for different-sex dyads compared to same-sex dyads (Table 6.4).

Table 6.4. Coefficients and significance of the test and control variables entered in the GLMM to compare PG tolerance between when the lower-ranking was the groomer or the groomee (N = 160).

Variables	Coefficient ± SE	Z	P	95% CIs	Significance
Groomer vs. Groomee	1.85 ± 1.36	1.36	0.17	-0.81 – 4.51	✗
Shareability	2.58 ± 0.89	2.89	0.004	0.83 – 4.32	✓
Groomer vs. Groomee * Shareability	-1.35 ± 1.13	-1.2	0.23	-3.56 – 0.86	✗
CSI of the dyad	0.09 ± 0.08	1.21	0.23	-0.06 – 0.24	✗
Sex of the dyad	-1.31 ± 0.56	-2.35	0.02	-2.41 – -0.22	✓
Rank difference	0.03 ± 0.04	0.77	0.44	-0.05 – 0.12	✗
Time of the day:					
Morning vs. Noon	-0.06 ± 0.57	-0.11	0.92	-1.17 – 1.05	✗
Morning vs. Afternoon	-0.16 ± 0.63	-0.25	0.8	-1.39 – 1.07	✗
Noon vs. Afternoon	-0.1 ± 0.68	-0.15	0.88	-1.43 – 1.23	✗
Grooming duration	-0.00004 ± 0.0007	-0.06	0.96	-0.001 – 0.001	✗

6.3.3. (3) Aggression over food would occur less often after grooming than in control condition, and more importantly so for shareable than non-shareable food.

All aggressive behaviours were directed from dominant to subordinate monkeys. When analysing all the data set, there was no significant difference between aggression received in PGs and controls, and between aggression received for non-shareable and shareable food (Table 6.5; Figure 6.2). There was no significant effect of the interaction between PG and control conditions and shareability of food on aggression (Table 6.5). The CSI values had no significant effect on aggression, but aggression was significantly lower for different-sex dyads than dyads of same sex (Table 6.5).

The results were similar when focusing on data where a subordinate monkey groomed a dominant monkey. Aggression was not significantly different in PG than control conditions, and with shareable than non-shareable food (Table 6.6). There was no significant effect of the interaction between PG and control conditions and shareability of food on aggression (Table 6.6). CSI values had no significant effect on aggression (Table 6.6). Aggression was significantly lower for different-sex than same-sex dyads (Table 6.6).

Table 6.5. Coefficients and significance of the test and control variables entered in the GLMM to compare aggression between PG and control conditions for all data (N = 386).

Variables	Coefficient ± SE	Z	P	95% CIs	Significance
PG vs. Control	0.73 ± 0.63	1.15	0.25	-0.51 – 1.96	✗
Shareability	0.22 ± 0.53	0.42	0.67	-0.82 – 1.26	✗
PG vs. Control * Shareability	0.95 ± 0.71	1.35	0.18	-0.43 – 2.33	✗
CSI of the dyad	0.03 ± 0.06	0.5	0.62	-0.08 – 0.14	✗
Sex of the dyad	1.32 ± 0.40	3.33	0.001	0.54 – 2.09	✓
Rank difference	-0.01 ± 0.02	-0.41	0.69	-0.04 – 0.03	✗
Time of the day: Morning vs. Noon	0.31 ± 0.38	0.81	0.42	-0.44 – 1.05	✗
Morning vs. Afternoon	-0.1 ± 0.44	-0.23	0.82	-0.96 – 0.75	✗
Noon vs. Afternoon	-0.41 ± 0.43	-0.96	0.34	-1.24 – 0.42	✗
Role reverse	0.79 ± 0.7	1.12	0.26	-0.59 – 2.17	✗
Grooming duration	-0.0002 ± 0.001	-0.25	0.8	-0.002 – 0.001	✗

Table 6.6. Coefficients and significance of the test and control variables entered in the GLMM to compare aggression between PG and control conditions for data when a subordinate monkey groomed a dominant monkey (N = 290).

Variables	**Coefficient ± SE**	**Z**	**P**	**95% CIs**	**Significance**
PG vs. Control	0.84 ± 0.89	0.95	0.34	-0.91 – 2.59	✗
Shareability	0.38 ± 0.81	0.47	0.64	-1.2 – 1.96	✗
PG vs. Control * Shareability	0.7 ± 0.92	0.76	0.45	-1.1 – 2.49	✗
CSI of the dyad	0.03 ± 0.07	0.4	0.69	-0.11 – 0.16	✗
Sex of the dyad	1.25 ± 0.44	2.82	0.01	0.38 – 2.12	✓
Rank difference	0.01 ± 0.02	0.54	0.59	-0.03 – 0.05	✗
Time of the day: Morning vs. Noon	0.16 ± 0.42	0.37	0.71	-0.67 – 0.99	✗
Morning vs. Afternoon	-0.3 ± 0.47	-0.62	0.54	-1.21 – 0.63	✗
Noon vs. Afternoon	-0.45 ± 0.48	-0.93	0.35	-1.39 – 0.5	✗
Grooming duration	-0.001 ± 0.002	-0.58	0.56	-0.01 – 0.003	✗

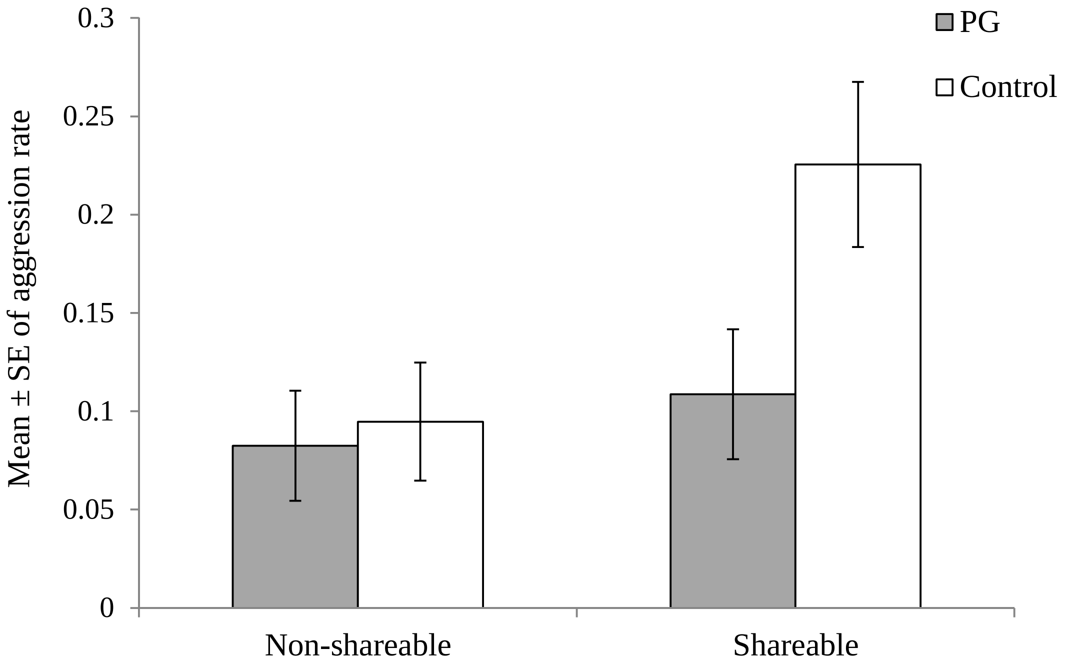


Figure 6.2. Mean ± SE of aggression rate (i.e. whether aggression occurred at least once or not for each session) in post-grooming (PG) and control conditions, for non-shareable and shareable food, including all data.

6.3.4. (4) Post-grooming aggression would occur less often when the lower-ranking monkey was the groomer than the groomee, and more importantly so for shareable than non-shareable food.

The lower-ranking monkeys did not receive less aggression in PG when they were the groomer than the groomee (Table 6.7). PG aggression was not significantly different between shareable and non-shareable food (Table 6.7). There was no significant effect of the interaction between the role of the lower-ranking monkey and shareability of food on PG aggression (Table 6.7). PG aggression was not affected by the CSI values of the dyads (Table 6.7). There was a non-significant tendency showing a lower aggression rate for different-sex dyads than same-sex dyads (Table 6.7).

Table 6.7. Coefficients and significance of the test and control variables entered in the GLMM to compare PG aggression between when the lower-ranking was the groomer or the groomee (N = 160).

Variables	Coefficient ± SE	Z	P	95% CIs	Significance
Groomer vs. Groomee	-0.65 ± 1.37	-0.48	0.63	-3.34 – 2.03	×
Shareability	0.18 ± 0.89	0.2	0.84	-1.57 – 1.93	×
Groomer vs. Groomee * Shareability	0.26 ± 1.31	0.2	0.85	-2.3 – 2.82	×
CSI of the dyad	-0.02 ± 0.11	-0.14	0.89	-0.22 – 0.19	×
Sex of the dyad	1.44 ± 0.78	1.85	0.06	-0.09 – 2.98	×
Rank difference	-0.07 ± 0.07	-0.92	0.36	-0.21 – 0.08	×
Time of the day:					
Morning vs. Noon	0.34 ± 0.65	0.52	0.6	-0.94 – 1.62	×
Morning vs. Afternoon	-0.92 ± 1.18	-0.78	0.44	-3.24 – 1.39	×
Noon vs. Afternoon	-1.27 ± 1.17	-1.08	0.28	-3.56 – 1.03	×
Grooming duration	-0.001 ± 0.001	-0.86	0.39	-0.004 – 0.001	×

6.3.5. (5) If dominant monkeys selectively allow subordinate monkeys around food resources, there would be no difference between aggression received when the lower-ranking monkey gets the food or not

No significant difference was found between aggression displayed when only the lower-ranking got the food or not (Table 6.8). There was no effect of CSI on aggression (Table 6.8). Aggression was lower for different-sex pairs than same-sex pairs (Table 6.8).

Table 6.8. Coefficients and significance of the test and control variables entered in the GLMM to compare aggression when the lower-ranking got the food or not (N = 367).

Variables	Coefficient ± SE	Z	P	95% CIs	Significance
Rank of who got the food	0.27 ± 0.46	0.58	0.56	-0.64 – 1.18	×
CSI of the dyad	-0.004 ± 0.06	-0.07	0.94	-0.11 – 0.1	×
Sex of the dyad	0.96 ± 0.36	2.69	0.01	0.26 – 1.66	✓
Rank difference	-0.01 ± 0.02	-0.7	0.48	-0.05 – 0.02	×
Food item	0.0003 ± 0.15	0.001	0.99	-0.3 – 0.3	×
Time of the day:					
Morning vs. Noon	0.19 ± 0.37	0.51	0.61	-0.54 – 0.92	×
Morning vs. Afternoon	-0.26 ± 0.43	-0.6	0.55	-1.11 – 0.59	×
Noon vs. Afternoon	-0.45 ± 0.43	-1.04	0.3	-1.3 – 0.4	×
Role reverse	0.48 ± 0.68	0.7	0.49	-0.87 – 1.82	×
Grooming duration	-0.001 ± 0.001	-1.44	0.15	-0.003 – 0.0005	×

6.4. DISCUSSION

The results of this study show no evidence of a short-term contingency between grooming and food tolerance in wild Barbary macaques, and this is regardless of the grooming role of the partners (Table 6.9). While tolerance was higher for shareable food, there was no effect of grooming interaction on tolerance over food. These results are consistent with a lack of short-term contingency between grooming and tolerance over food found in capuchin monkeys (Tiddi et al, 2011) and chimpanzees when controlling for social factors (Jaeggi et al, 2013). The results contrast with studies showing such evidence (e.g. de Waal, 1989, 1997), although the time frame was longer in those studies than the one used in this study (2 hours versus immediate effect).

Table 6.9. Summary of the main findings obtained for each prediction.

Predictions	Significance
(1) Tolerance over food would be higher after grooming than in control condition, and more importantly so for shareable than non-shareable food	✗
(2) Post-grooming tolerance (i.e. from dominant to subordinate monkeys) would occur more often when the lower-ranking monkey was the groomer than the groomee, and more importantly so for shareable than non-shareable food.	✗
(3) Aggression over food would occur less often after grooming than in control condition, and more importantly so for shareable than non-shareable food.	✗
(4) Post-grooming aggression would occur less often when the lower-ranking monkey was the groomer than the groomee, and more importantly so for shareable than non-shareable food.	✗
(5) If dominant monkeys selectively allowed subordinate monkeys around food resources, there would be no difference between aggression received when the lower-ranking monkey got the food or not	✗

Absence of short-term contingency between services given and received has also been found for the exchange of other services such as between food tolerance and mating opportunities (e.g. Gilby et al, 2010), and between reciprocity of food providing in experimental setups in chimpanzees (Melis et al, 2008; Brosnan et al, 2009; Yamamoto & Tanaka, 2009, 2010), capuchin monkeys (Pelé et al, 2010) and Tonkean macaques (*Macaca tonkeana*; Pelé et al, 2010). While in Chapter 5 a short-term contingency was found between the occurrence of grooming given and received, no evidence of short-term contingency between the amount of grooming given and received was found. Moreover, the short-term exchanges of different services may be more cognitively demanding as the value of each service may be different and may also varies depending on the partners involved (e.g. due to difference in their sex, age, social relationship and dominance relationship), or may involve different mechanisms than short-term reciprocity of same services (e.g. Boyd, 1992; Stevens & Gilby, 2004; Stevens & Hauser, 2004; Stevens et al, 2005; Melis & Semmann, 2010). How animals compare and value benefits and costs of different nature is still poorly understood (Stevens & Gilby, 2004).

While no contingency have been found between grooming and food tolerance, a positive relation between overall grooming received and food tolerance was found in captive Barbary macaques (Carne et al, 2011). Under the partner choice model, short-term contingencies are expected to be negligible if exchanges are affected by long-term relationship properties (Schino & Aureli, 2009, 2010). Thus, individuals would preferentially interact with partners from whom they have received the most benefits in the past over long time periods, regardless of the most recent interactions (Schino & Aureli, 2009, 2010). There is evidence that exchanges become more balanced over time in non-human primates (Schino et al, 2007; Frank & Silk, 2009; Gomes et al, 2009; Schino et al, 2009 Schino & Pellegrini, 2009; Jaeggi et al, 2010a; Tiddi et al, 2011; Jaeggi et al, 2013). For example, in a recent experiment of food tolerance in capuchin monkeys (*Cebus apella*), individuals preferred to reciprocate food tolerance according to long-term social bonds rather than according to recent food tolerance events (Sabbatini et al, 2012). Furthermore, in Barbary macaques females reciprocate grooming and interchange grooming for agonistic support and tolerance while feeding over long-time period (Carne et al, 2011). Moreover, in male Barbary macaques social affiliations such as close proximity and grooming during the non-mating season predict coalition formations during the mating season (Berghänel et al, 2011). Services may thus be exchanged according to long-term social interactions while single recent events may be negligible in Barbary macaques.

Long-term exchanges could be mediated by relationship quality, that is, individuals would make their decision about which partner to cooperate with based on the emotional states associated with each potential partner (Schino & Aureli, 2009). This mechanism obviates the need for scorekeeping and would thus not require high cognitively demanding abilities (Silk, 2002; Schino & Aureli, 2009; de Waal & Suchak, 2010; Schino & Aureli, 2010). Therefore, short-term contingencies may play a more important role in exchanges between individuals who rarely interact with each other (e.g. de Waal, 1997b; Jaeggi et al, 2013), rather than in stable social groups where social relationships are already established, such as the monkeys studied in this chapter (Roberts & Sherratt, 1998; Tan & Hare, 2013). Furthermore, the emotional mediation of reciprocity may facilitate the long-term exchanges of services of different nature (Schino & Aureli, 2009). Indeed, in the long-term the receipt of various services such as grooming, food tolerance and agonistic support may have similar emotional consequences in promoting the social bonds between individuals, and thus the overall exchanges of services between them (Schino & Aureli, 2009). Further studies would need to assess the long-term exchanges of grooming and food tolerance in wild Barbary macaques to determine whether the partner choice model can explain the lack of short-term contingency found in this study (Carne et al, 2011). While there was a tendency showing a higher level of tolerance between dyads of higher CSI values, this effect was not significant. However, it can be noted that the CSI index takes into account the frequency of proximity between individuals and the frequency of grooming interactions, but does not take into account the direction of grooming interactions and their duration.

Consequently it could not be assessed whether individuals direct more tolerance toward individuals from who they overall received more grooming in the long term (e.g. Carne et al, 2011). It is also possible that food tests are perceived as more competitive for animals than more naturally occurring feeding (Wobber et al, 2010; Jaeggi et al, 2013), especially if the food reward used is highly desirable and clumped, hindering food tolerance.

Aggression around food was not affected by grooming interaction. There is evidence that in the aftermath of grooming, aggression decreases in crested black macaques (*Macaca nigra*; Aureli & Yates, 2010), bonnet macaques (*Macaca radiate*; Silk, 1982), and long-tailed macaques (*Macaca fascicularis*; Gumert & Ho, 2008), and the probability for the monkeys to stay in proximity increases (Troisi et al, 1989; Gumert & Ho, 2008; Aureli & Yates, 2010). However, grooming may not decrease aggression in every context (e.g. Perry, 1996; Schino et al, 2005; Ventura et al, 2006). While no evidence has been found that aggression aound food decreases in the aftermath of grooming in Barbary macaques (see also Chapter 3), the rate of aggression remained low across conditions. Additionally, aggression directed toward the lower-ranking monkeys did not increase when only the lower-ranking monkeys got the food. This may suggest that the events of food tolerance observed in this study resulted in higher-ranking monkeys selectively allowing lower-ranking monkeys to feed in their proximity, that is, it did not consisted of lower-ranking monkeys stealing a part of food in front of higher-ranking monkeys, while risking to receive an aggressive response (de Waal, 1997b).

This study also highlights two main factors that may affect food tolerance in non-human primates. First, tolerance was higher for shareable than non-shareable food. When food resources can potentially be shared with other group members, the costs associated with sharing, such as a reduced food intake, may decrease, increasing the probability of food tolerance, even when food resources can be monopolisable (Kavanagh, 1972; Slocombe & Newton-Fisher, 2005; Jaeggi & van Shaik, 2011). The size, quality, availability and defendability of food resources affect food tolerance in animals (e.g. Elgar, 1986; Boccia et al, 1988; White & Wrangham, 1988; Goldberg et al, 2001; Mathy & Isbell, 2001; Johnson et al, 2004; Melis et al, 2006). Although the increase of tolerance for shareable food was not accompanied by a decrease of aggression, the aggression rate remained low.

Second, tolerance was higher and aggression lower for different-sex than same-sex dyads. This suggests that around food resources, the sex of the other group members affects the decision of an individual to be tolerant around the food or not. In this study, males favoured females around food resources. There is evidence of a positive relation between food tolerance and mating success in non-human primates (e.g. Tutin, 1979; Gomes & Boesch, 2009; van Noordwijk & van Schaik, 2009; Jaeggi & van Schaik, 2011; Dubuc et al, 2012). Future research may assess further the relation between food tolerance and mating success in Barbary macaques. Indeed, in a recent analyses conducted on 68 non-human primate species, Jaeggi and van Schaik (2011) revealed that male-female food tolerance co-evolved with the opportunities for female mate choice, that is, food possessors share with potential group mates who could provide or withhold mating opportunities. This may be also the case in Barbary macaques, where groups are multi-male-multi-female, and females mate with several males, giving opportunities for female mate choice (Heistermann et al, 2006).

In conclusion, wild Barbary macaques do not show short-term contingency between grooming and food tolerance. These findings add to the growing body of literature on exchanges of services in non-human primates (e.g. Noë, 2001; Silk, 2003; Mitani, 2006; Schino & Aureli, 2009; Jaeggi et al, 2010a; Schino & Aureli, 2010). The role of short-term contingencies in explaining reciprocal exchanges may be more complex than originally thought. The exchanges of grooming and food tolerance in non-human primates may be little affected by recent single events. Long-term exhanges between services given and received may be more balanced, and mediated by stable social relationships (Schino & Aureli, 2009, 2010; Jaeggi et al, 2013). The findings also highlight the important effect of sex of the individuals and shareability of the food resource, on food tolerance. This suggests that studies have to take into account these factors when comparing the exchanges of services in different contexts and species. Future studies would benefit to assess further the relation between long-term exchanges of food tolerance, grooming and mating opportunities in Barbary macaques and other non-human primate species to shed the light on the mechanisms underlying reciprocal exchanges.

6.5. REFERENCES

Akinyi, M. Y., Tung, J., Jeneby, M., Patel, N. B., Altmann, J. & Alberts, S. C. 2013. Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behaviour*, **85**, 559-568.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227-267.

Aureli, F. & Yates, K. 2010. Distress prevention by grooming others in crested black macaques. *Biology Letters*, **3**, 231-233.

Barelli, C., Reichard, U. H. & Mundry, R. 2011. Is grooming used as a commodity in wild white-handed gibbons, *Hylobates lar*? *Animal Behaviour*, **82**, 801-809.

Barrett, L. & Henzi, S. P. 2001. The utility of grooming in baboon troops. In: *Economics in nature: social dilemmas, mate choice and biological markets* (Ed. by R. Noë, J.

A. R. A. M. van Hooff & P. Hammerstein), pp. 119-145. Cambridge: Cambridge University Press.

Berghänel, A., Ostner, J., Schröder, U. & Schülke, O. 2011. Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, **81**, 1109-1116.

Blurton Jones, N. G. 1984. A selfish origin for human food sharing: tolerated theft. *Ethology and Sociobiology*, **5**, 1-3.

Blurton Jones, N. G. 1987. Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Social Science Information*, **26**, 31-54.

Boccia, M. L., Laudenslager, M. & Reite, M. 1988. Food distribution, dominance, and aggressive behaviors in bonnet macaques. *American Journal of Primatology*, **16**, 123-130.

Boesch, C. & Boesch, H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, **78**, 547-573.

Bolten, A. B., Robinson, F. A., Nation, J. L. & Yu, S. J. 1983. Food sharing between honeybee (*Apis mellifera*) colonies in flight cages. *Journal of Apicultural Research*, **22**, 90-100.

Brosnan, S., Silk, J., Henrich, J., Mareno, M., Lambeth, S. & Schapiro, S. 2009. Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Animal Cognition*, **12**, 587-597.

Brown, G. R., Almond, R. E. A. & van Bergen, Y. 2004. Begging, stealing, and offering: food transfer in nonhuman primates. *Advances in the Study of Behavior*, **24**, 265-295.

Bugnyar, T. & Kotrschal, K. 2002. Scrounging tactics in free-ranging ravens, *Corvus corax*. *Ethology*, **108**, 993-1009.

Bull, J. J. & Rice, W. R. 1991. Distinguishing mechanisms for the evolution of co-operation. *Journal of Theoretical Biology*, **149**, 63-74.

Carne, C., Wiper, S. & Semple, S. 2011. Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology*, **73**, 1127-1133.

Carter, G. & Wilkinson, G. 2013. Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B*, **280**, 1753.

Cheney, D. L., Moscovice, L. R., Heesen, M., Mundry, R. & Seyfarth, R. M. 2010. Contingent cooperation between wild female baboons. *Proceedings of the National Academy of Sciences*, **107**, 9562-9566.

Cords, M. 1995. Predator vigilance costs of allogrooming in wild blue monkeys. *Behaviour*, **132**, 559-569.

de Kort, S. R., Emery, N. J. & Clayton, N. S. 2003. Food offering in jackdaws (*Corvus monedula*). *Naturwissenschaften*, **90**, 238-240.

de Kort, S. R., Emery, N. J. & Clayton, N. S. 2006. Food sharing in jackdaws, *Corvus monedula*: what, why and with whom? *Animal Behaviour*, **72**, 297-304.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, **125**, 157-175.

de Waal, F. B. M. & Berger, M. L. 2000. Payment for labour in monkeys. *Nature*, **404**, 563.

de Waal, F. B. M. & Suchak, M. 2010. Prosocial primates: selfish and unselfish motivations. *Philosophical Transactions of the Royal Society B*, **365**, 2711-2722.

de Waal, F. B. M. 1989. Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution*, **18**, 433-459.

de Waal, F. B. M. 1997a. Food-transfers through mesh in brown capuchins. *Journal of Comparative Psychology*, **111**, 370-378.

de Waal, F. B. M. 1997b. The chimpanzee’s service economy: food for grooming. *Evolution and Human Behavior*, **18**, 375-386.

de Waal, F. B. M. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, **60**, 253-261.

Denault, L. K. & McFarlane, D. A. 1995. Reciprocal altruism between male vampire bats, *Desmodus rotundus*. *Animal Behaviour*, **49**, 855-856.

Dubuc, C., Hughes, K. D., Cascio, J. & Santos, L. R. 2012. Social tolerance in a despotic primate: co-feeding between consortship partners in rhesus macaques. *American Journal of Physical Anthropology*, **148**, 73-80.

Dunbar, R. I. M. & Sharman, M. 1984. Is social grooming altruistic? *Journal of comparative ethology*, **64**, 163-173.

Dunbar, R. I. M. 1991 Functional significance of social grooming in primates. *Folia Primatologica*, **57**, 121-131.

Elgar, M. A. 1986. House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour*, **34**, 169-174.

Feistner, A. & McGrew, W. 1989. Food-sharing in primates: a critical review. In: *Perspectives in primate biology. Vol. III* (Ed. by P. K. Seth & S. Seth), pp. 21-36. New Delhi: Today and Tomorrow's Printers and Publishers.

Frank, R. E. & Silk, J. B. 2009. Impatient traders or contingent reciprocators? Evidence for the extended time-course of grooming exchanges in baboons. *Behaviour*, **146**, 1123-1135.

Fruteau, C., Voelkl, B., van Damme, E. & Noë, R. 2009. Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences*, **106**, 12007-12012.

Gilby, I. C, Thompson, M. E., Ruane J. D. & Wrangham, R. W. 2010. No evidence of short-term exchange of meat for sex among chimpanzees. *Journal of Human Evolution,* **59**, 44-53.

Gilby, I. C. 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behaviour*, **71**, 953-963.

Goldberg, J. L., Grant, J. W. A. & Lefebvre, L. 2001. Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. *Behavioral Ecology*, **12**, 490-495.

Gomes, C. M. & Boesch, C. 2009. Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS One*, **4**, e5116.

Gomes, C. M., Mundry, R. & Boesch, C. 2009. Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B*, **276**, 699-706.

Goodall, J. 1986. *The chimpanzees of Gombe: patterns of behavior*. Cambridge, Massachusetts: Harvard University Press.

Gumert, M. D. & Ho, M. H. 2008. The trade balance of grooming and its coordination of reciprocation and tolerance in Indonesian long-tailed macaques (*Macaca fascicularis*). *Primates*, **49**, 176-85.

Hamilton, W. D. 1964. Genetical evolution of social behaviour. *Journal of Theoretical Biology*, **7**, 1-16.

Hattori, Y., Leimgruber, K., Fujita, K. & de Waal, F. B. M. 2012. Food-related tolerance in capuchin monkeys (*Cebus apella*) varies with knowledge of the partner's previous food-consumption. *Behaviour*, **149,** 171-185.

Hauser, M. D. 1992. Costs of deception: cheaters are punished in rhesus monkeys (*Macaca mulatta*). *Proceedings of the National Academy of Sciences*, **89**, 12137-12139.

Hauser, M. D., Chen, M. K., Chen, F., Chang, E. & Chuang, E. 2003. Give unto others: genetically unrelated cotton-top tamarin monkey preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society B*, **270**, 2363-2370.

Hauser, M. D., Teixidor, P., Fields, L. & Flaherty, R. 1993. Food-elicited calls in chimpanzees: effects of food quantity and divisibility. *Animal Behaviour*, **45**, 817-819.

Heistermann, M., Möhle, U., Wallner, B., Dittami, J., Shaw, E. & Hodges, K. 2006. Reproductive cycle and mating patterns in female Barbary macaques. In: *The Barbary macaque: biology, management and conservation* (Ed. by J. K. Hodges & J. Cortes), pp. 95-107. Nottingham: Nottingham University Press.

Hemelrijk, C. K. & Ek, A. 1991. Reciprocity and interchange of grooming and 'support' in captive chimpanzees. *Animal Behaviour*, **41**, 923-935.

Hemelrijk, C. K. 1994. Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, **48**, 479-481.

Hockings, K. J., Humle, T., Anderson, J. R., Biro, D., Sousa, C., Ohashi, G. & Matsuzawa, T. 2007. Chimpanzees share forbidden fruit. *PLoS ONE*, **2**, e886.

Hutchins, M. & Barash, D. P. 1976. Grooming in primates: implications for its utilitarian function. *Primates*, **17**, 145-150.

Jaeggi, A. V. & Gurven, M. 2013. Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis. *Proceedings of the Royal Society B*, **280**, 20131615.

Jaeggi, A. V. & van Schaik, C. P. 2011. The evolution of food sharing in primates. *Behavioral Ecology and Sociobiology*, **65,** 2125-2140.

Jaeggi, A. V., Burkart, J. M. & van Schaik, C. P. 2010a. On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of prosociality. *Philosophical Transactions of the Royal Society B*, **365**, 2723-2735.

Jaeggi, A. V., De Groot, E., Stevens, J. M. G. & van Schaik, C. P. 2013. Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, **34**, 69-77.

Jaeggi, A. V., Stevens, J. M. G. & van Schaik, C. P. 2010b. Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *American Journal of Physical Anthropology*, **143**, 41-51.

Johnson, C. A., Grant, J. W. A. & Giraldeau L.-A. 2004. The effect of patch size and competitor number on aggression among foraging house sparrows. *Behavioral Ecology*, **15**, 412-418.

Johnson, R. H. 1982. Food-sharing behavior in captive Amazon River dolphins (*Inia geoffrensis*). *Cetology*, **43**, 1-3.

Kaburu, S. S. K., MacLarnon, A., Majolo, B., Qarro, M. & Semple, S. 2012. Dominance rank and self-scratching among wild female Barbary macaques (*Macaca sylvanus*). *African Zoology*, **47**, 74-79.

Kapsalis, E. & Berman, C. M. 1996. Models of affiliative relationships among free ranging rhesus monkeys (*Macaca mulatta*) II. Testing predictions for three hypothesized organizing principles. *Behaviour*, **133**, 1235-1263.

Kavanagh, M. 1972. Food-sharing behavior within a group of douc monkeys (*Pygathrix nemaeus nemaeus*). *Nature*, **239**, 406-407.

Lehmann, J. & Boesch, C. 2008. Sex differences in chimpanzee sociality. *International Journal of Primatology*, **29**, 65-81.

Maestripieri, D. 1993. Vigilance costs of allogrooming in macaque mothers. *The American Naturalist*, **141**, 744-753.

Mathy, J. W. & Isbell, L. A. 2001. The relative importance of size of food and interfood distance in eliciting aggression in captive rhesus macaques (*Macaca mulatta*). *Folia Primatologica*, **72**, 268-277.

Melis, A. P., Hare, B. & Tomasello, M. 2006. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Animal Behaviour*, **72**, 275-286.

Melis, A. P., Hare, B. & Tomasello, M. 2008. Do chimpanzees reciprocate received favours? *Animal Behaviour*, **76**, 951-962.

Mitani, J. C. & Watts, D. P. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour*, **61**, 915-924.

Mitani, J. C. 2006. Reciprocal exchange in chimpanzees and other primates. In: *Cooperation in primates and humans: mechanisms and evolution* (Ed. by C. P. van Schaik & P. M. Kappeler), pp. 101-113. New-York: Springer.

Moore, J. 1984. The evolution of reciprocal sharing. *Ethology and Sociobiology*, **5**, 5-14.

Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y. & Uehara, S. 1992. Meat-sharing as a coalition strategy by an alpha male chimpanzee? In: *Topics in primatology* (Ed. by T. Nishida, W. C. McGrew, P. Marler, M. Pickford & F. B. M. de Waal), pp. 159-174. Tokyo: University of Tokyo Press.

Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of cooperation. In: *Economics in nature: social dilemmas, mate choice and biological markets* (Ed. by R. Noë, J. A. R. A. M van Hooff & P. Hammerstein), pp. 93-118. Cambridge: Cambridge University Press.

Noldus Information Technology. 2003. *Matman, software for matrix manipulation and analysis, version 1.1*. Wageningen, The Netherlands.

Pastor-Nieto, R. 2001. Grooming, kinship and co-feeding in captive spider monkeys (*Ateles geoffroyi*). *Zoo Biology*, **20**, 293-303.

Pelé, M., Thierry, B., Call, J. & Dufour, V. 2010. Monkeys failed to reciprocate in an exchange task. *Animal Cognition*, **13**, 745-751.

Perry, S. & Rose, L. 1994. Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capuchinus*. *Primates*, **35**, 409-415.

Perry, S. 1996. Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, **40**, 167-182.

Pinheiro, J. C. & Bates, D. M. 2000. *Mixed effects models in S and S-PLUS*. 1st edn. New York: Springer-Verlag.

Radford, A. N. & Du Plessis, M. A. 2006. Dual function of allopreening in the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*. *Behavioral Ecology and Sociobiology*, **61**, 221-230.

Roberts, G. & Sherratt, T. N. 1998. Development of cooperative relationships through increasing investment. *Nature*, **394**, 175-179.

Sabbatini G., De Bortoli Vizioli A., Visalberghi E. & Schino G. 2012. Food transfers in capuchin monkeys: an experiment on partner choice. *Biology Letters*, **8**, 757-759.

Sapolsky, R. M., Alberts, S. C. & Altmann, J. 1997. Hypercortisolism associated with social subordinate or social isolation among wild baboons. *Archive of General Psychiatry*, **54**, 1137-1143.

Scantlebury, M., Waterman, J. M., Hillegass, M., Speakman, J. R. & Bennett, N. C. 2007. Energetic costs of parasitism in the Cape ground squirrel *Xerus inauris*. *Proceedings of the Royal Society B*, **274**, 2169-2177.

Schino, G. & Aureli, F. 2008. Grooming reciprocation among female primates: a meta-analysis. *Biology Letters*, **4**, 9-11.

Schino, G. & Aureli, F. 2009. Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behavior*, **39**, 45-69.

Schino, G. & Aureli, F. 2010. Primate reciprocity and its cognitive requirements. *Evolutionary Anthropology*, **19**, 130-135.

Schino, G. & Pellegrini, B. 2009. Grooming in mandrills and the time frame of reciprocal partner choice. *American Journal of Primatology*, **71**, 884-888.

Schino, G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology,* **18**, 115-120.

Schino, G., Di Giuseppe, F. & Visalberghi, E. 2009. The time frame of partner choice in the grooming reciprocation of *Cebus apella*. *Ethology,* **115**, 70-76.

Schino, G., di Sorrentino, E. P. & Tiddi, B. 2007. Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame of reciprocation. *Journal of Comparative Psychology*, **121**, 181-188.

Schino, G., Ventura, R. & Troisi, A. 2005. Grooming and aggression in captive Japanese macaques. *Primates*, **46**, 207-209.

Silk, J. B. 1982. Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. *Behaviour,* **79**, 162-188.

Silk, J. B. 2002. Using the ‘F’ word in primatology. *Behaviour*, **139**, 421-446.

Silk, J. B. 2003. Cooperation without counting: the puzzle of friendship. In: *The genetic and cultural evolution of cooperation* (Ed. by P. Hammerstein), pp. 37-54. Cambridge: The MIT Press.

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P. & Shapiro, S. 2013. Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour*, **85**, 941-947.

Slocombe, K. E. & Newton-Fisher, N. E. 2005. Fruit sharing between wild adult chimpanzees (*Pan troglodytes schweinfurthii*): a socially significant event? *American Journal of Primatology*, **65**, 385-391.

Soltis, J. 2004. Mating systems. In: *Macaque societies: a model for the study of social organization* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 135-151. Cambridge: Cambridge University Press.

Stammbach, E. 1988. Group responses to specially skilled individuals in a *Macaca fascicularis* group. *Behaviour,* **107**, 241-266.

Stanford, C. B., Wallis, J., Mpongo, E. & Goodall, J. 1994. Hunting decisions in wild chimpanzees. *Behaviour,* **131**, 1-18.

Stevens, J. & Stephens, D. 2002. Food sharing: a model of manipulation by harassment. *Behavioral Ecology,* **13**, 393-400.

Stevens, J. R. & Gilby, I. C. 2004. A conceptual framework for non-kin food sharing: timing and currency of benefits. *Animal Behaviour,* **67**, 603-614.

Stevens, J. R. & Hauser, M. D. 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences,* **8**, 60-65.

Stevens, J. R. 2004. The selfish nature of generosity: harassment and food sharing in primates. *Proceedings of the Royal Society B*, **271**, 451-456.

Stevens, J. R., Cushman, F. A. & Hauser, M. D. 2005. Evolving the psychological mechanisms for cooperation. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 499-518.

Strum, S. C. 1981. Processes and products of change: baboon predatory behavior in Gilgil, Kenya. In: *Omnivorous primates: gathering and hunting in human evolution* (Ed. by R. S. O. Harding & G. Teleki), pp. 255-302. New York: Columbia University Press.

Tan, J. & Hare, B. 2013. Bonobos share with strangers. *PLoS ONE*, **8**, e51922.

Tanaka, I. & Takefushi, H. 1993. Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropological Science*, **101**, 187-193.

Tiddi, B., Aureli, F. & Schino, G. 2012. Grooming up the hierarchy: the exchange of grooming and rank-related benefits in a new world primate. *PLoS ONE*, **7**, e36641.

Tiddi, B., Aureli, F., di Sorrentino, E. P., Janson, C. H. & Schino, G. 2011. Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. *Behavioral Ecology*, **22**, 663-669.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *The Quarterly Review of Biology*, **46**, 35-57.

Troisi A., Schino G. & Aureli F. 1989. Allogrooming and interindividual proximity in two species of macaques (*Macaca fascicularis* and *M. nemestrina*). *Behaviour*, **111**, 196-206.

Tutin, C. E. G. 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, **6**, 29-38.

van Noordwijk, M. A. & van Schaik, C. P. 2009. Intersexual food transfer among orangutans: do females test males for coercive tendency? *Behavioral Ecology and Sociobiology*, **63**, 883-890.

Ventura, R., Majolo, B., Koyama, N., Hardie, S. & Schino G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology*, **68**, 1138-1149.

Watts, D. P. & Mitani, J. C. 2002. Hunting and meat sharing by chimpanzees at Ngogo, Kibale National Park, Uganda. In: *Behavioural diversity in chimpanzees and bonobos* (Ed. by C. Boesch, G. Hohmann & L. Marchant), pp. 244-255. Cambridge: Cambridge University Press.

Watts, D. P. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, **139**, 343-370.

Westergaard, G. C. & Suomi, S. J. 1997. Transfer of tools and food between groups of tufted capuchins (*Cebus apella*). *American Journal of Primatology*, **43**, 33-41.

Westergaard, G. C., Kuhn, H. E., Babitz, M. A. & Suomi, S. J. 1998. Aimed throwing as a means of food transfer between tufted capuchins (*Cebus apella*). *International Journal of Primatology*, **19**, 123-131.

White, F. J. & Wrangham, R. W. 1988. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour*, **105**, 148-163.

Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bat. *Nature*, **308**, 181-184.

Wobber, V., Hare, B., Maboto, J., Lipson, S., Wrangham, R. & Ellison, P. T. 2010. Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proceedings of the National Academy of Sciences*, **107**, 12457-12462.

Xue, M. & Su, Y. 2011. Food transfer in Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). *International journal of primatology*, **32**, 445-455.

Yamamoto, S. & Tanaka, M. 2009. Do chimpanzees (*Pan troglodytes*) spontaneously take turns in a reciprocal cooperation task? *Journal of Comparative Psychology*, **123**, 242-249.

Yamamoto, S. & Tanaka, M. 2010. The influence of kin relationship and reciprocal context on chimpanzees’ other-regarding preferences. *Animal Behaviour*, **79**, 595-602.

Zamma, K. 2002. Grooming site preferences determined by lice infection among Japanese macaques in Arashiyama. *Primates,* **43**, 41-49.

Chapter 7

Introducing a cooperative task to a wild group of Barbary macaques: performance and partner choice

Chapter 6 investigated the exchange of grooming for food tolerance by analysing the short-term contingency between these events. No evidence has been found of short-term contingency between grooming and food tolerance. The findings highlighted the important effect of sex of the individuals and shareability of the food resource, on food tolerance. The exchanges of grooming and food tolerance in non-human primates may be little affected by recent single events. The current Chapter investigates whether wild Barbary macaques succeed to cooperate in an experimental task to get food rewards, and which individual and social factors (i.e. sex, age, dominance status, tolerance, relationship quality and temperament) affect their choice of partners and their performance in solving the task.

7.1. INTRODUCTION

Cooperation is generally defined as any behaviour benefitting another individual (e.g. West et al, 2007). Cooperation increases individual success as by cooperating together animals can obtain benefits that they could not attain alone (e.g. West et al, 2007; Clutton-Brock, 2009; de Waal & Suchak, 2010; Melis & Semmann, 2010). Group hunting, group defence, cooperative breeding, tolerance around food resource, grooming and coalition have been considered as examples of cooperative behaviours (Boesch & Boesch, 1989; Dukatkin, 1997; Gazda et al, 2005; Clutton-Brock, 2009; Melis & Semmann, 2010). Cooperative behaviours include mutual cooperation (also called mutualism; de Waal, 2000), defined as cooperative interactions that yield simultaneously benefits to the participants involved, and reciprocity (Trivers, 1971), where individuals take turns in giving and receiving benefits (Noë, 2001, 2006; Melis & Semmann, 2010). This Chapter focuses on mutual cooperation and the exchange of services was discussed in Chapters 5 and 6. Since mutual cooperation produces benefits that are difficult to be obtained by an individual alone, the resulting cooperative interaction is principally self-serving, even if it benefits other participants at the same time (de Waal & Suchak, 2010). When analysing the cooperative hunting behaviour of wild chimpanzees (*Pan troglodytes*), Boesch and Boesch (1989) suggested different levels of cooperation depending on cognitive abilities, ranging from simple synchronous actions to division of labour among participants. Research in laboratory gives the advantage to test the cooperative abilities of animals in a more controlled environment in order to assess the mechanisms underlying cooperative events, such as cognitive abilities.

Cooperative tasks have been developed to test the ability of two animals to act simultaneously to reach a common goal. In most of the experiments, two individuals have to simultaneously manipulate two ropes or bars in order to get food (e.g. Hirata & Fuwa, 2007). While these tasks require cooperation, they do not necessarily demonstrate an understanding of this condition by the subjects (Mendres & de Waal, 2000), that is, simultaneous action may occur regardless to whether or not the subjects take into account the role of their partner in solving the task. Although simultaneity is an essential proximate mechanism of cooperation, comprehension of the partner's role is a cognitive ability that also requires to be assessed when running cooperative tests on animals (Noë, 2006). Comprehension of the partner's role would allow individuals to actively coordinate their actions with those of their partner, facilitating joint action, instead of showing 'simple' co-production, where individuals simultaneously but independently direct similar actions toward a common goal (Melis & Semmann, 2010).

A classic cooperative experiment was first conducted by Crawford (1937, 1941) to test the capacity of young chimpanzees to coordinate their movements to solve a task. The task required the two subjects to simultaneously pull two ropes to bring within arm's reach a heavy box containing food. The box was too heavy to be pulled by one chimpanzee alone. The subjects only succeeded to act simultaneously after being extensively trained to do so, and they failed to transfer their skill to a version of the test where the ropes needed to be pulled vertically instead of horizontally (Crawford, 1937, 1941). Crawford's paradigm (1937) has been conducted on a variety of species, sometime producing contrasting results. This is, for example, the case of studies conducted on tufted capuchin monkeys (*Cebus apella*) using Crawford's basic paradigm (1937). Capuchin monkeys were tested in a task requiring that two monkeys pulled a handle simultaneously in order to receive a food reward (Chalmeau et al, 1997b; Visalberghi et al, 2000). While the subjects were successful at pulling simultaneously, they did not increase their pulling when a partner was close to the other handle, that is, when cooperation might occur. The authors concluded that the success was due to random coaction, i.e. the co-occurrence of two monkeys pulling one handle at the same time due to chance, and that capuchins did not seem to take into account the behaviour of their partner (Chalmeau et al, 1997b; Visalberghi et al, 2000).

Mendres and de Waal (2000) tested the same species in a task requiring two monkeys to pull two bars attached to a tray with food cups. The tray was counter-weighted so that a single monkey could not pull the tray within reach alone. The capuchins succeeded to pull simultaneously, they pulled at higher rate when their partner was present than absent, and the elimination of visual contact (by using an opaque screen between the two monkeys) decreased the number of success (Mendres & de Waal, 2000). The authors concluded that capuchins did seem able to learn some aspect of their partner’s role in solving the task. Later, Hattori and colleagues (2005) showed that capuchins were able of division of labour to solve a task, that is, to divide an effective sequence of acts among partners to reach a common goal. Similar results were found in a recent study on chimpanzees (Melis & Tomasello, 2013). The difference of cognitive abilities shown by different subjects of the same species across studies is puzzling. One hypothesis proposed to explain the discrepancy of results across studies on capuchins was that the type of task used may affect the level of coordination achieved by the animals (Mendress & de Waal, 2000). For example, Mendres and de Waal (2000) proposed that tasks involving a device where the cause and effect relationship was more intuitive and closer to natural behaviour, such as tasks requiring pulling food toward themselves (e.g. Mendres & de Waal, 2000), might be more intuitive for the individuals and more ecologically valid than more complex mechanisms such as electronically mediated devices releasing food through an opaque tube (e.g. Chalmeau et al, 1997b). The puling task (Crawford, 1937; Mendres & de Waal, 2000; Hirata & Fuwa, 2007) has the advantage of both visual and kinesthetic feedback in the course of the simultaneous action toward the common goal (i.e. reaching the food reward). This may facilitate the understanding of the cause and effect relationship of the mechanism by the subjects (de Waal & Suchak, 2010). Moreover, the puling task is equivalent to natural resource acquisitions in the natural habitat of non-human primates, such as pulling branches toward self to reach fruits and leaves (Mendres & de Waal, 2000).

Success in simultaneous pulling, a few with some understanding of the partner's role (i.e. that the presence of the partner was needed to solve the task) has further been shown in orangutans (*Pongo pygmaeus*; Chalmeau et al, 1997a), cotton-top tamarins (*Saguinus oedipus*; Cronin et al, 2005), chimpanzees (*Pan troglodytes*; Chalmeau, 1994; Melis et al, 2006a, 2006b; Hirata & Fuwa, 2007), bonobos (*Pan paniscus*; Hare et al, 2007), and more recently in non-primate species such as rooks (*Corvus frugilegus*; Seed et al, 2008; Scheid & Noë, 2010), African grey parrots (*Psittacus erithacus*; Péron et al, 2011), hyenas (*Crocuta crocuta*; Drea & Carter, 2009), and Asian elephants (*Elephas maximus*; Plotnik et al, 2011). Pilot experiments showed that wolves were also able to coordinate their pulling to get food (*Canis lupus*; Möslinger et al, 2009). Furthermore, in a task where the arrival of the partner at the cooperative apparatus was delayed, chimpanzees (Melis et al, 2006a) and Asian elephants (Plotnik et al, 2011) were able to wait the arrival of their partner before pulling. The authors of these last studies concluded that the animals understood the need of their partner to solve the task. On the contrary, African grey parrots (Péron et al, 2011) and rooks (Seed et al, 2008) seemed unable to inhibit their pulling before the arrival of their partner.

Most of the experimental studies conducted so far on mutual cooperation have focused on simultaneity of actions and understanding of the partner's role. Nevertheless, partner choice is a significant mechanism of cooperation that still needs to be assessed in animals. Indeed, the choice of partner with whom to cooperate is key to initiate and maintain cooperative behaviours (Noë, 2006). Choosing the best available partner (e.g. in term of reliability or ability) improves the chances to establish a successful cooperative interaction and decreases the chances to be exploited (Noë, 2001, 2006). Unsatisfactory cooperative partners may be abandoned and replaced with other partners providing greater benefits (Noë & Hammerstein, 1994; de Waal & Suchak, 2010). In most of the cooperative tasks conducted so far, subjects were given no opportunity to choose their cooperative partner, or the choice was reduced to two individuals. For example, chimpanzees (*Pan troglodytes*) were able to recruit a cooperative partner (by unlocking the door of their partner to let them enter in the testing area) only when solving the problem required cooperation (Melis et al, 2006a). Moreover, chimpanzees recruited the most efficient partner for the cooperative task (chosen between two available individuals) based on their experience with each of them on a previous day (Melis et al, 2006a).

Group-living animals live in complex social group and can choose their social partners among several individuals differing in for example age, sex, abilities, competitive power, relationship quality and tolerance with the other animals, and temperament. The capacity to make effective choices among potential social partners is thus an important social skill. Therefore, it is necessary to assess the mechanism underlying the choice of cooperative partner in a social context. For this reason, experimental designs need to give to the subjects the opportunity of partner choice and partner switching (Noë, 2006). This would allow to assess which social and individual factors affect the choice of partners and their performance in solving cooperative tasks.

Tolerance between partners would improve the success of cooperation: subjects would be more motivated to cooperate with potential partners with whom they have a high level of tolerance (e.g. Melis et al, 2006b; Hare et al, 2007). This implies that more tolerant species would perform better in cooperative tasks than less tolerant species. For example, the capacity of two or more monkeys to push heavy stones to retrieve food hidden under it has been assessed in several monkey species. The simultaneous action by two or more individuals in moving the same stone was very rare in baboons (*Papio papio*; Fady, 1972), Japanese macaques (*Macaca fuscata*; Burton, 1977), and rhesus macaques (*Macaca mulatta*; Petit et al, 1992). Although it occurred more frequently in Tonkean macaques, no signs of coordination among partners and no improvement through learning were found (*Macaca tonkeana*; Petit et al, 1992). Petit and colleagues (1992) suggested that the simultaneous actions observed were dependent on the level of inter-individual tolerance of the subjects, the Tonkean macaques being more tolerant than rhesus and Japanese macaques (Petit et al, 1992; Thierry, 2000). Indeed, whereas rhesus macaques are characterized by strong dominance asymmetry and intense unidirectional aggression, dominance is more relaxed and aggression more bidirectional in Tonkean macaques (Thierry, 1985, 2000). Because of their social tolerance, the Tonkean macaques were more likely to produce similar behaviour simultaneously (i.e. pushing the same stone) than rhesus macaques (Petit et al, 1992). Similarly, higher level of inter-individual tolerance while cofeeding allowed bonobos to outperform chimpanzees on a cooperative task where the food reward was highly monopolisable (Hare et al, 2007). Bonobos maintain juvenile level of food tolerance into adulthood whereas chimpanzees become intolerant as they age (Wobber et al, 2010). Also, the high level of social tolerance of capuchin monkeys allowed them to obtain food through simultaneous actions without taking the role of their partner into account (Chalmeau et al, 1997b; Visalberghi et al, 2000).

Inter-individual tolerance between two animals of the same species would affect their performance when tested in tasks requiring joint effort. In chimpanzees, pairs that were more willing to share food outside the cooperative task, were more able to cooperate spontaneously by simultaneously pulling two ropes to get food (Melis et al, 2006b). Moreover, previously successful subjects stopped to cooperate if paired with a less tolerant partner (Melis et al, 2006b). Thus tolerance acted as a constraint on the ability of chimpanzees to solve the cooperative problem. In rooks, the performance of two birds in solving a cooperative task was higher when within-dyad tolerance was higher (Seed et al, 2008). In many of the studies conducted so far researchers have artificially paired up two subjects for a cooperative task without controlling for the tolerance level of the pairs. This lack of control for the tolerance level of the two subjects might partially explain the variance of the performances found in non-human primates (e.g. Chalmeau, 1994). Besides tolerance, there is a growing body of evidence showing that relationship quality between two animals positively affects prosocial behaviour and long-term reciprocity, as strong social bonds would reduce the uncertainty about the partner response (Noë, 2001; Silk, 2002, 2003; Brosnan et al, 2005; Noë, 2006; de Waal et al, 2008; Schino & Aureli, 2009; Chang et al, 2011; Tiddi et al, 2011; Cronin, 2012; Sabbatini et al, 2012; Jaeggi et al, 2013; Silk et al, 2013). Relationship quality between two animals may also affect mutual cooperation. Strong affiliative bonds may be based on kinship or on friendship between unrelated animals (Silk, 2002, 2005; Chapais, 2006; Silk, 2006; Jaeggi et al, 2010). For example, the success of capuchins in solving a cooperative task to receive clumped food was lower in non-kin than kin dyads (de Waal & Davis, 2003). However, the effect of relationship quality on the performance of animals in mutual cooperation still needs to be assessed.

Like tolerance and social bond, other factors such as the age, sex, dominance status and temperament of the subjects tested may affect their choice of partner and their performance in cooperative tasks, and should be controlled for. For example, in chimpanzees dominant individuals monopolised the cooperative apparatus, preventing lower-ranking subjects from solving the task (Chalmeau & Gallo, 1993). In hyenas, dyads involving the most dominant partner were relatively inefficient in solving the cooperative task compared to dyads of lower-ranking subjects, due to a higher rate of aggressive behaviours received from the most dominant subject (Drea & Carter, 2009). Capuchin monkeys cooperated less with dominant than subordinate subjects when the food reward was clumped (de Waal & Davis, 2003). Moreover, wild vervet monkeys (*Chlorocebus aethiops*) cooperated more with partners of similar dominance rank to their own (Pansini, 2011). The temperament of the individuals tested may also influence the cooperative success of the dyads (Bergmüller et al, 2010; McNamara & Leimar, 2010). In rooks, bolder birds were more willing to approach the apparatus and to solve the task than shier birds, that were willing to approach the apparatus only when another bird was already present (Scheid & Noë, 2010). Moreover, the subjects performed better in the cooperative task when paired with a bolder than shier partner (Scheid & Noë, 2010). Furthermore, capuchins (Mendres & de Waal, 2000) and cotton-top tamarins (Hauser et al, 2003) performed better in a cooperative task with same-sex than different-sex partners, contrary to wild vervet monkeys where a mixed effect was found (Pansini, 2011). Finally, the age of the subjects did not affect their cooperative performance in chimpanzees (Melis et al, 2006b) and wild vervet monkeys (Pansini, 2011). Therefore, there is still to assess the relative role of each of these factors in affecting partner choice and performances of animals belonging to the same population.

The aim of this chapter was to investigate the mechanisms underlying mutual cooperation with an experimental setting in wild Barbary macaques (*Macaca sylvanus*). In this study, a wild provisioned group of Barbary macaques was presented with a cooperative task. The monkeys could choose to interact or not with the apparatus and they had the opportunity to choose their cooperative partners among their group members (i.e. partners were not artificially paired up by the experimenter). This approach is expected to have a higher ecological validity than artificially pairing-up animals, and may bring important insights into the mechanisms underlying the choice of cooperative partners (Noë, 2006). The basic paradigm of Crawford's cooperative task (1937) was adapted to be conducted on wild macaques in their natural environment. This allowed to compare the results of this study with the results of laboratory studies using the same string pulling paradigm. To solve the task, two monkeys had to manipulate simultaneously the two ends of the same rope in order to bring within arm's reach a tray containing a food reward for each partner (Hirata & Fuwa, 2007). The Barbary macaque is a relatively tolerant species (Thierry et al, 2004; Thierry & Aureli, 2006; Chapter 2 of this thesis), also sharing some social features with more despotic macaque species such as low frequency of counter-aggression (Balasubramaniam et al, 2012), a steep dominance hierarchy (Kaburu et al, 2012), and grooming coercion (McFarland & Majolo, 2011b). There is evidence that Barbary macaques reciprocate and interchange grooming interactions, coalitions, and food tolerance (Widdig et al, 2000; Berghänel et al, 2011; Carne et al, 2011; Chapter 5 of this thesis). This species is thus of particular interest to experimentally assess cooperative behaviours. To my knowledge, this is the first study assessing cooperative behaviour with an experiment on a wild macaque species, and assessing the factors which may affect the choice of cooperative partners in a social context. Indeed, so far almost all the cooperative tasks have been conducted solely on captive animals artificially paired up in dyads (see Pansini, 2001 and Petit et al, 1992 for exceptions, respectively). More precisely, this chapter investigated:

(1) Whether wild Barbary macaques succeed to cooperate with a group member in an experimental task.

(2) Whether individual and social factors, that is, tolerance, relationship quality, dominance status, age, sex and temperament (i.e. shyness toward humans) affect their choice of partners and their performances in solving the task.

7.2. METHODS

7.2.1. Study subjects

Subjects were from the ‘Tourist group’, a wild partially-provisioned group of Barbary macaques living in the Middle Atlas Mountains of Morocco. The group was composed of 24 adult and sub-adult monkeys (11 males and 13 females), 12 juveniles (7 males and 5 females) and several infants. The group lived in the deciduous cedar and oak forest of the Ifrane National Park, between 1600 and 1860m a.s.l. The group was often close to tourists, who fed the monkeys with a variety of food such as fruits, bread and peanuts. See Chapter 2 for more details on the study animals and field site. Three juveniles (2 males and 1 female) deceased during the study period and were consequently not included in the analyses although they interacted with the experimental tasks. While the previous chapters focused only on sub-adults and adults, the juveniles were also included in the study of this chapter as they freely interacted a lot with the experiments. It is common to include juveniles in the analyses of cooperative experimental study (e.g. Crawford, 1937; Petit et al 1992; Chalmeau & Gallo, 1996; Chalmeau et al, 1997b;

Visalbergji et al, 2000; Hattori et al, 2005; Melis et al, 2006b; Hare et al, 2007; Pansini, 2011). However, because the data collection of this thesis was not initially planned to be conducted on juveniles, hourly scans and ad libitum data were not collected between juveniles (see Chapter 2). Two classes of age were considered in this chapter: adults (including sub-adults) from 4 years old for females and from 5 years old for males, and juveniles from 1 to 3 years old for females and from 1 to 4 years old for males. Infants (i.e. less than 1 year old) were not considered in this study.

7.2.2. Data collection

Data were collected from November 2010 to January 2012. During all the study period the monkeys were free to approach and interact with the experimental tasks. Moreover, the experimental tasks were always presented to the monkeys in the part of their home range where tourists often visit and feed them, which reduced the possible disruption effects that the introduction of the tasks could play on the monkeys.

7.2.2.1. Social and individual factors

Scan samples (Altmann, 1974) were collected every hour to assess the dyadic relationship quality and tolerance of the monkeys. Cofeeding frequency was used as a measure of tolerance. During these hourly scans, for each visible subject, their proximity (i.e. $\leq$ 1.5m but not grooming) or grooming with other group members were recorded, as well as the identity of their social partner (see Chapter 2 for further details). The occurrence of cofeeding, defined as a monkey feeding within 2m of another monkey, was also recorded as well as the identity of the cofeeding partner. Because research for this thesis was not initially planned to be conducted on juveniles, only data between two adults and between one adult and one juvenile, but no data between two juveniles were recorded during these hourly scans (see Chapter 2). Three females were considered to be juvenile at the beginning of the data collection of this thesis but sub-adult at the beginning of the experimental data collection. Thus, although their data were recorded as sub-adult during the experimental tasks of this Chapter, their data were recorded as juvenile during the hourly scans. Consequently, data between one juvenile and each one of these adults, as well as data between each of these adults, were not recorded during the hourly scans (see Chapter 2).

Ad libitum data (Altmann, 1974) were used to determine the dominance hierarchy of the monkeys. Ad libitum data were collected opportunistically on any observed dyadic conflicts not involving third parties and with a clear-cut result (i.e. one opponent displayed aggressive behaviour and the other opponent displayed submissive behaviour; see Chapter 2 for details on the aggressive and submissive behaviours recorded). Because the study was planned to be conducted mainly on adults and sub-adults, and because dominance status between juveniles is unstable and not properly defined, only dominance relationship between adults and sub-adults was assessed (see Chapter 2).

The experimenters were always present near the tasks to place food reward and check their proper functioning. Therefore, a temperament test was conducted on every monkey (i.e. adults, sub-adults and juveniles) of the group in order to assess individual differences in shyness toward humans. This test assessed at which distance a monkey would flee an approaching human. A test started when a monkey was seating without any other monkey within 1.5m around, and one experimenter was standing at 4m in front of the monkey. The experimenter first coughed to have the monkey focused on his presence, and then walked straight toward the animal at stable pace, without directly looking into their eyes. The test stopped (i.e. the experimenter stopped to walk) when the subject moved away from the experimenter or if the monkey did not move, when the experimenter arrived at 40cm in front of the monkey. The distance at which the subject started to move away from the experimenter was recorded. If the subject did not move at the end of the test, the distance of 40cm was attributed to that monkey. The shorter the distance was, the bolder the monkey was considered to be. Three tests were conducted for each monkey.

7.2.2.2. Apparatus

To test the ability of wild Barbary macaques to cooperate in an experimental setting, the Crawford's string pulling paradigm was used (1937). This paradigm has already been successfully conducted on a variety of primates species (e.g. Chalmeau et al, 1997a, 1997b; Mendres & de Waal, 2000; Visalberghi et al, 2000; Cronin et al, 2005; Melis et al, 2006a, 2006b), birds (e.g. Seed et al, 2008; Scheid & Noë, 2010), spotted hyenas (*Crocuta crocuta*; Drea & Carter, 2009) and Asian elephants (*Elephas maximus*; Plotnik, 2011). Moreover, similar tasks where monkeys had to pull the bar of a baited tray were conducted on long-tailed macaques (*Macaca fascicularis*; Massen et al, 2010), which suggests that the string pulling paradigm can be used with macaques.

The string pulling principle was kept in this study and the task was adapted to be used in the field with wild monkeys. The apparatus used in this study consisted of two identical boxes of 85 x 35 x 35cm each (L x H x W; Figure 7.1). Four 10cm legs assured the stability of each box on the ground. The sides and roof of the boxes were made of clear Perspex which allowed a see-through view of the inside of each box. Consequently, the entire mechanism of the apparatus, as well as the food rewards, were constantly visible for the monkeys. This allowed the monkeys to easily monitor the effect of their actions on the apparatus and the rewards (Mendres & de Waal, 2000). Each box contained a 10cm wide tray which could slide along the length of the box through a rail.

A jar lid was fixed in the middle of each tray and used to contain food rewards. The tray could be brought within arm's reach, from the back to the front of the box by pulling a rope from the front of the box. A total length of 75cm had to be pulled to bring the tray within arm's reach. Another rope could be pulled at the back of each box by the experimenters to bring back the tray to its initial position and bait it. In the middle of the front of each box, a 10cm diameter hole was made through the Perspex to allow the monkeys to introduce one hand and grab the food reward when the tray was within arm's reach. Underneath this hole, at the bottom, a smaller hole of 1.2cm diameter allowed the rope to extend outside the box. A flap was cut and placed at the back of each box and could be opened by the experimenters to bait the tray. Pilot tests determined that slices of fruits and vegetables, as well as peanuts, best motivated the monkeys to use the apparatus. More precisely, slices of mandarin, orange, apple, banana, tomato, courgette and carrot, as well as some peanuts were used to bait the trays.

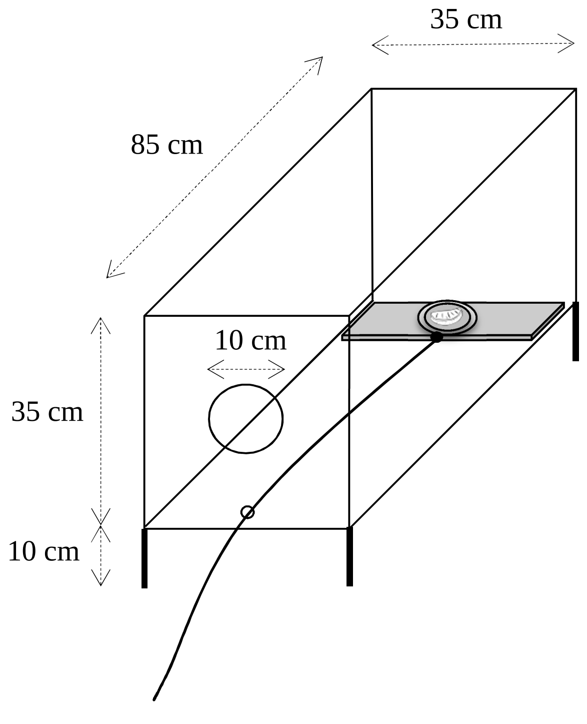


Figure 7.1. Schema detailing the features and dimensions of one box used for the experiment.

7.2.2.3. Training

The monkeys were first trained to use the apparatus from November 2010 to March 2011. During the training, only one box was used and one rope was directly attached to the tray (Figure 7.1). Through the shaping technique, the monkeys learned to use one box to get food, that is, to pull the rope to bring the tray within arm’s reach and get the food reward placed on it. The first phase was to get the wild monkeys habituated to the box and that they associated it with food. For this, the tray was baited and placed within arm’s reach at the front of the box. The monkeys had to introduce one hand into the front hole to reach the reward. Some food rewards were also dispersed around the box to attract the monkeys. When the subject became proficient in reaching the reward inside the box, the training moved to the second phase for the monkey.

During the second phase, the tray was baited but placed out of reach at the back of the box. The monkeys had to pull the rope to bring the tray within arm’s reach and grasp the reward inside the box. This sequence of behaviours is very similar to behaviours within the repertoire of non-human primates, such as pulling a branch to reach the food attached to it. For example, Barbary macaques often pull branches toward themselves to reach acorns. No more food was placed around the box during the second phase. A subject was considered trained when it performed the full sequence for a minimum of 15 times. Twenty one monkeys (7 males and 14 females, 17 adults and 4 juveniles) met this criterion during the training and were thus considered to be trained. Five additional monkeys (3 males and 2 females, all juveniles) learned to use the apparatus during the testing period without being trained by the experimenter. It is interesting to note that, contrary to chimpanzees (Chalmeau & Gallo, 1993), the most dominant monkeys in this study (i.e. higher-ranking males) were not interested in the apparatus, thus they did not get trained to use the apparatus and they never monopolised the tasks.

7.2.2.4. The cooperative test and control

The tasks were conducted from March 2011 to January 2012. The presentations of the cooperative and control tests were alternated during the study period. Individuals were free to interact with the tasks and to choose their partner. During the cooperative test, the two boxes were joined together at 215cm apart (Figure 7.2). The two trays (i.e. one for each box) were attached together with a wood plank (painted in blue colour) to form a longer tray across the boxes (Figure 7.2). The ‘loose string paradigm’ of Hirata and Fuwa (2007) was used. For this, a long rope went freely along the two boxes and tray, as well as through two pulleys placed on both extremities of the tray. Each end of the rope extended in front of each box. Consequently, the tray could only be brought within arm’s reach if two monkeys manipulated simultaneously both ends of the rope, either by pulling both ends, or by pulling one end and holding the other one. If only one monkey pulled one end of the rope, the rope moved freely through the pulleys and the tray did not move. In that case, the experimenters stopped the rope before the monkey could run away with it. Because of the 215cm distance between the two boxes it was not possible for one monkey alone to simultaneously manipulate the two ends of the rope. Food rewards were placed on both lids inside each box, and were always of the same kind and quantity across the two boxes. The trays were baited each time two monkeys succeeded to cooperate and finished consuming their reward.

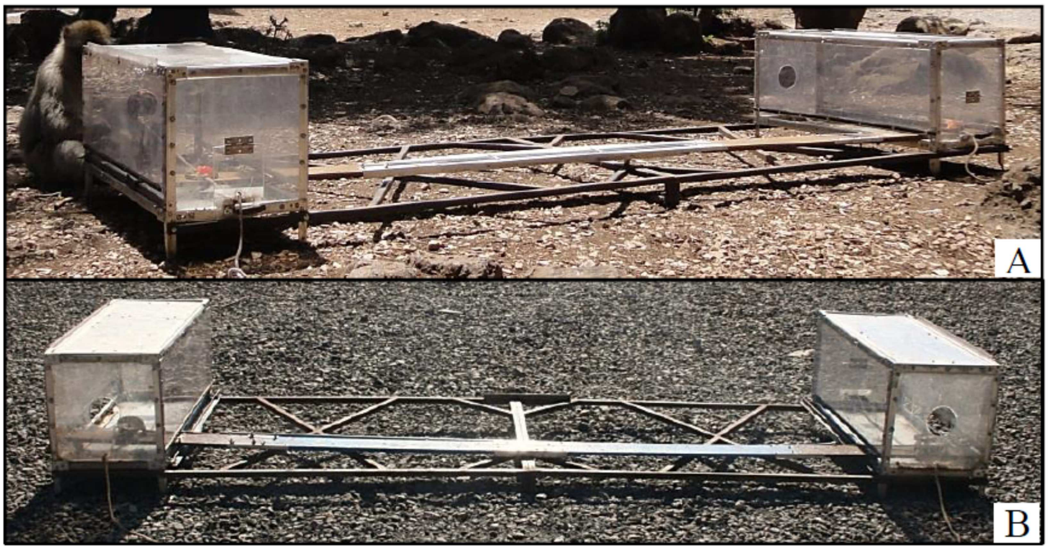


Figure 7.2. Pictures from the back (A) and front (B) of the cooperative test: in order for two monkeys to solve the task and both get a reward, they had to coordinate their movements and manipulate the two ends of the rope at the same time (pictures by S. Molesti).

During the control condition, the two boxes were also joined together, but not the trays. A rope was attached to each single tray (painted in brown colour). Consequently, the two trays worked independently and the monkeys did not need to act simultaneously to obtain food. One monkey alone could pull one rope to bring one tray within reach and get the reward, and could do this independently from each of the two boxes. Each tray was baited anew when a monkey got the reward and finished consuming it. The cooperative and control apparatuses were thus visually distinguishable: the cooperative apparatus contained a long blue tray across the two boxes, while the control apparatus contained two single brown trays inside each box. Because each side of the boxes was made of Perspex, for each apparatus the monkeys could monitor the effect of their behaviours on the movements of the tray, rope and food rewards.

The cooperative and control tests were made available to the monkeys during sessions of 40 minutes, several times per day. Sessions were stopped when no monkey approached the tasks for 10 minutes. During each session, focal sampling focusing on the tasks was used to continuously record the ID and behaviours of each monkey manipulating each box. For each monkey, the occurrences of pulling and holding the rope were recorded in relation to the presence or absence of a partner in front of the other rope or within 1.5m all around the tasks. Additionally, it was recorded whether the tray was successfully brought within arm's reach or not. Each behaviour had to be separated by 5 seconds to be considered two separate events.

The behaviours were then classified into three categories: (1) manipulating the rope alone, (2) manipulating the rope next to a partner, and (3) success. (1) 'Manipulating alone' was defined as a monkey pulling or holding the rope while no partner was present in front (i.e. within 50 cm) of the second rope for the control or in front of the other end of the rope for the cooperative test. (2) 'Manipulating next to' was defined as a monkey pulling or holding the rope while a partner was within arm's reach of the second rope for the control or in front of the other end of the rope for the cooperative test. For this last category, the partner could be manipulated the rope it was in front to or not. (3) 'Success' was defined as two monkeys manipulating simultaneously the two ends of the rope during the cooperative test and succeeded to bring the tray within arm's reach. This could be achieved by either two monkeys pulling simultaneously both ends of the rope, or by one monkey pulling one end while the partner held the other end. Consequently, the category 'manipulating next to' also included the successes for the cooperative test. For each monkey, their first success corresponded to the first time they solved the cooperative test. While by pulling the rope alone the monkeys could not get the reward during the cooperative test, the monkeys could bring the tray within arm's reach and get the reward by pulling alone during the control.

7.2.3. Data analysis

7.2.3.1. Social and individual factors

A composite sociality index (hereafter CSI) was calculated to measure the relationship quality between two individuals, based on the data collected during 929 hourly scans. For each dyad, their CSI was calculated based on the formula (Silk et al, 2006):

$$\frac{\sum_{i=1}^{2} \frac{x_i}{m_i}}{2}$$

x_i = dyad's value for each of the two behavioural measures (i.e. the proportion of hourly scans in which two monkeys of a dyad were grooming, or in proximity, divided by the total number of scans in which the general activity of the two animals was recorded).

m_i = group's mean value for the proportion of hourly scans spent grooming, or in proximity, by the whole group.

A high CSI indicates a high quality relationship between the two monkeys of the dyad. The CSI values ranged from 0 to 16.1 (mean CSI value ± SE = 1 ± 0.07). Dyads with a CSI value above the group's mean were labelled 'strong relationship' partners, whereas dyads with a CSI value under the group's mean were labelled 'weak relationship' partners. Cofeeding frequency was calculated as the proportion of hourly scans in which two monkeys were within 2m and at least one monkey was feeding, divided by the total number of scans in which the general activity of the two monkeys was recorded. Cofeeding frequencies ranged from 0 to 0.13 (mean cofeeding frequency ± SE = 0.01 ±

0.001). Dyads with a cofeeding frequency above the group’s mean were labelled ‘high tolerance’ partners, whereas dyads with a cofeeding frequency under the group’s mean were labelled ‘low tolerance’ partners.

Based on the dyadic conflicts collected ad libitum, a winner-loser socio-metric dominance matrix was constructed. Matman 1.1 (Noldus Information Technology, 2003; de Vries et al, 1993) was used to assign an ordinal dominance rank to each adult. All juveniles were assigned the same lowest rank of the group. The absolute value of the rank difference between two monkeys was calculated for each dyad, except for juvenile-juvenile dyads. The rank distances ranged from 1 to 24 (mean rank distance ± SE = 10.16 ± 0.29). Dyads with a rank distance under the group’s rank distance mean were labelled ‘close-rank’ partners whereas dyads with a rank distance above the group’s rank difference mean were labelled ‘distant-rank’ partners.

Based on the temperament tests, the mean distance at which the experimenter could approach a monkey before it fled was calculated for each monkey across the three tests. The distances ranged from 40 to 216.7cm (mean distance ± SE = 87.8 ± 8.2). Individuals with a distance under the group’s mean distance were labelled ‘bold’ whereas individuals with distance above the group’s mean distance were labelled ‘shy’. Additionally, the absolute value of the difference of distances between two monkeys was calculated for each dyad of the group. Smaller difference of distance indicated that the two monkeys were of more similar temperament.

Partial Kendall rowwise matrix correlations were used to assess whether the measures of CSI, tolerance and temperament were correlated. While the measure of CSI and tolerance were correlated, no significant correlation was found between the measures of CSI and temperament, and between tolerance and temperament (Table 7.1).

Table 7.1. Results of partial Kendall rowwise matrix correlations for the measures of CSI, tolerance and temperament.

Measures	N	P	τ_{rw}	Significance
CSI and Tolerance	462	0.0001	0.38	✓
CSI and Temperament	462	0.2	0.04	×
Tolerance and Temperament	462	0.47	0.003	×

Although the measures of CSI and tolerance were positively correlated, both measures were kept as two different factors in the analyses to provide a more comprehensive description of the experiment. Indeed, while the CSI index indicates the general strength of the relationship quality between two monkeys, including the time spend together and grooming, tolerance focuses more precisely on acceptance between two monkeys when feeding. Therefore these two factors may affect differently cooperative behaviours involving food.

7.2.3.2. Experiments

First of all, analyses were run to assess whether the monkeys learned that they needed to cooperate with a partner to obtain food in the cooperative test but not in the control. It was assumed that if a learning process was necessary, it would increase after the monkeys solved the cooperative test for the first time. For each individual, the percentage of manipulations performed either alone or next to a partner was calculated. First, the percentage of manipulations next to a partner for the cooperative test was compared before and after the monkeys first solved the cooperative test. If the monkeys learned that a partner was needed to solve the cooperative test, they would manipulate the rope next to a partner more often after than before their first success. Then, the percentage of manipulations next to a partner after the monkeys first succeeded was compared between the cooperative test and the control. If the monkeys differentiated between the mechanism of the cooperative test, which required cooperation with a partner, and the control, which did not, they would manipulate the rope next to a partner more often in the cooperative test than in the control, after their first success in the cooperative test. Finally, for the cooperative test and after the monkeys' first success, the percentage of manipulations next to a partner was compared with the percentage of manipulations alone. After the monkeys learned that a partner was needed to solve the cooperative test, they would refrain from manipulating the rope when no partner was available in the cooperative test. Wilcoxon signed rank tests for paired sample and two-tailed exact p-values were used to compare the individual percentages.

Second, analyses were run to assess which social and individual factors affected the percentage of successes of the monkeys in the cooperative test. Pairwise comparisons were run to assess whether, among all their successes, the monkeys succeeded more with (1) partners with whom they had a strong than weak relationship quality, (2) partners with whom they had a high than low level of tolerance, (3) juveniles than adults, (4) close-rank partners than more distant-rank partners, (5) same-sex partners than different-sex partners and (5) bolder than shier partners. Wilcoxon signed rank test for paired sample and two-tailed exact p-values were used to compare the percentage of successes. Three monkeys (2 juveniles and 1 adult) were not included in the analyses (1) and (2) as they only succeeded with juveniles and the CSI values and cofeeding frequencies were not available from the hourly scans for these subjects (see section 7.2.2.1. of this chapter). Two juveniles were not included in the analyses of rank distance as they only succeeded with juveniles and the hierarchy between juveniles was not measured (see

Chapter 2). Successes occurring between partners of unknown CSI value, cofeeding frequency or rank distance were not considered in the respective analyses (see section 7.2.2.1. of this chapter and Chapter 2).

Finally, partner choice among all the monkeys trained was tested using a generalised linear mixed model with a logistic distribution. Each potential dyad of trained monkeys was treated as a single data point in the model. The risk of sample inflation using this procedure was controlled for by adding to the models the ID of the two monkeys as crossed random factors (Pinheiro & Bates, 2000). The binary dependent variable was whether the dyads succeeded at least once the cooperative test or not. The test variables were ‘relationship quality’ (continuous: the CSI value of the dyads), ‘tolerance’ (continuous: the cofeeding frequency of the dyads), ‘rank distance’ (ordinal: absolute difference of rank status of the dyads), ‘temperament of the dyad’ (continuous: the absolute difference of fleeing distances of the dyads), ‘sex of the dyad’ (categorical: same-sex or different-sex dyads), and ‘age of the dyad’ (categorical: same-age or different-age dyads). Twenty six monkeys were trained. However, because the CSI value, cofeeding frequency and rank distance were not available for some dyads (see section 7.2.2.1. of this chapter), the model was run on 259 potential pairs instead of 325.

For each box plot presented below, the bottom and top sides of the boxes represent respectively the first and third quartiles of the data, the band inside the boxes represents the median, and the bottom and top ends of the whiskers represent respectively the minimum and maximum scores of the data set.

7.3. RESULTS

A total of 135 hours of focal sampling were recorded during the testing period. The presence of the experimenters near the apparatus did not affect the training of the monkeys as there was no significant difference between the shyness of the monkeys trained and not trained (Mann-Whitney U test; $z = -0.31$, $p = 0.77$, 26 monkeys trained and 7 monkeys not trained). Among the 26 monkeys trained, 22 (10 males and 12 females, 13 adults and 9 juveniles) succeeded at least once the cooperative test, that is, to pair up with a partner to bring the tray and the rewards within arm’s reach. Four adult females never succeeded the cooperative test: the top-ranking female of the group, two middle-ranking females and one low-ranking female. The cooperative successes were performed by 93 pairs out of 325 potential pairs. The number of cooperative successes ranged from 1 to 391 successes per monkey (mean per monkey ± SE = 94.82 ± 20.22), with a total of 800 cooperative successes recorded. The cooperative successes were performed by pulling simultaneously both ends of the rope at 95.4%, while 4.6 % were performed by one monkey pulling one end of the rope while its partner firmly held the other end of the rope. No subject spontaneously solved the cooperative task, that is, no subject succeeded to cooperate the first time they were presented with the task.

The monkeys significantly manipulated the rope next to a partner more often after than before their first success during the cooperative test ($z = -3.91$, $p = 0.001$, $N = 22$; Figure 7.3). Moreover, after they first succeeded the cooperative test, the monkeys significantly manipulated the rope next to a partner more often during the cooperative test than during the control ($z = -3.72$, $p = 0.001$, $N = 22$; Figure 7.3 and 7.4). During the cooperative test and after the monkeys first succeeded, there was no significant difference between the manipulation of the rope performed alone or next to a partner (z =

-0.26, p = 0.81, N = 22; Figure 7.3). However, during the cooperative test and after their first success, the monkeys manipulated the rope more often when a partner was in proximity (i.e. within 1.5m) of the apparatus than when no partner was in proximity (z = -3.52, p = 0.001, N = 22; Figure 7.5).

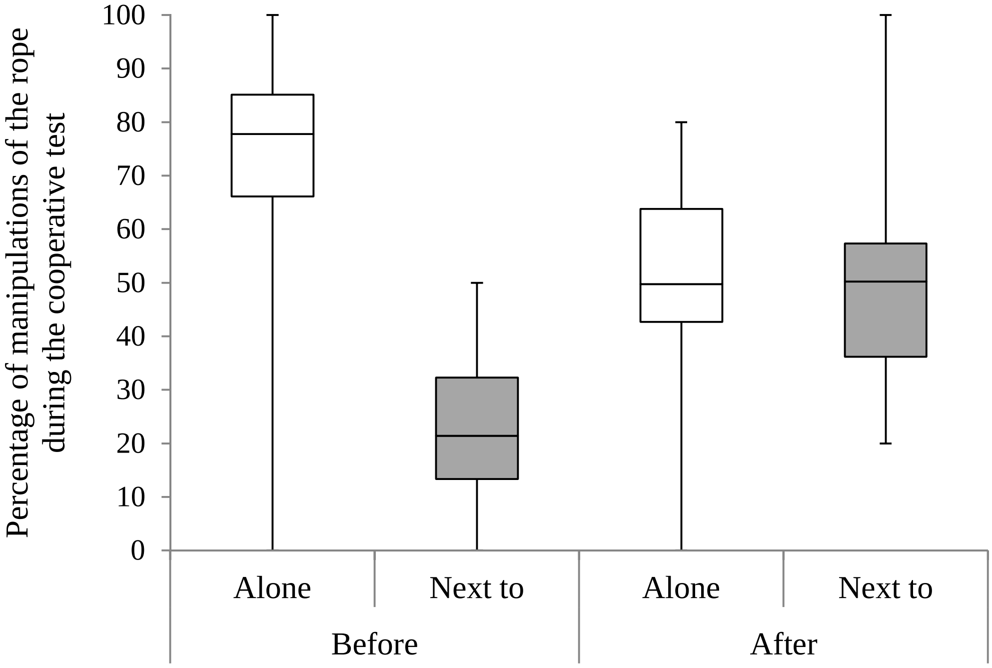


Figure 7.3. Among all the manipulations of the rope performed by each individual during the cooperative test, percentage of manipulations performed alone or next to a partner, before and after the subjects' first success (N = 22).

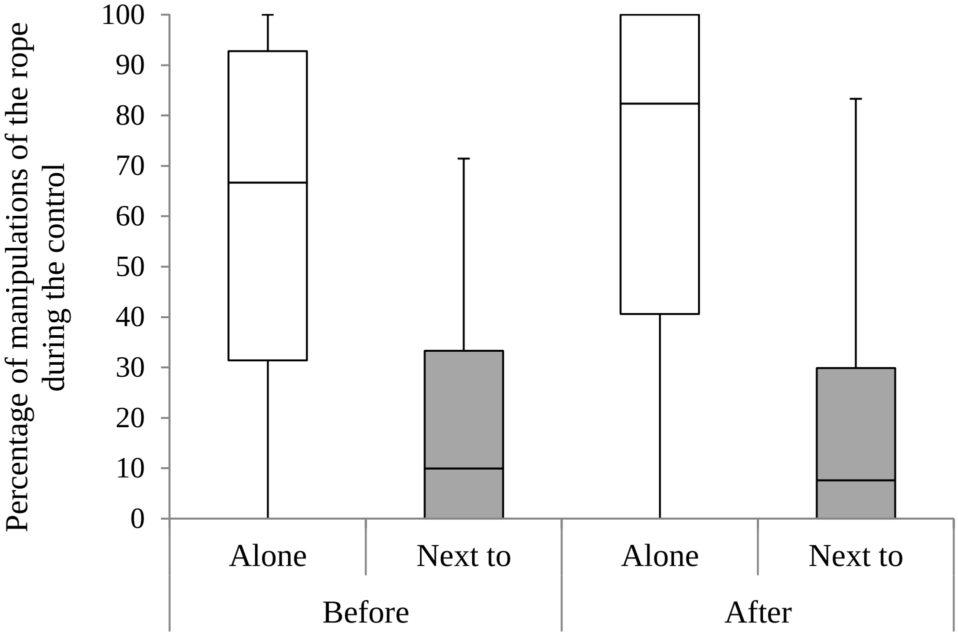


Figure 7.4. Among all the manipulations of the rope performed by each individual during the control, percentage of manipulations performed alone or next to a partner, before and after the subjects' first success in the cooperative test (N = 22).

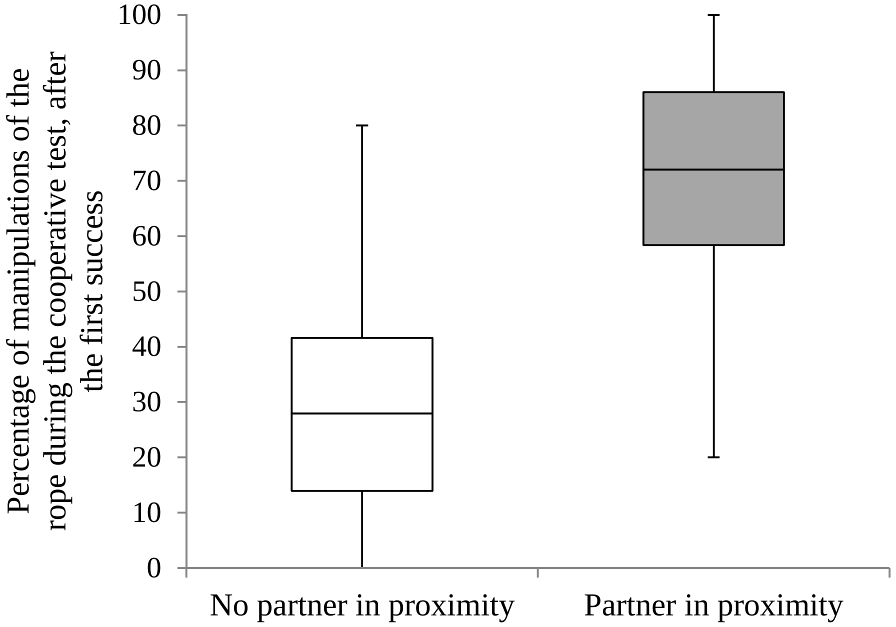


Figure 7.5. Among all the manipulations of the rope performed by each individual during the cooperative test and after the subjects' first success, percentage of manipulations performed when a partner was in proximity (i.e. within 1.5m) of the apparatus or when no partner was in proximity (N = 22).

The monkeys significantly succeeded more often with partners with whom they had a strong than weak relationship quality (z = -2.7, p = 0.005, N = 19; Figure 7.6). Although the monkeys succeeded more with partners with whom they had a high than low level of tolerance (68.3% of success between partners of high tolerance and 31.7% between partner of low tolerance), the difference was not significant (z = -1.73, p = 0.09, N = 19). The percentage of successes was not affected by the age of the partners (z = -0.54, p = 0.6, N = 22) and by the rank distance of the partners (z = -0. 3, p = 0.78, N = 20). The monkeys significantly succeeded to solve the cooperative test more often with same-sex than different-sex partners (z = -3. 11, p = 0.001, N = 22; Figure 7.7), and with bolder than shier partners (z = -4. 11, p = 0.001, N = 22; Figure 7.7).

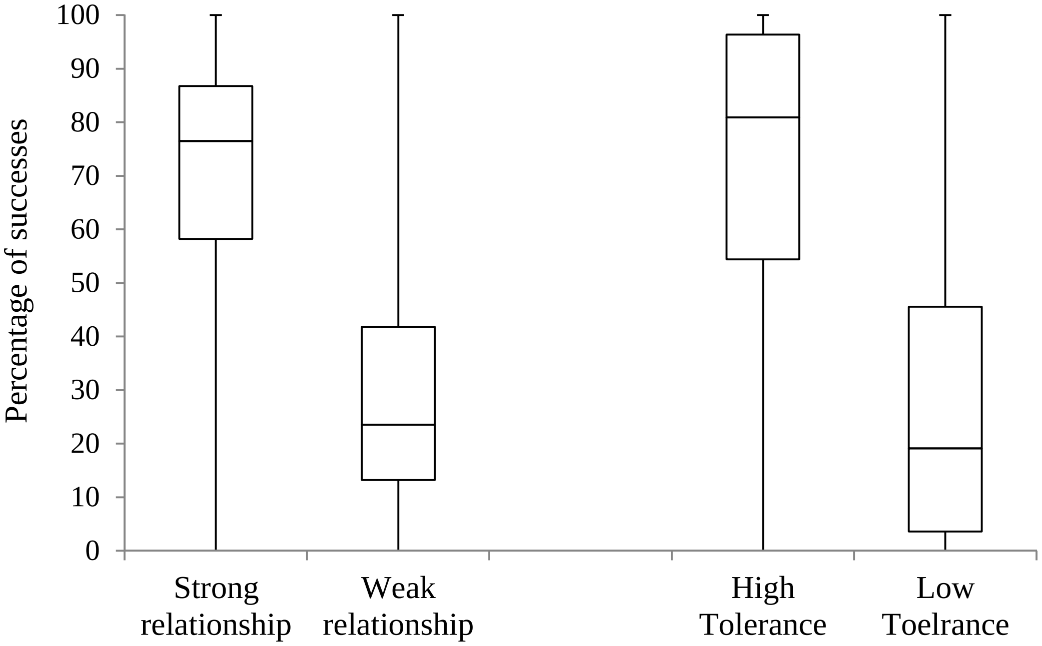


Figure 7.6. Among all the successes performed during the cooperative test by each individual, percentage of successes performed between partners of strong or weak relationship quality and between partner of high or low level of tolerance (N = 19).

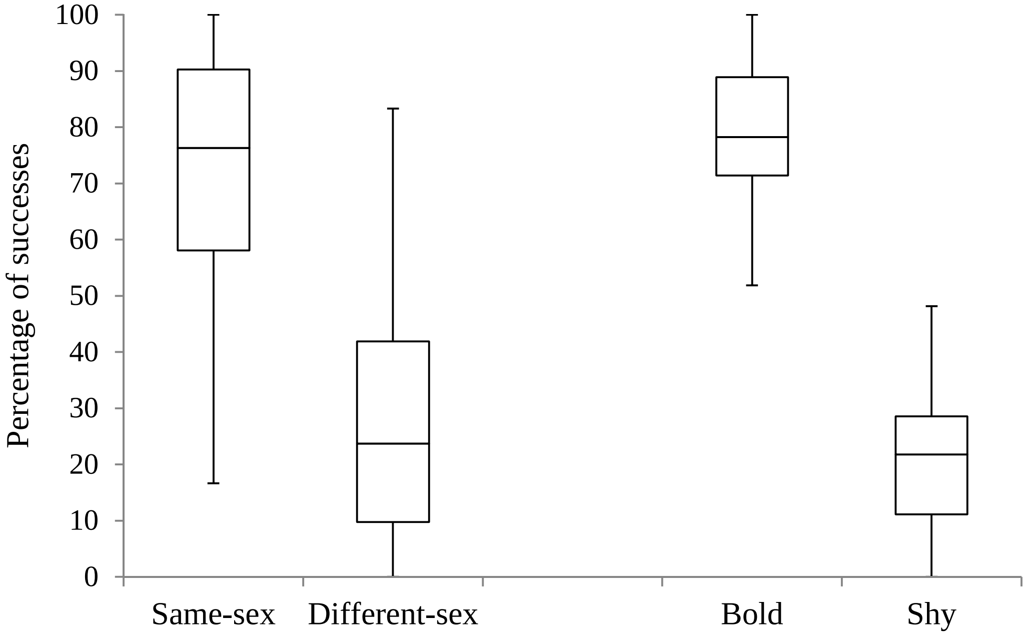


Figure 7.7. Among all the successes performed during the cooperative test by each individual, percentages of successes performed with same-sex or different-sex partners, and with bold or shy partners (N = 22).

The pairs who succeeded at least once had a higher tolerance level than potential pairs that never succeeded (Table 7.2). Partner choice was not affected by the rank distance of the monkeys, their age, sex, relationship quality and temperament (Table 7.2). However, because the measures of CSI and tolerance were correlated, the model was run again removing the test variable ‘tolerance’. In that case, successful pairs had a stronger relationship quality than potential pairs that never succeeded (GLMM, z = 2.74, p = 0.006), and the effect of the other test variables remained not significant (not presented here for the sake of brevity).

Table 7.2. Coefficients and significance of the variables entered in the GLMM with a logistic distribution to test which factors affect the occurrence of succeeding the cooperative test at least once among all the monkeys trained (N = 259).

Variable	**Coefficient ± SE**	**Z**	**P**	**95% CIs**	**Significance**
Relationship quality	-0.01 ± 0.16	-0.09	0.93	-0.33 – 0.3	✗
Tolerance	69.63 ± 19.9	3.5	0.001	30.62 – 108.63	✓
Rank distance	0.12 ± 0.06	1.96	0.05	0.0002 – 0.24	✗
Sex of the dyad	-0.16 ± 0.5	-0.32	0.75	-1.14 – 0.82	✗
Age of the dyad	0.46 ± 0.81	0.57	0.57	-1.13 – 2.06	✗
Temperament of the dyad	-0.01 ± 0.01	-1.85	0.06	-0.03 – 0.001	✗

7.4. DISCUSSION

This study showed that wild Barbary macaques succeed to cooperate to get food in a cooperative task, and that individual and social factors affect their choice of partners and their performance in solving the task. The string pulling cooperative task (Crawford, 1937; Hirata & Fuwa, 2007) was successfully adapted to be conducted on wild macaques: 79% of the monkeys of the group learnt to use the apparatus and freely participated in the task. Moreover, contrary to chimpanzees (Chalmeau & Gallo, 1993; Chalmeau, 1994), the most dominant monkeys of the group did not monopolise the apparatus; instead, they did not show interest in participating in the tasks, giving the opportunity for the rest of the group to participate.

The results showed that 85% of the monkeys trained succeeded to pair up with a partner and to solve the task by simultaneously manipulated the rope. To my knowledge, this is the first evidence of coordinated pulling in wild macaques. Because the string was loose (Hirata & Fuwa, 2007), the two ends needed to be manipulated exactly at the same time and along 75cm to bring the tray within arm's reach. Consequently, the successes observed were less likely to be only due to chance. Barbary macaques seem thus able to act simultaneously to reach a common goal, like observed in capuchins (Chalmeau et al, 1997b; Mendres & de Waal, 2000; Visalberghi et al, 2000), orangutans (Chalmeau et al, 1997a), cotton-top tamarins (Cronin et al, 2005), chimpanzees (Chalmeau, 1994; Melis et al, 2006a, 2006b; Hirata & Fuwa, 2007), bonobos (Hare et al, 2007), rooks (Seed et al, 2008; Scheid & Noë, 2010), African grey parrots (Péron et al, 2011), hyenas (Drea & Carter, 2009), Asian elephants (Plotnik et al, 2011), and wolves (Möslinger et al, 2009). Contrary to rooks (Seed et al, 2008), cotton-top tamarins (Cronin et al, 2005), capuchins (Mendres & de Waal, 2000), hyenas (Drea & Carter, 2009) and tolerant pairs of chimpanzees (Melis et al, 2006b), the subjects of this study did not spontaneously solve the task when first presented with it, but learnt through trial and error. For example, a pair of chimpanzees tested in another study (Hirata & Fuwa, 2007) and African grey parrots (Péron et al, 2011) also required learning before attaining a high success rate. However, it should be noted that spontaneous coordination does not necessarily mean a direct comprehension of the task by the subjects, as simultaneous pulling may initially occur by chance, that is, from a mutual attraction to the apparatus and food.

While simultaneity is an essential requirement of mutual cooperation, taking the role of the partner into account would facilitate the coordination of behaviours (Noë, 2006). When analysing the pulling behaviours according to the presence or absence of a partner, the subjects pulled one end of the rope when a partner was in front of the other end, more often after than before their first success in solving the cooperative task. After their first success (which may have occurred by chance), the subjects thus learned to pull when a partner was directly available, that is, when cooperation might occur. Moreover, after their first success the monkeys manipulated the rope next to a partner more often during the cooperative test than during the control. This suggests that the subjects learnt to discriminate between two different tasks that led to the same goal (i.e. obtaining food) but had different cooperative requirement: the cooperative task that required assistance of a partner to solve it, and the control where no cooperation was needed to reach the food. Similar results were found, for example, in hyenas (Drea & Carter, 2009) and African grey parrots (Péron et al, 2011). Discriminating between situations that required the assistance of a partner and situations that do not may allow individuals to avoid risk of conflict when a resource can be obtained alone. Further studies, for example studies assessing recruitment behaviours before cooperative interactions, may reveal whether macaques recruit a partner only when help is necessary (e.g. Melis et al, 2006a).

Although these results suggest that the monkeys may have some understanding of the need of a partner to solve the cooperative task, this study does not allow to fully apprehend to what extent the monkeys understand the role of their partner in solving the task. Even if the subjects learned to refrain their pulling when no partner was available in front of the rope in the cooperative task, they did not significantly stop this behaviour. Capuchins and cotton-top tamarins also continued to pull, although less frequently, when the partner was out of the testing room (Mendres & de Waal, 2000; Cronin et al, 2005). Several hypotheses may explain this result. First, even if the subjects continued to pull when no partner was in front of the other rope, they significantly pulled more often when a partner was in proximity of the apparatus than when no partner was present around the apparatus. Although perhaps unlikely, there is a probability that at the end of the testing period, the monkeys might still be learning, and after more exposures to the task they might progressively learn to precise their pulling by pulling exclusively when a partner is directly available at the rope. Second, it cannot be ruled out that pulling while being in proximity of another monkey may either be used by the monkeys to actively recruit a potential partner, by communicating their interest in obtaining the food, or may act as a local stimulus which enhanced the approach of potential partners (Jaeggi et al, 2010; Schwab et al, 2012). To clarify this point, further studies may analyse the communication between potential partners during the manipulation of the apparatus. Communication may allow individuals to actively coordinate their actions with those of their partner by recruiting potentials partners and facilitating the coordination during the joint action. For example, visual contact has been showed to improve cooperation in capuchins, and the monkeys increased glances during coordinated actions (Mendres & de Waal, 2000). Back glance (i.e. a side directed behaviour) is used by non-human primates to recruit group members for coalitions and group movement (e.g. de Waal & van Hooff, 1981; Freese & Oppenheimar, 1981; Leca et al, 2003; Meunier et al, 2008; Sueur & Petit, 2009), and may be also used during other cooperative interactions. Third, it is possible that the monkeys were too impulsive when presented with a food reward (fully visible to the monkeys during the task), preventing them from totally refraining the inefficient pulling. There is evidence that many animals have difficulties to inhibit a learned response (here pulling a string) to get food (Stevens & Hauser, 2004; Péron et al, 2011). Because the monkeys had free access to the experiments, the synchrony of manipulation could not be explained by a simultaneous release of the animals in the testing area like in laboratory studies (e.g. Seed et al, 2008; Scheid & Noë, 2010). For example, the subjects may have learned the contingency between the co-occurrence of their manipulations and the food rewards through trial and error. Thus, these results suggest that, although it is unlikely that the successes observed in this cooperative task were achieved through random action, it remains unclear to what extent the monkeys understood the role of their partner in solving the cooperative task.

This study also investigated the individual and social factors affecting the choice of partners and performances of the individuals in solving the cooperative task. It can be noted that a complete set of all the successes observed could not be analysed as measures of tolerance, relationship quality and dominance were not available for juveniles, and so the results have to be interpreted with caution. The successful pairs had a higher level of tolerance (measured as naturally occurring cofeeding) than potentials pairs that never succeeded. There was no effect of the age, sex, dominance status, and temperament of the potentials dyads on their capacity to form a successful cooperative interaction. While relationship quality also had a positive effect on successful pairing, tolerance was the determinant factor. This result adds to the growing body of evidence showing that tolerance is necessary for the initiation of successful cooperative behaviours (e.g. Melis et al, 2006b; Hare et al, 2007). Melis and colleagues (2006b) showed that tolerance constrains chimpanzees' cooperation even in subjects who understand the cooperative problem they have to solve. Tolerance has thus an important impact on cooperative behaviour and further studies conducting cooperative task on animals should control for baseline tolerance level between subjects. Barbary macaques succeeded better in this study than more tolerant (grade 4, census Thierry, 2000) Tonkean macaques succeeded when tested in their capacity to simultaneously manipulate a stone (Petit et al, 1992). However, the results of the two studies cannot be directly compared because the two tasks were different, and the distance required for two monkeys to move a stone may be shorter than the distance required (2.15m) for cooperation in this study. Further studies could be run using the string pulling cooperative task on different macaques species, differing in their level of inter-individual tolerance, to assess whether the tolerance style of the species affect their performance in cooperative task. Furthermore, in this study dominance status did not seem to affect the performance of the monkeys. In Barbary macaques, the difference of dominance status between two individuals does not have a key effect on their relationship quality (McFarland & Majolo, 2011a). It is possible that the tolerance level between two monkeys in this study is irrespective of the difference of dominance status between them. Thus tolerance would improve cooperation, and this would be regardless of the difference of dominance status between individuals. The high level of tolerance between two macaques (i.e. their capacity to feed in proximity) may have allowed them to be in proximity around the food rewards of the task, and so to have a chance to manipulate the rope at the same time, giving them the opportunity to learn the connection between their behaviour, the partner's behaviour and the food reward, facilitating further success.

Moreover, individuals succeeded more often with partners with whom they had a high than low relationship quality. This suggests that while tolerance was necessary to initiate a successful cooperative interaction, relationship quality between two monkeys facilitated the maintenance of success. There is a growing body of evidence showing that strong social bonds enhance cooperative behaviours in animals and humans (Silk, 2002, 2003; Majolo et al, 2006; Schino & Aureli, 2009; de Waal & Suchak, 2010; Cronin, 2012). Individuals would make their decision about which partner to cooperate with in the long-term based on the emotional states associated with each potential partner (Schino & Aureli, 2009). Supporting this view, neurotransmitters such as oxytocin underlie social bonding in humans and animals and may play a role in modulating cooperative behaviours (Insel & Shapiro, 1992; Insel & Young, 2001; Kosfeld et al, 2005; Schino & Aureli, 2009; Soares et al, 2010; Chang et al, 2012). Additionally, while age, dominance status and tolerance had no significant effect on the number of successes performed, individuals succeeded more often with same-sex than difference-sex partners. Same-sex partners would be more efficient in solving cooperative tasks than different-sex partners (Mendres & de Waal, 2000; Hauser et al, 2003). In animals, sex of the individuals affect cooperative behaviours such as grooming interaction (Mitchell & Tokunaga, 1976; Lehmann & Boesch, 2008). Moreover, in Barbary macaques relationships quality is affected by the sex of the individuals, high quality social bonds being more frequent between individuals of the phylopatric sex, that is, between females (McFarland & Majolo, 2011a).

Individuals were more successful with bold than shy partners. Because experimenters were always near the experiments, the presence of a bolder partner may have reassured shier monkeys in approaching and manipulating the apparatus, although the shyness of the individuals did not affect their training in using the tasks. Individual temperament in term of shyness and boldness, such as the propensity to take risk, to react to stressful situation or to explore new environment, may affect the participation of individual in cooperative interactions (e.g. Wilson et al, 1994; McNamara et al, 2004). Scheid and Noë (2010) proposed that bold individuals function as catalysers which allow shier individuals to cooperate even in situation they perceived as risky (Wilson et al, 1994; Groothuis & Carere, 2005; Gilby et al, 2008). Shier individuals would benefit from a diluted perceived risk by joining bolder individuals (Scheid & Noë, 2010). For example, when a fish joins another one to inspect a predator to assess the potential danger, they both share the risk of being eaten (Milinski, 1990; Milinski et al, 1990; Dugatkin & Alfieri, 1991; Pitcher, 1992; Huntingford et al, 1994; Godin & Davis, 1995; Dugatkin, 1997; Milinski et al, 1997). This effect of temperament may thus be more important in risky cooperative interactions such as naturally occurring agonistic intergroup encounters, and need to be further explored (e.g. Huntingford, 1976; Heinsohn & Packer, 1995; Fairbanks, 2001; Wilson et al, 2001; Nunn & Deaner, 2004; Harris, 2006).

In conclusion, wild Barbary macaques were successful at pairing up with a partner to solve a cooperative task. Moreover, individual and social factors such as tolerance, relationship quality, sex and temperament affected, to some extent, partner choice and cooperation. High level of tolerance was necessary for the initiation of successful cooperation, while strong relationship quality sustained the success. Sex and shyness of the subjects affected their performance and also need to be taken into account when running cooperative experiment on animals. More work is needed to reveal the full extents and limits of cooperation in animals. This study stresses the importance of studying both cognitive and individual and social factors underlying cooperative behaviours in animals, in order to gain important insights into the evolutionary roots of cooperation, fundamental to human social behaviour. Human-like cooperation may have evolved following a transition from non-tolerant social systems to more egalitarian social systems. Thus, tolerant relationships may have been a prerequisite for the evolution of cognitively complex cooperation (Melis et al, 2006b; Hare, 2007; Hare et al, 2007; Melis & Semmann, 2010).

7.5. REFERENCES

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227-267.

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B., Ogawa, H., Schino, G., Thierry, B. & de Waal, F. B. M. 2012. Hierarchical steepness, counter-aggression, and macaque social style scale. *American Journal of Primatology*, **74**, 915-925.

Berghänel, A., Ostner, J., Schröder, U. & Schülke, O. 2011. Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, **81**, 1109-1116.

Bergmüller, R., Schürch, R. & Hamilton, I. M. 2010. Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. *Philosophical Transactions of the Royal Society B*, **365**, 2751-2764.

Boesch, C. & Boesch, H. 1989. Hunting behavior of wild chimpanzees in the Tai national park. *American Journal of Physical Anthropology*, **78**, 547-573.

Brosnan, S. F., Schiff, H. & de Waal, F. B. M. 2005. Tolerance for inequity increases with social closeness in chimpanzees. *Proceedings of the Royal Society B*, **272**, 253-258.

Burton, J. J. 1977. Absence de comportement coopératif spontané dans une troupe de *Macaca fuscata* en présence de pierres appâtées. *Primates*, **18**, 359-366.

Carne, C., Wiper, S. & Semple, S. 2011. Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology*, **73**, 1127-1133.

Chalmeau, R. & Gallo, A. 1993. Social constraints determine what is learned in the chimpanzee. *Behavioural Processes*, **28**, 173-180.

Chalmeau, R. & Gallo, A. 1996. What chimpanzees (*Pan troglodytes*) learn in a cooperative task. *Primates*, **37**, 39-47.

Chalmeau, R. 1994. Do chimpanzees cooperate in a learning task? *Primates*, **37**, 39-47.

Chalmeau, R., Lardeux, K., Brandibas, P. & Gallo, A. 1997a. Cooperative problem solving by Orangutans (*Pongo pygmaeus*). *International Journal of Primatology*, **18**, 23-32.

Chalmeau, R., Visalberghi, E. & Gallo, A. 1997b. Capuchin monkeys, *Cebus apella*, fail to understand a cooperative task. *Animal Behaviour*, **54**, 1215-1225.

Chang, S. W. C., Barter, J. W., Ebitz, R. B., Watson, K. K. & Platt, M. L. 2012. Inhaled oxytocin amplifies both vicarious reinforcement and self-reinforcement in rhesus macaques (*Macaca mulatta*). *Proceedings of the National Academy of Sciences*, **109**, 959-964.

Chang, S. W. C., Winecoff, A. A. & Platt, M. L. 2011. Vicarious reinforcement in rhesus macaques (*Macaca mulatta*). *Frontiers in Neuroscience*, **5**, 27.

Chapais, B. 2006. Kinship, competence and cooperation in primates. In: *Cooperation in primates and humans: mechanisms and evolution* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 47-64. New-York: Springer.

Clutton-Brock, T. 2009. Cooperation between non-kin in animal societies. *Science*, **462**, 51-57.

Crawford, M. P. 1937. The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs*, **14**, 1-88.

Crawford, M. P. 1941. The cooperative solving by chimpanzees of problems requiring serial responses to color cues. *The Journal of Social Psychology*, **13**, 259-280.

Cronin, K. A. 2012. Prosocial behaviour in animals: the influence of social relationships, communication and rewards. *Animal Behaviour*, **84**, 1085-1093.

Cronin, K. A., Kurian, A. V. & Snowdon, C. T. 2005. Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). *Animal Behaviour*, **69**, 133-142.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. Matman: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, **125**, 157-175.

de Waal, F. B. M. & Davis, J. M. 2003. Capuchin cognitive ecology: cooperation based on projected returns. *Neuropsychologia*, **41**, 221-228.

de Waal, F. B. M. & Suchak, M. 2010. Prosocial primates: selfish and unselfish motivations. *Philosophical Transactions of the Royal Society B*, **365**, 2711-2722.

de Waal, F. B. M. & van Hooff, J. A. R. A. M. 1981. Side-directed communication and agonistic interactions in chimpanzees. *Behaviour*, **77**, 164-198.

de Waal, F. B. M. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, **60**, 253-261.

de Waal, F. B. M., Leimgruber, K. & Greenberg, A. R. 2008. Giving is self-rewarding for monkeys. *Proceedings of the National Academy of Sciences*, **105**, 13685-13689.

Drea, C. M. & Carter, A. N. 2009. Cooperative problem solving in a social carnivore. *Animal Behaviour*, **78**, 967-977.

Dugatkin, L. A. & Alfieri, M. 1991. Guppies and the Tit-for-tat strategy: preference based on past interaction. *Behavioral Ecology and Sociobiology,* **28**, 243-246.

Dugatkin, L. A. 1997. *Cooperation among animals: an evolutionary perspective*. Oxford: Oxford University Press.

Fady, J. C., 1972. Absence de cooperation de type instrumental en milieu nature1 chez *Papio papio*. *Behaviour*, **93**, 157-164.

Fairbanks, L. A. 2001. Individual differences in response to a stranger: social impulsivity as a dimension of temperament in vervet monkeys (*Cercopithecus aethiops sabaeus*). *Journal of Comparative Psychology*, **115**, 22-28.

Freese, C. H. & Oppenheimer, J. R. 1981. The capuchin monkeys, genus *Cebus*. In: *Ecology and behavior of neotropical primates, vol. 1*. (Ed. by A. F. Coimbra-Filho & R. A. Mittermeier), pp. 331-390. Rio de Janeiro: Academia Brasileira de Ciências.

Gazda, S. K., Connor, R. C., Edgar, R. K. & Cox, F. 2005. A division of labour with rule specialization in group hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society B,* **272**, 135-140.

Gilby, I. C., Eberly, L. E. & Wrangham, R. W. 2008. Economic profitability of social predation among wild chimpanzees: individual variation promotes cooperation. *Animal Behaviour*, **75**, 351-360.

Godin, J. G. G & Davis, S. A. 1995. Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proceedings of the Royal Society B*, **259**, 193-200.

Groothuis, T. G. G. & Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience & Biobehavioral Reviews*, **29**, 137-150.

Hare, B. 2007. From nonhuman to human mind: what changed and why. *Current Directions in Psychological Science,* **16**, 60-64.

Hare, B., Melis, A. P., Woods, V., Hastings, S. & Wrangham, R. W. 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology,* **17**, 619-623.

Harris, T. R. 2006. Within- and among-male variation in roaring by black and white colobus monkeys (*Colobus guereza*): what does it reveal about function? *Behaviour,* **143,** 197-218.

Hattori, Y., Kuroshima, H. & Fujita, K. 2005. Cooperative problem solving by tufted capuchin monkeys (*Cebus apella*): spontaneous division of labor, communication, and reciprocal altruism. *Journal of Comparative Psychology*, **119**, 335-342.

Hauser, M. D., Chen, M. K., Chen, F. & Chuang, E. 2003. Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society B*, **270**, 2363-2370.

Heinsohn, R. & Packer, C. 1995. Complex cooperative strategies in group-territorial African lions. *Science*, **269**, 1260-1262.

Hirata, S. & Fuwa, K. 2007. Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates,* **48,** 13-21.

Huntingford, F. A. 1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour*, **24,** 245-260.

Huntingford, F. A., Lazarus, J., Barrie, B. D. & Webb, S. 1994. A dynamic analysis of cooperative predator inspection in sticklebacks. *Animal Behaviour*, **47**, 413-423.

Insel, T. R. & Shapiro, L. E. 1992. Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. *Proceedings of the National Academy of Sciences,* **89**, 5981-5985.

Insel, T. R. & Young, L. J. 2001. The neurobiology of attachment. *Nature Review of Neuroscience*, **2**, 129-136.

Jaeggi, A. V., Burkart, J. M. & van Schaik, C. P. 2010. On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of prosociality. *Philosophical Transactions of the Royal Society B*, **365**, 2723-2735.

Jaeggi, A. V., De Groot, E., Stevens, J. M. G. & van Schaik, C. P. 2013. Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, **34**, 69-77.

Kaburu, S. S. K., MacLarnon, A., Majolo, B., Qarro, M. & Semple, S. 2012. Dominance rank and self-scratching among wild female Barbary macaques (*Macaca sylvanus*). *African Zoology*, **47,** 74-79.

Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U. & Fehr, E. 2005. Oxytocin increases trust in humans. *Nature*, **435**, 673-676.

Leca, J. B., Gunst, N., Thierry, B. & Petit, O. 2003. Distributed leadership in semifree-ranging white-faced capuchin monkeys. *Animal Behaviour*, **66**, 1035-1044.

Lehmann, J. & Boesch, C. 2008. Sex differences in chimpanzee sociality. *International Journal of Primatology*, **29**, 65-81.

Majolo, B., Ames, K., Brumpton, R., Garratt, R., Hall, K. & Wilson, N. 2006. Human friendship favours cooperation in the iterated Prisoner’s Dilemma. *Behaviour*, **143**, 1383-1395.

Massen, J. J. M., van den Berg, L. M., Spruijt, B. M. & Sterck, E. H. M. 2010. Generous leaders and selfish underdogs: pro-sociality in despotic macaques. *PLoS ONE*, **5,** e9734.

McFarland, R. & Majolo, B. 2011a. Exploring the components, asymmetry and distribution of relationship quality in wild Barbary macaques (*Macaca sylvanus*). *PLoS ONE*, **6,** e28826.

McFarland, R. & Majolo, B. 2011b. Grooming coercion and the post-conflict trading of social services in wild Barbary macaques. *PLoS ONE*, **6**, e26893.

McNamara, J. M. & Leimar, O. 2010. Variation and the response to variation as a basis for successful cooperation. *Philosophical Transactions of the Royal Society B*, **365**, 2627-2633.

McNamara, J. M., Barta, Z. & Houston, A. I. 2004. Variation promotes cooperation in the Prisoner's Dilemma game. *Nature*, **428**, 745-747.

Melis, A. P. & Semmann, D. 2010. How is human cooperation different? *Philosophical Transactions of the Royal Society B*, **365**, 2663-2674.

Melis, A. P. & Tomasello, M. 2013. Chimpanzees' (*Pan troglodytes*) strategic helping in a collaborative task. *Biology Letters*, **9**, 20130009.

Melis, A. P., Hare, B. & Tomasello, M. 2006a. Chimpanzees recruit the best collaborators. *Science*, **311**, 1297-1300.

Melis, A. P., Hare, B. & Tomasello, M. 2006b. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Animal Behaviour,* **72,** 275-286.

Mendres, K. A & de Waal, F. B. M. 2000. Capuchins do cooperate: the advantage of an intuitive task. *Animal Behaviour*, **60**, 523-529.

Meunier, H., Deneubourg, J. L. & Petit, O. 2008. How many for dinner? Recruitment and monitoring by glances in capuchins. *Primates*, **49**, 26-31.

Milinski, M. 1990. No alternative to Tit-for-tat cooperation in sticklebacks. *Animal Behaviour*, **39**, 989-991.

Milinski, M., Külling, D. & Kettler, R. 1990. Tit-for-Tat: sticklebacks *Gasterosteus aculeatus* trusting a cooperating partner. *Behavioral Ecology*, **1**, 7-11.

Milinski, M., Luthi, J., Eggler, R. & Parker, G. 1997. Cooperation under predation risk: experiments on costs and benefits. *Proceedings of the Royal Society B*, **264**, 831-837.

Mitchell, G. & Tokunaga, D. H. 1976. Sex differences in nonhuman primate grooming. *Behavioural Processes*, **4**, 335-345.

Möslinger, H., Kotrschal, K., Huber, L., Range, F. & Virányi, Z. 2009. Cooperative string-pulling in wolves. *Journal of Veterinary Behavior: Clinical Applications and Research*, **4**, 99.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism, and mating. *Behavioral Ecology and Sociobiology*, **35**, 1-11.

Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of cooperation. In: *Economics in nature: social dilemmas, mate choice and biological markets* (Ed. by R. Noë, J. A. R. A. M van Hooff & P. Hammerstein), pp. 93-118. Cambridge: Cambridge University Press.

Noë, R. 2006. Cooperation experiments: coordination through communication versus acting apart together. *Animal Behaviour*, **71**, 1-18.

Noldus Information Technology. 2003. *Matman, software for matrix manipulation and analysis, version 1.1.* Wageningen, The Netherlands.

Nunn, C. L. & Deaner, R. O. 2004. Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*). *Behavioral Ecology and Sociobiology*, **57,** 50-61.

Pansini, R**.** 2011. Induced cooperation to access a sharable reward increases the hierarchical segregation of wild vervet monkeys. *PLoS ONE,* **6**, e21993.

Péron, F., Rat-Fischer, L., Lalot, M., Nagle, L. & Bovet, D. 2011. Cooperative problem solving in African grey parrots (*Psittacus erithacus*). *Animal Cognition*, **14**, 545-553.

Petit, O., Desportes, C. & Thierry, B., 1992. Differential probability of ‘coproduction’ in two species of macaque (*Macaca tonkeana, M. mulatta*). *Ethology,* **90**, 107-120.

Pinheiro, J. C. & Bates, D. M. 2000. *Mixed effects models in S and S-PLUS.* 1st edn. New York: Springer-Verlag.

Pitcher, T. J. 1992. Who dares, wins: the function and evolution of predator inspection behaviour in shoaling fish. *Netherlands Journal of Zoology*, **42**, 371-391.

Plotnik, J. M., Lair, R., Suphachoksahakun, W. & de Waal, F. B. M. 2011. Elephants know when they need a helping trunk in a cooperative task. *Proceedings of the National Academy of Sciences,* **108**, 5116-5121.

Sabbatini, G., De Bortoli Vizioli, A., Visalberghi, E. & Schino, G. 2012. Food transfers in capuchin monkeys: an experiment on partner choice. *Biology Letters*, **8**, 757-759.

Scheid, C. & Noë, R. 2010. The performance of rooks in a cooperative task depends on their temperament. *Animal Cognition*, **13**, 545-553.

Schino, G. & Aureli, F. 2009. Reciprocal altruism in primates: partner choice, cognition and emotions. *Advances in the Study of Behavior*, **39**, 45-69.

Schwab, C., Swoboda, R., Kotrschal, K. & Bugnyar, T. 2012. Recipients affect prosocial and altruistic choices in jackdaws, *Corvus monedula*. *PLoS ONE*, **7**, e34922.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2008. Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society B*, **275**, 1421-1429.

Silk, J. B. 2002. Using the 'F' word in primatology. *Behaviour*, **139**, 421-446.

Silk, J. B. 2003. Cooperation without counting: the puzzle of friendship. In: *The genetic and cultural evolution of cooperation* (Ed. by P. Hammerstein), pp. 37-54. Cambridge: The MIT Press.

Silk, J. B. 2005. The evolution of cooperation in primate groups. In: *Moral sentiments and material interests: on the foundations of cooperation in economic life* (Ed. by H. Gintis, S. Bowles, R. Boyd & E. Fehr), pp. 43-73. Cambridge: The MIT Press.

Silk, J. B. 2006. Practicing Hamilton's rule: kin selection in primate groups. In: *Cooperation in primates and humans: mechanisms and evolution* (Ed. by P. M. Kappeler & C. P. van Schaik). New-York: Springer.

Silk, J. B., Altmann, J. & Alberts S. 2006. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, **61**, 183-195.

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P. & Shapiro, S. 2013. Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour*, **85**, 941-947.

Soares, M. C., Bshary, R., Fusani, L., Goymann, W., Hau, M., Hirschenhauser, K. & Oliveira, R. F. 2010. Hormonal mechanisms of cooperative behaviour. *Philosophical Transactions of the Royal Society B*, **365**, 2737-2750.

Stevens, J. R. & Hauser, M. D. 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences*, **8**, 60-65.

Sueur, C. & Petit, O. 2009. Signals use by leaders in *Macaca tonkeana* and *Macaca mulatta*: group-mate recruitment and behaviour monitoring. *Animal Cognition*, **13**, 239-248.

Thierry, B. & Aureli, F. 2006. Barbary but not barbarian: social relations in a tolerant macaque. In: *The Barbary macaque: biology, management and conservation* (Ed. by J. K. Hodges & J. Cortes), pp. 29-45. Nottingham: Nottingham University press.

Thierry, B. 1985. Patterns of agonistic interactions in three species of macaque (*Macaca mulatta, M fascicularis, M tonkeana*). *Aggressive Behavior*, **11**, 223-233.

Thierry, B. 2000. Covariation of conflict management patterns in macaque societies. In: *Natural conflict resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 106-128. Berkeley: University of California Press.

Thierry, B., Singh, M. & Kaumanns, W. 2004. *Macaque societies: a model for the study of social organization*. Cambridge: Cambridge University Press.

Tiddi, B., Aureli, F., Polizzi di Sorrentino, E., Janson, C. H. & Schino, G. 2011 Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. *Behavioral Ecology*, **22**, 663-669.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35-57.

Visalberghi, E., Quarantotti, B. P. & Tranchida, F. 2000. Solving a cooperation task without taking into account the partner’s behavior: the case of capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, **114**, 297-301.

West, S. A., Griffin, A. S. & Gardner, A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, **20**, 415-432.

Widdig, A., Streich, W. & Tembrock, G. 2000. Coalition formation among male Barbary macaques (*Macaca sylvanus*). *American Journal of Primatology*, **50**, 37-51.

Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994. Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, **9**, 442-446.

Wilson, M. L., Hauser, M. D. & Wrangham, R. D. 2001. Does participation in intergroup conflict depend on numerical assessement, range location, or rank for wild chimpanzees? *Animal Behaviour*, **61**, 1203-1216.

Wobber, V., Wrangham, R. & Hare, B. 2010. Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology*, **20**, 226-230.

Chapter 8

General discussion

A male Barbary macaque (picture by S. Molesti).

8.1. GROOMING, RECIPROCITY, AND PARTNER CHOICE

Cooperation is a phenomenon that has attracted research from many different disciplines working with humans (e.g. psychology, sociology, anthropology, economics) or animals (e.g. ethology, behavioural ecology, evolutionary ecology) (Noë, 2006). The study of cooperative behaviours has been crucial to research on the evolution of social living in human and animal societies (e.g. Silk, 2003, 2007; Clutton-Brock, 2009; Schino & Aureli, 2009; Jaeggi et al, 2010; Melis & Semmann, 2010). Grooming interaction has notably been use as model to investigate the functions and mechanisms of exchanges of services in non-human primates. Using both established and novel advanced methodologies to test a large set of predictions, this thesis brings a novel contribution to the understanding of grooming interactions and cooperation in wild Barbary macaques.

It is important to have a comprehensive idea of the costs and benefits of grooming interactions, and of the effect of grooming interaction on the anxiety of the grooming partners (Russell & Phelps, 2013). Indeed, a short-term change of anxiety following grooming may affect the exchange of this service between group members and the establishment and maintenance of social relationships. This thesis revealed that a reduction in anxiety may not be a key benefit of grooming, at least not once the grooming interaction is ended. This highlights the need to investigate further the link between grooming and emotions, particularly at a physiological level, in order to assess how social relationships are emotionally mediated (Aureli & Schino, 2004; Dunbar & Shultz, 2010). Moreover, this thesis showed that dominant individuals may aggressively disrupt grooming interactions of other group members to access grooming opportunities and sustain their social and dominant position within the group. Thus, dominant individuals may affect the grooming distribution within a group and so the social relationships of other group members, at their own advantages. This has to be taken into account when analysing grooming distribution and the formation and maintenance of social relationships in non-humans primates (Clutton-Brock & Parker, 1995).

This thesis also revealed the key role of direct reciprocity but not of indirect and generalised reciprocity in the distribution of grooming in Barbary macaques. This result adds to the growing body of evidence showing that direct but not indirect and generalised reciprocity play a role in the exchanges of services in non-human primates (Schino & Aureli, 2008; Melis & Semmann, 2010; Clutton-Brock, 2009; Majolo et al, 2012). Direct reciprocity may be proximately driven by partner-specific emotional bond that develops as a consequence of past interactions exchanged such as grooming (Schino & Aureli, 2009). In Barbary macaques, partner-specificity seems to play a key role in the exchange of services. The role of neuroendocrinological mechanisms, such as those involving oxytocin, in social bonding and exchange of services could be further investigated in non-human primates.

Two main mechanisms have been proposed to explain the exchange of services such as grooming in non-human primates: temporal contingency between a service given and received, and the overall exchange of services over longer time frames between partners. Although evidence of temporal contingency in the exchange of services in non-human primates is mixed, short-term contingency between services given and received is traditionally used as the basic mechanism to explain and demonstrate reciprocity (Silk, 2007; Schino & Aureli, 2009). The results of this thesis revealed that temporal contingency, particularly for the exchange of grooming for food tolerance, may not play a key role in the exchange of services in Barbary macaques. It is hypothesised that short-term contingencies may be negligible if exchanges are overall balanced in relation to long-term relationships between partners (Schino & Aureli, 2009, 2010), which may be the case in Barbary macaques (Carne et al, 2011). Short-term contingencies between services exchanged may play a more important role between partners who rarely interact together (Silk, 2007; Schino & Aureli, 2009; Hare & Tan, 2012; Jaeggi et al, 2013).

Finally, this thesis showed for the first time that wild Barbary macaques are able to cooperate in an experimental setting to get food. This study highlighted, to some extents, the importance of tolerance and relationship quality in the establishment and maintenance of cooperative interactions in a cooperative task. This adds to the growing body of evidence showing that tolerance constrains cooperative behaviours in animals (e.g. Melis et al, 2006b; Hare et al, 2007; Hare & Tan, 2012; Schneider et al, 2012; Silk et al, 2013). Moreover, it suggests to investigate further the key role of partner choice in the establishment and maintenance of cooperation in animals (Noë, 2006). Future experimental studies investigating cooperative behaviour in animals would need to take into account the tolerance level of the species and the tolerance level between partners within a species.

These findings in Barbary macaques make an important contribution to our understanding of social interactions and cooperative behaviours in non-humans primates. Humans-like cooperation may have evolved following a transition from non-tolerant social systems to more egalitarian social systems, which would have favoured the evolution of the wide and complex forms of cooperation observed in humans, especially among strangers (e.g. Melis & Semmann, 2010; Hare & Tan, 2012; Tomasello et al, 2012).

8.2. THESIS SUMMARY AND IMPLICATIONS

The following sections summarise the contribution each Chapter of this thesis has made to further understanding grooming interactions and cooperation in wild Barbary macaques, and discuss some potential implications these findings may have for research on social relationship and cooperation in animals and humans.

8.2.1. Grooming and anxiety (Chapter 3)

Grooming has been proposed to reduce anxiety in the grooming partners, which would favour subsequent social interactions between animals as well as their choice of social partners. Chapter 3 used a new methodological approach (i.e. data were simultaneously collected on both grooming partners) to investigate the post-grooming anxiety of both the donor and recipient of the same grooming interactions. Self-scratching and self-grooming were used as behavioural indicators of anxiety (Maestripieri et al, 1992; Schino et al, 1996; Troisi, 2002). This study showed that a short-term increase of anxiety follows the termination of grooming interaction in both donor and recipient in wild Barbary macaques. The frustration due to the termination of grooming and the emotional consequences following behavioural transitions may influence post-grooming anxiety. The release of anxiety after grooming may not be a key benefit of grooming in wild Barbary macaques, and the social and hygienic benefits of grooming may out-weigh its short-term cost in term of anxiety. This need to be taken into account when investigating the proximate costs and benefits of grooming interactions (Russell & Phelps, 2013), notably to assess the exchange of services as well as the establishment and maintenance of social bonds in animals. These findings highlight the importance of conducting further research to explore the relation between grooming and emotions in animals, as understanding the proximate mechanisms of grooming is essential to shed light on the factors influencing the choice of social partners and exchange of services.

Emotions play an important role in social relationships in animals and humans. For example, there is evidence that receiving grooming stimulates the release of β-endorphins (Keverne et al, 1989; Dunbar, 2010) similarly to receiving massage in humans (Kaada & Torsteinbø, 1989). In humans, endorphins activate opiate receptors, creating a feeling of pleasure and relaxation (Hawkes, 1992; Goats, 1994). This effect may play a role in social interactions of animals and humans by promoting social contact (van Ree et al, 2000; Graves et al, 2002). For example, in rat the injection of β-endorphins promotes social contact including grooming (van Ree & Niesink, 1983). The sensory pleasure an individual gains from a specific partner may constitute a partner-specific emotional experience that would favour social bonding (van Ree et al, 2000; Russel & Phelps, 2013). However, the pleasure experienced during grooming may dissipate in the course of the grooming interaction, following habituation to the stimulus (even though the area groomed changes in the course of the grooming interaction, Russel & Phelps, 2013), and thus decrease the motivation to continue the interaction (Yaksh et al, 1982; McSweeney & Swindell, 1999; Russell & Phelps, 2013). Consequently, the calming effect experienced at the beginning of grooming may not last once the grooming interaction is terminated. Further studies are thus necessary to investigate how long the physiological calming effect of grooming lasts. The results of this thesis suggest that the relaxing effect of grooming on recipients, if present, stops once the grooming interaction is terminated. It remains unclear whether donors experience a physiological relaxing effect during grooming, as so far physiological data during or just before and after grooming interactions have not been collected on donors (Shutt et al, 2007; Aureli & Yates, 2010; Radford, 2012; Russell & Phelps, 2013). The results of this thesis suggest that if donors experience a relaxing effect during grooming, this effect does not last once the grooming interaction is terminated. Thus, we still know little about the underlying mechanisms supporting the emotional mediation of social interactions such as grooming in animals (Dunbar & Shultz, 2010). This is certainly due to the difficulty to conceive proper tests to investigate these hypotheses. Studies using methods such as pharmacological manipulation of emotional states, neuroimaging of brain and measure of neuroendocrine environment may be necessary to bring essential contribution to this topic (Schino & Aureli, 2009; Dunbar & Shultz, 2010; Russel & Phelps, 2013).

8.2.2. Grooming disruption (Chapter 4)

Because of the potential hygienic and social benefits of grooming exchanges and since time for grooming is limited, individuals compete over valuable grooming partners (Dunbar, 1991, 1992). Grooming disruption has been proposed as resulting from such competition over access to grooming partner (Cheney & Seyfarth, 1990). However, no study has so far investigated the benefits the disrupters gain from disruption and whether this behaviour is potentially risky. The results of this thesis showed that grooming disruption can be costly for the disrupters as it increases aggression risk (when one grooming partner is higher-ranking than the disrupter), but it gives direct grooming benefits to the disrupters and it is successful at stopping the disruptees from grooming each other. By stopping grooming interactions, the disrupter may gain access to grooming partners that would not be available otherwise, and obtain the hygienic and social benefits of grooming, while preventing the disruptees from accessing those benefits. Individuals may maintain their social and dominance positions in the group by controlling the social relationships of other group members, notably by controlling their grooming exchanges. This may allow individuals to influence the social relationships of other group members at their own advantage. This does not necessarily imply that animals plan disruption to get benefits. Mechanisms based on emotion may play a role in grooming disruption in animals. For example, an individual may experience a negative emotional response when viewing a ‘friend’ (i.e. a partner with whom the subject has a strong social relationship) grooming with an ‘enemy’ (i.e. a partner with whom the subject has a weak social relationship), which may trigger the disruption of the grooming interaction. The need to be groomed because of a high parasite infection may also trigger individuals to approach group members to request to be groomed, regardless of whether the group members are already engaged in a grooming interaction or not. Grooming disruption has to be taken into account when analysing grooming distribution and the formation and maintenance of social relationships in non-humans primates. Further studies are necessary to shed the light on the mechanism and function of grooming disruption in animals. For instance, it would be necessary to investigate which kind of grooming interaction is more likely to be disrupted (e.g. in terms of social and dominance relationships between the grooming partners), and which animal is more likely to be a disrupter. For example, a grooming interaction between partners having a low relationship quality may be more likely disrupted by a disputer who has a strong relationship quality with one of the grooming partner, in order to sustain the existing strong social bond. Moreover, it would be useful to assess the choice of grooming partner by the disrupter following grooming disruption in order to investigate the function of grooming disruption in term of grooming coercion and competition for accessing valuable grooming partner. Finally, it would also be necessary to assess the long-term consequences of grooming disruption, that is, whether grooming disruptions affect social relationships and social networks within a group.

Grooming disruption may be related to the set of strategies under the maxim ‘divide and rule’, successfully employed in political, military and economic contexts in humans. These strategies consist in gaining and maintaining power by breaking up existing enemies structures and preventing smaller groups from linking up. For example, in humans history ‘divide and rule’ strategies can be related to labour law, constitutional design, imperial and colonial powers, international law and market competition (Posner et al, 2010). ‘Divide and rule’ strategies imply to encourage those who are willing to cooperate and prevent non-cooperators from forming alliances that could challenge the power. This prevention can be achieved for example by destroying communication channels, limiting the frequency or duration of interactions and spreading threat of punishment (Posner et al, 2010). Following this view, grooming disruption may limit the frequency and duration of friendly interactions between partners whose social relationship could be a threat to the social and dominance relationships of other group members.

In humans, individuals respond to actions that are likely to reduce their fitness with behaviour that reduces the fitness of the investigators and discourage or prevent them from reiterating the actions (Clutton-Brock & Parker, 1995). Punishment thus provides future benefits for the punishers such as the reduction of behaviours that transgress their interest. Grotius (1738) also defined punishment behaviours as the infliction of an ill suffered for an ill done. There is evidence that punishment promotes cooperation in humans (Fehr & Gächter, 2000, 2002; Boyd et al, 2003; Cinyabugama, 2005; Henrich, 2006; Shinada & Yamagishia, 2007; Gächter et al, 2008; Boyd et al, 2010; Jensen, 2010; Balliet et al, 2011; Wolf, 2012). However, it is unclear whether punishment occurs and promotes cooperative behaviours and influences social behaviours in animals (e.g. Hauser, 1992; Clutton-Brock & Parker, 1995; Gardner &

West, 2004; Bshary & Grutter, 2005; Silk, 2005; Bernstein, 2006; Cant & Johnstone, 2006; Henrich, 2006; Koyama et al, 2006; Chancellor & Isbell, 2008; Jensen, 2010; Raihani et al, 2010; Bshary & Bronstein, 2011; Nakao & Machery, 2012; Raihani et al, 2012). In the blue-streak cleaner wrasse (*Labroides dimidiatus*), clients chase cleaners fishes when they feed on their mucus, terminating the cleaner-client interaction, which results in a reduction of cheating behaviour (i.e. eating the mucus) by the cleaner fishes (Bshary & Grutter, 2002, 2005). Moreover, during male-female pairs inspection of model client, male aggressively punishes female that cheats and causes the client to leave (Bshary et al, 2008; Raihani et al, 2010). In non-humans primates, dominant individuals may use aggression to punish subordinate individuals that infringed their interest, for instance when a subordinate individual does not let a higher-ranking individual accessing a food resource in priority, or when it tries to mate with a female guarded by a higher-ranking individual (de Waal & Luttrell, 1988; Hauser, 1992; Silk, 1992; Clutton-Brock & Parker, 1995; Silk, 2005; Jensen, 2010). For example, dominant chimpanzees (*Pan troglodytes*) retaliate subordinates that stole their food (Jensen et al, 2007), and in geladas (*Theropithecus gelada*) extra-pair copulations elicit post-copulatory aggression (Le roux et al, 2013). In the same way, the concept of punishment may be applied to social relationships in general, and to grooming disruption in particular (Clutton-Brock & Parker, 1995b). For example, individuals may target the disruption of grooming interactions involving monkeys whose social bonds may become a threat for them. For instance, an individual may disrupt grooming interactions involving one of its ‘friends’ with one of its ‘enemies’. This may be risky as the individual may receive aggression, but it may preserve the advantages the individual usually gets from its relationship with its friend (e.g. support during agonistic interaction against its enemies), and discourage its friend from socialising with other individuals. Grooming disruption may also be applied to the notion of relational aggression in humans, where individuals damage others' social relationships and social status at their own advantage (e.g. Crick & Grotpeter, 1995; Bowie, 2007). In humans, relational aggression can take the form of excluding others from social activities and relationships, and damaging their reputation. Further studies would need to assess whether grooming disruption significantly modify the subsequent grooming distributions and social relationships of the partners that were targeted.

8.2.3. Grooming reciprocity (Chapter 5)

8.2.3.1. Reciprocity, emotion and neural basis

The role of direct, indirect and generalised reciprocity in explaining grooming exchanges was investigated in wild Barbary macaques. The results revealed a temporal contingency between grooming given and received according to direct reciprocity, but not according to indirect or generalised reciprocity. This supports the hypothesis that direct reciprocity but not indirect or generalised reciprocity plays an important role in the reciprocation of services in non-human primates. Although the act of giving grooming was reciprocated in the short-term, the duration of grooming received was not matched to the duration given. In Barbary macaques, direct contingent reciprocation of grooming may thus follows a 'rule of thumb', that is, the relevant aspect of short-term contingency may be the act to receive grooming, not the amount received. Nevertheless, it is possible that the duration of grooming exchanged may be balanced in the long-term (Manson et al, 1999; Schino et al, 2003; Manson et al, 2004; Gomes et al, 2009; Schino & Aureli, 2009; Schino et al, 2009; Frank & Silk, 2009; Carne et al, 2011; Majolo et al, 2012). Further studies may asses the overall dyadic amount of grooming given and received in Barbary macaques, irrespective of the time frames, to investigate whether the overall amount of grooming exchanged is balanced, and whether social factors such as dominance relationships influence the amount of services exchanged (e.g. following the biological market theory, Noé & Hammerstein, 1994; Barrett et al, 1999; Noë et al, 2001). Direct reciprocity may be proximately driven by partner-specific emotional bonds that develop between partners as a consequence of past interactions such as grooming (Schino & Aureli, 2009).

In humans, emotions such as gratitude (i.e. the positive emotion individuals feel after they have received something valuable) and sense of fairness are known to promote cooperative behaviours and reciprocity (Fehr & Schmidt, 1999; Bolton & Ockenfels, 2000; Nowak et al, 2000; McCullough et al, 2001, 2002; Fehr & Fischbacher, 2003; Emmons & McCullough, 2004; Bartlett & DeSteno, 2006; Rand et al, 2013). People compare their own efforts and pay-offs with those of others, and react negatively to inequity. For example, in the ultimatum game (Güth et al, 1982) two subjects, the proposer and the responder, are faced with a sum of money. The proposer has to do a proposal on how to divide the money between the two participants. Then the responder has the choice to accept or reject the proposed division. If the responder accepts the proposal, the division of money is made and the money is distributed to both participants. If the responder rejects the proposal, both subjects receive no money. In order to maximize its own payoff, the proposer would offer the least amount possible to the responder, and the responder would accept it. However, in most studies the average offer by the proposers for the responders is about 40%, and below a proposal share of around 25% of the money, most responders reject the proposal (Güth & Tietz, 1990; Hoffman et al, 1996; Cameron, 1999; List & Cherry, 2000; Camerer & Thaler, 1995; Henrich et al, 2001; Fehr & Fischbacher, 2003). These results have been interpreted as people not maximising their benefits and having a sense of fairness. When the proposal is experienced as unfair, the responder punishes the proposer for the violation of equity, and as a consequence if the game is played for several rounds, the proposer is more likely to make more equal proposals in the future (Fehr & Fischbacher, 2003). When the responders have no option to reject the offer (e.g. in the dictator game), proposers give less to the responders than in the ultimatum game (Forsythe et al, 1994; Hoffman et al, 1994). Reactions to unfairness elicit activity in brain areas related to both cognition (dorsolateral prefrontal cortex) and emotion (the anterior insula, an area also involved in aversive emotions such as disgust: Phillips et al, 1997) (Sanfey et al, 2003). Participants to the ultimatum game also experienced more emotional arousal, measured by skin conductance activity, when receiving an unfair offer and rejecting it (van't Wout et al, 2006). Thus, in humans emotions favour social relationships and cooperative behaviours. There is also evidence that aversion to inequity varies depending on the quality of the relationship between the individuals involved; people showing less response to inequity for close than distant relationships (Clark & Grote, 2003).

It remains unclear and highly debated whether animals experience inequity aversion like humans do, and whether inequity aversion plays a role in the evolution of cooperative behaviours (Henrich, 2004; Brosnan, 2006; Chen & Santos, 2006; de Waal, 2006; Silberberg et al, 2006; Brosnan, 2008, 2009, 2011; Bräuer & Hanus, 2012; Price & Brosnan, 2012; Yamamoto & Takimoto, 2012; Brosnan, 2013; DeAngelo & Brosnan, 2013). Inequity aversion has been tested in experimental settings in several species including non-human primates (Brosnan & de Waal, 2003; Brosnan et al, 2005; Bräuer et al, 2006; Dubreuil et al, 2006; Roma et al, 2006; Jensen et al, 2007; van Wolkenten et al, 2007; Fletcher, 2008; Bräuer et al, 2009; Neiworth et al 2009; Silberberg et al, 2009; Brosnan et al, 2011; Talbot et al, 2011; Massen et al, 2012; Kaiser et al, 2012; Proctor et al, 2013), dogs (Range et al, 2009; Horowitz, 2012; Range et al, 2012), birds (Wascher & Bugnyar, 2013), and fishes (Raihani et al, 2012). For example, Brosnan and colleagues found that chimpanzees (*Pan troglodytes*) and capuchins (*Cebus apella*) respond negatively when receiving less benefits than a partner for the same effort, and they suggested that these species show inequity aversion (Brosnan & de Waal, 2003; Brosnan et al, 2005; Brosnan et al, 2010). In chimpanzees, the longer individuals had lived together the lower their response to iniquity was (Brosnan et al, 2005), but this was not the case in long-tailed macaques (*Macaca fascicularis*; Massen et al, 2012). However, the debate of fairness in non-human primates is still on-going (e.g. Henrich, 2004; Bräuer et al, 2006; Bräuer & Hanus, 2012). The species' degree of social tolerance and the relative dominance rank between partners may also influence response to inequity in food distribution in animals (Amici et al, 2012). Jensen and colleagues (2007) tested chimpanzees in a mini-ultimatum game where the proposer was given a choice between making one of two pre-set offers of food, and the responder could accept or reject it. The responder's acceptance led to both subjects being able to reach their respective share of food, whereas rejection led to both subjects getting no food. The proposer made the proposal by first pulling half-way a platform with the two chosen shares of food, and the responder either pulled the platform the remaining distance so that both got their share of food, or rejected the offer by not pulling during one minute. Thus, while in humans the rejection of an offer is usually active in the ultimatum game, the rejection of an offer by chimpanzees in this study was passive. The results showed that when given the opportunity, proposers did not make fair offers, and responders tended to accept any offer, regardless of the difference in gains between the two partners, which maximised their pay-off (Jensen et al, 2007). However, in control conditions where the subjects were alone, they still pulled the tray when no food could be gained, which may indicates an inability to inhibit pulling for food. In another study, chimpanzees and bonobos (*Pan paniscus*) did not reject any non-zero offer, even when the proposers stole food from the responders' shares (Kraiser et al, 2012). When the game of Jensen and colleagues (2007) was replicated with humans (i.e. subjects were asked to wait 5 minutes before to refuse an offer to match the minute of inactivity required to reject an offer in chimpanzees), participants also did not reject most of the offers and maximised their pay-off (Smith & Silberberg, 2010). A recent study showed that, in a modified ultimatum game where proposers had to choose between an equal and selfish split of rewards, chimpanzees and children proposers chose the equal split if their partner's cooperation was required to get the reward, and responders accepted the offers (Proctor et al, 2013). It remains thus unclear whether animals have a sense of fairness or act to maximize their immediate benefits. Humans seem to treat fairness more as a social norm, and people also respond to receiving more than their partner (i.e. advantageous inequity) and to equity for others (Silk et al, 2005; Brosnan, 2009). There is no clear evidence of advantageous inequity aversion in non-human primates (e.g. Brosnan & de Waal, 2003; Henrich, 2004; Brosnan et al 2005; Brosnan et al, 2010; Yamamoto & Takimoto, 2012). More studies are still necessary to understand the diversity and evolution of human responses to inequity, and the link between inequity aversion and cooperative behaviours.

There is evidence in humans and animals that neurotransmitters such as oxytocin promote social bonding and so may favour cooperative behaviours (Donaldson & Young, 2008; Insel, 2010). Oxytocin is a neurosecretory hormone synthesized by hypothalamic neurons in the mammals brain (Donaldson & Young, 2008). Oxytocin is thought to be important for bonding in parental relationships of mammals, including humans (Pedersen, 1999; Feldman et al, 2007). For example, even in a non-pregnant ewe, oxytocin facilitated acceptance of an alien lamb, within 30 seconds of intra-cerebral ventricular injection (Kendrick et al, 1987; Keverne & Kendrick, 1992). Recent studies suggest that oxytocin, or its close relative vasopressin (whose sequence differs from oxytocin by two amino acids), are also involved in bonding between adults (Insel & Young, 2001). For example, oxytocin and vasopressin facilitate pair bonding in voles (*Microtus* species: Insel & Shapiro, 1992; Young & Wang, 2004). Recent studies show that oxytocin also affects social bonding in highly social mammals species such as non-human primates. For example, pharmacological manipulations of oxytocin activity modified social behaviour during male-female pair interactions in marmosets (*Callithrix penicillata;* Smith et al, 2010). The stimulation of oxytocin’s activity (by intranasal administration of oxytocin) favoured social behaviours such as body contact, proximity and food tolerance, whereas the inhibition of oxytocin’s activity (by oral administration of an oxytocin-receptor antagonist) reduced these behaviours (Smith et al, 2010). Moreover, inhaled oxytocin favoured prosocial choices (i.e. rewarding another monkey when the alternative choice was to reward no one) in rhesus macaques (*Macaca mulatta;* Chang et al, 2012). In a recent study of grooming in wild chimpanzees, Crockford and colleagues (2013) measured urinary oxytocin following grooming interactions. Oxytocin levels were higher after grooming between partners having a strong relationship quality, regardless of kinship and role of the partner (i.e. donor or recipient; Crockford et al, 2013). This suggests that the oxytocin system may have further been specialized to process partner-specific affiliative interactions (Chang et al, 2013). Moreover, injection of oxytocin to meerkats (*Suricata suricatta*) promoted contribution to communal activities such as guarding and pup-feeding, and reduced aggressive behaviours (Madden & Clutton-Brock, 2011). Oxytocin would also favour memory of social partners in animals (Dantzer et al, 1987; Ferguson et al, 2000).

In humans, inhaled oxytocin enhanced trust (Kosfeld et al, 2005; Zak, 2005; Zak et al, 2005), empathy (by inferring the mental state of someone by interpreting social cues; Domes et al, 2007), social memory (memory of facial identity and expression; Savaskan et al, 2008), and generosity (in the ultimatum and dictator game; Zak et al, 2007). Trust is defined as the willingness to be vulnerable to the actions of someone else (Zak et al, 2005). Trust is an important component of the human capacity for altruism, and it facilitates the formation and maintenance of social bonds, reducing the uncertainty about the partner response (Hinde, 1997; Kosfeld et al, 2005). Empathy (i.e. sharing the emotional state of others) may also promote altruistic acts in humans (Batson, 2002; Preston & de Waal, 2002; de Vignemont & Singer, 2006; Barraza & Zak, 2009). Finally, oxytocin treatment improves social skills in people with autism (Hollander et al, 2007; Andari et al, 2010; Insel, 2010). Thus in animals and humans, cooperative relationships may be facilitated by an endocrinological mechanism involving oxytocin.

8.2.3.2. Generalised reciprocity

In this thesis, no evidence was found that Barbary macaques exchanged grooming interactions according to generalised reciprocity. The importance of partner specificity in the exchange of grooming interaction may explain the lack of evidence for generalised reciprocity. Generalised reciprocity is thought to be driven by a general benevolent mood which makes individuals more willing to reciprocate altruistic act to anyone else (i.e. ‘paying it forward’, Emmons & McCullough, 2004; Nowak & Roch, 2007). In animals, if mechanisms of reciprocity are affected by change in emotional state, this may be partner-specific and not generalisable to other individuals.

Generalised reciprocity does not required partner recognition and partner choice as individuals can base their decision solely on the outcome of the last interaction they experienced (Berkowitz & Daniels, 1964; Boyd & Richerson, 1989; Nowak & Sigmund, 2005; Pfeiffer et al, 2005; Rankin & Taborsky, 2009; Barta et al, 2011). In humans, receiving benefits would increase the willingness to help strangers (Berkowitz & Daniels, 1964; Dufwenberg et al, 2001; Fischbacher et al, 2001; Güth et al, 2001; Greiner & Levati, 2003; Hamilon & Taborsky, 2005; Bartlett & de Steno, 2006; Nowak & Roch, 2007). However, when interactions involve also known partners, would direct reciprocity play a more important role in the exchange of benefits than generalised reciprocity? Emotions such as gratitude that may favour generalised reciprocity are also known to favour social relationships and direct reciprocity (Emmons & McCullough, 2004; Bartlett & de Steno, 2006). After receiving help, although gratitude favoured help toward benefactors and strangers, humans were more helpful toward their benefactors than toward strangers (Bartlett & de Steno, 2006). In a two parts dictator game, the correlation between amounts received and amounts given to the other players was higher in the case of direct than generalised reciprocity (Ben-Ner et al, 2004). Direct reciprocity may play a role in interactions with known partners, while generalized reciprocity may promote cooperation when interactions involve unknown partners (Pfeiffer et al, 2005). This is compatible with a ‘hierarchical information hypothesis’, where the information about the cooperative propensity of known partners would be used when available to decide whether to cooperate or not, otherwise social experience with strangers would be used instead (Rutte & Taborsky, 2007, 2008). Thus direct reciprocity would play a role in cooperation when the propensity to cooperate of known partners is available, otherwise generalised reciprocity would take place. This would maintain cooperation even when direct information about known partners is unavailable or costly to obtain (Rutte & Taborsky, 2007, 2008). In humans, generalised reciprocity may thus be a by-product of emotional mechanisms that initially evolved to facilitate direct reciprocity (Bartlett & de Steno, 2006; Nowak & Roch, 2007).

Models have been developed to analyse the evolution of generalised reciprocity. In a well-mixed population (i.e. when each individual interacts with every other individual with equal likelihood) of cooperators and defectors, generalised reciprocity would not evolved because individuals would indiscriminately give benefits to strangers who will not necessarily return the cooperation, favouring defectors (Rankin & Taborsky, 2009). Some models suggest that generalized reciprocity could evolve either in very small groups (i.e. two to four individuals: Pfeiffer et al, 2005), in combination with group leaving strategies (i.e. a win-stay in the group and lose-leave the group rule: Hamilton & Taborsky, 2005), in connection with direct reciprocity (Nowak & Roch, 2007), or in population with assortment of encounters (e.g. individuals are more likely to interact with others playing the same strategy, such as cooperating between relatives: Rankin & Taborsky, 2009). Real populations are not well-mixed and spatial structures and social networks influence how individuals interact with each other (e.g. Nowak, 2006; Iwagamia & Masudavan, 2010; Fehl et al, 2011; van Doorn & Taborsky, 2012).

To date, there is no evidence that generalised reciprocity play a key role in the exchange of services in animals (e.g. de Waal, 1997; de Waal & Brosnan, 2006; Rutte & Taborsky, 2008; Majolo et al, 2012). Within a group, non-human primates do not interact anonymously, they have knowledge of the identity, social and dominance relationships of others group members, and they often interact together (Cheney & Seyfarth, 1982; Cheney & Seyfarth, 1990; Cheney et al, 1995; Silk, 1999; Bergman et al 2003; Kitchen et al, 2005; Schino et al, 2006; Slocombe & Zuberbuehler, 2007; Shettleworth, 2010; Adachi & Hampton, 2011; Cheney, 2011; Schell et al, 2011; Borgeaud et al, 2013). Thus direct reciprocity may play a more important role in non-human primates than generalised reciprocity. There is evidence that when the cooperative propensity of known partners is available, direct reciprocity play a more important role than generalised reciprocity in the exchange of services in animals (de Waal, 1997; Hauser et al, 2003; Rutte & Taborsky, 2008). In non-human primates, partner-specificity seem thus to play a key role in the exchange of services. Further studies may assess whether generalised reciprocity favour cooperation in population structures where interactions occur between anonymous individuals, and where repeated interaction between the same individuals is rare. Moreover, further studies may modulate the availability of known partners and strangers and investigate the relative role of direct and generalised reciprocity in explaining exchange of services, as well as investigate partner choice based on benefits received by known partners or by strangers.

8.2.3.3. Indirect reciprocity

In this thesis, no evidence was found that Barbary macaques exchange grooming interactions according to indirect reciprocity. Indirect reciprocity assumes that giving grooming increases the donor’s reputation, and so its chance to receive grooming from bystanders, that gained the grooming propensity of the donor by eavesdropping, increases (McGregor, 2005; Bshary & Grutter, 2006). Although grooming is a conspicuous behaviour that can potentially be observed by group members, reputation does not seem to affect the contingency of grooming exchanges in Barbary macaques. Individual may have had the opportunity to gain information on the cooperative propensity (i.e. the tendency to give grooming or not) of each potential partner through direct interactions. Gaining the cooperative propensity of group members through observing their grooming interactions may, if present, play a less important role than direct experience in this species. Thus Barbary macaques direct their grooming toward individuals from who they received grooming rather than toward individuals who gave grooming to other group members.

In humans, people regularly interact with unknown potential partners (Seabright, 2005). There is a wide range of evidence showing that humans invest in their own reputation and use the reputation they gather on third-parties interactions to make decision about with whom being cooperative among strangers (Nowak & Sigmund, 1998; Wedekind & Milinski, 2000; Milinski et al, 2001; Hammerstein, 2003; Panchanathan & Boyd, 2003, 2004; Haley & Fessler, 2005; Nowak & Sigmund, 2005; Semmann et al, 2005; Bateson et al, 2006; Nowak, 2006; Seinena & Schram, 2006; Sommerfeld et al, 2007; Roberts, 2008; Engelmann & Fischbacher, 2009; Sylwester & Roberts, 2010; Tennie et al, 2010; Pfeiffer et al, 2012). Reputation thus promotes cooperation in humans (Nowak & Sigmund, 1998; Wedekind & Milinski, 2000; Milinski et al 2002; Wedekind & Braithwaite, 2002; Brandt et al, 2003; Barclay, 2004; Brandt & Sigmund, 2005; Nowak & Sigmund, 2005; Semmann, 2012; Rand & Nowak, 2013). In humans, reputation-based decision making may involve some form of meta-representation (e.g. thinking about what others think of us, Amodio & Frith, 2006; Izuma, 2012). A brain area involved in meta-representations (the medial prefrontal cortex) is also involved in reputation management (Izuma et al, 2010; Izuma, 2012). Moreover, many of the means for gathering indirect information include the use of language (i.e. gossip, Nakamaru & Kawata, 2004; Nowak & Sigmund, 2005; Sommerfeld et al, 2007), and the accuracy of the information gathered indirectly may increase through multiple gossip sources (Sommerfeld et al, 2008).

To adjust to changing ecological and social environment, animals reduce uncertainty by gathering information either directly or indirectly (i.e. by observing the behaviour of other animals) (Dall & Johnstone, 2002; Dall et al, 2005). Non-human primates gain information about social and dominance relationships by direct interactions with group members and by observing third-parties interactions, and use this information to behave accordingly (Hinde, 1976, 1979; Cheney & Seyfarth, 1980; Hinde, 1983; Dasser, 1988; Bergman et al, 2003; Silk, et al, 2004; McGregor, 2005; Crockford et al, 2007; Aureli et al, 2012). For example, individuals adjust their fighting behaviour according to information they gathered about fighting abilities during third-parties' conflicts (e.g. Johnstone, 2001; Earley & Dugatkin, 2002; Peake et al, 2002; Johnstone & Bshary, 2004; McGregor, 2005; Amy & Leboucher, 2007; Earley, 2010; Le Roux & Bergman, 2012). However, evidence that animals eavesdrop and use the information gathered in a cooperative context is scarce. For example, evidence of indirect reciprocity in grooming exchange of long-tailed macaques was limited (Majolo et al, 2012). In another study, chimpanzees (*Pan troglodytes verus*), but not bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla gorilla*), and orangutans (*Pongo pygmaeus abelii*), preferred to approach an experimenter they have just witnessed as cooperative rather than non-cooperative (i.e. giving or not giving food) in an interaction with another experimenter (Russel et al, 2008). Herrmann and colleagues (2013) found that orangutans and chimpanzees, but not bonobos, took into account the actions of the experimenter toward third-parties in forming reputations. Species differences among the apes and across studies are notably unclear and may be further investigated. Capuchin monkeys (*Cebus apella*) accepted food less frequently from experimenters who rejected another experimenter's requests for help (Anderson et al, 2013), but did not learn to prefer reliable experimenters from watching other monkeys-experimenters interactions (Brosnan & de Waal, 2009). Similar experiments also led to mixed results in dogs (Kundey et al, 2011; Marshall-Pescini et al, 2011; Nitzschner et al, 2012). However, these experiments always involved humans as partners and consequently they do not provide a test of an effect of eavesdropping on cooperative decision between conspecifics. Moreover, the response measured was rather indirect (e.g. time spend in proximity) instead of more explicit such as giving grooming. When chimpanzees are asked to choose to beg food (a more explicit response than time spend in proximity) to an experimenter they witnessed as being either cooperative or non-cooperative toward another experimenter, the results are mixed (Subiaul et al, 2008). Additionally, there is no evidence that non-human primates increase their cooperative behaviour in the presence of other group members (Engelmann et al, 2012; Yamamoto & Takimoto, 2012). Moreover in a recent study, chimpanzees were not sensitive to cues of conspecific observation (Nettle et al, 2013). The only evidence of an effect of reputation on cooperative behaviours comes from studies on cleaning mutualism involving cleaner wrasses (*Labroides dimidiatus*) and client reef fishes. Clients invite more for inspection cleaners they have witnessed as more cooperative (Pinto et al, 2001; Bshary, 2002; Bshary & Grutter, 2006), and cleaners are more cooperative in the presence of bystanders (Bshary & D'Souza, 2005). Cleaners interact with over 2,000 clients per day, and they constantly received feedback on the consequences of their foraging on clients' behaviours (Bshary & Grutter, 2006). Indirect reciprocity in cleaning mutualism in fishes probably requires only simple cognitive processes as clients react immediately to what they have just observed, and thus do not need to remember several third-parties interactions (Bshary & Grutter, 2006). Whether indirect reciprocity in non-human primates, if present, involved cognitively demanding mechanisms is still unknown. Notably, as there is no evidence that indirect reciprocity may be mediated by emotion, mechanisms such as image-scoring of past grooming interactions of several known group members may require too cognitively demanding capacities for animals (Stevens & Hauser, 2004; Stevens et al, 2005).

Thus, so far there is little evidence that non-human primates use information gathered through observation of third-parties interactions to regulate their cooperative interactions. Gaining the cooperative propensity of potential partners by direct interactions is likely to provide more accurate information than gathering information indirectly (Axelrod, 1984; Alexander, 1987; Hauser et al, 2003). Further experimental studies may investigate partner choice based on the observation of interactions between unknown conspecifics (in order to control for direct reciprocity), for example in the context of food tolerance (e.g. Melis et al, 2006a; Sabbatini et al, 2012). Indirect reciprocity may play a more important role as direct encounters between potential partners are infrequent (e.g. before the first direct interaction) and/or potentially risky (e.g. assessing the strength or dominance status of others, Axelrod, 1984, 1987; Sommerfeld et al, 2007; Herrmann et al, 2013). Indeed, models suggest that when encounters between known partners increase, direct reciprocity dominates over indirect reciprocity (Robert, 2008). Gaining the cooperative propensity of potential partners through eavesdropping is thus an important factors in humans and may potentially occur in animals where the same conditions of encounter between partners are met (e.g. Bshary, 2002; Bshary & D'Souza, 2005; Tan & Hare, 2013). In humans, the effect of reputation may also be linked to the risk that non-cooperative behaviour may be punished by others (Jaeggi et al, 2010; Jensen, 2010). Because humans regularly interact with strangers, it may have favoured the evolution of cognitive mechanisms that manage reputations and indirect reciprocity (Nowak & Sigmund, 2005). Exchanging social information about others is a very important capacity which contributes to the very high level of cooperation in human societies (Melis & Semmann, 2010).

8.2.4. Exchange of grooming and food tolerance (Chapter 6)

Non-human primates not only exchange grooming for itself, but also exchange grooming for other services such as support during agonistic interactions and food tolerance (e.g. Barrett & Henzi, 2001; Watts, 2002; Ventura et al, 2006 ; Carne et al 2011). In this thesis, the exchange of grooming for food tolerance was investigated by analysing the short-term contingency between these events in a wild partially-provisioned group of Barbary macaques. Food tolerance was assessed by conducting food tests after the end of grooming interactions. The results showed no evidence of a short-term contingency between grooming and food tolerance in Barbary macaques. Under the partner choice model, short-term contingencies are expected to be negligible if exchanges are explained by long-term relationship properties (Schino & Aureli, 2009, 2010). A positive relation between overall grooming received and tolerance given have been found in captive Barbary macaques (Carne et al, 2011). Thus the exchanges of grooming and food tolerance in Barbary macaques may be little affected by recent single events. Moreover in this thesis, males favoured females around food resources. Future research may assess further the relation between long-term exchanges of grooming, food tolerance and mating opportunities (Jaeggi & van Schaik, 2011).

While there is extensive evidence of a correlation between grooming and food tolerance in non-human primates over long-time frames (Kapsalis & Berman, 1996; Pastor-Nieto, 2001; Mitani, 2006; Ventura et al, 2006; Carne et al, 2011; Tiddi et al, 2011; Tiddi et al, 2012), evidence for short term contingency is mixed (de Waal, 1989, 1997; Melis et al, 2008; Tiddi et al, 2011; Jaeggi et al, 2013) and may be influenced by other mechanisms such as harassment (Silk et al, 2013). Moreover, in chimpanzees the contingency between grooming and food tolerance was higher between individuals who rarely groom each other than between individuals who frequently exchange grooming (de Waal, 1997). In a recent experimental study on food tolerance, capuchin monkeys chose more their partners according to the long-term social bonds they had with them, rather than according to the recent events of food tolerance they experienced with them (Sabbatini et al, 2012). Thus, although non-human primates exchange grooming and food tolerance over longer time frames, short-term contingency seems to play little effect. This is consistent with a growing body of evidence showing that the exchanges of services in non-human primates are more balanced over time (Schino et al, 2003; Manson et al, 2004; Schino, 2007; Schino et al, 2007; Melis et al, 2008; Frank & Silk, 2009; Gomes et al, 2009; Schino & Aureli, 2009; Schino & Pellegrini, 2009; Schino et al, 2009; Jaeggi et al, 2010; Cheney, 2011; Tiddi et al, 2011; Sabbatini et al, 2012; Jaeggi et al, 2013). Individuals may preferentially interact with partners with whom they have strong social bonds, regardless of the most recent interactions (Schino & Aureli, 2009, 2010). Short-term contingency may play a more important role between partners who rarely interact together, and/or at the beginning of a new relationship (e.g. Seyfarth & Cheney, 1984; de Waal, 1997; Roberts & Sherratt, 1998; Schino & Aureli, 2009; Jaeggi et al, 2013; Tan & Hare, 2013). Indeed, in humans friends do not keep accurate track of each benefit given and received (but do so with strangers), but the costs and benefits are overall balanced within the relationships (Deutsch, 1975; Clark & Mills, 1979; Argyle & Henderson, 1984; Clark, 1984; O’Connor, 1992; Shackelford & Buss, 1996; Hinde, 2002; Silk, 2003; Stewart-Williams, 2007). Thus, close friendships in humans is independent of short-term contingent reciprocation. Neuroimaging studies in humans may assess whether cooperating with friends or with strangers activate similar brain area or not. It may be supposed that cooperating with friends may activate regions more involved in emotion whereas cooperating with strangers may activate regions more involved in cognition (e.g.

Krueger et al, 2007). Further long-term studies in non-human primates may follow individuals during several years from their first interactions with unknown individuals to their stable relationships within the group (e.g. when a new group is artificially formed in a zoo or when individuals migrate to other groups in nature). This may allow to investigate how services are exchanged in relation to the establishment and maintenance of social relationships.

In this thesis, a temporal contingency for grooming reciprocation occurred in Barbary macaques whereas no temporal contingency between grooming and food tolerance was found. It is possible that food tests are perceived as more competitive for animals than more naturally occurring feeding (Wobber et al, 2010a; Tiddi et al, 2011; Jaeggi et al, 2013), especially if the food reward used is highly desirable, hindering food tolerance. How animals compare and value different services is still poorly understood (Stevens & Gilby, 2004). Indeed, it is difficult to assess the exchange of different services because the value of each service is difficult to assess and compare (Seyfarth & Cheney, 1988), and may varies depending on the partners involved due to difference for example in sex, age, social relationships and dominance relationships (Boyd, 1992; Melis & Semmann, 2010). The emotional mediation of reciprocity through social relationships may facilitate the long-term exchanges of different services (Schino & Aureli, 2009). Indeed, the receipt of various services, such as grooming, food tolerance and agonistic support, may have qualitatively similar emotional consequences and thus may have similar effect on the probability of returning the services in the long-term (Schino & Aureli, 2009). Further studies such as neuroimaging studies may investigate whether the neural correlates of the receipt of different services are similar or different (Schino & Aureli, 2009).

8.2.5. Cooperative task and partner choice (Chapter 7)

Although the cognitive mechanisms underlying mutual cooperation have been often investigated with experimental approaches, no study has so far assessed the mechanisms underlying partner choice in mutual cooperation. However, the choice of partner with whom to cooperate is key to initiate and maintain mutual cooperation. In this thesis, the string-pulling cooperative task, commonly used in laboratory to assess mutual cooperation (Crawford, 1937; Hirata & Fuwa, 2007), was presented to a group of wild Barbary macaques to assess which social and individual factors affect their choice of cooperative partners and their performances. This study showed that wild Barbary macaques succeed to cooperate in an experimental task to get food. This is the first evidence of coordinated pulling in a wild macaque species. Although it remains unclear to what extend individuals 'understand' the role of their partner in solving the task, the results show that, to some extents, food tolerance and relationship quality affect their choice of partners and their success. Food tolerance between partners facilitated the initiation of successful cooperative interactions, while strong social bonds sustained their cooperative success. These results highlight the importance of testing the choice of cooperative partners in a social context, and add to the growing body of evidence showing that tolerance constrains cooperative behaviours in animals (Petit et al, 1992; Werdenich & Huber, 2002; de Waal & Davis, 2003; Melis et al, 2006b; Hare et al, 2007; Seed et al, 2008; Schneider et al, 2012; Silk et al, 2013).

If tolerance constrains cooperation, more tolerant species would perform better in cooperative task than less tolerant species and, within species, more tolerant partners would perform better than less tolerant partners. When individuals have the opportunity to cooperate to obtain resources such as food, the level of social tolerance of the group influences the ability of individuals to be in proximity to one another in the presence of this resource (Visalberghi et al, 1997; Cronin & Sanchez, 2012). Consequently, in groups with low level of social tolerance, only selected individuals sharing a high level of social tolerance would be able to gather together around the food resource without the risk of receiving aggression (Cronin & Sanchez, 2012). For example, because bonobos have a higher willingness to share food than chimpanzees, bonobos outperformed chimpanzees in a cooperative task to retrieve monopolizable food rewards (Hare et al, 2007). The high level of social tolerance of adult bonobos compared to adult chimpanzees would result from a shift in their development (Wobber et al, 2010b). Indeed, bonobos maintain juvenile level of food tolerance into adulthood whereas chimpanzees become less tolerant as they age (Wobber et al, 2010b). Moreover, male bonobos and chimpanzees showed a different physiological response preceding their release in a room full of food with a partner. When unable of sharing food, male chimpanzees experienced an increase of testosterone, consistent with competitive interaction and avoidance of contact, whereas male bonobos did not (Salvador & Costa, 2009; Wobber et al, 2010a; Hare & Tan, 2012). The experimental study presented in this thesis may be replicated in other species with known differences in social tolerance levels to investigate to what extent the social tolerance of a species affect the performance of individuals and the choice of partners in cooperative tasks. Further studies may also reward only one individual instead of both for each cooperative interaction, in order to investigate the factors influencing partner choice and performance of the individuals in a social context for altruism and reciprocity. Indeed, altruism is more risky than mutual cooperation as the return benefit is not guaranteed, and the effect of social tolerance and relationship quality may become stronger as the risk increases.

There is a growing body of evidence showing that social tolerance (including strong socials bonds) enhance cooperative behaviours in animals and humans (e.g. Silk, 2002, 2003; Majolo et al, 2006; Schino & Aureli, 2009; de Waal & Suchak, 2010; Massen et al, 2010; Melis & Semmann, 2010; Cronin, 2012; Cronin & Sanchez, 2012; Schneider et al, 2012). Humans-like cooperation may have evolved following a transition from non-tolerant social systems to more egalitarian social systems, relative to the *Pan-Homo* common ancestor 6 million years ago (Hare & Wrangham, 2002; Leach, 2003; Hare & Tomasello, 2005; Tomasello et al, 2012). Tolerant relationships may have been a prerequisite for the evolution of cognitively complex cooperation in humans (Leach, 2003; Hare & Tomasello, 2005; Melis et al, 2006b; Hare, 2007; Hare et al, 2007; Melis & Semmann, 2010; Hare & Tan, 2012). Thus it may be only after humans became more tolerant that socio-cognitive skills such as forming shared goals, intentions and experiences, as well as cooperative communication, have been favoured by selection and shaped the humans' complex and wide cooperative behaviours (Tomasello et al, 2005; Melis et al, 2006b; Moll & Tomasello, 2007). For example, children are able to intentionally coordinate their behaviour, but also to communicate to guide their partners during cooperation (e.g. Warneken et al, 2006). Humans are maybe uniquely motivated to share their intention and emotion in cooperation and to impose sanction on non-cooperators, such as third-party punishment (i.e. individuals punish a non-cooperator or norm violator even when they are not affected themselves, Fehr & Fischbacher, 2004) (Fehr & Gachter, 2002; Fehr & Fischbacher, 2003; Gintis et al, 2003; Tomasello et al, 2005; Warneken & Tomasello, 2009; Melis & Semmann, 2010; Cheney, 2011; Riedl et al, 2012). Control mechanism such as punishment, reputation and ostracism enforce cooperative behaviours in large group in humans (Lau et al, 2009; Melis & Semmann, 2010). In non-human primates, shunning (i.e. avoiding to interact with non-preferred social partners) may maintain cooperative behaviours without the need of costly punishment (Barret et al, 1999; Melis et al, 2006a; Hare & Tan, 2012). The increase of social tolerance in the evolution of humans likely resulted in an expanded social network of unrelated individuals which further enabled widespread cooperation (Tomasello, 2009; Foley & Gamble, 2009; Hill, 2011; Tomasello et al, 2012; Tan & Hare, 2013).

8.3. FUTURE DIRECTIONS

The following sections discusse potential future researches to complete and expand the results of this thesis. Moreover, potential improvements to the methodology used in this thesis are discussed.

8.3.1. Relationship quality

To facilitate cooperation, partners should maximise opportunity to be at the same place at the same time, that is, they need to coordinate and synchronise their activities with those of their preferred social partners (Dunbar & Shultz, 2010). In humans, psychologist defined friendship notably as physical togetherness and sharing of activities (Berscheid et al, 1989; Dunbar & Shultz, 2010). This poses the question of whether animals sharing high relationship quality coordinate their distance and activities to get more chances to interact together. Data can be collected to assess whether wild macaques sharing strong relationships coordinate and synchronise more their daily activities compare to individuals sharing weak relationships, as well as which pattern of inter-individual distances characterize those dyads (e.g. whether individuals spend all the day in proximity of their preferred partner, or whether they live more ‘independently’ but regularly ‘visit’ each other for particular activities). For this, each individual of dyads sharing a strong or weak relationship can be simultaneously followed by two observers during focal sessions. Thus two simultaneous focal sessions would be collected for each dyad. During a focal session, the frequency and duration of all activities and social behaviours involving the focal monkey would be continuously recorded, as well as the full GPS track of the focal monkey. Baseline data on average activities and distance between group members and on average group spread would be also necessary. These data can be analysed to examine whether relationship quality influence the coordination of daily activities and the patterns of inter-individual distances. Temporal and spatial coordination may promote cooperation in individuals sharing high relationship quality.

8.3.2. Grooming and anxiety

Self-directed behaviours increase after grooming, possibly due to the frustration caused by the termination of grooming and/or because SDBs peak around behavioural transitions from one activity to another (Chapter 3). Individuals may experience frustration when it is the other partner that ends the grooming interaction. In the groomees, post-grooming anxiety where the groomer ended the grooming interaction might be compared to post-grooming anxiety where the groomee ended the grooming interaction. If self-directed behaviours increase due to the frustration caused by the termination of grooming, it would be expected that groomees experience more anxiety when they did not ended the grooming interaction. Similar analysis might be conducted on the groomers. Furthermore, self-scratching frequency could be simultaneously collected before, during and after grooming interaction in groomer and groomee (e.g. Semple et al, 2013). This would allow to investigate further the relation between anxiety and grooming. For example, anxiety may be lower during grooming compared to before and after. Physiological data collected before, during and after grooming may be also very useful to investigate the physiological changes in relation to grooming interaction, but are more difficult to collect. The occurrence and duration of self-directed behaviours would also need to be investigated for various behavioural transitions, such as from travelling to feeding, from resting to travelling and so on, in order to examine whether self-directed behaviours also increases during other behavioural transitions than the ones involving grooming. Because self-scratching and self-grooming have different behavioural/temporal constrains and different functions (e.g. self-grooming has also a hygienic function), it may be necessary to investigate whether those behaviours are similar or different in term of behavioural indicators of anxiety, and what is the equivalence of intensity of anxiety between these two behaviours.

8.3.3. Grooming disruption

In Chapter 4, while at the beginning of post-disruption sessions the disrupters were in proximity of the disruptees, the disrupter may not be in proximity of other group members at the beginning of control sessions. There is a possibility that the differences observed between post-disruption and control sessions, in term of grooming opportunities and aggression received, were influenced by proximity to other group members at the beginning of the sessions. Thus, additionally to the control sessions analysed in this thesis, a second kind of control session might be collected to control for the potential effect that proximity may play on the probability of grooming and agonistic behaviours to occur. For example, this control can consist in 10-minutes focal sessions where the focal monkey (i.e. the disrupter of the post-disruption session) would be in proximity (i.e. within 1.5m) of two grooming partners, but without the grooming interaction being disrupted. However, the situations in which a monkey is in proximity of two grooming partners without interrupting the grooming interaction occur very rarely, so this kind of control would be very time consuming to collect. Moreover, data from Chapter 5 (i.e. the 60-minutes control sessions) showed that only 11.1% of proximity events observed between two monkeys were followed by a grooming interaction between them.

Chapter 4 provided evidence of the costs and benefits of grooming disruption for the disrupter. Further studies are needed to investigate in which conditions a grooming interaction is more likely to be disrupted and which individuals are more likely to disrupt grooming interactions. This could not be investigated in this thesis because post-disruption sessions were collected in an opportunistic way and baseline focal data would be necessary to assess these questions. For example, data related to the identity, sex, relationship quality and dominance status of disrupters and partners of grooming interactions disrupted or not disrupted, as well as data on the audience present around grooming interactions would need to be collected. Moreover, further studies may investigate the short-term costs of disruption on disruptees, such as an increase of anxiety, and the long-term effects of grooming disruption on social relationships and exchange of services in the disrupters and disruptees. In order to assess the effect of disruption on the anxiety of the disruptees, focal sessions would need to be collected simultaneously on each disruptee following the disruption, and the frequency and duration of behavioural indicators of anxiety such as self-directed behaviours would be recorded. These data could be compared to the baseline level of anxiety of the individual, to the level of anxiety the individual experiences after receiving aggression when not engaged in a grooming interaction, and to the level of anxiety the individual experiences after a grooming interaction not disrupted. The data collection to assess the dynamic of social relationships in relation to grooming disruption may involve the collection of focal sessions during several months or years and so might be time consuming.

8.3.4. Exchange of services

Chapter 5 and 6 analysed the temporal contingency between grooming given and received, and between grooming and food tolerance. However, across-dyads, individuals can also overall give more benefits toward individuals from who they received more benefits, irrespective of the time frames. Further studies may thus assess the relative role of these two mechanisms in the exchange of services of the same population. Baseline focal sessions may be conducted on all the individuals of the ‘Green group’ and ‘Tourist group’ to collect data on the overall exchanges of grooming and food tolerance (e.g. Carne et al, 2011). This would allow to assess whether the giving and receiving of theses services is related, irrespective of the time frames. According to the partner choice model, temporal contingency may be neglected if overall individuals give more benefits toward individuals from who they received more benefits. Moreover, these data may also be compared between dyads of partners sharing high and low relationship quality, as the role of temporal contingency in the exchanges of services may be more important in individuals who rarely interact with each other. Additionally to grooming and food tolerance, other services such as mating opportunities and support during agonistic interactions may also be investigated.

Different results may be found depending on the degree of tolerance of the species studied and depending on variation of food resources within populations. In species with higher degree of social tolerance, it is expected that dominant individuals would not tend to restrict access to food resources, and therefore subordinate individuals would not exchange grooming for food tolerance, but would instead exchange more grooming for itself (e.g. Barrett et al, 1999). Moreover according to biological market theory, the availability of resources may influence the exchanges of services within populations (Noé & Hammerstein, 1994; Noë et al, 2001). For example in the Tourist group, if the presence of tourists (and so the presence of food given by tourists to the monkeys) is higher during the summer than during the winter, competition for food may be higher during the winter because of the scarcity of food resources compare to the summer (e.g. Barrett et al, 1999; Chancellor & Isbell, 2009; Fruteau et al, 2009). In that case, grooming may be more exchanged for food tolerance during the winter than during the summer.

8.3.5. Partner choice

In Chapter 7, juvenile individuals were also included in the data analysis together with adults and sub-adults. The data collection of this thesis was planned to be conducted only on adults and sub-adults. For this reason, the hourly scans were conducted on the adults and sub-adults of the groups, and only the identity, distance and activity of the nearest juvenile of each adult and sub-adult were recorded (see Chapter 2). Thus no data involving two juveniles were recorded during the hourly scans. The hierarchy of juveniles was also not investigated, thus dyadic conflicts involving two juveniles were not collected ad libitum. Three females were considered juvenile at the beginning of the study and sub-adult when the experimental data collection started. Consequently, although their data were recorded as sub-adult during the experimental tasks in Chapter 7, their data were recorded as juvenile during the hourly scans. Therefore, because juveniles of the ‘Tourist group’ were included in the data analysis of Chapter 7 a-posteriori, data on relationship quality, cofeeding frequency and hierarchy were not available within juveniles and could not be included in the analyses. Thus before the submission of the results of Chapter 7 to a peer-reviewed journal, these data would need to be completed and analysed, or the study would need to be focused only on adults and sub-adults.

Chapter 7 showed that several factors such as food tolerance and relationship quality influence the choice of partners and performances of monkeys in a cooperative task. Choosing the appropriate partner promotes the chance of success of cooperative interactions. Thus it may be favourable to be able to choose an appropriate partner according to its efficiency in a particular task. For example, chimpanzees were able to choose the more efficient of two partners for a cooperative task, based on previous cooperative attempts they experienced with each of them (Melis et al, 2006a). In a study on wild vervet monkeys (*Chlorocebus aethiops*), two individuals were only allowed to get food from a black feeder, while the rest of the group could only get food from a white feeder (Pansini, 2011). When the black and white feeders were joined together, one monkey from the black class and one monkey from the white class had to sit in proximity in front of their respective colour feeder to be allowed to access the food. Most of the monkeys cooperated with partners of the appropriate class and they preferred to do so with specific combinations of individuals. This study showed that induced cooperation modified the social network of the group (Pansini, 2011). In another experimental study, vervet monkeys recognised the capacity of some individuals to provide food for the group by operating a food dispenser, and in response they groomed more these individuals (Fruteau et al, 2009). In a recent study on chimpanzees, individuals were able to cooperate in a cooperative task requiring a different role for each partner, and they also distinguished which particular action the partner needed to perform, as they transferred to the partner the right tool it needed to perform its role (Melis & Tomasello, 2013). Thus, the experimental paradigm conducted in Chapter 7 may be used to assess whether non-human primates are able to recognise the specific skills of potential partners, and to use this knowledge to pair up with the adequate partner in a cooperative task. For this, three boxes (e.g. the same as the one used in Chapter 7) of different colour such as red, blue and yellow (for species with a trichromatic vision, such as Barbary macaques) might be used. During the training phase, only certain individuals would be able to get the food from a box of a specific colour (e.g. by using remote controls that activate and deactivate the possibility to pull the rope). This would allow to artificially create a difference of skills between individuals. The number and identity of individuals present around a monkey manipulating the box (i.e. the audience) during the training phase might be also recorded, to assess whether individuals monitor group members to gain knowledge of their specific capacities. Then during the testing phase, the cooperative task would be presented in combination of two boxes of different and/or same colour. Only two partners from the appropriate colour classes would be allowed to use the apparatus and pull together to get the rewards. It would be important to ensure that the combination of colours involved potential partners that are tolerant around food resource. If individuals take into account the specific skills of potential partners that are needed to solve the cooperative task, they should attempt to pull the rope more often in the presence of an ‘adequate’ partner than in the presence of a ‘non-adequate’ partner or alone. They should also attempt to pull more often the rope corresponding to the box of their specific than non-specific colour. Individuals may acquire the knowledge of the specific skill of potential partners either by indirect observation during the training phase, and/or by direct experience with potential partners during the testing phase. This experiment may then be conducted again by changing the allocation of the colours of the individuals to investigate whether the capacity to choose appropriate partners is partner specific and flexible, and whether monkeys regularly monitor the capacity of group members for specific tasks. Modification of colours allocation to the monkeys may also be done in such a way to analyse the relative role of conflicting factors (such as colour allocation and food tolerance) on the decision to choose a partner for a cooperative task. These experiments can be conducted with wild non-human primates, or in a more control environment such as in a laboratory or zoo (e.g. Melis et al, 2006a). For example, in a control setting individuals would have to choose to recruit a partner between two or three potential partners, depending on their specific skills such as the capacity to pull a rope of a particular colour, based on previous indirect observations of the potential partners' skills and/or on direct experiences with each of them (Melis et al, 2006a).

8.4. CONCLUSION

The findings of this thesis have made novel contributions to our understanding of grooming interactions and cooperation in wild Barbary macaques. This study highlighted the importance of studying further the role of anxiety and emotion in grooming interactions and it pointed out that dominant monkeys may affect the social interactions of other group members to sustain their social and dominance positions within the group. Furthermore, this thesis provided evidence that direct reciprocity play a key role in the exchange of services in non-humans primates, but not indirect and generalised reciprocity. It suggested that temporal contingency may not be a key mechanism of reciprocity but, instead, other mechanisms such as those involving an emotional mediation based on long-term social bonds between partners, may play a more important role and need to be further investigated. Finally, this thesis strengthened the important role of tolerance and relationship quality in the establishment and maintenance of cooperative interactions.

8.5. REFERENCES

Adachi, I. & Hampton, R. R. 2011. Rhesus monkeys see who they hear: spontaneous cross-modal memory for familiar conspecifics. *PLoS ONE*, **6**, e23345.

Alexander, R. D. 1987. *The biology of moral systems.* New York: Aldine De Gruyter.

Amici, F., Call, J. & Aureli, F. 2012. Aversion to violation of expectations of food distribution: the role of social tolerance and relative dominance in seven primate species. *Behaviour*, **149**, 345-368.

Amodio, D. M. & Frith, C. D. 2006. Meeting of minds: the medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, **268**, 268-277.

Amy, M. & Leboucher, G. 2007. Male canaries can visually eavesdrop on conspecific food interactions. *Animal Behaviour*, **74**, 57-62.

Andari, E., Duhamel, J.-R., Zalla, T., Herbrecht, E., Leboyer, M. & Sirigu, A. 2010. Promoting social behavior with oxytocin in high-functioning autism spectrum disorders. *Proceedings of the National Academy of Sciences*, **107**, 4389-4394.

Anderson, J. R., Kuroshima, H., Takimoto, A. & Fujita, K. 2013. Third-party social evaluation of humans by monkeys. *Nature Communications*, **4**, 1561.

Argyle, M. & Henderson, M. 1984. The rules of friendship. *Journal of Social and Personal Relationships*, **1**, 211-237.

Aureli, F. & Schino, G. 2004. The role of emotions in social relationships. In: *Macaque societies: a model for the study of social organization* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 38-60. Cambridge: Cambridge University Press.

Aureli, F. & Yates, K. 2010. Distress prevention by grooming others in crested black macaques. *Biology Letters*, **6**, 27-29.

Aureli, F., Fraser, O. N., Schaffner, C. M. & Schino, G. 2012. The regulation of social relationships. In: *The evolution of primate societies* (Ed. by J. Mitani, J. Call, P. Kappeler, R. Palombit & J. Silk), pp. 531-551. Chicago: University of Chicago Press.

Axelrod, R. 1984. *The evolution of cooperation*. New York: Basic Books.

Balliet, D., Mulder, L. B. & van Lange, P. A. M. 2011. Reward, punishment, and cooperation: a meta-analysis. *Psychological Bulletin*, **137**, 594-615.

Barclay, P. 2004. Trustworthiness and competitive altruism can also solve the ‘tragedy of the commons’. *Evolution and Human Behavior*, **25**, 209-220.

Barraza, J. & Zak, P. J. 2009. Empathy towards strangers triggers oxytocin release and subsequent generosity. *Annals of the New York Academy of Sciences,* **1167**, 182-189.

Barrett, L. & Henzi, S. P. 2001. The utility of grooming in baboon troops. In: *Economics in nature: social dilemmas, mate choice and biological markets* (Ed. by R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein), pp. 119-145. Cambridge: Cambridge University Press.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999. Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B,* **266**, 665-670.

Barta, Z., McNamara, J. M., Huszár, D. B. & Taborsky, M. 2011. Cooperation among non-relatives evolves by state-dependent generalized reciprocity. *Proceedings of the Royal Society B*, **278**, 843-848.

Bartlett, M. Y. & de Steno, D. 2006. Gratitude and prosocial behavior: helping when it costs you. *Psychological Science,* **17**, 319-325.

Bateson, M., Nettle, D. & Roberts, G. 2006. Cues of being watched enhance cooperation in a real-world setting. *Biology Letters*, **2**, 412-414.

Batson, C. D. 2002. Addressing the altruism question experimentally. In: *Altruism and altruistic love* (Ed. by S. G. Post, L. G. Underwood, J. P. Schloss & W. B. Hurlbut), pp. 89-105. Oxford: Oxford University Press.

Ben-Ner, A., Putterman L., Kong, F. & Magan, D. 2004. Reciprocity in a two-part dictator game. *Journal of Economic Behavior and Organization,* **53**, 333-352.

Bergman, T. J., Beehner, J. C, Cheney, D. L. & Seyfarth, R. M. 2003. Hierarchical classification by rank and kinship in baboons. *Science,* **302,** 1234-1236.

Berkowitz, L. & Daniels, L. 1964. Affecting the salience of the social responsibility norm: effects of past help on the response to dependency relationships. *Journal of Abnormal Psychology,* **68**, 275-281.

Bernstein, I. S. 2006. Social mechanisms in the control of primate aggression. In: *Primates in perspective* (Ed. by C. J. Campbell, A. Fuentes, K. C. Mackinnon, M. Panger & S. K. Bearder), pp. 562-571. New York: Oxford University Press.

Berscheid, E., Snyder, M. & Omoto, A. M. 1989. The relationship closeness inventory: assessing the closeness of interpersonal relationships. *Journal of Personality and Social Psychology*, **57**, 792-807.

Bolton, G. E. & Ockenfels, A. 2000. Erc: A theory of equity, reciprocity, and competition. *American Economic Review,* **90**, 166-193.

Borgeaud, C., van de Waal, E. & Bshary, R. 2013. Third-party ranks knowledge in wild vervet monkeys (*Chlorocebus aethiops pygerythrus*). *PLoS ONE,* **8,** e58562.

Bowie, B. H. 2007. Relational aggression, gender, and the developmental process. *Journal of Child and Adolescent Psychiatric Nursing,* **20**, 107-15.

Boyd, R. & Richerson, P. J. 1989. The evolution of indirect reciprocity. *Social Networks*, **11**, 213-238.

Boyd, R. 1992. The evolution of reciprocity when conditions vary. In: *Coalitions and alliances in humans and other animals* (Ed. by A. Harcourt & F. B. M. de Waal), pp. 473-489. New York: Oxford University Press.

Boyd, R., Gintis, H. & Bowles, S. 2010. Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science*, **328**, 617-620.

Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J**.** 2003. The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences*, **100**, 3531-3535.

Brandt, H. & Sigmund, K. 2005. Indirect reciprocity, image scoring, and moral hazard. *Proceedings of the National Academy of Sciences,* **102**, 2666-2670.

Brandt, H., Hauert, C. & Sigmund, K. 2003. Punishment and reputation in spatial goods games. *Proceedings of the Royal Society B*, **270**, 1099-1104.

Bräuer, J. & Hanus, D. 2012. Fairness in non-human primates? *Social Justice Research*, **25**, 256-276.

Bräuer, J., Call, J. & Tomasello, M. 2006. Are apes really inequity averse? *Proceedings of the Royal Society B*, **273**, 3123-3128.

Bräuer, J., Call, J. & Tomasello, M. 2009. Are apes inequity averse? New data on the token-exchange paradigm. *American Journal of Primatology*, **71**, 175-181.

Brosnan, S. & de Waal, F. B. M. 2009. *Cebus apella* tolerate intermittent unreliability in human experimenters. *International Journal of Primatology*, **30**, 663-674.

Brosnan, S. F. & de Waal, F. B. M. 2003. Monkeys reject unequal pay. *Nature*, **425**, 297-299.

Brosnan, S. F. 2006. Nonhuman species' reactions to inequity and their implications for fairness. *Social Justice Research,* **19**, 153-185.

Brosnan, S. F. 2008. How primates (including us!) respond to inequity. *Advances in Health Economics and Health Services Research,* **20,** 99-124.

Brosnan, S. F. 2009. Responses to inequity in non-human primates. In: *Neuroeconomics: decision making and the brain* (Ed. by P. W. Glimcher, E. Fehr, C. Camerer & R. A. Poldrack*),* pp. 285-301. London: Academic Press.

Brosnan, S. F. 2011. A hypothesis of the co-evolution of cooperation and responses to inequity. *Frontiers in Neuroscience,* **5,** 43.

Brosnan, S. F. 2013. Justice- and fairness-related behaviors in nonhuman primates. *Proceedings of the National Academy of Sciences*, **110**, 10416-10423.

Brosnan, S. F., Schiff, H. C. & de Waal, F. B. M. 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society B,* **272**, 253-258.

Brosnan, S. F., Talbot, C., Ahlgren, M., Lambeth, S. P. & Schapiro, S. J. 2010. Mechanisms underlying responses to inequitable outcomes in chimpanzees, *Pan troglodytes*. *Animal Behaviour*, **79,** 1229-1237.

Brosnan, S. F., Flemming, T., Talbot, C. F., Mayo, L. & Stoinski, T. 2011. Orangutans *(Pongo pygmaeus)* do not form expectations based on their partner's outcomes**.** *Folia Primatologica*, **82**, 56-70.

Bshary, R. & Bronstein, J. L. 2011. A general scheme to predict partner control mechanisms in pairwise cooperative interactions between unrelated individuals. *Ethology,* **117**, 1-13.

Bshary, R. & D'Souza, A. 2005. Cooperation in communication networks: indirect reciprocity in interactions between cleaner fish and client reef fish. In: *Animal communication networks* (Ed. by P. K. McGregor), pp. 521-539. Cambridge: Cambridge University Press.

Bshary, R. & Grutter, A. S. 2002. Asymmetric cheating opportunities and partner control in the cleaner fish mutualism. *Animal Behaviour,* **63**, 547-555.

Bshary, R. & Grutter, A. S. 2005. Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biology Letters,* **1**, 396-399.

Bshary, R. & Grutter, A. S. 2006. Image scoring and cooperation in a cleaner fish mutualism. *Nature*, **441**, 975-978.

Bshary, R. 2002. Biting cleaner fish use altruism to deceive image scoring clients. *Proceedings of the Royal Society B,* **269**, 2087-2093.

Bshary, R., Grutter, A. S., Willener, A. S. T. & Leimar, O. 2008. Pairs of cooperating cleaner fish provide better service quality than singletons. *Nature,* **455**, 964-966.

Camerer, C. & Thaler, R. H. 1995. Anomalies: ultimatums, dictators and manners. *Journal of Economic Perspectives,* **9**, 209-219.

Cameron, L. A. 1999. Raising the stakes in the ultimatum game: experimental evidence from Indonesia. *Economic Inquiry*, **37**, 47-59.

Cant, M. A. & Johnstone, R. A. 2006. Self-serving punishment and the evolution of cooperation. *Evolutionary Biology*, **19**, 1383-1385.

Carne, C., Wiper, S. & Semple, S. 2011. Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology*, **73**, 1127-1133.

Chalmeau, R., Visalberghi, E. & Gallo, A. 1997. Capuchin monkeys, *Cebus apella*, fail to understand a cooperative task. *Animal Behaviour*, **54**, 1215-1225.

Chancellor, R. L. & Isbell, L. A. 2008. Punishment and competition over food in captive rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, **75**, 1939-1947.

Chancellor, R. L. & Isbell, L. A. 2009. Female grooming markets in a population of gray-cheeked mangabeys (*Lophocebus albigena*). *Behavioral Ecology*, **20**, 79-86.

Chang, S. W. C., Barter, J. W., Ebitz, R. B., Watson, K. K. & Platt, M. L. 2012. Inhaled oxytocin amplifies both vicarious reinforcement and self-reinforcement in rhesus macaques (*Macaca mulatta*). *Proceedings of the National Academy of Sciences*, **109**, 959-964.

Chang, S. W. C., Brent, L. J. N., Adams, G. K., Klein, J. T., Pearson, J. M., Watson, K. K. & Platt, M. L. 2013. Neuroethology of primate social behavior. *Proceedings of the National Academy of Sciences*, **110**, 10387-10394.

Chen, K. M. & Santos, L. 2006. Some thoughts on the adaptive function of inequity aversion: an alternative to Brosnan’s social hypothesis. *Social Justice Research*, **19**, 201-207.

Cheney, D. L. & Seyfarth, R. M. 1980. Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour*, **28**, 362-367.

Cheney, D. L. & Seyfarth, R. M. 1982. Recognition of individuals within and between groups of free-ranging vervet monkeys. *American Zoologist*, **22**, 519-529.

Cheney, D. L. & Seyfarth, R. M. 1990. *How monkeys see the world: inside the mind of another species*. Chicago: University of Chicago Press.

Cheney, D. L. 2011. Extent and limits of cooperation in animals. *Proceedings of the National Academy of Sciences*, **108**, 10902-10909.

Cheney, D. L., Seyfarth, R. M. & Silk, J. B. 1995. The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: evidence for causal reasoning? *Journal of Comparative Psychology*, **109**, 134-141.

Cinyabuguma, M., Page, T. & Putterman, L. 2005. Cooperation under the threat of expulsion in a public goods experiment. *The Experimental Approaches to Public Economics*, **89**, 1421-1435.

Clark, M. S. & Grote, N. K. 2003. Close relationships. In: *Handbook of psychology, volume 5: personality and social psychology* (Ed. by T. Millon & M. J. Lerner), pp. 447-461. New York: John Wiley & Sons, Inc.

Clark, M. S. & J. Mills. 1979. Interpersonal attraction in exchange and communal relationships. *Journal of Personality and Social Psychology,* **37,** 2-24.

Clark, M. S. 1984. Record keeping in two types of relationships. *Journal of Personality and Social Psychology*, **47**, 549-557.

Clutton-Brock, T. 2009. Cooperation between non-kin in animal societies. *Science*, **462**, 51-57.

Clutton-Brock, T. H. & Parker, G. A. 1995. Punishment in animal societies. *Nature*, **373**, 209-216.

Crawford, M. P. 1937. The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs*, **14**, 1-88.

Crick, N. R. & Grotpeter, J. K. 1995. Relational aggression, gender, and social-psychological adjustment. *Child Development*, **66**, 710-722.

Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K. & Deschner, T. 2013. Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B,* **280**, 20122765.

Crockford, C., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2007. Baboons eavesdrop to deduce mating opportunities. *Animal Behaviour*, **73**, 885-890.

Cronin, K. A. & Sànchez, A. 2012. Social dynamics and cooperation: the case of nonhuman primate and its implications for human behavior. *Advances in Complex Systems*, **15**, 1250066.

Cronin, K. A. 2012. Prosocial behaviour in animals: the influence of social relationships, communication and rewards. *Animal Behaviour*, **84**, 1085-1093.

Dall, S. R. X. & Johnstone, R. A. 2002. Managing uncertainty: information and insurance under the risk of starvation. *Philosophical Transactions of the Royal Society B,* **357**, 1519-1526.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M. & Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, **20**, 187-193.

Dantzer, R., Bluthe, R. M., Koob, G. F. & Moal, M. 1987. Modulation of social memory in male rats by neurohypophyseal peptides. *Psychoparmacology*, **91**, 363-368.

Dasser, V. 1988. A social concept in java monkeys. *Animal Behaviour*, **36**, 225-230.

de Vignemont, F. & Singer, T. 2006. The empathic brain: how, when and why? *Trends in Cognitive Sciences*, **10**, 435-441.

de Waal, F. B. M. & Brosnan, S. F. 2006. Simple and complex social reciprocity in monkeys and apes. In: *Cooperation in primates and humans: mechanisms and evolution* (Ed. by P. Kappeler & C. van Schaik), pp. 79-99. New-York: Springer.

de Waal, F. B. M. & Davis, J. M. 2003. Capuchin cognitive ecology: cooperation based on projected returns. *Neuropsychologia*, **41**, 221-228.

de Waal, F. B. M. & Luttrell, L. M. 1988. Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethology and Sociobiology*, **9,** 101-118.

de Waal, F. B. M. & Suchak, M. 2010. Prosocial primates: selfish and unselfish motivations. *Philosophical Transactions of the Royal Society B*, **365**, 2711-2722.

de Waal, F. B. M. 1989. Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution*, **18**, 433-459.

de Waal, F. B. M. 1997. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, **18**, 375-386.

de Waal, F. B. M. 2006. Joint ventures require joint pay-offs: fairness among primates. *Social Research*, **73**, 349-364.

DeAngelo, G. & Brosnan, S. F. 2013. The importance of risk tolerance and knowledge when considering the evolution of inequity responses across the primates. *Journal of Economic Behavior & Organization*, **90,** 105-112.

Deutsch, M. 1975. Equity, equality, and need: what determines which value will be used as the basis of distributive justice? *Journal of Social Issues*, **31**, 137-150.

Domes, G., Heinrichs, M., Michel, A., Berger, C. & Herpertz, S. C. 2007. Oxytocin improves 'mind-reading' in humans. *Biological psychiatry*, **61**, 731-733.

Donaldson, Z. R. & Young, L. J. 2008. Oxytocin, vasopressin, and the neurogenetics of sociality. *Science*, **322**, 900-904.

Dubreuil, D., Gentile, M. S. & Visalberghi, E. 2006. Are capuchin monkeys (*Cebus apella*) inequity averse? *Proceedings of the Royal Society B,* **273**, 1223-1228.

Dufwenberg, M., Gneezy, U., Güth, W. & van Damme, E. 2001. Direct vs. indirect reciprocity: an experiment. *Homo Oeconomicus*, **18**, 19-30.

Dunbar, R. I. M. & Shultz, S. 2010. Bondedness and sociality. *Behaviour*, **147**, 775-803.

Dunbar, R. I. M. 1991. Functional significance of social grooming in primates. *Folia Primatologica*, **57**, 121-131.

Dunbar, R. I. M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology,* **31**, 35-49.

Dunbar, R. I. M. 2010. The social role of touch in humans and primates: behavioural function and neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews*, **34**, 260-268.

Earley, R. L. & Dugatkin, L. A. 2002. Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking. *Proceedings of the Royal Society B*, **269**, 943-952.

Earley, R. L. 2010. Social eavesdropping and the evolution of conditional cooperation and cheating strategies. *Philosophical Transactions of the Royal Society B*, **365**, 2675-2686.

Emmons, R. A. & McCullough, M. E. 2004. *The psychology of gratitude*. New York: Oxford University Press.

Engelmann, D. & Fischbacher, U. 2009. Indirect reciprocity and strategic reputation building in an experimental helping game. *Games and Economic Behavior*, **67**, 399-407.

Engelmann, J. M., Herrmann, E. & Tomasello, M. 2012. Five-year olds, but not chimpanzees, attempt to manage their reputations. *PLoS ONE*, **7**, e48433.

Fehl, K., van der Post, D. J. & Semmann, D. 2011. Co-evolution of behaviour and social network structure promotes human cooperation. *Ecology Letters*, **14**, 546-551.

Fehr, E. & Fischbacher, U. 2003. The nature of human altruism. *Nature*, **425**, 785-791.

Fehr, E. & Fischbacher, U. 2004. Third-party punishment and social norms. *Evolution and Human Behavior,* **25**, 63-87.

Fehr, E. & Gächter, S. 2000. Cooperation and punishment in public goods experiments. *American Economic Review*, **90**, 980-994.

Fehr, E. & Gächter, S. 2002. Altruistic punishment in humans. *Nature*, **415**, 137-140.

Fehr, E. & Schmidt, K. M. 1999. A theory of fairness, competition, and cooperation. *Quarterly Journal of Economics*, **114**, 817-868.

Feldman, R., Weller, A., Zagoory-Sharon, O. & Levine, A. 2007. Evidence for a neuroendocrinological foundation of human affiliation: plasma oxytocin levels across pregnancy and the postpartum period predict mother-infant bonding. *Psychological Science*, **18**, 965-970.

Ferguson, J. N., Young, L. J., Hearn, E. F., Matzuk, M. M., Insel, T. R. & Winslow, J. T. 2000. Social amnesia in mice lacking the oxytocin gene. *Nature Genetics*, **25**, 284-288.

Fischbacher, U., Gächter, S. & Fehr, E. 2001. Are people conditionally cooperative? Evidence from a public goods experiment. *Economics Letters,* **71**, 397-404.

Fletcher, G. E. 2008. Attending to the outcome of others: disadvantageous inequity aversion in male capuchin monkeys (*Cebus apella*). *American Journal of Primatology,* **70**, 901-905.

Foley, R. & Gamble, C. 2009. The ecology of social transitions in human evolution. *Philosophical Transactions of the Royal Society B,* **364**, 3267-3279.

Forsythe, R., Horowitz, J. L., Savin, N. E. & Sefton, M. 1994. Fairness in simple bargaining experiments. *Games and Economic Behavior*, **6**, 347-369.

Frank, R. E. & Silk, J. B. 2009. Impatient traders or contingent reciprocators? Evidence for the extended time course of grooming exchanges in baboons. *Behaviour,* **146**, 1123-1135.

Fruteau, C., Voelkl, B., van Damme, E. & Noë, R. 2009. Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences*, **106**, 12007-12012.

Gächter, S., Renner, E. & Sefton, M. 2008. The long-run benefits of punishment. *Science,* **322**, 1510-1510.

Gardner, A. & West, S. A. 2004. Cooperation and punishment, especially in humans. *American Naturalist*, **164**, 753-764.

Gintis, H., Bowles, S., Boyd, R. & Fehr, E. 2003. Explaining altruistic behavior in humans. *Evolution and Human Behavior*, **24**, 153-172.

Goats, G. C. 1994. Massage, the scientific basis of an ancient art: part 2. Physiological and therapeutic effects. *British Journal of Sports Medicine,* **28**, 153-156.

Gomes, C. M., Mundry, R. & Boesch, C. 2009. Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B,* **276**, 699-706.

Graves, F. C., Wallen, K. & Maestripieri, D. 2002. Opioids and attachment in rhesus macaques (*Macaca mulatta*) abusive mothers. *Behavioral neuroscience,* **116**, 489-493.

Greiner, B. & Levati, M. V. 2003. Indirect reciprocity in cyclical networks: an experimental study. *Journal of Economic Psychology*, **26**, 711-731.

Grotius. 1738. *De Jure Bellict Pacis*. London: Innys

Güth, W. & Tietz, R. 1990. Ultimatum bargaining behavior: a survey and comparison of experimental results. *Journal of Economic Psychology*, **11**, 417-449.

Güth, W., Königstein, M., Marchand, N. & Nehring, K. T. 2001. Trust and reciprocity in the investment game with indirect reward. *Homo Oeconomicus*, **18**, 241-262.

Güth, W., Schmittberger, R. & Schwarze, B. 1982. An experimental analysis of ultimatum bargaining. *Journal of Economic Behavior & Organization*, **3**, 367-388.

Haley, K. J. & Fessler, D. M. T. 2005. Nobody's watching? Subtle cues affect generosity in an anonymous economic game. *Evolution and Human Behavior*, **26**, 245-256.

Hamilton, I. M. & Taborsky, M. 2005. Contingent movement and cooperation evolve under generalised reciprocity. *Proceedings of the Royal Society B*, **272**, 2259-2267.

Hammerstein, P. 2003. Why is reciprocity so rare in social animals? A protestant appeal. In: *Genetic and cultural evolution of cooperation* (Ed. by P. Hammerstein), pp. 83-93. Cambridge: The MIT Press.

Hare, B. & Tan, J. 2012. How much of our cooperative behavior is human? In: *The primate mind: built to connect with other minds* (Ed. by F. B. M. de Waal & P. F. Ferrari), pp. 175-193. Cambridge: Harvard University Press.

Hare, B. & Tomasello, M. 2005. Human-like social skills in dogs? *Trends in Cognitive Sciences*, **9**, 439-444.

Hare, B. & Wrangham, R. 2002. Integrating two evolutionary models for the study of social cognition. In: *The cognitive animal: empirical and theoretical perspectives on animal cognition* (Ed. by M. Bekoff, C. Allen & G. M. Burghardt), pp. 363-370. Cambridge: The MIT Press.

Hare, B. 2007. From non-human to human mind: what changed and why. *Current Directions in Psychological Science*, **16**, 60-64.

Hare, B., Melis, A. P., Woods, V., Hastings, S. & Wrangham, R. W. 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, **17**, 619-623.

Hauser, M. D. 1992. Costs of deception: cheaters are punished in rhesus monkeys (*Macaca mulatta*). *Proceedings of the National Academy of Sciences*, **89**, 12137-12139.

Hauser, M. D., Chen, M. K., Chen, F. & Chuang, E. 2003. Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society B*, **270**, 2363-2370.

Hawkes, C. 1992. Endorphins: the basis of pleasure? *Journal of Neurology, Neurosurgery & Psychiatry*, **55**, 247-250.

Henrich, J. 2004. Inequity aversion in capuchins. *Nature*, **428**, 139.

Henrich, J. 2006. Cooperation, punishment, and the evolution of human institutions. *Science,* **312**, 60-61.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Gintis, H., McElreath, R. & Fehr, E. 2001. In search of homo economicus: experiments in 15 small-scale societies. *American Economic Review*, **91**, 73-79

Herrmann, E., Keupp, S., Hare, B., Vaish, A. & Tomasello, M. 2013. Direct and indirect reputation formation in nonhuman great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, **127**, 63-75.

Hill, K. 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, **331,** 1286-1289.

Hinde, R. A. 1976. Interactions, relationships and social structure. *Man*, **11**, 1-17.

Hinde, R. A. 1979. *Towards understanding relationships*. London: Academic Press.

Hinde, R. A. 1983. A conceptual framework. In: *Primate social relationships: an integrated approach* (Ed. by R. A. Hinde), pp. 1-7. Oxford: Blackwell Scientific Publications.

Hinde, R. A. 1997. *Relationships: a dialectical perspective*. Brighton: Psychology Press.

Hinde, R. A. 2002. *Why good is good: the sources of morality*. London: Routledge.

Hirata, S. & Fuwa, K. 2007. Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates,* **48,** 13-21.

Hoffman, E., McCabe, K. A. & Smith, V. L. 1996. On expectations and monetary stakes in ultimatum games. *International Journal of Game Theory,* **25,** 289-301.

Hoffman, E., McCabe, K. A., Shachat, K. & Smith, V. 1994. Preferences, property rights and anonymity in bargaining games. *Games and Economic Behavior*, **7**, 346-380.

Hollander, E., Bartz, J., Chaplin, W., Phillips, A., Sumner, J., Soorya, L., Anagnostou, E. & Wasserman, S. 2007. Oxytocin increases retention of social cognition in autism. *Biological psychiatry,* **61**, 498-503.

Horowitz, A. 2012. Fair is fine, but more is better: limits to inequity aversion in the domestic dog. *Social Justice Research,* **25**, 195-212.

Insel, T. R. & Shapiro, L. E. 1992. Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. *Proceedings of the National Academy of Sciences,* **89**, 5981-5985.

Insel, T. R. & Young, L. J. 2001. The neurobiology of attachment. *Nature Review of Neuroscience*, **2**, 129-136.

Insel, T. R. 2010. The challenge of translation in social neuroscience: a review of oxytocin, vasopressin, and affiliative behaviour. *Neuron*, **65**, 768-779.

Iwagami, A. & Masuda, N. 2010. Upstream reciprocity in heterogeneous networks. *Journal of Theoretical Biology*, **265**, 297-305.

Izuma, K. 2012. The social neuroscience of reputation. *Neuroscience Research*, **72,** 283-288.

Izuma, K., Saito, D. N., Sadato, N. 2010. The roles of the medial prefrontal cortex and striatum in reputation processing. *Social Neuroscience,* **5**, 133-147.

Jaeggi, A. V. & van Schaik, C. P. 2011. The evolution of food sharing in primates. *Behavioral Ecology and Sociobiology,* **65,** 2125-2140.

Jaeggi, A. V., Burkart, J. M. & van Schaik, C. P. 2010. On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of prosociality. *Philosophical Transactions of the Royal Society B*, **365**, 2723-2735.

Jaeggi, A. V., De Groot, E., Stevens, J. M. G. & van Schaik, C. P. 2013. Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, **34**, 69-77.

Jensen, K. 2010. Punishment and spite, the dark side of cooperation. *Philosophical Transactions of the Royal Society B*, **365**, 2635-2650.

Jensen, K., Call, J. & Tomasello, M. 2007. Chimpanzees are vengeful but not spiteful. *Proceedings of the National Academy of Sciences*, **104**, 13046-13050.

Johnstone, R. A. & Bshary, R. 2004. The evolution of spiteful behaviour. *Proceedings of the Royal Society B*, **271**, 1917-1922.

Johnstone, R. A. 2001. Eavesdropping and animal conflict. *Proceedings of the National Academy of Sciences*, **98**, 9177-9180.

Kaada, B. & Torsteinbø, O. 1989. Increase of plasma β-endorphins in connective tissue massage. *General Pharmacology*, **20**, 487-489.

Kaiser, I., Jensen, K., Call, J. & Tomasello, M. 2012. Theft in an ultimatum game: chimpanzees and bonobos are insensitive to unfairness. *Biology Letters*, **8**, 942-945.

Kapsalis, E. & Berman, C. M. 1996. Models of affiliative relationships among free ranging rhesus monkeys (*Macaca mulatta*) II. Testing predictions for three hypothesized organizing principles. *Behaviour*, **133**, 1235-1263.

Kendrick, K. M., Keverne, E. B. & Baldwin, B. A. 1987. Intracerebroventricular oxytocin stimulates maternal behaviour in the sheep. *Neuroendocrinology*, **46**, 56-61.

Keverne, E. & Kendrick, K. 1992. Oxytocin facilitation of maternal behavior in sheep. *Annals of the New York Academy of Sciences*, **652**, 83-101.

Keverne, E. B., Martensz, N. D. & Tuite, B. 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, **14**, 155-161.

Kitchen, D. M., Cheney, D. L. & Seyfarth, R. M. 2005. Male chacma baboons (*Papio hamadryas ursinus*) discriminate loud call contests between rivals of different relative ranks. *Animal Cognition*, **8**, 1-6.

Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U. & Fehr, E. 2005. Oxytocin increases trust in humans. *Nature*, **435**, 673-676.

Koyama, N. F, Caws, C. & Aureli, F. 2006. Interchange of grooming and agonistic support in chimpanzees. *International Journal of Primatology*, **27**, 1293-1309.

Krueger, F., McCabe, K., Moll, J., Kriegeskorte, N., Zahn, R., Strenziok, M., Heinecke, A. & Grafman, J. 2007. Neural correlates of trust. *Proceedings of the National Academy of Sciences*, **104**, 20084-20089.

Kundey, S. A., Los Reyes, A., Royer, E., Molina, S., Monnier, B., German, R. & Coshun, A. 2011. Reputation-like inference in domestic dogs (*Canis familiaris*). *Animal Cognition*, **14**, 291-302.

Lau, G., Moulds, M. L. & Richardson, R. 2009. Ostracism: how much it hurts depends on how you remember it. *Emotion*, **9**, 430-434.

Le Roux, A. & Bergman, T. J. 2012. Indirect rival assessment in a social primate, *Theropithecus gelada*. *Animal Behaviour*, **83**, 249-255.

Le Roux, A., Snyder-Mackler, N., Roberts, E., Beehner, J. & Bergman, T. 2013. Evidence for tactical concealment in a wild primate. *Nature communications*, **4**, 1462.

Leach, H. M. 2003. Human domestication reconsidered. *Current Anthropology*, **44**, 349-368.

List, J. A. & Cherry, T. L. 2000. Learning to accept in ultimatum games: evidence from an experimental design that generates low offers. *Experimental Economics*, **3**, 11-29.

Madden, J. R. & Clutton-Brock, T. H. 2011. Experimental peripheral administration of oxytocin elevates a suite of cooperative behaviours in a wild social mammal. *Proceedings of the Royal Society B*, **278**, 1189-1194.

Maestripieri, D., Schino, G., Aureli, F. & Troisi, A. 1992. A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour*, **44**, 967-979.

Majolo, B., Ames, K., Brumpton, R., Garratt, R., Hall, K. & Wilson, N. 2006. Human friendship favours cooperation in the iterated Prisoner's Dilemma. *Behaviour*, **143**, 1383-1395.

Majolo, B., Schino, G. & Aureli, F. 2012. The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges. *Animal Behaviour*, **83**, 763-771.

Manson, J. H., Navarrete, C. D., Silk, J. B. & Perry, S. 2004. Time matched grooming in female primates? New analyses from two species. *Animal Behaviour*, **67**, 493-500.

Manson, J. H., Rose, L. M., Perry, S. & Gros-Louis, J. 1999. Dynamics of female-female relationships in wild *Cebus capucinus*: data from two Costa Rican sites. *International Journal of Primatology*, **20**, 679-706.

Marshall-Pescini, S., Passalacqua, C., Ferrario, A., Valsecchi, P. & Prato-Previde, E. 2011. Social eavesdropping in the domestic dog. *Animal Behaviour*, **81**, 1177-1183.

Massen, J. J. M., van den Berg, L. M., Spruijt, B. M. & Sterck, E. H. M. 2010. Generous leaders and selfish underdogs: pro-sociality in despotic macaques. *PLoS ONE*, **5,** e9734.

Massen, J. J. M., van den Berg, L. M., Spruijt, B. M. & Sterck, E. H. M. 2012. Inequity aversion in relation to effort and relationship quality in long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, **74**, 145-156.

McCullough, M. E., Emmons, R. A. & Tsang, J. 2002. The grateful disposition: a conceptual and empirical topography. *Journal of Personality and Social Psychology*, **82**, 112-127.

McCullough, M. E., Kilpatrick, S. D., Emmons, R. A. & Larson, D. B. 2001. Is gratitude a moral affect? *Psychological Bulletin*, **127**, 249-266.

McGregor, P. K. 2005. *Animal communication networks*. Cambridge: Cambridge University Press.

McSweeney, F. K. & Swindell, S. 1999. General-process theories of motivation revisited: the role of habituation. *Psychological Bulletin*, **125**, 437-457.

Melis, A. P. & Semmann, D. 2010. How is human cooperation different? *Philosophical Transactions of the Royal Society B*, **365**, 2663-2674.

Melis, A. P. & Tomasello, M. 2013. Chimpanzees' (*Pan troglodytes*) strategic helping in a collaborative task. *Biology Letters*, **9**, 20130009.

Melis, A. P., Hare, B. & Tomasello, M. 2006a. Chimpanzees recruit the best collaborators. *Science*, **311**, 1297-1300.

Melis, A. P., Hare, B. & Tomasello, M. 2006b. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Animal Behaviour*, **72,** 275-286.

Melis, A. P., Hare, B. & Tomasello, M. 2008. Do chimpanzees reciprocate received favours? *Animal Behaviour*, **76**, 951-962.

Milinski, M., Semmann, D. & Krambeck, H. J. 2002. Reputation helps solve the 'tragedy of the commons'. *Nature*, **415,** 424-426.

Milinski, M., Semmann, D., Bakker, T. C. M. & Krambeck, H. 2001. Cooperation through indirect reciprocity: image scoring or standing strategy? *Proceedings of the Royal Society B*, **268**, 2495-2501.

Mitani, J. C. 2006. Reciprocal exchange in chimpanzees and other primates. In: *Cooperation in primates: mechanisms and evolution* (Ed. by C. P. van Schaik & P. M. Kappeler), pp. 101-113. New-York: Springer.

Moll, H. & Tomasello, M. 2007. Cooperation and human cognition: the Vygotskian intelligence hypothesis. *Philosophical transactions of the Royal Society B*, **362**, 639-648.

Nakamaru, M. & Kawata, M. 2004 Evolution of rumours that discriminate lying defectors. *Evolutionary Ecology Research*, **6**, 261-283.

Nakao, H. & Machery, E. 2012. The evolution of punishment. *Biology & Philosophy*, **27**, 833-850.

Neiworth, J. J., Johnson, E. T., Whillock, K., Greenberg, J. & Brown, V. 2009. Is a sense of inequity an ancestral primate trait? Testing social inequity in cotton top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, **123**, 10-17.

Nettle, D., Cronin, K. A. & Bateson, M. 2013. Responses of chimpanzees to cues of conspecific observation. *Animal Behaviour*, **86**, 595-602.

Nitzschner, M., Melis, A. P., Kaminski, J. & Tomasello, M. 2012. Dogs (*Canis familiaris*) evaluate humans on the basis of direct experiences only. *PLoS ONE*, **7**, e46880.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism, and mating. *Behavioral Ecology and Sociobiology*, **35**, 1-11.

Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of cooperation. In: *Economics in nature: social dilemmas, mate choice* *and biological markets* (Ed. by R. Noë, J. A. R. A. M van Hooff & P. Hammerstein), pp. 93-118. Cambridge: Cambridge University Press.

Noë, R. 2006. Cooperation experiments: coordination through communication versus acting apart together. *Animal Behaviour*, **71**, 1-18.

Noë, R., van Hooff, J. A. R. A. M. & Hammerstein, P. 2001. *Economics in nature: social dilemmas, mate choice and biological markets.* Cambridge: Cambridge University Press.

Nowak, M. A. & Roch, S. 2007. Upstream reciprocity and the evolution of gratitude. *Proceedings of the Royal Society B*, **274**, 605-610.

Nowak, M. A. & Sigmund, K. 1998. Evolution of indirect reciprocity by image scoring. *Nature*, **393**, 573-577.

Nowak, M. A. & Sigmund, K. 2005. Evolution of indirect reciprocity. *Nature*, **437**, 1291-1298.

Nowak, M. A. 2006. Five rules for the evolution of cooperation. *Science*, **314**, 1560-1563.

Nowak, M. A., Page, K. M. & Sigmund, K. 2000. Fairness versus reason in the ultimatum game. *Science,* **289**, 1773-1775.

O’Connor, P. 1992. *Friendships between women: a critical review*. New York: Guilford.

Panchanathan, K. & R. Boyd. 2003. A tale of two defectors: the importance of standing for the evolution of indirect reciprocity. *Journal of Theoretical Biology,* **224,** 115-126.

Panchanathan, K. & R. Boyd. 2004. Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature,* **432**, 499-502.

Pansini, R**.** 2011. Induced cooperation to access a sharable reward increases the hierarchical segregation of wild vervet monkeys. *PLoS ONE,* **6**, e21993.

Pastor-Nieto, R. 2001. Grooming, kinship and co-feeding in captive spider monkeys (*Ateles geoffroyi*). *Zoo Biology,* **20**, 293-303.

Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. 2002. Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proceedings of the Royal Society B*, **269**, 1925-1929.

Pedersen, C. A. 1999. Oxytocin control of maternal behavior: regulation of sex steroids and offspring stimuli. In: *The integrative neurobiology of affiliation* (Ed. by C. S. Carter, I. Lederhendler & B. Kirkpatrick), pp. 301-320. Cambridge: The MIT Press.

Petit, O., Desportes, C. & Thierry, B. 1992. Differential probability of 'coproduction' in two species of macaque (*Macaca tonkeana, M. mulatta*). *Ethology*, **90**, 107-120.

Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M. & Bonhoeffer, S. 2005. Evolution of cooperation through generalised reciprocity. *Proceedings of the Royal Society B*, **272**, 1115-1120.

Pfeiffer, T., Tran, L., Krumme, C. & Rand, D. G. 2012. The value of reputation. *Journal of the Royal Society Interface*, **9**, 2791-2797.

Phillips, M. L., Young, A. W., Senior, C., Brammer, M., Andrew, C., Calder, A. J., Bullmore, E. T., Perrett, D. I., Rowland, D., Williams, S. C. R., Gray, J. A. & David, A. S. 1997. A specific neural substrate for perceiving facial expressions of disgust. *Nature*, **389**, 495-498.

Pinto, A., Oates, J., Grutter, A. & Bshary, R. 2011. Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Current Biology*, **21**, 1140-1144.

Posner, E. A., Spier, K. E. & Vermeule, A. 2010. Divide and conquer. *Journal of Legal Analysis*, **2**, 417-471.

Preston, S. D. & de Waal, F. B. M. 2002. Empathy: its ultimate and proximate bases. *Behavioral and Brain Sciences*, **25**, 1-72.

Price, S. & Brosnan, S. 2012. To each according to his need? Variability in the responses to inequity in non-human primates. *Social Justice Research,* **25**, 140-169.

Proctor, D., Williamson, R. A., de Waal, F. B. M. & Brosnan, S. F. 2013. Chimpanzees play the ultimatum game. *Proceedings of the National Academy of Sciences,* **110**, 2070-2075.

Radford, A. N. 2012. Post-allogrooming reductions in self-directed behaviour are affected by role and status in the green woodhoopoe. *Biology Letters*, **8**, 24-27.

Raihani, N. J., Grutter, A. S. & Bshary, R. 2010. Punishers benefit from third-party punishment in fish. *Science*, **327**, 171-171.

Raihani, N. J., McAuliffe, K., Brosnan, S. F. & Bshary, R. 2012. Are cleaner fish, *Labroides dimidiatus*, inequity averse? *Animal Behaviour*, **84**, 665-674.

Rand, D. G. & Nowak, M. A. 2013. Human cooperation. *Trends in Cognitive Sciences,* **17,** 413-425.

Rand, D. G., Tarnita, C. E., Ohtsuki, H. & Nowak, M. A. 2013. Evolution of fairness in the one-shot anonymous ultimatum game. *Proceedings of the National Academy of Sciences,* **110**, 2581-2586.

Range, F., Horn, L., Viranyi, Z. & Huber, L. 2009. The absence of reward induces inequity aversion in dogs. *Proceedings of the National Academy of Sciences*, **106**, 340-345.

Range, F., Leitner, K. & Viranyi, Z. 2012. The influence of the relationship and motivation on inequity aversion in dogs. *Social Justice Research*, **25**, 170-194.

Rankin, D. & Taborsky, M. 2009. Assortment and the evolution of generalized reciprocity. *Evolution*, **63**, 1913-1922.

Riedl, K., Jensen, K., Call, J. & Tomasello, M. 2012. No third-party punishment in chimpanzees. *Proceedings of the National Academy of Sciences*, **109**, 14824-14829.

Roberts, G. & Sherratt, T. N. 1998. Development of cooperative relationships through increasing investment. *Nature*, **394**, 175-179.

Roberts, G. 2008. Evolution of direct and indirect reciprocity. *Proceedings of the Royal Society B*, **275**, 173-179.

Roma, P. G., Silberberg, A., Ruggiero, A. M. & Suomi, S. J. 2006. Capuchin monkeys, inequity aversion, and the frustration effect. *Journal of Comparative Psychology*, **120**, 67-73.

Russell, Y. I. & Phelps, S. 2013. How do you measure pleasure? A discussion about intrinsic costs and benefits in primate allogrooming. *Biology & Philosophy*, **28**, 1005-1020.

Russell, Y. I., Call, J. & Dunbar, R. I. M. 2008. Image scoring in great apes. *Behavioural Processes*, **78**, 108-111.

Rutte, C. & Taborsky, M. 2007. Generalised reciprocity in rats. *PLoS Biology*, **5**, 1421-1425.

Rutte, C. & Taborsky, M. 2008. The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): direct vs. generalised reciprocity. *Behavioral Ecology and Sociobiology*, **62**, 499-505.

Sabbatini, G., De Bortoli Vizioli, A., Visalberghi, E. & Schino, G. 2012. Food transfers in capuchin monkeys: an experiment on partner choice. *Biology Letters*, **8**, 757-759.

Salvador, A. & Costa, R. 2009. Coping with competition: neuroendocrine responses and cognitive variables. *Neuroscience and Biobehavioral Reviews*, **33,** 160-170.

Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E. & Cohen, J. D. 2003. The neural basis of economic decision-making in the ultimatum game. *Science*, **300**, 1755-1758.

Savaskan, E., Ehrhardt, R., Schulz, A., Walter, M. & Schächinger, H. 2008. Post-learning intranasal oxytocin modulates human memory for facial identity. *Psychoneuroendocrinology,* **33**, 368-374.

Schell, A., Rieck, K., Schell, K., Hammerschmidt, K. & Fischer, J. 2011. Adult but not juvenile Barbary macaques spontaneously recognize group members from pictures. *Animal Cognition,* **14**, 503-509.

Schino, G. & Aureli, F. 2008. Grooming reciprocation among female primates: a meta-analysis. *Biology Letters,* **4**, 9-11.

Schino, G. & Aureli, F. 2009. Reciprocal altruism in primates: partner choice, cognition and emotions. *Advances in the Study of Behavior,* **39**, 45-69.

Schino, G. & Aureli, F. 2010. Primate reciprocity and its cognitive requirements. *Evolutionary Anthropology,* **19**, 130-135.

Schino, G. & Pellegrini, B. 2009. Grooming in mandrills and the time frame of reciprocal partner choice. *American Journal of Primatology,* **71**, 884-888.

Schino, G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology,* **18**, 115-120.

Schino, G., di Giuseppe, F. & Visalberghi, E. 2009. The time frame of partner choice in the grooming reciprocation of *Cebus apella*. *Ethology,* **115**, 70-76.

Schino, G., Perretta, G., Taglioni, A. M., Monaco, V. & Troisi, A. 1996. Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety,* **2**, 186-191.

Schino, G., Polizzi di Sorrentino, E. & Tiddi, B. 2007. Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame of reciprocation. *Journal of Comparative Psychology,* **121**, 181-188.

Schino, G., Tiddi, B. & Di Sorrentino, E. P. 2006. Simultaneous classification by rank and kinship in Japanese macaques. *Animal Behaviour,* **71**, 1069-1074.

Schino, G., Ventura, R. & Troisi, A. 2003. Grooming among female Japanese macaques: distinguishing between reciprocation and interchange. *Behavioral Ecology,* **14**, 887-891.

Schneeberger, K., Dietz, M. & Taborsky, M. 2012. Reciprocal cooperation between unrelated rats depends on cost to donor and benefit to recipient. *BMC Evolutionary Biology,* **12**, 41.

Schneider, A.-C., Melis, A. P. & Tomasello, M. 2012. How chimpanzees solve collective action problems. *Proceedings of the Royal Society B,* **279**, 4946-4954.

Seabright, P. 2005. *In the company of strangers*. Princeton: Princeton University Press.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2008. Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society B*, **275**, 1421-1429.

Seinena, I. & Schram, A. 2006. Social status and group norms: indirect reciprocity in a repeated helping experiment. *European Economic Review*, **50**, 581-602.

Semmann, D. 2012. Conditional cooperation can hinder network reciprocity. *Proceedings of the National Academy of Sciences*, **109**, 12846-12847.

Semmann, D., Krambeck, H.-J. & Milinski, M. 2005. Reputation is valuable within and outside one's own social group. *Behavioral Ecology and Sociobiology*, **57**, 611-616.

Semple, S., Harrison, C. & Lehmann, J. 2013. Grooming and anxiety in Barbary macaques. *Ethology*, **119**, 779-785.

Seyfarth, R. M. & Cheney, D. L. 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, **308**, 541-543.

Seyfarth, R. M. & Cheney, D. L. 1988. Empirical tests of reciprocity theory: problems in assessment. *Ethology and sociobiology*, **9**, 181-187.

Shackelford, T. K. & Buss, D. M. 1996. Betrayal in mateships, friendships, and coalitions. *Personality and Social Psychology Bulletin*, **22**, 1151-1164.

Shettleworth, S. 2010. *Cognition, evolution, and behavior*. 2nd edn. New York: Oxford University Press.

Shinada, M. & Yamagishi, T. 2007. Punishing free riders: direct and indirect promotion of cooperation. *Evolution and Humans Behavior*, **28**, 330-339.

Shutt, K., MacLarnon, A., Heistermann, M. & Semple, S. 2007. Grooming in Barbary macaques: better to give than to receive? *Biology Letters*, **3**, 231-233.

Silberberg, A., Crescimbene, L., Addessi, E., Anderson, J. & Visalberghi, E. 2009. Does inequity aversion depend on a frustration effect? A test with capuchin monkeys (*Cebus apella*). *Animal Cognition*, **12**, 505-509.

Silberberg, A., Roma, P. G., Ruggiero, A. M. & Suomi, S. J. 2006. On inequity aversion in nonhuman primates. *Journal of Comparative Psychology*, **120**, 76.

Silk, J. B. 1992. The patterning of intervention among male bonnet macaque: reciprocity, revenge, and loyalty. *Current Anthropology*, **33**, 318-325.

Silk, J. B. 1999. Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour*, **58**, 45-51.

Silk, J. B. 2002. Using the ‘F’ word in primatology. *Behaviour*, **139**, 421-446.

Silk, J. B. 2003. Cooperation without counting: the puzzle of friendship. In: *The genetic and cultural evolution of cooperation* (Ed. by P. Hammerstein), pp. 37-54. Cambridge: The MIT Press.

Silk, J. B. 2005. The evolution of cooperation in primate groups. In: *Moral sentiments and material interests: on the foundations of cooperation in economic life* (Ed. by H. Gintis, S. Bowles, R. Boyd & E. Fehr), pp. 43-73. Cambridge: The MIT Press.

Silk, J. B. 2007. The strategic dynamics of cooperation in primate groups. *Advances in the Study of Behaviour*, **37**, 1-42.

Silk, J. B., Alberts, S. C. & Altmann, J. 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour*, **67**, 573-582.

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P. & Shapiro, S. 2013. Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour*, **85**, 941-947.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., Lambeth, S. P., Mascaro, J. & Schapiro, S. J. 2005. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, **437**, 1357-1359.

Slocombe, K. E. & Zuberbuehler, K. 2007. Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, **104**, 17228-17233.

Smith, A. S., Ågmo, A., Birnie, A. K. & French, J. A. 2010. Manipulation of the oxytocin system alters social behavior and attraction in pair-bonding primates, *Callithrix penicillata*. *Hormones and Behavior*, **57**, 255-262.

Smith, P. & Silberberg, A. 2010. Rational maximizing by humans (*Homo sapiens*) in an ultimatum game. *Animal Cognition*, **13**, 671-677.

Sommerfeld, R. D., Krambeck, H.-J. & Milinski, M. 2008. Multiple gossip statements and their effect on reputation and trustworthiness. *Proceedings of the Royal Society B*, **275**, 2529-2536.

Sommerfeld, R. D., Krambeck, H.-J., Semmann, D. & Milinski, M. 2007. Gossip as an alternative for direct observation in games of indirect reciprocity. *Proceedings of National Academy of Sciences*, **104**, 175435-175440.

Stevens, J. R. & Gilby, I. C. 2004. A conceptual framework for non-kin food sharing: timing and currency of benefits. *Animal Behaviour*, **67**, 603-614.

Stevens, J. R. & Hauser, M. D. 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences*, **8**, 60-65.

Stevens, J. R., Cushman, F. A. & Hauser, M. D. 2005. Evolving the psychological mechanisms for cooperation. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 499-518.

Stewart-Williams, S. 2007. Altruism among kin vs. non-kin: effects of cost of help and reciprocal exchange. *Evolution and Human Behavior*, **28**, 193-198.

Subiaul, F., Vonk, J., Okamoto-Barth, S. & Barth, J. 2008. Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. *Animal Cognition*, **11**, 611-623.

Sylwester, K. & Roberts, G. 2010. Cooperators benefit through reputation-based partner choice in economic games. *Biology Letters*, **6,** 659-662.

Talbot, C. F., Freeman, H. D., Williams, L. E. & Brosnan, S. F. 2011. Squirrel monkeys' response to inequitable outcomes indicates a behavioural convergence within the primates. *Biology Letters*, **7**, 680-682.

Tan, J. & Hare, B. 2013. Bonobos share with strangers. *PLoS ONE*, **8**, e51922.

Tennie, C., Frith, U. & Frith, C. D. 2010. Reputation management in the age of the world-wide web. *Trends in Cognitive Sciences*, **14**, 482-488.

Tiddi, B., Aureli, F. & Schino, G. 2012. Grooming up the hierarchy: the exchange of grooming and rank-related benefits in a new world primate. *PLoS ONE*, **7**, e36641.

Tiddi, B., Aureli, F., di Sorrentino, E. P., Janson, C. H. & Schino, G. 2011. Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. *Behavioral Ecology*, **22**, 663-669.

Tomasello, M. 2009. *Why we cooperate*. Cambridge: The MIT press.

Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. 2005. Understanding and sharing intentions: the origins of cultural cognition. *Behavioral and Brain Sciences*, **28**, 675-691.

Tomasello, M., Melis, A. P., Tennie, C., Wyman, E. & Herrmann, E. 2012. Two key steps in the evolution of human cooperation: the interdependence hypothesis. *Current Anthropology*, **53**, 673-692.

Troisi, A. 2002. Displacement activities as behavioural measures of stress in non-human primates and human subjects. *Stress*, **5**, 42-54.

van Doorn, G. S. & Taborsky, M. 2012. The evolution of generalised reciprocity on social interaction networks. *Evolution*, **66**, 651-664.

van Ree, J. M. & Niesink, R. J. M. 1983. Low doses of β-endorphin increase social contacts of rats tested in dyadic encounters. *Life Sciences*, **33**, 611-614.

van Ree, J. M., Niesink, R. J. M, van Wolfswinkel, L., Ramsey, N. F., Kornet, M. L. M. W., van Furth, W. R., Vanderschuren, L. J. M. J., Gerrits, M. A. F. M. & van den Berg, C. L. 2000. Endogenous opioids and reward. *European Journal of Pharmacology*, **405**, 89-101.

van Wolkenten, M., Brosnan, S. F. & de Waal, F. B. M. 2007. Inequity responses in monkeys are modified by effort. *Proceedings of the National Academy of Sciences*, **104**, 18854-18859.

Ventura, R., Majolo, B., Koyama, N., Hardie, S. & Schino G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology*, **68**, 1138-1149.

Visalberghi, E. 1997. Success and understanding in cognitive tasks: a comparison between *Cebus apella* and *Pan troglodytes*. *International Journal of Primatology*, **18**, 811-830.

Warneken, F. & Tomasello, M. 2009. Varieties of altruism in children and chimpanzees. *Trends in Cognitive Sciences*, **13**, 397-402.

Warneken, F., Chen, F. & Tomasello, M. 2006. Cooperative activities in young children and chimpanzees. *Child Development*, **77**, 640-663.

Wascher, C. A. F. & Bugnyar, T. 2013. Behavioral responses to inequity in reward distribution and working effort in crows and ravens. *PLoS ONE*, **8,** e56885.

Watts, D. P. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, **139**, 343-370.

Wedekind, C. & Braithwaite, V. A. 2002. The long-term benefits of human generosity in indirect reciprocity. *Current Biology*, **12**, 1012-1015.

Wedekind, C. & Milinski, M. 2000. Cooperation through image scoring in humans. *Science*, **288**, 850-852.

Werdenich, D. & Huber, L. 2002. Social factors determine cooperation in marmosets. *Animal Behaviour*, **64**, 771-781.

Wobber, V., Hare, B., Maboto, J., Lipson, S., Wrangham, R. & Ellison, P. T. 2010a. Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proceedings of the National Academy of Sciences*, **107,** 12457-12462.

Wobber, V., Wrangham, R. & Hare, B. 2010b. Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology*, **20,** 226-230.

Wolff, I. 2012. Retaliation and the role for punishment in the evolution of cooperation. *Journal of Theoretical Biology*, **315**, 128-138.

Wout, M., Kahn, R., Sanfey, A. & Aleman, A. 2006. Affective state and decision-making in the ultimatum game. *Experimental Brain Research*, **169**, 564-568.

Yaksh, T. L., Gross, K. E. & Li, C. H. 1982. Studies on the intrathecal effect of β-endorphin in primate. *Brain Research*, **241**, 261-269.

Yamamoto, S. & Takimoto, A. 2012. Empathy and fairness: psychological mechanisms for eliciting and maintaining prosociality and cooperation in primates. *Social Justice Research*, **25**, 233-255.

Young, L. J. & Wang, Z. X. 2004. The neurobiology of pair bonding. *Nature Neuroscience*, **7**, 1048-1054.

Zak, P. J. 2005. Trust: a temporary human attachment facilitated by oxytocin. *Behavioral and Brain Sciences*, **28**, 368-369.

Zak, P. J., Kurzban, R. & Matzner, W. T. 2005. Oxytocin is associated with human trustworthiness. *Hormones and Behavior*, **48**, 522-527.

Zak, P. J., Stanton, A. A. & Ahmadi, S. 2007. Oxytocin increases generosity in humans. *PLoS ONE*, **2**, e1128.

Appendix

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Grooming increases self-directed behaviour in wild Barbary macaques, *Macaca sylvanus*

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self-scratching

Allogrooming has hygienic and social functions. Moreover, anxiety is thought to be reduced in the first few minutes after a grooming interaction is terminated. Few data exist on postgrooming reduction in anxiety, and mostly concern the recipient of grooming and captive animals. We analysed whether anxiety is reduced after grooming and whether this reduction differs between the donor and recipient of grooming. We collected 10 min postgrooming and matched-control (PG–MC) focal data on the donor and recipient of the same grooming interaction in wild Barbary macaques. We recorded all the occurrences of self-directed behaviours (i.e. self-scratching and self-grooming) as these are reliable indicators of anxiety. The occurrence of self-directed behaviour was greater in PGs than in MCs for both the donor and recipient. This increase in postgrooming anxiety was more evident for the recipient than for the donor. The postgrooming increase in anxiety was not due to a higher risk of receiving aggression after grooming. Unlike previous studies, our results indicate that anxiety may increase after grooming in Barbary macaques. If so, the social and hygienic benefits of grooming may outweigh its short-term anxiety cost. Self-directed behaviour may increase because of the emotional response to the change in activity (e.g. from grooming to travelling) and/or frustration at the termination of grooming. Our findings highlight the need to investigate further the link between emotions and grooming.

In many mammals and birds, allogrooming (hereafter grooming) and allopreening have a hygienic function, as animals exchange this behaviour to remove dirt and parasites from parts of the body that they cannot reach through self-grooming (Zamma 2002; Radford & Du Plessis 2006). Grooming also has a social function, because it plays an important role in the establishment and maintenance of social bonds (e.g. Dunbar 1991; Henzi & Barrett 1999). The giving of grooming is assumed to be a costly activity, as it interferes with vigilance against predators and/or competitors and the time available for other activities (e.g. feeding; Dunbar & Sharman 1984; Maestripieri 1993; Scantlebury et al. 2007), whereas receiving grooming has a positive effect on physical condition (e.g. Terry 1970; Zamma 2002; see below). For these reasons, grooming can be exchanged for itself (e.g. Schino & Aureli 2008a; Majolo et al. 2012), or it can be used as a trading commodity for other social services, such as support in aggression or tolerance over food (Noë & Hammerstein 1994; Henzi & Barrett 1999; Schino 2007).

Grooming is also thought to have an anxiety reduction benefit (Terry 1970). However, only a few studies have tested the hypothesis that a short-term reduction in anxiety follows the termination of grooming in the social partners. These studies have shown that the recipient of grooming (i.e. groomee) experiences a reduced heart rate during grooming (Boccia et al. 1989; Aureli et al. 1999), and a release of opioids in the blood (Keverne et al. 1989; Martel et al. 1995). Moreover, in the first few minutes after grooming, the groomee displays a lower frequency of self-directed behaviours (hereafter SDBs), such as self-scratching and self-grooming (Schino et al. 1988; Radford 2012).

SDBs are linked to anxiety and are often used as noninvasive, reliable behavioural manifestations of anxiety in animals (Maestripieri et al. 1992; Schino et al. 1996; Troisi 2002). Nonhuman primates display a lower frequency of SDBs following the administration of anxiolytic drugs (Schino et al. 1991, 1996; Cilia & Piper 1997; Barros et al. 2000), and a higher frequency following the administration of anxiogenic drugs (Schino et al. 1996). Moreover, SDBs increase during, or in the first few minutes after, events known to increase anxiety (e.g. close proximity to a higher-ranking animal or an agonistic interaction; Troisi & Schino 1987; Pavani et al. 1991; Aureli 1997; Castles et al. 1999; Koski et al. 2007; Schino et al. 2007).

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