

'FRIENDSHIP' IN MACAQUES

Economics and Emotions

Jorg J. M. Massen

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‘FRIENDSHIP’ IN MACAQUES

Economics and Emotions

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Economie en Emoties

(met een samenvatting in het Nederlands)

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*Aan pap en mam,
Omdat jullie me in elke keuze tot hier gesteund hebben*

*Aan Kim
Mijn muze*

"A friend may well be reckoned the masterpiece of nature."
Ralph Waldo Emerson (1803 - 1882)

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Chapter 1

A general introduction to friendship
and macaques

"Fate chooses your relations, you choose your friends."
Jacques Delille (1738 - 1813)

Chapter 1

A GENERAL INTRODUCTION TO FRIENDSHIP AND MACAQUES

The Altruism Conundrum

Natural selection (Darwin 1859) assumes that any trait that benefits an individual will prevail in future generations, while traits that are costly to or harm an individual will disappear. Altruistic behaviour poses a cost to the actor, while someone else is benefited. Consequently, the evolution of altruistic behaviour is a conundrum.

Kin-selection (Hamilton 1964) provides a solution to this conundrum with regard to altruistic behaviour among related individuals. Since related individuals share part of their genes, altruistic helping of those related individuals contributes, albeit in a diluted form, to the perpetuation of one's own genes. While altruistic behaviours do indeed occur rather frequent among kin (e.g., Silk 2002a), kin selection cannot explain altruistic behaviours among non-related individuals.

The solution to the altruism conundrum regarding unrelated individuals resides in reciprocation (Trivers 1971). Consider a well-fed individual that shares some food with someone who is literally starving. Although this obviously poses some costs to the 'altruist', these costs are trivial compared to the benefits for the one starving. Yet, when we consider this as an isolated event, the altruist still only poses costs on his own fitness. However, if in future time the roles are reversed and the previously starving individual reciprocates the favour, both individuals are saved from death by starvation at relatively small costs to both. By helping each other, these two individuals ultimately are better off than those that act alone (Trivers 1971). However, the mechanism of reciprocal altruism is prone to free riders; i.e., individuals that exploit the altruistic behaviour of others and do not reciprocate. Consequently, as a strategy, reciprocal altruism does not easily develop in an asocial world.

If, however, individuals meet on a regular base, free riders can be designated as such and excluded from future reciprocal exchanges. Altruistic acts are then only provided to those individuals that also reciprocate those acts, following a rule like: "I'll scratch your back, if you scratch mine." This tit-for-tat strategy (Axelrod & Hamilton 1981), in which the starting point is altruistic and thereafter decisions to cooperate are based on the previous action of the other, is able to develop in an asocial world and can resist invasion of free riders, making it an evolutionary stable strategy.

Chapter 1

Friendship and Reciprocal Altruism

Humans and other animals generally do not treat each group member equally, but instead show marked preferences in affiliative behaviour for particular individuals in their group (e.g., Smuts 1985; Cords 2002). These preferences can be attributed to kin-relations, yet also comprise unrelated individuals. In humans such affiliative relations between unrelated individuals are referred to as friends.

Preferences for particular individuals have been attributed to the value of such an individual (Kummer 1978), suggesting that 'good relations' among animals are social tools that enhance one's fitness. Indeed, there is a growing body of evidence for the adaptive value of both 'good relations' of animals and friendships of humans (e.g., House et al. 1988; Silk 2002b). Whereas these findings are interesting and provide us with some new insights in why friendships evolved, there is little to no research on what behavioural decision rules underlie and maintain friendships and by which strategy friendship becomes adaptive (Smuts 1985).

Since friendships concern unrelated individuals, the most common way to explain their occurrence and adaptive nature is through the mechanism of reciprocal altruism. Yet, in the social sciences there is a broad consensus that short-term, tit-for-tat reciprocity is not a feature of close friendship (Silk 2003). Moreover, requesting immediate reciprocation from friends is considered inappropriate, and for example selling your car to a friend often leads to awkward and difficult situations (Deutsch 1975). Therefore, Clark and Mills (1979) suggested that friends use different behavioural guidelines from strangers or acquaintances when providing help to each other. Whereas strangers and acquaintances only benefit each other with the expectation of reciprocation, friends are concerned with the other's welfare, and benefits provided do not create any obligations (Clark & Mills 1979). Furthermore, theoretical work (Boyd 1992) shows that reciprocity can be delayed when it is part of a long-term friendly relationship in which there can be considerable tolerance for prolonged imbalances in payoffs. Consequently, a tolerance for short-term imbalances may preserve valuable long-term (reciprocal) relationships (Silk 2002b). Whether these different behavioural guidelines for friends and non-friends also are apparent in non-human animals, and if consequently human and non-human friendships show homologous patterns, remains until now unclear.

Therefore, in this thesis, I explore the role of friendship in social behaviour in two macaque species, where individuals live in groups with differentiated social relationships. I test whether friendship determines benefits provided to group members, both through observations of patterns in this social behaviour and in

experimental set-ups. Thereby, I can also investigate whether ‘friends’ use different, less conditional, behavioural decision rules from other dyads within that social group. In addition, I determine experimentally whether friends are more tolerant to differences in benefits (i.e., inequity) than non-friends. Finally, I use my results in a literature review to establish whether human and macaque friendships are homolog phenomena or have a different origin.

THE STUDY SPECIES

This thesis reports studies on rhesus macaques (*Macaca mulatta*) and long-tailed macaques (*Macaca fascicularis*). Both macaque species live in relatively large social groups and show complex social behaviour. Although affiliative behaviour does concentrate around kin relations (Kapsalis & Berman 1996a), these macaques also commonly show affiliative behaviour towards non-kin. Moreover, in both species distinct patterns of affiliative behaviour can be observed, i.e., individuals show marked preferences in their affiliative behaviour for some and not for others. Altogether, this makes both macaque species interesting study subjects for the study of friendship in non-human animals. In addition, by studying two different macaque species, more general conclusions about macaque friendships can be drawn.

Rhesus and Long-tailed Macaques’ Ecology and Socio-Ecology

The behaviour of an animal is inseparably related to its ecology and socio-ecology. Therefore, I present a short introduction into the ecology and socio-ecology of the rhesus macaque and the long-tailed macaque. Both species belong to the genus *Macaca* and to the family *Cercopithecidae*. The group composition of both the rhesus and long-tailed macaque group I studied can be found in the appendix of this thesis.

The Rhesus Macaque

The rhesus macaque can be found almost throughout whole mainland Asia. Its geographical distribution ranges from Afghanistan in the west to China in the east and from both Thailand and India in the south to central China in the north. Apart from humans, rhesus macaques have the broadest geographic distribution of all primates (Southwick et al. 1996). Their success in ‘invading’ the world has been attributed to their Machiavellian nature (Maestripietri 2007), but may also be a result of their exceptional adaptation to coexist with humans (Richard et al. 1989). In

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general, they can be found in almost all habitats (e.g. semi deserts, temperate forests, tropical forests and mangrove swamps) in these regions (Fooden 2000).

Rhesus macaques have a dusty brown to auburn fur and a medium sized tail of about 21 cm. Their reddish-pink faces have no fur. As many macaque species, rhesus macaques are sexually dimorphic: males are about 53 cm high and weigh approximately 8 kg, whereas females are about 47 cm high and weigh approximately 5.5 kg (Fooden 2000). The average life span of rhesus macaques is 25 years in the wild, but in captivity they may reach 30 years. Their age of first reproduction is approximately 3 years (Rawlins & Kessler 1986), but in captivity they have been reported to start reproducing at 2 years of age (Catchpole & van Wagenen 1975). From their first reproduction onwards, females are theoretically able to give birth every year until they are about 20 years of age (Rawlins & Kessler 1986), but mostly have some pauses in between separate offspring. Rhesus macaques have distinct birth seasonality; i.e. they mate in winter (Oct-Jan) and babies are born at the end of the rainy season or during the period of highest food abundance, i.e. spring. During the mating season both males as females in a group mate promiscuously (Lindburg 1971).

Rhesus macaques live in multi-male/multi-female groups ranging in size between ten to more than a hundred individuals (Lindburg 1971). Females are philopatric, i.e. they remain in their natal group for the rest of their lives. In contrast, males disperse and emigrate from their natal group just before they hit puberty. Thereafter, males try to join a different group or stay in male bachelor groups for a while.

Rhesus macaques in a group form distinct and clear dominance hierarchies. Among a scale of all macaque species, rhesus macaques are considered among the most despotic macaques (Thierry 2000). Females form a dominance hierarchy according to their matrilineal kinship, creating family ranks, e.g. an alpha family, a beta family etc. After birth females gain a rank position just below their mother, but higher in rank than their siblings. Therefore, whenever an old matriarch becomes weak, disappears or dies, her youngest daughter replaces her in the dominance hierarchy. Although takeovers between families sometimes occur, female rank relations are generally very stable (Seth 2000). In contrast, male dominance hierarchies are relatively unstable. Like immature females, immature males inherit the rank of their mother. However, during maturation, their dominance status changes based on a combination of aggressive and social skills (Lindburg 1971; Berard 1999). When they leave their natal group at puberty, these aggressive and social skills become even more important in trying to join a different group. They

will need aggressive skills and strength to overpower resident males and social skills to be accepted by the resident females. If a male succeeds in becoming the most dominant male in a group, i.e. the alpha male, he will only enjoy this rank for an average of two years before being replaced by another male (Bercovitch 1997). If male rhesus macaques take over the alpha position, they can be infanticidal (Louwerse, pers. comm.), killing infants that are unlikely to be sired by themselves. Females losing a nursing infant will come into estrus faster than if they reared the infant completely. By inducing cycling in females, infanticidal males increase their chances of siring offspring as soon as possible after a take-over (Hrdy 1974).

Finally, rhesus macaques are omnivores and feed on a wide variation of plant products, e.g. leaves, fruit, roots, flowers etc., and on various invertebrates. Moreover, their coexistence with humans has led them to forage by picking through garbage, and they also raid crops (Goldstein & Richard 1989; Richard et al. 1989). Especially because of their opportunistic foraging on human byproducts, rhesus macaques are usually not affected much by loss of habitat and most rhesus macaque populations are thriving (Zhang 1998). By raiding crops, stealing food and threatening children and elderly they, however, have become a menace to small villages. This leads to low levels of tolerance of humans towards rhesus macaques and may end in killing these animals (Imam et al. 2002; Wolfe 2002; Rao 2003). Rhesus macaques are therefore a rare case in which the overabundance of a species is a major problem for its conservation.

The Long-tailed Macaque

Long-tailed macaques can be found on almost all large Indonesian Islands, as well as on mainland Southeast Asia in Malaysia, Burma, Vietnam, Laos and Cambodia. They inhabit tropical rain forests characterized by a warm, humid climate and heavy seasonal rainfall (Supriatna et al. 1996; Umapathy et al. 2003). They prefer forests near water and are commonly found along riverbanks, lakeshores and along the seacoast (van Schaik et al. 1996).

Long-tailed macaques have a grayish fur and, as their name predicts, an extraordinary long tail of about 55 cm. Both males and females have cheek whiskers, moustaches and beards covering their pinkish-brown face. Additionally, long-tailed macaques have white colourations on their eyelids (Rowe 1996). Also long-tailed macaques are sexually dimorphic: males are about 50 cm high and weigh approximately 6 kg, whereas females are only about 45 cm high and weigh approximately 4.5 kg (Fa 1989). The average lifespan of long-tailed macaques is 30 years in the wild, whereas in captivity they may reach 35 years. The age of first

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reproduction is approximately 5.5 years (Varavudhi et al. 1992), but in captivity they may start reproducing at an age of 3 years (pers. Observation). From their first reproduction onwards, females are theoretically able to give birth every year until they are about 24 years of age, however, they are more likely to skip a year after giving birth to a surviving infant (van Noordwijk & van Schaik 1999). This leads to an average interbirth interval of approximately 18 months (van Schaik & van Noordwijk 1988). Long-tailed macaques do exhibit birth seasonality, albeit not as distinct as that of the rhesus macaque. Moreover, birth seasonality in long-tailed macaques varies across populations and seems linked to food abundance, which varies with mast years (van Noordwijk & van Schaik 1987; van Schaik & van Noordwijk 1988). Because of the lack of a truly distinct birth and mating season, both males and females mate promiscuously throughout the year.

Long-tailed macaques live in multi-male/multi-female groups ranging in size between 6 to 60 individuals (van Schaik & van Noordwijk 1985). Like rhesus macaques, female long-tailed macaques are philopatric, and males disperse and emigrate from their natal group just before they hit puberty. Thereafter, males try to join a different group or stay in male bachelor groups for a while (van Noordwijk & van Schaik 2001).

Long-tailed macaques also form clear dominance hierarchies. And, albeit not as despotic as rhesus macaques, also long-tailed macaques are known for their despotic nature (Thierry 2000). Similar to rhesus macaques, female long-tailed macaques form stable dominance hierarchies according to their matrilineal kinship, and males form unstable dominance hierarchies according to their aggressive and social skills (de Jong et al. 1994; van Noordwijk & van Schaik 1999). Male long-tailed macaques migrate very often and stay in one group only for approximately 45 months (van Noordwijk & van Schaik 1999; 2001). Only at age 9 they start trying to take over the alpha position, and if they succeed they will keep that position for approximately 3 years before being overthrown themselves (de Jong et al. 1994). As in the rhesus macaques, after a take-over in long-tailed macaques, the group conditions are conducive to infanticide (Gosselt pers. comm; de Ruiter 1994).

Finally, long-tailed macaques are mainly frugivorous. However, in the dry season, when fruit is less abundant, they also feed on different plant products, various invertebrates, mushrooms, bird eggs and even frogs and crabs (which is why they are also called crab-eating monkeys)(Sussman & Tattersall 1986; Son 2003). Like rhesus macaques, also long-tailed macaques have become very crafty in coexisting with humans. They commonly beg for food from humans, steal food from kitchens and even raid crops. This has made them a pest and humans often

shoot the monkeys and can eliminate entire local populations (Wheatley et al. 1999). Nonetheless, fortunately they are currently not a threatened species.

Rhesus and Long-tailed Macaques' Social Intelligence

Living in a group provides several advantages, e.g., social benefits like better protection from predators, the ability to compete with conspecific groups for resources and improved mating opportunities (Alexander 1974; Bertram 1978; Wrangham 1980; van Schaik 1983). However, group living also has various disadvantages, e.g., a greater risk of infection by diseases and social costs like competition over food, space and mating partners (Bertram 1978; Gompper 1996). However, exactly these problems of balancing social benefits and costs, resulting in a complex social life, are believed to be at the basis of the evolution of primate intellect (e.g., The Machiavellian Intelligence Hypothesis: Byrne & Whiten 1988; The Social Brain Hypothesis: Dunbar 1998). According to the Machiavellian intelligence hypothesis, certain cognitive mechanisms have evolved that allow animals to deal with this complex social life (Byrne & Whiten 1988; Byrne 1997). These mechanisms are of great importance to both rhesus and long-tailed macaques, since both species live in complex groups with repeated opportunity for interaction with conspecifics. An important component of Machiavellian intelligence is knowledge about the social environment (Call 2004).

Recognition of Others and their Relations

A key mechanism to allow for reciprocal relations among individuals is the ability to recognize others (Axelrod & Hamilton 1981). Both rhesus and long-tailed macaques can recognize each individual of their group (rhesus macaques: Rosenfeld & van Hoesen 1979; long-tailed macaques: Dittrich 1990). Moreover, considering their nepotistic biases (e.g., their matrilineally organized dominance hierarchies)(Silk 2009), their kin preference in grooming behaviour (rhesus macaques: Kapsalis & Berman 1996a), and the large frequencies of kin-support in conflicts (rhesus macaques: Kapsalis & Berman 1996b; long-tailed macaques: de Waal 1977), they apparently also recognize their own kin. Furthermore, they also seem to understand the kin-relations of others (rhesus macaques: Rendall et al. 1996; long-tailed macaques: Dasser 1988), and interestingly, long-tailed macaques use such third-party information when they redirect aggression towards the kin of the opponent of the previous fight, which is sometimes referred to as 'vendetta' (Aureli & van Schaik 1991a).

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Furthermore, macaques of both species show ritualized behaviours to express their subordination to dominant individuals (i.e., bare teeth display and make room)(de Waal 1976). Therefore, individuals of both species seem to understand their dominance position in relation to others. Moreover, it has been shown that they also understand other animals' (i.e. third-party) rank relations (rhesus macaques: Bovee & Washburn 2003; long-tailed macaques: Dasser 1987). This suggests that both macaque species not only live in groups in which all individuals are known, but that the network of kin and dominance relationships are also part of their view on group characteristics.

Agonistic Aiding and Conflict Resolution

Rhesus macaques and long-tailed macaques are both relatively aggressive species. They quarrel a lot, and this is not always just between two individuals but can involve many more group members. Macaques of both species cooperate in fights and regularly form coalitions against others (rhesus macaques: Lindburg 1971; long-tailed macaques: de Waal et al. 1976). As mentioned before, they more frequently support kin than non-kin (rhesus macaques: Kapsalis & Berman 1996b; long-tailed macaques: de Waal 1977). Moreover, in their support behaviour they also reflect knowledge about rank relations, since the majority of coalitions in rhesus macaques are all down coalitions in which they support a higher ranked individual against an individual that both the aggressor and the supporter outrank (Kaplan 1978; Bernstein & Ehardt 1985). This suggests that rhesus macaques employ an opportunistic strategy in their support behaviour by which they can strengthen their own dominance position.

Conflicts are stressful, can lead to wounds and can damage relationships with group members, and should, therefore, be prevented or remedied if possible (Aureli & de Waal 2000). A dominance hierarchy, and its related ritualized expressions of submission, is an apt mechanism to avoid conflicts among known individuals (Preuschoft & van Schaik 2000). When conflicts nevertheless occur, the combatants have to deal with or remedy the negative consequences. To tackle these negative consequences, both rhesus and long-tailed macaques can reconcile conflicts (rhesus macaques: de Waal & Yoshihara 1983; long-tailed macaques: Aureli & van Schaik 1991a). Reconciliation has been shown to reduce the stress-levels of previous opponents (Aureli & van Schaik 1991b; Das et al. 1998), and is believed to repair social bonds that have been damaged through a conflict (Cords & Aureli 2000). Consequently, reconciliation occurs more frequent among kin and with 'valuable' partners (Cords & Turnheer 1993; Aureli et al. 1997).

Understanding of Others' Behaviour

Paying attention to what others do in a group can be beneficial, since others may have information you do not have. Moreover, they may see things you have not seen yet or cannot see from your position. To tap into this rich source of information, both species are able to follow the gaze of their conspecifics (rhesus macaques: Tomasello et al. 1998; long-tailed macaques: Goossens et al. 2008) and do this more often when the gaze of the other is accompanied by a facial expression that shows the salience of what the animal is seeing (e.g. the bare-teeth display)(Goossens et al. 2008). This gaze following is not based on a simple co-orientation mechanism, but instead on a more sophisticated perception of what the other sees, since at least long-tailed macaques are also able to follow a gaze to a hidden location (Goossens 2008). Moreover, macaques of both species seem to make use of their knowledge of what others can and cannot see, since subordinate males tend to hide their mating behaviour from the more dominant males (rhesus macaques: Overduin-de Vries et al. MS ; long-tailed macaques: Gyax 1995). Furthermore, it has been reported that rhesus macaques also know what others can and cannot hear (Santos et al. 2006).

Finally, long-tailed macaques have been reported to use tools (Watanabe et al 2007; Malaivijitnond et al. 2007; Gumert et al. 2009), and seem to learn using these tools by looking at members of their group that already master the skill (Masataka et al. 2009). Social learning of artificial object-reward associations, furthermore, has also been reported for rhesus macaques (Meunier et al. 2007).

To summarize, macaques of both species seem to have a well-developed understanding of their social environment and seem to take the behaviour of their conspecifics into account when making decisions about their own behaviour.

Chapter 1

HOW TO DEFINE FRIENDSHIPS?

The Cambridge Advanced Learner's Dictionary defines friendship and friends as follows:

friendship *noun*

/ˈfrend.ʃɪp/ [C or U]

- when two people are friends

friends *noun*

/frend/ [C]

- a person who you know well and who you like a lot, but who is usually not a member of your family
- someone who is not an enemy and who you can trust

Who is befriended with whom in human studies is commonly derived from questionnaires. However, this technique cannot be applied to non-human animals. Furthermore, friendships in humans are mainly described by emotional states, which are also very difficult to measure in non-human animals (Silk 2002b). Therefore, to define friendship, I use two objective measures that occur frequently, are frequently used to describe friendships of non-human animals (Smuts 1985; Cords 2002), and can be used to measure human friendships as well: i.e., proportion of time spent sitting in contact and proportion of time spent physically touching each other (e.g., social grooming).

Frequency of Physical Proximity

Although human friends are able to endure long separations, time spent together is one of the main measures of friendships in humans (Baxter et al. 1997). Even in contemporary Western society, in which people are equipped with cell-phones and e-mail and can be members of various social networking websites, reported emotional closeness is strongly related to frequency of face-to-face contact (Hill & Dunbar 2003): humans report to be emotionally closer to those people with whom they also have frequent close physical proximity. Frequency of contact is a measure that can also easily be quantified in any group living animal. Moreover, in many animal species frequency of contact correlates strongly with affiliative behaviours such as social grooming (Smuts 1985; Cords 2002). Altogether, this makes

frequency of contact a useful and objective measure of friendship in both humans and non-human animals.

Frequency of Physical Touch (Social Grooming)

Humans have an extensive lexicon and talking is considered very important in maintaining relationships. Therefore, there seems to be no need for tactile communication in the maintenance or development of social bonds in humans. However, there is ample evidence that physical touch does play an important role in human relationships. Although humans may not be aware of it, they still exhibit several forms of physical contact in the form of patting, petting and cuddling. These touches are confined to the more intimate relations (Dunbar 2010), thereby making them predictive of the nature of a relationship.

The social grooming of primates is all about touch. Nonetheless, it was at first assumed that it served a hygienic function, hence the name grooming. However, the frequency of grooming, primates can spend up to 20 % of their daytime on grooming, exceeds the time necessary for cleaning the fur by far, and the body language of those being groomed suggest that it is also pleasurable (Kummer 1978; Dunbar 1991). Like humans, primates focus these close social touches to a select group of individuals and, for example, the amount of grooming of rhesus macaques is related to their degree of genetic relatedness (e.g. Kapsalis & Berman 1996a). Moreover, it is assumed that grooming relations create social bonds that affect group cohesion (Dunbar, 1996), and that grooming bonds determine the degree of familiarity and predictability of each other's behaviour (Dunbar 1988). In conclusion, grooming and touch seem, comparable to frequency of physical proximity, to be useful and objective measures of close bonds or friendship in humans and non-human primates.

Chapter 1

Definitions

To be Friends or not to be Friends

For my research question, I had to establish who are friends and who are not. First of all, by definition, friends are always non-kin. To distinguish friends from non-friends within a group of individuals, I conducted time-sample scan observations (2-4 times a day, with at least one hour between each observation) of all group members during an extensive period of time (minimally 8 months), to assess who is sitting with whom (contact-sitting, i.e. sitting within arm reach of each other) and who is grooming whom. The 'friends' of an individual are then defined as the upper quarter of individuals of contact sitting and grooming, i.e. the animals with whom the individual was most often together and which he/she groomed the most, and bad relationships are maintained with individuals in the lower quarter of contact sitting and grooming, i.e., animals with whom the individual was least often together and which he/she groomed the least. Only individuals that score highest or lowest in these two measures, i.e., both contact sitting and grooming, are considered friends or non-friends respectively. Furthermore, since measures of (non-)friendship in a dyad can be asymmetric, only dyads in which both individuals are categorized as friend or as non-friend for the other are considered. Other relations were considered neutral relations. In figure 1 I show an example of the contact-sitting data of two individuals that according to these data are considered friends, provided that the same criteria are met in the grooming data (figure 1).

Relationship Quality on a Continuous Scale

To measure relationship quality on a continuous scale, I also used the data of contact sitting and grooming. I ordered relationship quality based on the degree of contact sitting and grooming per individual. In a group of for example 35 subjects, the individual with whom they sat most often in contact was given number 1 and with whom they sat least often together was given number 34. When an individual sat a same proportion of time together with two individuals, they were given the average number, e.g. if they were 4 and 5, they were both numbered 4.5. If an individual sat the least together with several individuals, they were all given number 34. The same was done for grooming. For each partner both numbers were added and divided by two, leading to a 'relationship quality' ordering ranging between 1 ('best friends') and 34 (the least affiliative bonds).

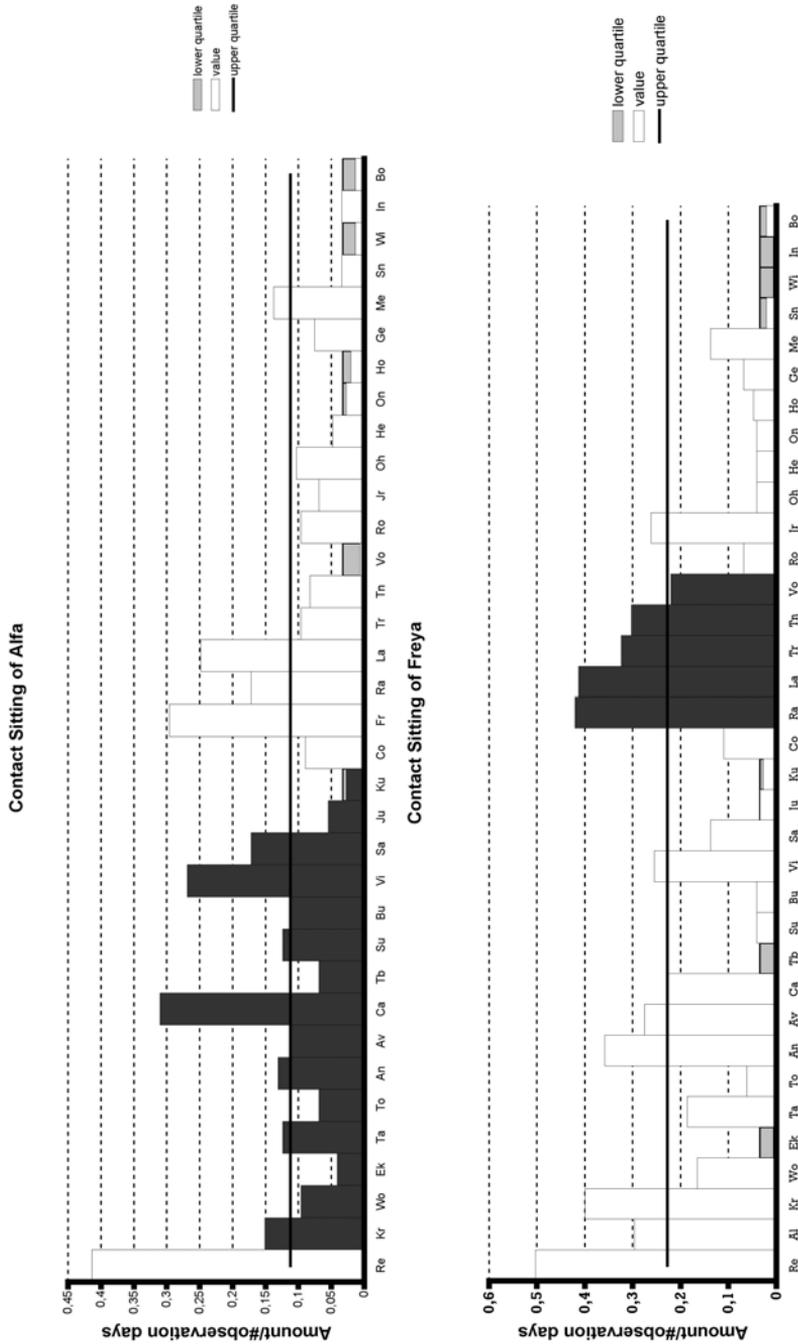


Figure 1. The relative frequency of contact sitting with all group members of two individuals (Alfa (Al) and Freya (Fr)). Dark grey bars represent relatives of the subject. The solid line represents the upper quartile of contact sitting for the subject, while the light grey area represents the lower quartile. The two individuals are not related and are in each others upper quartile. If the same pattern is found in their grooming data, they can be considered friends.

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THE AIMS AND OUTLINE OF THIS STUDY

The research described in this thesis was part of an interdisciplinary research on tolerance for underbenefitting in human and non-human friendships. By interchanging concepts, measures and research designs from the social and the life sciences, and the inclusion of both human and non-human subjects, we aimed to overcome differences in the explanation of what a friendship is between the social and the life sciences. The aim of my study was to study friendship in non-human animals, i.e., macaques. In particular, the aim of my research was to address the question whether macaque ‘friends’ are more tolerant to underbenefitting than non-friends. I addressed this question by means of both observational and experimental studies, of which this thesis is the result.

In the first study (chapter 2) I investigate the different strategies male rhesus macaques can use to obtain mating access to females. In primates, but also in many other animal species, with multi-male multi-female groups, male mating success depends on the males’ dominance rank (e.g. Cowlshaw & Dunbar 1991). If this determines male mating success, it is expected that only the alpha male mates unless there are several receptive females and the alpha male cannot monopolize them all, in which case also the beta male mates (Altmann 1962). However, low-ranked males may still gain mating access by using alternative strategies. For example, it has been suggested that long-tailed macaques ‘pay’ for sex with grooming (Gumert 2007a). Alternatively, others (Smuts 1985; Palombit 2003) argue that long-term friendships lead to mating access.

My study tests these different hypotheses about male mating strategies. Firstly, whether male dominance hierarchy is related to the males’ sexual behaviour. Secondly, the study focuses on the exchange of grooming for sex. I investigate whether such an exchange exists and what the time frame of such an exchange is: either short-term, reflecting a sort of payment, or long-term, reflecting a strong social bond (e.g. friendship) which may be unaffected by temporal imbalances in the exchange relation.

The second study (chapter 3) also investigates exchange patterns. It has been argued that altruistic acts can be exchanged for similar acts or interchanged for other acts, commodities or services (Hemelrijk & Ek 1991). Such reciprocal relations (Trivers 1971) are ultimately beneficial for both actors. Several proximate mechanisms explaining reciprocal altruism have been proposed. Reciprocity can be based on symmetrical features of the individuals involved, i.e., *symmetry based reciprocity*, on the attitude an individual shows towards another individual due to its recent behaviour, i.e., *attitudinal reciprocity*, or on active scorekeeping of the

amount and value of what has been given and received, i.e., *calculated reciprocity* (Brosnan & de Waal 2002). Alternatively it has been proposed that reciprocal relations arise due to the strength of a social bond built up during a (long) series of interactions, i.e., *emotionally based bookkeeping* (Schino et al. 2007).

My study investigates the exchanges of grooming for grooming and support for support, as well as the interchanges of grooming for support and support for grooming in long-tailed and rhesus macaques. I focus on the time frame of these exchange and interchanges, thereby underpinning the proximate mechanism. Moreover, I investigate in this study whether the monkeys use differential decision rules for friends and non-friends, e.g. more tolerant for temporal imbalances towards their friends compared to non-friends.

The third study (chapter 4 & 5) experimentally investigates in long-tailed macaques whether friends are in general more pro-social towards each other compared to non-friends. Pro-social behaviour i.e., benefiting others without direct reciprocation, has long been regarded uniquely human. However, pro-social behaviour has been reported for several primate species (common marmosets: Burkart et al. 2007; capuchin monkeys: de Waal et al. 2008; and bonobos: Hare & Kwetuenda 2010). In contrast, several studies reported mixed evidence for pro-sociality in chimpanzees (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008). This leads to the suggestion that pro-sociality is a trait usually expressed by tolerant species, and not often shown by more despotic species such as chimpanzees (Lakshminarayanan & Santos 2009).

The first part of this study (**chapter 4**) considers whether despotic long-tailed macaques show pro-sociality. Moreover, in this experiment I specifically test what the effect of the dominance hierarchy is on the pro-social behaviour of the group members. The hierarchy may affect pro-sociality in two opposed ways: subordinate individuals may be more pro-social towards dominant individuals, presumably to gain tolerance or future support (Seyfarth 1977). Alternatively, dominants may be more pro-social to either enhance or maintain their status (Moore 1984; de Waal 1989). By testing individuals varying in their dominance position in the group for their pro-social tendencies, I aim to test these hypotheses.

If friends are tolerant to underbenefitting, it can be expected that friends benefit each other without expecting direct reciprocation, i.e., among friends pro-social behaviour will be more likely than among non-friends. In the second part of this study (**chapter 5**), I specifically address that question by means of two experiments. In the first experiment I test for pro-sociality within pairs that vary in relationship quality (i.e., from 'best friends' to the least affiliative bonds). In the

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second experiment I test subjects with two partners. Subjects are given the choice to either benefit their 'friend' or to benefit a 'non-friend' By relating relationship quality to pro-sociality and by comparing the frequency of pro-social choices for a 'friend' and a 'non-friends', I aim to test the hypothesis that individuals are more pro-social to friends than to non-friends.

The fourth study (chapter 6) addresses the question whether friends are more tolerant to underbenefiting, using an experimental approach. In this study I tested whether long-tailed macaques show inequity aversion and how their relationship quality affects this behaviour. Inequity aversion, the aversive reaction to an unequal pay-off (Adams 1963), has also long been regarded uniquely human. Recently however, inequity aversion has been reported in several non-human species (capuchin monkeys: Brosnan & de Waal 2003; chimpanzees: Brosnan et al. 2005; cottontop tamarins; Neiworth et al. 2009; and domestic dogs: Range et al. 2009a). Social scientists have argued that in contrast to strangers, human friends are not focused on an equal distribution, but distribute resources mainly according to differences in need (Deutsch 1975; Clark & Mills 1979). Data on both chimpanzees and domestic dogs also suggest that more tolerant bonds show less inequity aversion (Brosnan et al. 2005; Range et al. 2009b). However, the role of relationship quality in an inequity response in non-human animals remains to be tested experimentally.

My study encompasses two experiments with long-tailed macaques. The first experiment tests whether long-tailed macaques show inequity aversion. Moreover, in this experiment inequity aversion is tested in relation to the relationship quality of the tested duo. In the second experiment I specifically compare the inequity response of friends and non-friends. In this experiment subjects are tested twice: once with a friend and once with a non-friend. By comparing the inequity response of individuals with their friends and with non-friends, I aim to investigate whether indeed friends are less focused on inequity and thus are more tolerant to underbenefiting.

The last study (chapter 7) is a literature review of functions and mechanisms of friendship in animals and man. In this review I address the notion that the social sciences and the life sciences have very different ideas about friendship. Whereas biologists conceive friendship as a fitness enhancing relationship, i.e., through reciprocal exchange of benefits between two individuals (Kummer 1978), social scientist describe friendships as a 'deep engagement' (Tooby & Cosmides 1996), in which resources are distributed according to need and in which receiving a benefit does not create an obligation (Clark and Mills 1979).

Rather than reflecting a true difference, these differences may reflect differences in interpretation of the nature of friendship due to differences in measures and a mix-up of proximate and ultimate causes (Tinbergen 1963) of behaviour leading to friendship. Therefore, a careful examination of friendship in humans and animals and their proximate and ultimate causes is needed.

In the first part of this chapter I review the measures used to describe friendships and I aim to find similar and objective measures that can be used to define both human and non-human friendships. In the second part of this chapter I review studies on the ultimate benefits of friendship, exploring the adaptive benefits of non-human and human friendship. Thirdly, I review studies on the proximate mechanisms that may underlie friendship in both human and non-human animals. Here I explore the motivations of friendly behaviour for their conditionality, i.e., are friendly behaviours motivated by the prospect of future reciprocation or not? In the last part of this chapter I review studies on hormonal and neuronal correlates of friendship. Here I examine whether there are similarities between humans and other animals in neuronal and hormonal structures and pathways involved in social behaviour and attachment. The basis of human friendly behaviour may be old and many animals may share similar underlying structures facilitating such friendly behaviour. Finally, I hope to answer the question whether human and non-human friendships are truly different or may be based on homologue patterns.

Altogether, the studies described in this thesis contribute to our understanding of what comprises friendship in macaques, how these friendships relate to reciprocal altruism and whether these friendships in macaques are similar to or different from human friendships. This is achieved by examining the proximate mechanisms underlying the macaques' differential behaviour towards friends and others using both observational and experimental approaches, and positioning the results of these studies in the framework of literature on friendship in humans and other animals.

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Chapter 2

Male mating tactics in captive rhesus macaques, *Macaca mulatta*:
Dominance, markets or relationship quality?

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"She's beautiful, and therefore to be wooed;
She is a woman, therefore to be won"
William Shakespeare (1564 - 1616)

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ABSTRACT

Male mating success in a multi-male multi-female group can depend on several variables: dominance, coalitions, or an exchange of services for mating access. Furthermore, exchange patterns may be determined by market effects or social relationships. We studied the male mating tactics in a captive multi-male group of rhesus macaques. Male rank was positively related to the total number of copulations and the number of mating partners, but could not completely explain male mating success. Grooming by the male was not directly exchanged for male mating access and supply or quality of fertile females did not affect the amount of male grooming, suggesting that market effects could not explain male mating success. However, a long-term correlation existed between grooming and mating access for both males and females, indicating that social relationships were important for male mating success. Therefore, we suggest that the exchange of grooming for male mating access is best explained by 'emotional bookkeeping'. In conclusion, both male rank and male-female 'friendship' determine male mating access in rhesus macaques.

INTRODUCTION

Males competing for mating access to females will use mating tactics (i.e., distinct behavioural patterns leading to mating access) depending on their own and their competitor's characteristics (Andersson 1994). Strong or dominant males can gain mating access based on their fighting abilities or dominance rank (e.g., anthropoid primates: Cowlshaw & Dunbar 1991; mountain goats, *Oreamnos americanus*: Mainguy et al. 2008; meerkats, *Suricata suricata*: Spong et al. 2008), while subordinate males may use other tactics (e.g., special relationships in olive baboons, *Papio anubis*: Smuts 1985; coalitions in savanna baboons, *Papio cynocephalus*: Noë & Sluifjter 1990; satellite males in fallow deer, *Dama dama*: Apollonia et al. 1992; 'coursing' in mountain goats: Mainguy et al. 2008). Male mating success, however, not only depends on the behaviour of other males, but also results from female mating tactics (Trivers 1972). Females may prefer particular males (Anderson 1994) or mate promiscuously with many males (Nikitopoulos et al. 2005). Especially promiscuous mating preferences of females will allow mating access for multiple males that employ different tactics. In primates, where multiple males can live in the same group with multiple promiscuously mating females (Dixson 1997), there are ample opportunities for males to employ different mating tactics. Primate male mating tactics may depend on the male dominance hierarchy (Cowlshaw & Dunbar 1991), male-male coalitions (Noë & Sluifjter 1990), the exchange of grooming for male mating access in a mating market (Noë & Hammerstein 1994; Gumert 2007a) or special relationships among particular males and females (Smuts 1985; Palombit 2003). Here we aim to determine the mating tactics that result in the mating pattern observed in a multi-male multi-female rhesus macaque (*Macaca mulatta*) group.

Hierarchy Based Mating Tactics

In many species males form clear dominance hierarchies (e.g., primates: Smuts et al. 1987; cooperatively breeding carnivores: Creel & Sands 2003; spotted hyenas, *Crocuta crocuta*: Drea & Frank 2003; elephants: Payne 2003). Male hierarchies often play a major role in male mating opportunities, since many studies find a positive correlation between male dominance rank and mating activity (e.g., primates: Cowlshaw & Dunbar 1991; mountain goats: Mainguy et al. 2008) and mating success (e.g., lions, *Panthera leo*: Packer et al. 1991; macaques, *Macaca sp.*: Rodriguez-Llanes et al. 2009). In rhesus macaques, males can monopolize only one female at a time (Carpenter 1942). This combination of hierarchy and monopolization led Altmann (1962) to propose his 'Priority-of-Access' model (PoA), where male dominance rank and number of simultaneously sexually

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receptive females determine the probability that a male will get mating access to a receptive female. If there is only one receptive female, mating will be monopolized by the alpha male, if there are two receptive females, one will be monopolized by the alpha male and one by the beta male, etcetera. Some studies find a mating pattern that supports this model (olive baboons: Packer 1979; savanna baboons: Bulger 1993), while in other studies subordinate males have more mating access to females than predicted (olive baboons: Smuts 1985; savanna baboons: Bercovitch 1986; Noë & Sluijter 1990). This suggests that subordinate males employ other tactics or that females have other preferences. For example, middle-ranking males may form coalitions against high-ranking males to gain access to females (i.e., revolutionary coalitions: Noë & Sluijter 1990; van Schaik et al. 2004). However, not only male aggression, but also male affiliation with females may lead to mating opportunities.

Grooming for Mating Access

Low-ranking males may entice females to mate with them when they provide them with benefits. Grooming is a service that can be interchanged against other benefits, e.g., mating opportunities (Barrett & Henzi 2006). Accordingly, males groom more frequently fertile than infertile females (chimpanzees, *Pan troglodytes*: Hemelrijk et al. 1992; hamadryas baboons, *Papio hamadryas hamadrya*: Colmenaris et al. 2002) and subsequently may mount these females (bonnet macaques, *Macaca radiata*: Kurup 1988; chimpanzees: Hemelrijk et al. 1992; long-tailed macaques, *Macaca fascicularis*: Gumert 2000). This indirect evidence indicates that male grooming may constitute a mating strategy that males employ in the short term (i.e., biological market for mating behaviour, Noë et al. 1991) or long term (i.e., good social relationships, Smuts 1985) to gain access to females.

Short-Term Tactics: Mating Market

The biological market theory describes social behaviour from an economic perspective. Social acts, such as grooming or mating access, are considered valuable commodities that two classes of individuals exchange within a biological market to the benefit of both parties (Noë et al. 1991; Noë & Hammerstein 1994). These commodities cannot be taken by force and the exchange is preceded by partner choice. The 'price' of a commodity is influenced by supply and demand: when there is little supply and much demand, prices will be high, and vice versa (Noë & Hammerstein 1994, 1995). In a primate mating market, males will be the demanding class and females can supply mating access. Therefore, males will groom females in exchange for mating access and grooming reciprocation by females is not

expected. Recently, market effects have been found in the mating context (wood mouse, *Apodemus sylvaticus*: Stopka & MacDonald 1999; long-tailed macaques: Gumert 2007a). Alternatively, males may employ long-term tactics.

Long-Term Relationships: 'Friendship'

Primates maintain differential relationships with groupmembers, varying from good to bad. Individuals with a good relationship have frequent affiliative interactions (e.g., grooming), high proximity levels, often support each other in conflicts, are tolerant towards each other and show low degrees of stress when together (Silk 2002b). Non-kin individuals with a good social relationship are often referred to as 'friends' (Smuts 1985; Palombit et al. 1997). Friendships between males and females have been reported for baboons (olive baboons, Smuts 1985; chacma baboons, *Papio urcines*: Lemasson et al. 2008). A friendship's functional significance for males is probably related to mating access (Palombit 2003) and females obtain protection against infanticide (chacma baboons: Palombit et al. 1997) or against non-lethal harassment (Lemasson et al. 2008). Since both sexes will benefit from such a relation, both the male and female are expected to groom each other to maintain the social relationship. Although within friendships mating access is not exchanged directly for grooming, on the long-term a male's grooming behaviour will predict his access to mating partners.

The exchange of commodities or services can be explained by three different hypothetical proximate mechanisms: symmetry-based reciprocity, attitudinal reciprocity and calculated reciprocity (de Waal & Luttrell 1988; Brosnan & de Waal 2002). *Symmetry-based reciprocity* is based on symmetrical features of individuals (e.g., kinship, rank, social class or age) that make both parties react similarly to each other. *Attitudinal reciprocity* expresses the willingness of an individual to cooperate based on the attitude that the partner shows in the long term (also called 'emotional bookkeeping' (Schino et al. 2007)) or has recently shown towards him (de Waal 2000). In contrast, *calculated reciprocity* is based on mental scorekeeping of the precise costs and benefits of exchanged behaviour (Brosnan & de Waal 2002). While long-term tactics may depend on all three proposed reciprocity mechanisms, short-term tactics require attitudinal or calculated reciprocity.

In this study we investigate the different possible male mating tactics in a multi-male multi-female group of captive rhesus macaques. Female rhesus macaques mate promiscuously (Manson 1992; Dixson 1998; Overduin-de Vries et al. MS) and are

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seasonal breeders. Both male and female rhesus macaques have a clear linear dominance hierarchy (Thierry 2000), creating ample possibilities for hierarchy based mating tactics, female choice, and differences in value of commodities in a possible mating market. Using an observational approach, we aim to determine whether male mating tactics concur with dominance rank, whether mating access is exchanged for grooming, and whether this exchange is governed by short-term market effects or by long-term affiliative patterns ('friendships') between mating partners. In addition, we aim to establish what the underlying proximate mechanism of a possible interchange of grooming and mating access is.

METHODS

Study Group and Housing Conditions

The study group was a captive group of Burmese rhesus macaques (*M. m. mulatta*)(Wodka group), housed at the Biomedical Primate Research Centre, Rijswijk, the Netherlands. The group contained between 30 and 39 individuals. Changes in group composition were due to demographic processes, births, maturation and deaths, and management reasons. The group was composed of 1 adult non-natal male, between 7 and 8 sub-adult natal males (2-7 years of age), between 7 and 9 adult females in 3 matriline, between 3 and 4 sub-adult females (2-5 years of age) and between 11 and 18 immatures (0-2 years of age). Sub-adult animals were included in the study, since they mated and captive sub-adult rhesus macaques can be considered sexually mature since they reproduce at this age (Catchpole & van Wagenen 1975; BPRC, unpublished colony management data)(table 1).

Male Mating Tactics

Table 1. The age and rank of all males in the study per mating season, their female mating partners and the number of matings observed.

2006/2007	Male	Age	Rank	Mating Partner	# Mating-days	Age partner	Rank Partner
	Robbedoes	11	1	Mona	1	10	2
				Natasha	2	10	14
	Timon	5	4	Lisa	4	3	3
				Priegel	1	4	5
				Saravi	1	5	6
				Emoe	1	10	11
				Wenk	1	18	16
	Jam	3	8	Nala	1	6	7
				Epha	7	18	19
	Moer	4	10	Lisa	3	3	3
				Yota	3	2	17
	Bout	4	12	Lisa	1	3	3
				Priegel	2	4	5
	Kaas	5	15	Saravi	1	5	6
	Ham	2	18	Yota	2	2	17
				Epha	7	18	19
	Zier	3	21	-			
2007/2008	Male	Age	Rank	Mating Partner	# Matings	Age partner	Rank Partner
	Robbedoes	12	1	Mona	15	11	2
				Saravi	1	6	4
				Natasha	4	11	14
	Moer	5	5	Lisa	4	4	7
				Emoe	1	11	10
				Girl	6	2	13
	Jam	4	7	Natsaha	16	11	14
				Wenk	4	19	17
				Epha	21	19	19
	Bout	5	9	Priegel	3	5	3
				Saravi	1	6	4
	Kaas	6	11	Priegel	1	5	3
	Ham	3	12	Girl	1	2	13
	Zier	4	15	-			
	Dremel	3	16	Yota	1	3	18

The group was housed in an indoor enclosure, 72 m² and 2.85 m high, and an outdoor enclosure, 208 m² and 3.1 m high, connected by two tunnels. The indoor enclosure had sawdust bedding, the outdoor enclosure sand. Both enclosures had multiple elevated sitting locations and enrichment devices. The animals were fed a diet of monkey chow (ssniff® Pri), fruits, vegetables and grains. Water was available ad libitum.

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Data Collection

Data were collected between November 2006 and February 2007 and between September 2007 and Augustus 2008, encompassing two consecutive breeding- and non-breeding seasons. During the observations, the animals were locked in the outdoor enclosure.

Scan Data

We took 4 scans a day, 4-5 days a week, during the whole data collection period, recording for all group members who was sitting in contact with whom and who groomed whom. Scans were at least one hour apart and divided randomly over the course of the day.

Focal Data

A total of 518 hours of focal observations were recorded. Focal observations were recorded during the 2006/2007 breeding season (November 2006 – February 2007), the 2007 pre-breeding season (September 2007 – October 2007), the 2007/2008 breeding season (November 2007 – March 2008), and during the 2008 post-breeding season (May 2008 – August 2008), by several observers (Inter-observer reliability between all other observers and J.J.M.M. calculated by Cohen's kappa ranged between 0.93 and 0.96). During these periods the group was studied 4-5 days a week. 15-min focal samples of all agonistic, affiliative and sexual behaviour of all sexually active animals (2006/2007: 9 females and 8 males; 2007/2008: 10 females and 8 males) were recorded in The Observer 5.0 and XT (Noldus) according to a semi-random time schedule. The behaviour was recorded continuously (Martin & Bateson 1993). We employed an ethogram of rhesus macaque's social behaviour based on Altmann (1962) and supplemented by Angst (1974). Comparable to Gumert (2007a), we subdivided grooming behaviour in normal grooming and sexual grooming. Sexual grooming was defined as grooming that either directly preceded sexual activity or grooming in between sexual activity, whereas normal grooming did not concur with any sexual activity between a male and female.

Ad Libitum Data

During the two breeding seasons, all sexual behaviours observed were recorded *ad libitum*. Matings were defined as each interaction containing one or more of the following elements: sexual mounts, copulations and thrusts without, and with ejaculation. In addition, unidirectional submissive behaviour (i.e., bare teeth and make room) was recorded.

Dominance Hierarchy

To calculate the dominance hierarchy, we used the unidirectional submissive behaviour elements bare teeth and make room. These behaviours were arranged in a socio-matrix with actors in rows and recipients in columns. MatMan 1.1 was used to calculate Landau's linearity indices and to reorder matrices according to hierarchy (de Vries 1995; 1998). In both the 2006/2007 data and the 2007/2008 data a significantly linear hierarchy was found (2006/2007: Landau's linearity index (h) = 0.249, $p < 0.001$; 2007/2008: Landau's linearity index (h) = 0.453, $p < 0.001$). The hierarchy of both years was comparable, with few changes in the relative position of individuals in the hierarchy, mainly due to changes in group composition.

Female Receptivity

To test the PoA model and to assess supply and demand in a possible mating market, female receptivity, i.e., a female's willingness to mate (Beach 1976), had to be determined. We defined female receptivity by the actual mating behaviour of a female, i.e., females were defined receptive on days they did mate and were defined non-receptive on days they did not mate.

Data Processing and Analyses

To study exchange patterns of grooming and mating access, these behaviours were arranged in socio-matrices with actors in rows and recipients in columns. Exchange patterns were then calculated in MatMan 1.1 with row-wise matrix correlations (de Vries et al. 1993), using Kendall's tau as a correlation statistic (Hemelrijk 1990a). Partial row-wise correlations (Hemelrijk 1990b) were used to assess the effect of rank, proximity and grooming received from the females on these exchange patterns. The effect of these variables is then reflected in their effect on the correlation statistic tau compared to the original correlation. For a detailed explication of why we prefer to use rowwise matrix correlations instead of linear mixed models see appendix 1 of chapter 2.

Since our data were not normally distributed, we used non-parametric tests. All statistic tests in this study were $\alpha = 0.05$. Tests were 2-tailed, unless directional predictions allowed the use of 1-tailed probabilities.

Since our data encompass two consecutive breeding seasons, we first tested whether there were differences between these two breeding seasons. When no significant differences were found, we only show overall data and statistics. When differences were significant, we report the separate results.

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RESULTS

Dominance Rank

The dominance position of a male may determine how often and with how many females he mates. High-ranking males had a significantly higher number of female mating partners than low-ranking males (Spearman's rank correlations: 2006/2007 data: $r_s = -0.868$, $n = 8$, $p = 0.005$; 2007/2008 data: $r_s = -0.801$, $n = 8$, $p = 0.017$)(figure 1). In the 2007/2008 data, the number of matings was significantly higher for high than low-ranking males (Spearman's rank correlation: $r_s = -0.854$, $n = 8$, $p = 0.007$), and in the 2006/2007 data there was a similar, but non-significant, relationship between the number of days with mating activity and male rank (Spearman's rank correlation: $r_s = -0.590$, $n = 8$, $p = 0.123$)(figure 1). These results indicate that high-ranking males have better mating access to females and the PoA model may explain the male mating pattern.

If PoA explains mating patterns in our group, we expect the alpha male to mate on each day a female was observed mating, the beta male to mate on each day two females were observed mating, the gamma male to mate on each day three females were observed mating, and so on. The expected- and actual-proportion of mating-days were calculated for all males in both years. The observed and expected proportion of mating days, however, differed significantly ($\chi^2 = 82.16$, 5 df, $p < 0.001$). This indicates that the PoA model does not explain the observed male mating pattern.

Grooming for Mating Access

A male may use grooming to obtain mating access to a female. The distribution of grooming during the breeding season tends to differ from the distribution of grooming during the non-breeding season (scan data: Univariate test; $n = 9$ males & 10 females, $F = 3.859$, 3 df, $p = 0.058$)(figure 2), since both males and females groomed individuals of their own sex more often during the non-breeding season and the opposite sex more often during the breeding season. This opens the possibility that males may use grooming to gain access to a particular mating partner.

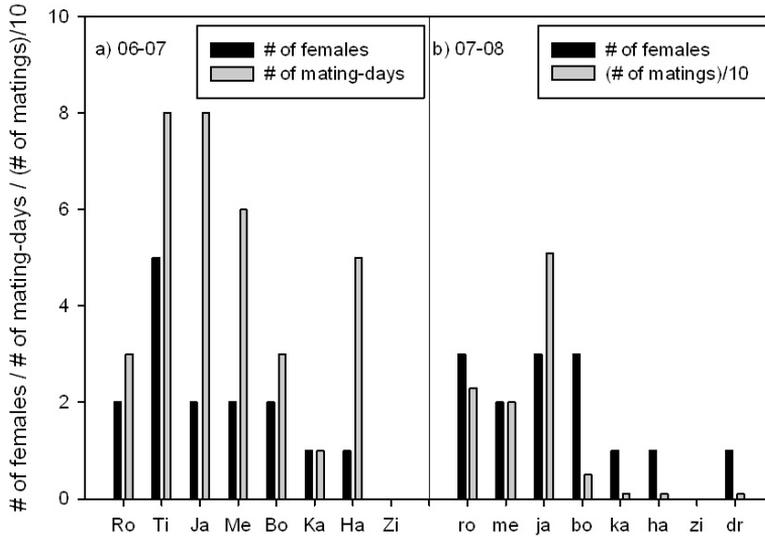


Figure 1. **a:** Number of female partners and observed mating days of all (sub-)adult males in the 2006/2007 breeding season, **b:** Number of female partners and number of observed matings (#/10) off all (sub-)adult males in the 2007/2008 breeding season. The males are listed in order of dominance hierarchy at that time, with the alpha male on the left.

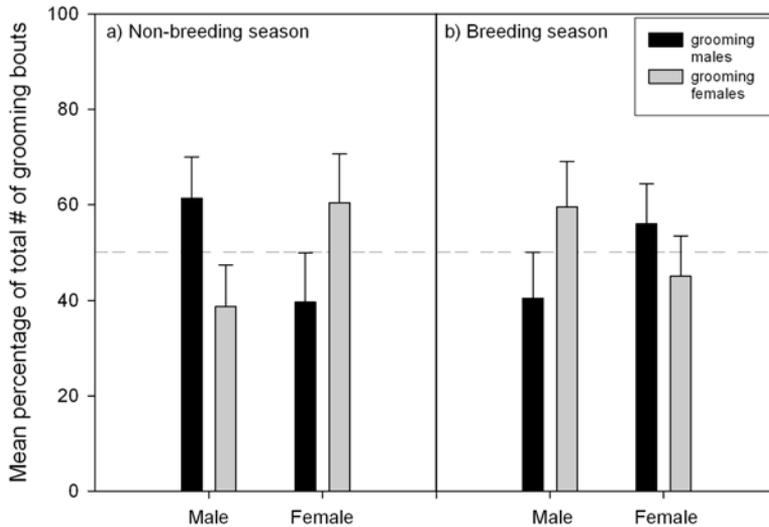


Figure 2. Mean percentage + SEM of the total number of grooming bouts from males and females directed towards males or females, in the **a:** non-breeding season and in the **b:** breeding season. Data of 2006/2007 and 2007/2008 are combined.

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To investigate a possible exchange of grooming for mating access, the grooming patterns of males during the breeding season were determined in relation to their mating access to females. First we used matrix correlations of all male grooming of females and mating data to determine whether male grooming may predict their mating access. Indeed, there was a significant positive correlation between male grooming (both number of grooming bouts and duration of grooming) and mating access (number of mating-days in the 2006/2007 data, and number of matings in the 2007/2008 data)(Kendall's τ_{rw} : $0.24 < \tau < 0.44$, $n = 7$ males, 10/11 females, right-tailed probability < 0.05)(for all statistics see table 2). Therefore, the grooming given to a female in a mating season predicts male mating access to this female.

Second, in the breeding season males tended to groom their female mating partners more often and longer compared to their grooming of these females in the non-breeding season (Friedman tests: number of grooming bouts: $\chi^2 = 4.923$, $n = 7$, 2 df, $p = 0.085$; duration of grooming: $\chi^2 = 4.923$, $n = 7$, 2 df, $p = 0.085$), whereas males did not differ significantly in the number of grooming bouts and grooming duration in the breeding and non-breeding season towards females they did not mate with (Friedman tests: number of grooming bouts: $\chi^2 = 0.783$, $n = 7$, 2 df, $p = 0.676$; duration of grooming: $\chi^2 = 1.652$, $n = 7$, 2 df, $p = 0.438$)(figure 3).

Third, we determined variation in male grooming within the breeding season. Males in the 2007/2008 breeding season groomed their mating partners significantly more and longer compared to the females they did not mate with in the breeding season (Wilcoxon signed rank tests: number of grooming bouts: $Z = -2.197$, $n = 7$, $p_{1\text{tailed}} = 0.014$; duration of grooming: $Z = -1.69$, $n = 7$, $p_{1\text{tailed}} = 0.045$), and the data from the 2006/2007 breeding season showed a similar trend (Wilcoxon signed rank test: number of grooming bouts: $Z = -1.352$, $n = 7$, $p_{1\text{tailed}} = 0.088$; duration of grooming: $Z = -1.352$, $n = 7$, $p_{1\text{tailed}} = 0.088$)(figure 3). The specific allocation of grooming of males towards the females they mated with, and only during the relevant period, opens the possibility of a mating market.

Male Mating Tactics

Table 2. Rowwise matrix correlations of grooming bouts (Gr#) and number of matings (sex#) of males and females in both breeding seasons, and of grooming duration (Grdur) and number of matings, and (partial) rowwise matrix correlations of the effect of rank, proximity and received grooming on these correlations.

Breeding Season 2006/2007							
Male							
	K. tau _{rw}	p	Partialled out	K. tau _{rw;XY,Z}	p	K. tau _{rw;XZ}	K. tau _{rw;YZ}
Gr#vs.Sex#	0,2431	0,0190	Rank	0,245576	0,0170	0,06084	-0,03086
			Proximity	0,193446	0,0450	0,37507	0,17772
			Received gr,	0,211245	0,0320	0,21019	0,19251
Grdurvs,Sex#	0,3664	0,0030	Rank	0,369704	0,0010	0,07068	-0,03086
			Proximity	0,017157	0,4385	0,22505	0,24197
			Received gr,	0,294135	0,0085	0,32435	0,31579
Female							
	K. tau _{rw}	p	Partialled out	K. tau _{rw;XY,Z}	p	K. tau _{rw;XZ}	K. tau _{rw;YZ}
Gr#vs.Sex#	0,2502	0,0260	Rank	0,264587	0,0210	0,12677	-0,08827
			Proximity	0,178122	0,0785	0,35014	0,25376
			Received gr,	0,173852	0,0775	0,29756	0,31079
Grdurvs,Sex#	0,4163	0,0015	Rank	0,436634	0,0000	0,15273	-0,08827
			Proximity	0,178122	0,0705	0,35014	0,25376
			Received gr,	0,300380	0,0120	0,37945	0,43926
Breeding Season 2007/2008							
Male							
	K. tau _{rw}	p	Partialled out	K. tau _{rw;XY,Z}	p	K. tau _{rw;XZ}	K. tau _{rw;YZ}
Gr#vs.Sex#	0,3922	0,0005	Rank	0,396655	0,0005	0,12158	-0,01222
			Proximity	0,278616	0,0045	0,46427	0,34609
			Received gr.	0,209464	0,0270	0,49488	0,46735
Grdurvs.Sex#	0,4432	0,0005	Rank	0,444902	0,0005	0,06265	-0,01222
			Proximity	0,374845	0,0015	0,31690	0,34609
			Received gr.	0,382790	0,0000	0,25549	0,42075
Female							
	K. tau _{rw}	p	Partialled out	K. tau _{rw;XY,Z}	p	K. tau _{rw;XZ}	K. tau _{rw;YZ}
Gr#vs.Sex#	0,4905	0,0005	Rank	0,479826	0,0010	-0,11629	-0,22334
			Proximity	0,429424	0,0005	0,27665	0,41779
			Received gr.	0,382364	0,0005	0,41077	0,42647
Grdurvs.Sex#	0,4753	0,0005	Rank	0,458138	0,0005	-0,15202	-0,22334
			Proximity	0,466146	0,0005	0,13303	0,41779
			Received gr.	0,419141	0,0015	0,24837	0,47755

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Figure 3. Mean relative duration (seconds / focal hours) + SEM of male grooming directed towards those females they mated with during the breeding season or towards the other females, in the 2006/2007 breeding season, in the two months preceding the 2007/2008 breeding season (Pre-Br. 2007/2008), in the 2007/2008 breeding season and in the 5 months after the 2007/2008 breeding season (Post-Br. 2007/2008). * $p < 0.05$.

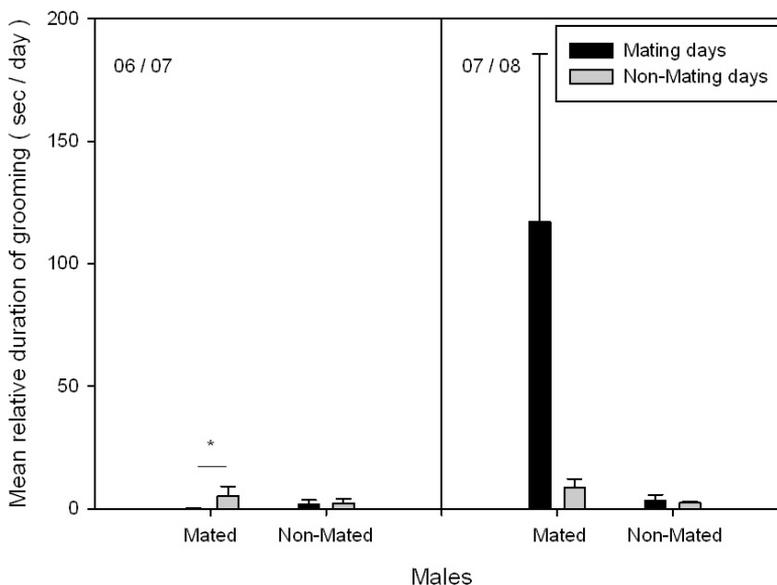


Figure 4. Mean relative duration (seconds / focalhours) + SEM of grooming of mated and non-mated males directed at females on days those females mated (black bars) and on days those females did not mate (grey bars) with the male. * $p < 0.05$.

Mating Market

If grooming is exchanged for mating access, it is expected that males groom their female mating partners more often and longer when they are receptive. However, in the 2007/2008 data no significant difference was found between the number of grooming bouts (Wilcoxon signed rank tests: $Z = -1.120$, $n = 10$, $p = 0.263$), or in the duration of grooming (Wilcoxon signed rank tests: $Z = -1.363$, $n = 10$, $p = 0.173$) on mating days and non-mating days (figure 4). Moreover, the data of 2006/2007 show, opposite to expectation, that males groomed their mating partners more (number of grooming bouts, Wilcoxon signed rank tests: $Z = -2.521$, $n = 10$, $p = 0.012$) and longer (duration of grooming, Wilcoxon signed rank tests: $Z = -2.366$, $n = 10$, $p = 0.018$) on days they did not mate compared to actual mating days (figure 4). In addition, sexual grooming (Gumert 2007a) was rare and only observed twice in the two breeding seasons. These results indicate that, contra to what is expected when there is a mating market, there is no direct interchange of grooming for mating access on the actual day of mating.

A biological 'mating' market further predicts that partner choice is based on competition among the demanding class. Therefore, females that mated may also have been particularly attractive to males that were not their mating partner. This may create a mating market effect where non-mating males try to outbid their competitors by grooming mating females more than males that mate. However, on days they were receptive, females did not receive more or longer grooming of males they did not mate with versus days they were not receptive (Wilcoxon signed rank tests; number of grooming bouts: $Z = -0.978$, $n = 11$, $p = 0.32$; duration of grooming: $Z = -1.156$, $n = 11$, $p = 0.248$)(figure 4). This is not consistent with a biological mating market.

To investigate whether there was an influence of supply and demand, another characteristic of a biological market, we determined the number of grooming bouts and the duration of grooming of males towards their female mating partners depending on the number of mating females per day (1-6 females per day). However, regression analysis showed no effect of the number of mating females on the number of male grooming bouts or the duration of male grooming, when all cases of no grooming were taken into account (linear regression: number of grooming bouts: $r = 0.076$, $r^2 = 0.006$, $F_{1,65} = 0.374$, $p = 0.543$; duration of grooming: $r = 0.034$, $r^2 = 0.001$, $F_{1,65} = 0.077$, $p = 0.783$), and when cases of no grooming were considered missing values (linear regression: number of grooming bouts: $r = 0.041$, $r^2 = 0.002$, $F_{1,6} = 0.010$, $p = 0.924$; duration of grooming: $r = 0.405$, $r^2 = 0.164$, $F_{1,6} =$

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1.175, $p = 0.320$). Therefore, there are no indications that supply, i.e., the number of receptive females on a day, determines male grooming behaviour.

Finally, the biological market theory predicts that the quality of a commodity influences its 'price'. Both male and female dominance rank are proposed to influence the amount of grooming needed for mating access (Gumert 2007a). However, partial rowwise correlations of male grooming of females and mating access with dominance rank showed that rank does not play a significant role in the interchange between grooming and mating, since Kendall's tau does not change substantially when rank is partialled out (see table 2), indicating no effect of this variable (Vervaecke et al. 2000). This indicates that neither high-ranking males groom less to 'get' mating access compared to low-ranking males, nor is more grooming 'needed' to get mating access to a high-ranking female compared to a low-ranking female.

'Friendship'

The relation between male grooming of and mating access to females may also be due to the quality of the male-female relationship. If male mating distribution is explained by the quality of affiliative social relationships, such as friendships, and males use grooming to invest into a relationship, it is expected that also females invest in particular males. Therefore, we investigated whether females were active or passive participants in the pattern of male grooming. The distribution of female grooming of males differed between the breeding and the non-breeding season. As the males, also the females groomed their own sex more often in the non-breeding season and the opposite sex more often in the breeding season, suggesting that females also invest in males during the breeding season (figure 2). Also, female grooming of males predicted mating behaviour, since there was a significant correlation between female grooming (both number of grooming bouts and duration of grooming) and mating access (number of mating-days in the 2006/2007 data, and number of matings in the 2007/2008 data) (Kendall's τ_{rw} : $0.25 < \tau < 0.49$, $n = 7$ males, 10/11 females, right-tailed probability < 0.05) (for all statistics see table 2). Therefore, the female grooming pattern predicts mating behaviour: the more a female grooms a particular male, the greater the chance that this female mates with that male. Thus, both male and female grooming patterns of the opposite sex correlate with mating behaviour. Furthermore, 'friendships' or close social relationships are characterized by several variables such as mutual grooming and proximity. Therefore, we investigated how these variables affect the interchange of grooming and mating access using partial rowwise correlations. These partial

rowwise correlations showed that female grooming as well as proximity did change the Kendall's tau of the correlation between male grooming and mating access substantially (see table 2). This indicates that those male-female dyads that mate have a mutual grooming relation and spent much time in each other's proximity as well.

DISCUSSION

In this study we determined the mating tactics employed by male rhesus macaques. We investigated whether the distribution of matings was best explained by male dominance rank or whether mating access was exchanged for grooming, governed by either market effects or by general affiliative patterns. Furthermore, we determined the proximate mechanism underlying such an exchange.

Dominance Status and Mating Access

The male hierarchy is a good predictor for mating success: high-ranking males mate more often and with more females. This suggests that the PoA model could explain the distribution of mating partners. However, the distribution of mating partners expected by the PoA model did not match the observed distribution of mating partners. Young (some only 3 years of age) low-ranking males were also observed mating. Consequently, the PoA model did not explain the distribution of mating partners in our group of captive rhesus macaques.

Coalitions between middle ranking males have been suggested as an explanation for such different distributions of mating partners (Noë & Sluiter 1990). However, the formation of coalitions did not determine male mating success in our group, since in both years no male coalitions have been observed. In contrast, coalitions among adult males have been observed in free-ranging rhesus macaque populations (Altmann 1962). Since the formation of coalitions may require experience and also a good chance of winning (Noë 1994), the absence of coalitions in our study may result from the young age of the subordinate males compared to male age in other studies where coalitions were observed.

Although male-male competition thus can explain part of the distribution of mating, it still cannot explain the mating access of young subordinate males. Furthermore, since we observed that female rhesus macaques cannot be habitually forced to mate by the males (see also Manson 1992), and females show marked promiscuity (table 1; Lindburg 1971; Overduin-de Vries et al. MS), female choice probably plays a role in male- and female mating success. Therefore, males can

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compete with each other by enticing the females to prefer them over other males. Grooming has been suggested to serve such a function, through a mating market (Noë & Hammerstein 1994; Gumert 2007a) or through the formation of special relationships (Smuts 1985; Palombit et al. 1997).

Grooming for Mating Access

We investigated male-female grooming patterns over two years. In the non-breeding season both sexes groom their own sex more often than the opposite sex, which is in accordance with the species dispersal pattern. Females typically remain in the group throughout their lives and, therefore, female-female relations are very important. Males leave the group at puberty (Melnick et al. 1984) and they may invest in future coalitions with male peers from their natal group. In contrast, during the breeding season both males and females groom the opposite sex more often, suggesting that in the mating context grooming may enhance access to mating partners. Indeed, in the breeding season males groomed specifically those females they mated with more often and longer than the females that they did not mate with. Moreover, in the breeding season males groomed their mating partners more often and longer than in the non-breeding season. Therefore, grooming and mating access are related, and short-term market effects or long-term relationship quality may determine this relation.

Mating Market

A biological market predicts competition for commodities (Noë & Hammerstein 1994; 1995). Thus, in a mating market, successful males are expected to groom females in exchange for mating access. However, on the actual days of mating, the females did not receive more grooming of the males they mated with compared to other days, suggesting there is no direct exchange of grooming for mating access. Accordingly, sexual grooming almost never occurred. In addition, not only the successful males, the ones that actually mate, but also their competitors are expected to groom a female more on the days that a female is receptive. However, there is apparently no such competition between males on the days females are receptive, since females also did not receive more grooming on these days of males they did not mate with.

The biological market further predicts the laws of supply and demand apply (Noë & Hammerstein 1994; 1995). We, however, did not find any effect of the number of receptive females available on the amount of grooming received by those females.

Finally, the biological market predicts that the value of a commodity predicts the 'price to be paid' (Noë & Hammerstein 1994; 1995). For example, males may groom high-ranking females more than low-ranking females, and high ranking males may groom less than low-ranking males to gain mating access (Gumert 2007a). Mating opportunities with high-ranking females have a greater value, since high-ranking females produce more offspring with better survivorship chances compared to low-ranking females (long-tailed macaques: van Noordwijk & van Schaik 1999). High-ranking males may provide more genetic benefits to a female or be better able to force a female to mate than low-ranking males (Gumert 2007a). An alternative explanation for the effects of male dominance argues that a more dominant male has to pay less since he can provide better protection for the female and her future offspring (Smuts 1985). However, in our study, high-ranking males did not groom less often their female mating partners compared to low-ranking males, nor did high-ranking females receive more grooming for mating compared to low-ranking females. Altogether, these results suggest that there is no mating market in our group. Furthermore, female grooming data support that there is no mating market. Although male grooming of females may be viewed as a 'payment for sex' (Gumert 2007a), the grooming of male mating partners by females counters this interpretation since market theory predicts that only the demanding class (i.e., males) grooms. Altogether, the fact that males do not specifically groom the females they mate with more on the actual day of mating, the low occurrence of sexual grooming, and the lack of grooming competition on these days further underlines that, at least in our group of captive rhesus macaques, the data are not conform to the mating market theory (Noë & Hammerstein 1994; Gumert 2007a).

'Friendship'

Male-female 'friendships' may lead to mating access (Smuts 1985). Although within a friendship mating access is not 'paid' for immediately, on the long-term a male's grooming behaviour may still predict his mating access, since grooming is seen as an investment in a social relationship (Silk 2002b). Indeed, matrix correlations revealed an interchange of grooming for mating access. In addition, the interchange of grooming and mating was strongly influenced by proximity and reciprocal grooming. Moreover, not only males, but also females groom mating partners more often than non-mating partners. This suggests that a mutual good relationship between a male and female is important in securing mating opportunities (Hinde 1979; Silk 2002b). Accordingly, in our group of captive rhesus macaques the relationship between grooming and mating access is mostly explained by affiliation

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during a particular breeding season towards particular individuals and the formation of long-lasting stable social relationships between males and females. This is similar to the male-female 'friendships' (Smuts 1985; Palombit et al. 1997) found in other multi-male multi-female primate groups. While the baboon male-female 'friendships' described by Smuts (1985) preceded and possibly led to mating, those described by Palombit and colleagues (1997) succeeded mating association and males may provide protection for the female and her offspring. In our population the time frame of a male-female 'friendship' seemed to differ between males and females. Males seemed to invest more in their social bond with a female prior to and during the mating season, and their investment ceased after the breeding season. In contrast, females did not seem to invest in male-female 'friendships' prior to the breeding season, but invested in this relationship during and after the breeding season. This suggests that males invest in male-female 'friendships' to ensure mating access, and females try to sustain these 'friendships' to ensure male protection for her and her offspring.

Proximate Mechanism of Grooming - Mating Access Exchange

The time frame of the exchange of grooming and mating access gives us insight to the possible proximate mechanism underlying this exchange. In rhesus macaques, the exchange of grooming for mating access does not seem to take place within one day. This is in accordance with data on grooming reciprocation in Japanese macaques (Schino et al. 2003), capuchin monkeys (Schino et al. 2009), and chimpanzees (Gomes et al. 2009)(for a meta-analysis on more primate species see Schino & Aureli 2008), and also in accordance with data on the exchange of grooming for support in Japanese macaques (Schino et al. 2007). Instead, the timeframe of this exchange is found over a relatively long time span of weeks or months. Accordingly, emotionally mediated reciprocity (Schino et al. 2007) that allows for short-term imbalances seems to be the most plausible (i.e., low-level) mechanism underlying this exchange. Alternatively, symmetry-based reciprocity (Brosnan & de Waal 2002) may also explain long-term exchange patterns. However, in our group of rhesus macaques the identity of mating partners does not seem to depend on symmetrical features, e.g., rank or age, of the individuals involved (see table 1).

We conclude that for captive rhesus macaques male mating access is partly explained by male dominance hierarchy. In addition, males exchange grooming for mating access. However, this exchange is not on the short-term or driven by a biological market and seems not to involve cognitive bookkeeping. Instead, grooming of both males and females seems to be exchanged for mating access on the long run and emotional bookkeeping seems the best proximate explanation of these long-term exchange patterns. Consequently, we can conclude that in our group of rhesus macaques, instead of truly exchanging grooming for mating access, males and females create a 'good' relationship by grooming each other. Having such a 'friendship' allows them to mate.

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Long-term social bonds mediate
exchange and interchange of
grooming and support in
Macaca fascicularis and *M. mulatta*

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"Thus nature has no love for solitude, and always leans,
as it were, on some support; and the sweetest support
is found in the most intimate friendship."

Cicero (106-43 BC)

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ABSTRACT

Reciprocal ex- and interchange patterns of social behaviour have been described in a variety of species. However, the proximate mechanism and temporal characteristics of these reciprocal patterns are poorly understood. In this study the proximate mechanism and temporal characteristics of the ex- and interchange patterns of grooming and support in two macaque species, *Macaca fascicularis* and *Macaca mulatta*, were examined. Macaques of both species exchange grooming for grooming and support for support and interchange grooming for support and vice versa. Symmetrical features of a dyad could not explain these patterns. Furthermore, the timeframe of reciprocity in these exchange patterns exceeded the period of a day, and close social bonds substantially influenced ex- and interchange patterns. Moreover, monkeys with close social bonds supported each other at significantly higher frequencies than those with less close bonds. Thus, rather than claiming that macaques groom in order to obtain support, we conclude that support in a conflict is mediated by the social bonds of these macaques. Therefore, our data support the hypothesis that the long-term social bond is the main mediator of ex- and interchange of grooming and support.

Ex- and Interchange of Grooming and Support

INTRODUCTION

Non-kin altruism has been difficult to explain in light of the theory of evolution. The main explanation for altruistic behaviours towards unrelated individuals is reciprocal altruism (Trivers 1971). Reciprocity arises when the performer of an altruistic act receives an altruistic act in return. Within reciprocal relations, services, goods or commodities can be traded for themselves, which is referred to as exchange (i.e., grooming for grooming), or traded for other services, goods or commodities, which is dubbed interchange (i.e., grooming for support)(Hemelrijk & Ek 1991). Although there are ample examples of reciprocity (Dugatkin 1997), these are mostly based on correlational data. Consequently, the proximate mechanism (i.e., the underlying motivation) of these exchanges and interchanges remains unknown.

Many species are cognitively constrained to keep track of large numbers of interactions (Stevens & Hauser 2004). Therefore, highly cognitive decision rules that depend on active scorekeeping of the value and amount of what has been given and received (i.e., *calculated reciprocity*, de Waal & Luttrell 1988), are unlikely to explain the observed reciprocal relations, maybe even in humans. In his seminal paper on reciprocal altruism, Trivers (1971) already suggested that reciprocal exchange patterns are probably mediated by emotions (e.g., *emotionally mediated reciprocity*, Schino et al. 2007; *attitudinal reciprocity*, de Waal 2000; Brosnan & de Waal 2002). Emotionally mediated reciprocity proposes that the probability of an individual to cooperate depends on the strength of the partner-specific emotional bond built up during a *long* series of interactions (Schino et al. 2007). In contrast, attitudinal reciprocity is described as a decision rule in which an individual's probability to give depends on the attitude towards a partner due to the *recently* shown behaviour towards him (de Waal 2000). These two emotional decision rules differ in their time frame: either short-term attitudes or long-term emotional bonds determine reciprocity. Therefore, Schino and coworkers (2007) argued that in trying to investigate the underlying proximate mechanism of reciprocity it is very important to take the temporal characteristics of ex- and interchange patterns into account.

Alternatively, reciprocal ex- and interchange patterns may be explained by a system where individuals solely interact based on symmetrical features of their relation, such as age, rank or kinship (i.e., *symmetry-based reciprocity*, de Waal & Luttrell 1988). Since these features are symmetrical, both parties act similarly to each other, leading to reciprocal interactions, and no cognitive or emotional scorekeeping is required to generate reciprocity (de Waal & Luttrell 1988).

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In this study we examined which of the three proposed mechanisms; symmetrical features, short-term attitude or long-term emotional bonds, best explains our data on the exchange of grooming for grooming and support for support, and the interchange of grooming for support and support for grooming in two macaque species: long-tailed macaques, *Macaca fascicularis*, and rhesus macaques, *M. mulatta* (Hereafter sometimes referred to as ltm and rhm). Macaques of both species do groom each other regularly (ltm: $\pm 8.3\%$ of total daytime, van Noordwijk & van Schaik 1985; rhm: $\pm 15\%$ of total daytime, Teas et al. 1980) and support each other in agonistic conflicts (ltm: $\pm 25\%$ of all conflicts, de Waal et al. 1976; rhm: $\pm 30\%$ of all conflicts, Lindburg 1971). To date there is some support for the exchange of grooming for grooming in both species (Schino & Aureli 2008), and for the exchange of grooming for support (ltm: Hemelrijk 1994; rhm: de Waal & Luttrell 1986; Kapsalis & Bernstein 1996b), albeit mostly correlational and these studies do not take the temporal characteristics of these ex- and interchanges into account (apart from Hemelrijk 1994). In this study we investigate the temporal characteristics of these ex- and interchanges, and thereby aim to understand the proximate mechanism underlying them.

Firstly, in species with a clear dominance hierarchy that is maintained by coalitions, such as long-tailed and rhesus macaques (Thierry 2000), grooming is expected to be directed up the hierarchy (Seyfarth 1977). Presumably this attraction to high-ranking individuals is due to their value as potential allies in a conflict. This suggests that, in addition to grooming being directed up the hierarchy, support is expected to be directed down the hierarchy.

Secondly, to investigate ex- and interchange patterns of grooming and support, we first established in our groups whether there was overall exchange of grooming for grooming, exchange of support for support, and interchange of grooming for support and vice versa. To investigate the underlying proximate mechanism of reciprocity we used a bottom up approach, in which we try to explain the found ex- and interchanges by the different proposed mechanisms, starting with the least complex mechanism. To determine whether these ex- and interchanges rely on symmetrical features, or symmetry-based reciprocity, we investigated the role of the symmetrical features rank difference and age difference in these ex- and interchanges.

When symmetrical features of a dyad did not or only partly explained the found long-term reciprocity, we tried to distinguish between the two remaining hypotheses to explain the reciprocation on a proximate level. Therefore, we

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investigated the temporal characteristics of ex- and interchange. Attitudinal reciprocity is described as contingent on the immediately preceding behaviour of the partner (Brosnan & de Waal 2002), and thus short-term reciprocity is expected. In contrast, in emotionally mediated reciprocity short-term reciprocity is not required, but long-term reciprocity is predicted (Schino et al. 2007). To distinguish the two mechanisms, we tested for short- and long-term contingency of ex- and interchanges. Furthermore, within emotionally mediated reciprocity, features of a long-term social bond, such as degree of contact sitting and reciprocated grooming (i.e., grooming received from the other individual in each dyad)(Hinde & Atkinson 1970), are expected to explain the probability of giving a service. The influence of these two bond-indicating factors was assessed by controlling for both in the correlational data.

Finally, in addition to the correlational data, we also compared the amount of support given between animals with close social bonds ('friends') and distant social bonds ('non-friends'). Since 'friendships' in our study were defined by the amount of mutual grooming, a similar comparison for grooming given was superfluous.

METHODS

Subjects and Housing

This study was conducted on a captive social group of long-tailed macaques (Roza group) and on a captive social group of rhesus macaques (Wodka group). The long-tailed macaques were housed at the 'Ethologie station' of the Utrecht University, the Netherlands, in an indoor enclosure (235 m³) with access to an outdoor compound (800 m³). The rhesus macaques were housed at the Biomedical Primate Research Centre (BPRC) in Rijswijk, the Netherlands. They had an indoor enclosure (205 m³) that was connected to an outdoor enclosure (605 m³). For the sake of visibility during the observations, the long-tailed macaques were locked in the indoor compartment of their enclosure, whereas the rhesus macaques were locked in the outdoor compartment of their enclosure. The enclosures of both the long-tailed and rhesus macaques had plenty of climbing facilities and the monkeys were regularly provisioned with enrichment. The monkeys were fed a diet of commercially available monkey chow supplemented with alternately fruit, vegetables or bread. Water was available ad libitum.

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At the start of the observation period the group of long-tailed macaques consisted of 33 individuals, with males and females from all life stages. The group of rhesus macaques consisted of 35 individuals, with males and females from all life stages. During the study one long-tailed macaque and five rhesus macaques were born. All newborns and two long-tailed and seven rhesus macaque infants (< 1 yr.) were excluded from data analyses, resulting in a sample size of 31 long-tailed macaques and 28 rhesus macaques. All maternal genealogies were known, since all animals were born in captivity, and these were entered as a coefficient of maternal relatedness (r) into analyses. Subjects were defined as kin if matrilineal relatedness coefficient equalled or exceeded 0.125 (Chapais 2001; Silk 2002a).

Data Collection

Data on the long-tailed macaques were collected between January and June 2008 by I.J.A.F.L. and a total of 214.5 hr of observation were completed. Data on the rhesus macaques were collected between April and July 2009 by C.B. and a total of 178 hr of observation were completed. The used data collection techniques were similar in both species.

Sampling consisted of observations during multiple periods of 30 minutes on one day. During these 30-minute intervals, grooming interactions were recorded using the 1-minute scan sampling method (Altmann 1974). The unprovoked submissive behaviours 'bare teeth' and 'make room' were recorded ad libitum to calculate a dominance hierarchy. All occurrences of conflict and support were recorded according to the sequence sampling method during the 30-minute intervals (Altmann 1974; Koyama et al. 2006). A conflict was defined as a dyadic interaction that started when an individual, the aggressor, displayed aggressive behaviour towards another individual, i.e., the victim. Aggression was present when an individual displayed threats, chases, physical contact and/or bites (for the ethogram see Altman 1962; Angst 1974). Within a conflict we identified the aggressor, the victim and the supporter. Only support involving overt aggression (threats, chases, or physical assaults) was considered. Two supporters could start their support at the same time and for the same individual. This was recorded as two separate supports. When the supporters entered the same conflict sequentially on the same side, it was not clear if the support of the second supporter was on behalf of the individual that was in the original conflict, or on behalf of the first supporter. In such cases, only the first support was recorded. In the group of long-tailed macaques a total of 2713 conflicts (12.6 per hour), including 455 supports (93.4% of the supports was directed against an individual lower in rank than the

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supporter), were observed. In the group of rhesus macaques a total of 548 conflicts (3.1 per hour), including 182 supports (89.6% of the supports was directed against an individual lower in rank than the supporter), were observed. The rates of grooming observed were 58.2 and 43.1 grooming bouts per hour for the groups of long-tailed macaques and rhesus macaques respectively.

To investigate the role of social bonds, we used data on grooming from the one-minute scan samples and on contact sitting from time-sample scan observations (see below) of all dyads in the correlational analyses. Secondly, we used a measure of 'friendship'. To measure friendship, we conducted time-sample scan observations (2-4 times a day) of all [independent] group members during the studies, to assess who was sitting with whom within contact reach (but without grooming) and who was grooming whom. For each individual, potential 'friends' were individuals in the upper quartile of contact sitting and grooming, while potential 'non-friends' were in the lower quartile of contact sitting and grooming. Only individuals that scored highest or lowest in both measures were considered 'friends' or 'non-friends' respectively. Since measures of friendship in a dyad can be asymmetric, only dyads in which both individuals were categorized as 'friend' or 'non-friend' for the other were considered to be '(non-) friends'. All other dyads were considered neutral dyads. With these conditions of '(non-) friends' we found 25 pairs of 'friends' and 48 pairs of 'non-friends' out of in total 391 non-kin dyads in the group of long-tailed macaques, and 16 pairs of 'friends' and 41 pairs of 'non-friends' out of in total 308 non-kin dyads in the group of rhesus macaques. There were, furthermore, 73 kin dyads in the group of long-tailed macaques and 70 kin dyads in the group of rhesus macaques.

Data Analysis

Dominance Hierarchy

To determine a dominance hierarchy, the unprovoked submissive behaviours were arranged in a socio-matrix with actors in rows and recipients in columns. The dominance order most consistent with a linear hierarchy was determined with MatMan 1.1 (de Vries 1995; 1998). The results for the group of long-tailed macaques show a linearity index h' of 0.59 ($p < 0.001$) and for the group of rhesus macaques the results show a linearity index h' of 0.41 ($p < 0.001$), which indicate that a significant degree of linearity is present in both matrices of dominance relationships. Rank numbers were afterwards assigned with 1 for the most dominant individual and 31 (ltm)/ 28 (rhM) for the most subordinate individual.

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Long-Term Ex- and Interchange Patterns

To examine long-term ex- and interchange patterns, we carried out correlational analyses. Data on grooming and support were arranged in socio-matrices with actors in rows and recipients in columns and correlations were calculated in MatMan 1.1 with rowwise matrix correlations (de Vries et al. 1993), using rowwise Kendall's tau (Hemelrijk 1990a; de Vries 1993) as correlation coefficient. p values were calculated on the basis of 10,000 permutations. Partial rowwise correlations (Hemelrijk 1990b; de Vries 1993) were used to assess the effect of the symmetrical variables age difference and rank distance, and of the bonding variables contact sitting and reciprocated grooming (i.e., grooming received from the other individual in each dyad) on those exchange patterns. Moreover, relatedness was partialled out to test for the effect of kin selection (Hamilton 1964). The effect of these variables is reflected in the change of the tau correlation statistic relative to the tau of the original, non-partial correlation (Vervaecke et al. 2000).

Recently, linear mixed models have been used instead of matrix correlation methods to analyse reciprocity of grooming (Gomes et al. 2009). An advantage of these models is that more than one variable at a time can be controlled for. Yet, we opted for rowwise matrix correlation methods using Kendall's tau for several reasons. A detailed explication of why we prefer to use rowwise matrix correlations instead of linear mixed models is given in appendix 1 of this chapter.

Short-Term Ex- and Interchange Patterns

In this study we defined short-term as within one day (cf. Gomes et al. 2009). To examine short-term exchange patterns in grooming, we first calculated the daily grooming balance and the grooming balance over the whole study period. The daily grooming balance was calculated as the mean absolute difference in grooming bouts given and received in each dyad per day per individual. The grooming balance over the whole study period was calculated as the mean absolute difference in grooming bouts given and received in each dyad over the whole study period per individual. Grooming is then perfectly balanced if it is zero. To examine whether the reciprocation of grooming occurred within one day, we compared the daily grooming balance with the grooming balance over the whole study period divided by the number of days. If reciprocation of grooming occurred mainly within one day, the daily balance will be equal or smaller than the grooming balance over the whole study period. If reciprocation of grooming is mainly in the long run, it is expected that the daily grooming balance is larger than the grooming balance over the whole study period. Since it seems implausible that monkeys can time match the

Ex- and Interchange of Grooming and Support

amount of grooming given and received, we did not analyse the differences in grooming-time given and received.

To examine short-term interchange patterns, we compared the relative amount of grooming given on a day to an individual before conflicts in which that individual supported the subject, with the relative amount of grooming given on a day to the same individual before conflicts in which that individual did not support the subject (see also Hemelrijk 1994; Koyama et al. 2006). The same was done with the relative amount of grooming after supported and non-supported conflicts.

To assess the role of social bonds, we compared the frequencies of support of individuals towards their 'friends' with those towards their 'non-friends'.

In all comparisons of pairwise data we used Wilcoxon signed rank tests, because the data deviated from normality. All statistic tests were two-tailed at the $\alpha = 0.05$ level.

Apart from the analyses on the time window for the exchange of grooming, all other analyses on grooming were conducted for both the number of grooming bouts and grooming-time (minutes). Patterns in both analyses were almost always similar. For the sake of brevity, here we only report the results of the analyses on grooming bouts. Results of grooming-time are only reported when they deviate from the results on number of grooming bouts. The results of the other analyses on grooming-time can be found in appendix 2 of this chapter.

RESULTS

Direction of Grooming and Support Within the Dominance Hierarchy

To investigate whether macaques groom in accordance with the rank of the receiver, we correlated the amount of grooming bouts given with rank and found a significant negative correlation for the long-tailed macaques (Kendall's $\tau_{rw} = -0.14$, $p < 0.001$), but not for the rhesus macaques (Kendall's $\tau_{rw} = -0.09$, $p = 0.108$). Although the correlations are weak, they do suggest that long-tailed macaques groom up the hierarchy (note that the correlation is negative since high-ranking individuals have low rank numbers). However, rhesus macaques seem to groom indifferently both up and down the hierarchy.

It has been suggested that dominant individuals will support lower-ranking individuals. To investigate this, we correlated support given with rank and found a significant negative correlation for the long-tailed macaques (Kendall's $\tau_{rw} = -0.17$, $p < 0.001$), but no significant correlation for the rhesus macaques (Kendall's $\tau_{rw} = 0.041$, $p = 0.353$). For the long-tailed macaques these results suggests that support is

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actually directed up the hierarchy and not, contra to expectation, down the hierarchy. In rhesus macaques support given does not depend on dominance rank.

Long-Term Ex- and Interchange Patterns

To examine long-term exchange patterns of grooming, we correlated grooming given with grooming received, using matrix correlations. We found a significant positive correlation for both the long-tailed and the rhesus macaques (Kendall's $\tau_{rw} = 0.42$ and 0.54 ; table 1), suggesting there is long-term exchange of this commodity. To examine long-term exchange patterns of support, we correlated support given with support received, using matrix correlations. We found a significant positive correlation for both the long-tailed and the rhesus macaques (Kendall's $\tau_{rw} = 0.35$ and 0.15 ; table 1), albeit rather low. Nonetheless, these results suggest a long-term exchange of this commodity.

To rule out kin selection as an explanation for the found exchange patterns, we controlled these correlations for relatedness. Using partial rowwise matrix correlations we found that relatedness only slightly reduces the Kendall's tau of the grooming for grooming (table 1) in both species. The Kendall's tau correlation of support for support is reduced more and in the rhesus macaques this correlation even becomes non-significant. The other three correlations remained significant, even after controlling for relatedness. This indicates that relatedness does not affect the exchange of grooming, but does affect the exchange of support. While in rhesus macaques it is the main determinant of this exchange of support, in long-tailed macaques support may be affected by additional factors.

To examine long-term interchange patterns of grooming and support, we correlated grooming given with support received, and support given with grooming received, using matrix correlations. We found a significant positive correlation between grooming given and support received in both long-tailed and rhesus macaques (Kendall's $\tau_{rw} = 0.19$ and 0.27 ; table 2), and also a significant positive correlation between support given and grooming received in both long-tailed and rhesus macaques (Kendall's $\tau_{rw} = 0.22$ and 0.27 ; table 2), suggesting there is long-term interchange of grooming for support and vice versa. Again, we controlled for relatedness and found that controlling for relatedness decreased the original correlation somewhat, but all four correlations remained significant (table 2).

Ex- and Interchange of Grooming and Support

Symmetry-Based Reciprocity

To investigate if the found reciprocity was based on symmetrical features of a relationship, we corrected the original correlations for the symmetrical features age difference and rank difference using partial rowwise matrix correlations. These two features did not reduce Kendall's tau much. Therefore, we found no clear effect of the independent variables age difference and rank difference on the original ex- and interchange correlations (table 1 & 2).

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Table 1. Long-term exchanges: Grooming-grooming, support-support.

Correlations of grooming bouts given and received and of support given and received for all long-tailed macaques and rhesus macaques, and the effect of partialling out various variables from these correlations. Bold numbers represent substantial deviations from the original correlations.

<i>Grooming-grooming</i>					
Long-tailed macaques (n = 31)			Rhesus macaques (n = 28)		
	Kendall's τ_{rw}	<i>p</i>		Kendall's τ_{rw}	<i>p</i>
Original correlation	0.42	<0.001	Original correlation	0.54	<0.001
Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>	Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>
Age difference	0.42	<0.001	Age difference	0.54	<0.001
Rank difference	0.41	<0.001	Rank difference	0.54	<0.001
Relatedness	0.38	<0.001	Relatedness	0.48	<0.001
Contact sitting	0.18	<0.001	Contact sitting	0.38	<0.001
<i>Support-support</i>					
	Kendall's τ_{rw}	<i>p</i>		Kendall's τ_{rw}	<i>p</i>
Original correlation	0.35	<0.001	Original correlation	0.15	<0.01
Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>	Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>
Age difference	0.33	<0.001	Age difference	0.13	<0.01
Rank difference	0.29	<0.001	Rank difference	0.13	<0.01
Relatedness	0.25	<0.001	Relatedness	0.06	0.117
Contact sitting	0.28	<0.001	Contact sitting	0.08	0.04

Table 2. Long-term interchanges: Grooming-support, support-grooming.

Correlations of grooming bouts given and support received and of support given and grooming bouts received for all long-tailed macaques and rhesus macaques, and the effect of partialling out various variables from these correlations. Bold numbers represent substantial deviations from the original correlations.

<i>Grooming-support</i>					
Long-tailed macaques (n = 31)			Rhesus macaques (n = 28)		
	Kendall's τ_{rw}	<i>p</i>		Kendall's τ_{rw}	<i>p</i>
Original correlation	0.19	<0.001	Original correlation	0.27	<0.001
Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>	Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>
Age difference	0.19	<0.001	Age difference	0.26	<0.001
Rank difference	0.17	<0.001	Rank difference	0.26	<0.001
Relatedness	0.13	<0.001	Relatedness	0.19	<0.001
Contact sitting	0.05	0.123	Contact sitting	0.18	<0.001
Grooming received	0.08	0.026	Grooming received	0.16	<0.001
<i>Support-grooming</i>					
	Kendall's τ_{rw}	<i>p</i>		Kendall's τ_{rw}	<i>p</i>
Original correlation	0.22	<0.001	Original correlation	0.27	<0.001
Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>	Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>
Age difference	0.20	<0.001	Age difference	0.25	<0.001
Rank difference	0.18	<0.001	Rank difference	0.24	<0.001
Relatedness	0.13	<0.001	Relatedness	0.17	<0.001
Contact sitting	0.07	0.044	Contact sitting	0.15	<0.001
Grooming given	0.11	<0.01	Grooming given	0.14	<0.001

Ex- and Interchange of Grooming and Support

Short-Term Exchange and Interchange Patterns

We investigated whether the described ex- and interchanges took place on the short term (i.e., short-term reciprocity within a day).

Exchange of Grooming

For the exchange of grooming we compared the daily grooming balance with the grooming balance over the whole study period. We found that the balance of grooming given and received over the whole period was significantly better, i.e., more balanced, than the average daily balance: the average absolute difference in number of grooming bouts given and received per day was significantly larger than the average absolute difference in number of grooming bouts given and received over the whole period (Wilcoxon signed ranks tests: ltm: $T^+ = 496$, $n = 31$, $p < 0.001$; rhm: $T^+ = 406$, $n = 28$, $p < 0.001$)(figure 1a). Since opportunities to support an individual do not occur sufficiently often each day, we did not conduct a similar analysis for the exchange of support. Nevertheless, from the grooming data we can conclude that grooming is not reciprocated on the short-term (i.e., one day), but the amount of grooming given does, however, seem more balanced in the long run.

Interchange of Grooming for Support

We investigated whether grooming and support are interchanged within one day. Therefore, we calculated per single day the relative number of grooming bouts towards an individual before and after that individual supported the grooming individual, and compared that to the relative number of grooming bouts towards the same individual before and after a conflict in which that individual did not support the grooming individual. We found no significant difference in the relative number of grooming bouts before a conflict with support compared to a conflict without support (Wilcoxon signed ranks tests: ltm: $T^+ = 192$, $n = 25$, $p = 0.241$; rhm: $T^+ = 39$, $n = 16$, $p = 0.685$)(figure 2a), suggesting that the amount of grooming received does not predict whether an individual supports the grooming individual later on the same day. In addition, we did not find a significant difference in the relative number of grooming bouts after a conflict with support compared to a conflict without support (Wilcoxon signed ranks tests: ltm: $T^+ = 182$, $n = 25$, $p = 0.375$; rhm: $T^+ = 58$, $n = 16$, $p = 0.761$)(figure 3a), suggesting that giving support also does not predict the amount of grooming received later on the same day.

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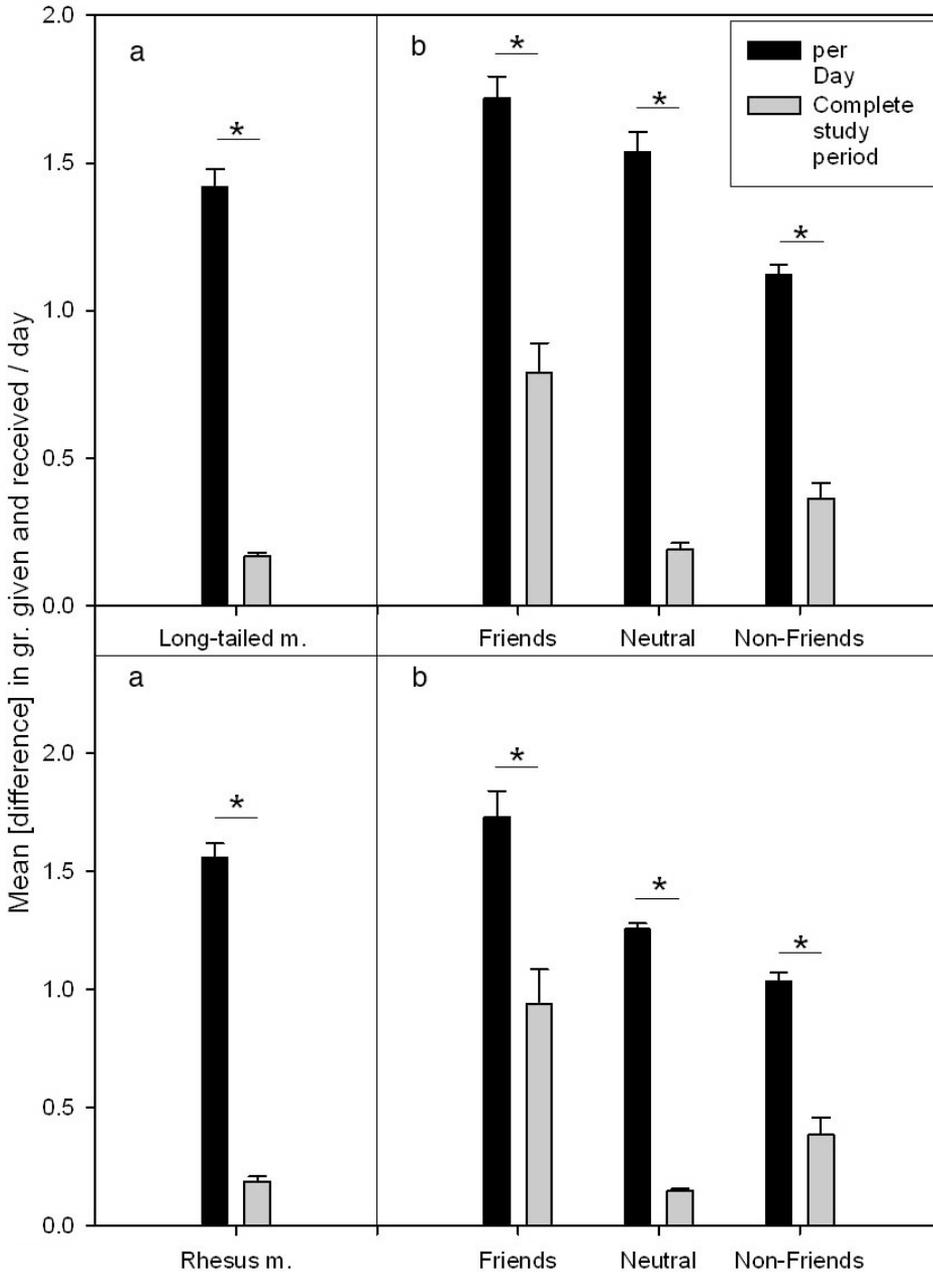


Figure 1. The mean absolute difference + SEM in number of grooming bouts given and received per day (black bars) and over the whole study period (grey bars) in long-tailed (top) and rhesus macaques (bottom): **a:** for all animals (ltm: n = 31; rhm: n = 28), **b:** for friends (ltm: n = 24; rhm: n = 20), neutral dyads (ltm: n = 31; rhm: n = 28) and non-friends (ltm: n = 23; rhm: n = 20) separately. * p < 0.05.

Ex- and Interchange of Grooming and Support

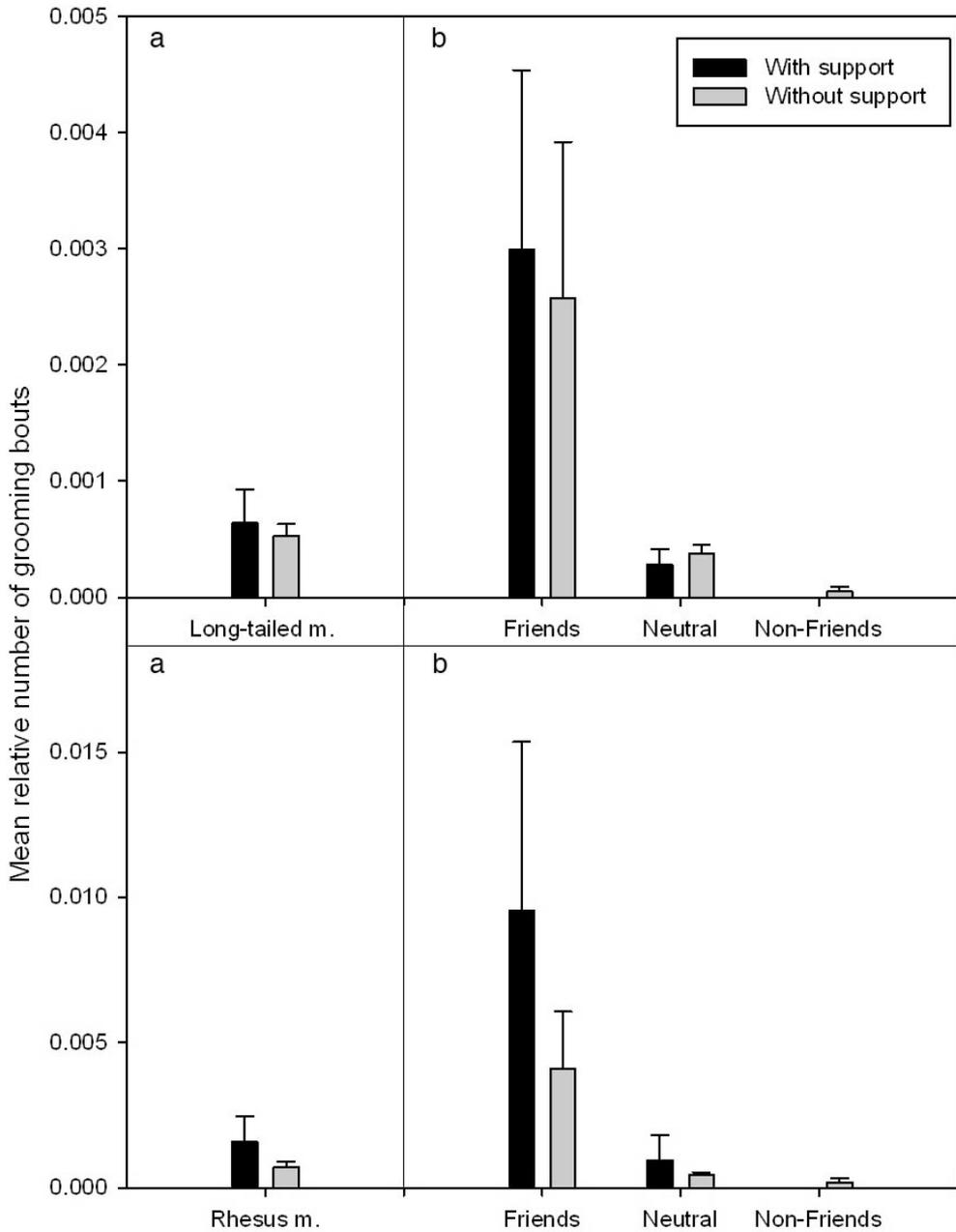


Figure 2. The mean relative number of grooming bouts + SEM on the same day *before* a conflict to an individual that supported in that conflict (black bars) and towards the same individual before a conflict in which that individual did not support the grooming individual (grey bars), for long-tailed (top) and rhesus macaques (bottom): **a**: for all animals (ltm: n = 25; rhm: n = 16), **b**: for friends (ltm: n = 13; rhm: n = 6), neutral dyads (ltm: n = 24; rhm: n = 13) and non-friends (ltm: n = 5; rhm: n = 4) separately.

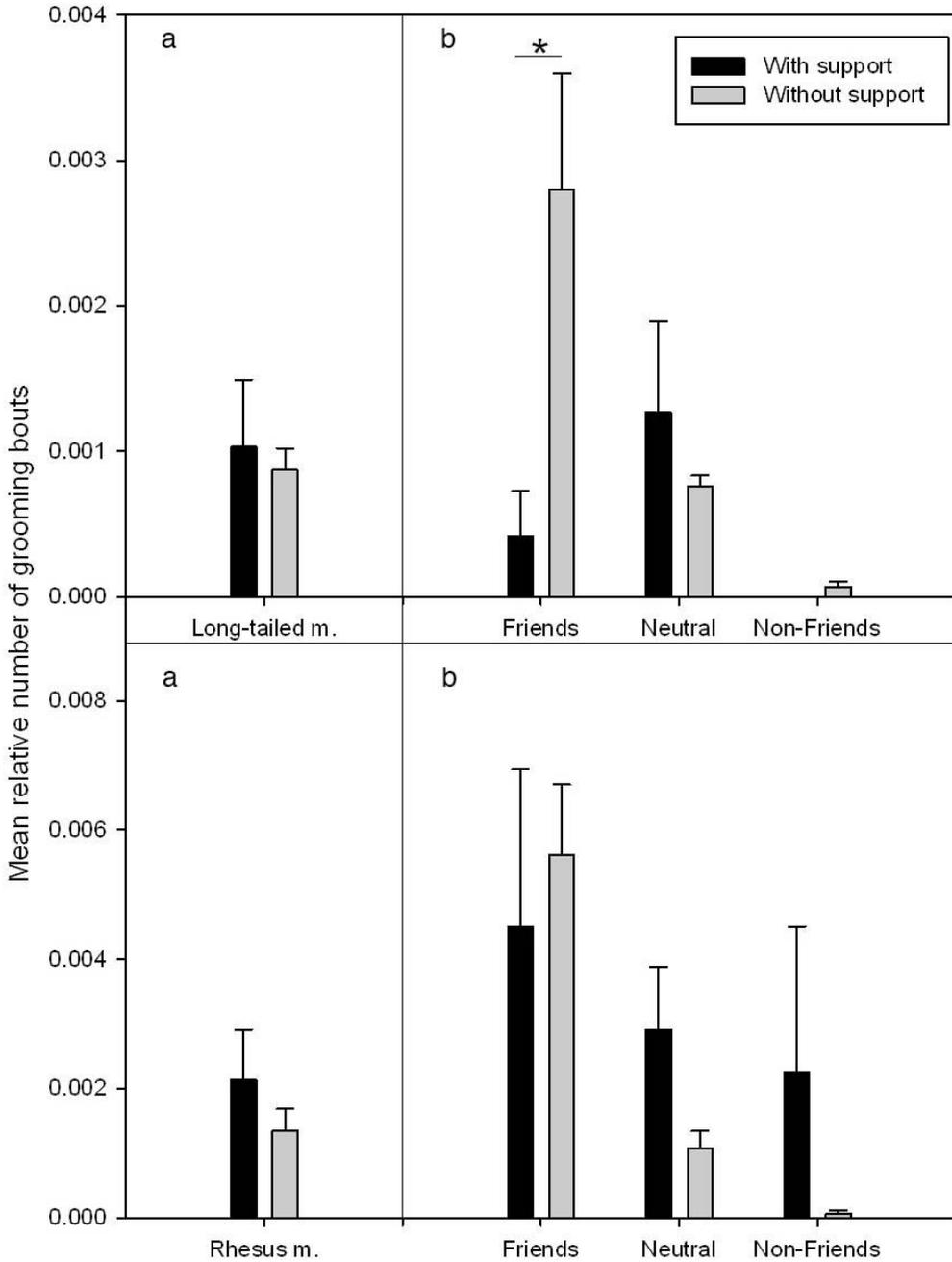


Figure 3. The mean relative number of grooming bouts + SEM on the same day *after* a conflict to an individual that supported in that conflict (black bars) and towards the same individual before a conflict in which that individual did not support the grooming individual (grey bars), for long-tailed (top) and rhesus macaques (bottom): **a**: for all animals (ltm: n = 25; rhm: n = 16), **b**: for friends (ltm: n = 13; rhm: n = 6), neutral dyads (ltm: n = 24; rhm: n = 13) and non-friends (ltm: n = 5; rhm: n = 4) separately. * p < 0.05.

Ex- and Interchange of Grooming and Support

Social Bonds

Strong social bonds are characterized by frequent contact sitting and affiliative interactions. Therefore, we first analysed what effects such independent variables have on the ex- and interchange patterns of grooming and support.

To assess the role of social bonds in the long-term exchange patterns of grooming and support, we first analysed whether contact sitting had an effect on the correlations between grooming and grooming and between support and support. We found that controlling for contact sitting reduces the Kendall's tau of the original correlation between grooming and grooming substantially, while the correlation between support and support is also, but less, reduced (table 1), suggesting an important role for the social bond in these exchanges, especially the grooming exchange.

To assess the role of social bonds in the long-term interchange patterns of grooming and support, we analysed whether contact sitting and reciprocated grooming (i.e., grooming received from the other individual in each dyad) had an effect on the correlations between grooming and support and vice versa. Both contact sitting and reciprocated grooming reduced Kendall's tau substantially (see table 2). Moreover, the correlation between grooming and support of the long-tailed macaques became insignificant when contact sitting was partialled out. In conclusion, these data suggest that social bonds do play an important role in the interchange both of grooming for support and support for grooming as well.

Secondly, we investigated whether 'friends' support each other more than 'non-friends'. We found a significant difference in the mean number of support from and to 'friends' compared to support from and to 'non-friends' for the long-tailed macaques. A difference in the same direction, but not significant, was found for the rhesus macaques (Wilcoxon signed ranks tests: ltm: $T^+ = 98$, $n = 21$, $p = 0.002$; rhm: $T^+ = 23.5$, $n = 17$, $p = 0.125$)(figure 4). 'Friends' seem to support each other more often than 'non-friends'.

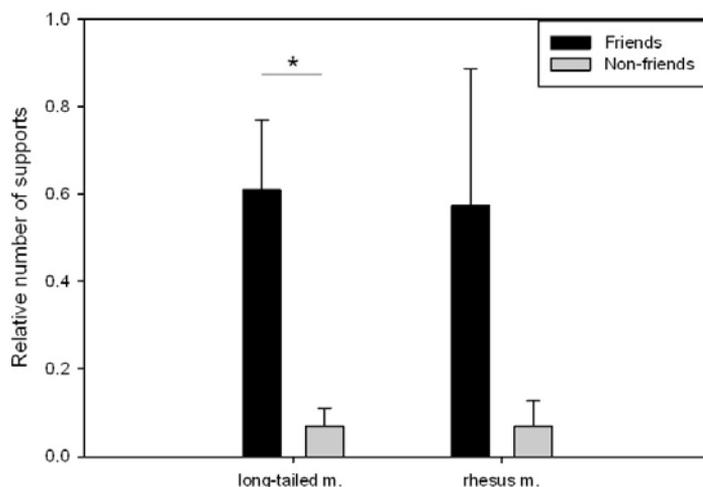


Figure 4. Mean relative number of support + SEM for ‘friends’ (black bars) and ‘non-friends’ (grey bars) in long-tailed ($n = 21$) and rhesus macaques ($n = 17$). * $p < 0.05$

Different Decision Rules for ‘Friends’ and ‘Non-Friends’

‘Friends’ may use different decision rules in their ex- and interchange relations than ‘non-friends’: i.e., ‘friends’ might be less focused on the balance between services given and received compared to ‘non-friends’. To test whether the lack of contingency within one day of the grooming exchange and the grooming for support interchange might be due to all friendly dyads, we split our data into ‘friend’ dyads, neutral dyads and ‘non-friend’ dyads. To investigate differences between the three dyad types in their difference in balance between the different time windows (i.e., one day or the whole study period), we first calculated the difference between the balances of the two time windows per type of dyad. Using Kruskal-Wallis tests, we found a significant difference between the types of dyad (ltm: $\text{Chi}^2 = 32.924$, 2 df, $p < 0.001$; rhm: $\text{Chi}^2 = 26.442$, 2 df, $p < 0.001$). However, in all types of dyads the balance of grooming given and received over the whole period was significantly better (i.e., more balanced) than the average daily balance: ‘friend’ dyads (Wilcoxon signed ranks tests: ltm: $T^+ = 300$, $n = 24$, $p < 0.001$; rhm: $T^+ = 171$, $n = 20$, $p < 0.001$), neutral dyads (Wilcoxon signed ranks tests: ltm: $T^+ = 496$, $n = 31$, $p < 0.001$; rhm: $T^+ = 406$, $n = 28$, $p < 0.001$), ‘non-friend’ dyads (Wilcoxon signed ranks tests: ltm: $T^+ = 231$, $n = 23$, $p < 0.001$; rhm: $T^+ = 136$, $n = 20$, $p < 0.001$)(figure 1b), suggesting no difference in decision rules for the different dyad types.

Ex- and Interchange of Grooming and Support

To investigate differences between the dyad types in their contingency of reciprocation in the grooming for support interchange, we first calculated the difference in amount of grooming before or after a conflict between a conflict with and without support per dyad identity. Using Kruskal-Wallis tests, we found no significant difference in the contingency of the different types of dyad concerning grooming *before* the conflict (with or without support)(# grooming bouts before conflict: ltm: $\text{Chi}^2 = 3.753$, 2 df, $p = 0.153$; rhm: $\text{Chi}^2 = 0.107$, 2 df, $p = 0.948$)(figure 2b). However, we did find a significant difference between the dyad types in their contingency concerning grooming *after* a conflict (with or without support) for the long-tailed macaques (# grooming bouts after conflict: $\text{Chi}^2 = 12.083$, 2 df, $p < 0.01$), but not for the rhesus macaques (# grooming bouts after conflict: $\text{Chi}^2 = 1.337$, 2 df, $p = 0.513$). The long-tailed macaques groomed their 'friends' significantly more often after a conflict in which their 'friends' did not support them compared to when they did support them (Wilcoxon signed ranks test: 'friends': $T^+ = 86$, $n = 13$, $p < 0.01$)(figure 3b). For neutral dyads and 'non-friends' no such difference was found ('neutral' dyads: $T^+ = 155$, $n = 24$, $p = 0.900$; 'non-friends': $T^+ = 6$, $n = 5$, $p = 0.250$). Although interesting in itself, these results point in the opposite direction from the predictions and do not provide us with any proof of differential decision rules for 'friends' and 'non friends' in these long-tailed macaques. Moreover, we also found a significant difference between the dyad types in their contingency concerning grooming-time *after* a conflict (with or without support) for the long-tailed macaques (grooming-time after conflict: $\text{Chi}^2 = 9.578$, 2 df, $p < 0.01$). However, for non of the dyad types there was a significant difference in the time of grooming after a conflict in which the groomed individual did support and did not support (Wilcoxon signed ranks tests: 'friends': $T^+ = 68$, $n = 13$, $p = 0.127$; neutral dyads: $T^+ = 163$, $n = 24$, $p = 0.726$; 'non-friends': $T^+ = 6$, $n = 5$, $p = 0.256$), which contrasts to the grooming bout data. Altogether, the data do not support the hypothesis of different decision rules for 'friends', neutral individuals and 'non-friends' in either macaque species.

DISCUSSION

In this study we examined which of three proposed mechanisms, symmetrical features, short-term attitude or long-term emotional bonds, best explains our data on the exchange of grooming for grooming and support for support, and the interchange of grooming for support and support for grooming in two macaque species.

Chapter 3

Direction of Grooming and Support Within the Dominance Hierarchy

The influential model of grooming distribution among female monkeys (Seyfarth 1977) predicts that monkeys are attracted to high-ranking individuals and that therefore grooming is directed up the hierarchy. We indeed found that long-tailed macaques groom preferentially those animals higher in rank. Similarly, a meta-analysis on 27 different social primate groups belonging to 14 different species of 8 genera showed a significant role for attraction to high rank in the distribution of grooming of these groups (Schino 2001). However, we could not confirm these results with the data on the rhesus macaques. Furthermore, an assumption of Seyfarth's model is that grooming is directed up the hierarchy because monkeys are attracted to higher-ranking individuals due to their potential value as an ally in a conflict (Seyfarth 1977). Therefore, support in a conflict is expected to be mostly directed down the hierarchy. However, we found that not only grooming, but also support is directed up the hierarchy in the long-tailed macaques. Moreover, the supports observed in both groups were almost always (ltm: 93.4%; rhm: 89.6%) directed against an individual lower in rank than the supporting individual. Therefore, we can conclude that the majority of supports observed within the groups in our study concern status quo maintaining, non-rank changing and all-down coalitions (van Schaik et al. 2004); i.e., both supporting and supported individual outrank the opponent. These data confirm earlier findings that report for rhesus macaques that the amount of all down coalitions covers about 73% of all coalitions within this species (Kaplan 1978; Bernstein & Ehardt 1985). Consequently, it seems that the macaques in our study groups employ an opportunistic strategy by supporting a higher-ranking individual against a lower-ranking individual, thereby strengthening their own dominance position. The above described relations between grooming and rank and support and rank were, however, weak and there might be more factors explaining both the distribution of grooming and of support in these macaque species.

Long-Term Ex- and Interchange Patterns

When altruistic acts are returned from the recipient to the actor this is called reciprocal altruism (Trivers 1971). Altruistic acts can be exchanged for similar acts or interchanged for other acts, commodities or services (Hemelrijk & Ek 1991). Our data pooled over the whole study period showed that long-tailed and rhesus macaques indeed groom preferentially those individuals that groom them most. Similarly, our data pooled over the whole study period also showed that both macaque species preferentially support those individuals that support them most.

Ex- and Interchange of Grooming and Support

Although grooming and support are not only directed towards kin, kin selection (Hamilton 1964) may be an important factor in their occurrence. Relatedness had some influence on the correlations between grooming given and received and support given and received. However, after controlling for relatedness, almost all these correlations remained significant, suggesting that kin selection cannot explain them completely.

Our results fit nicely with results from a recent meta-analysis in which a similar exchange of grooming was found, using similar methods, for primates of 48 social groups belonging to 22 different primate species of 12 genera (Schino & Aureli 2008). Reciprocation of support in kind was also found in a different group of rhesus macaques, in chimpanzees, *Pan troglodytes*, in stump-tailed macaques, *Macaca arctoides* (all in de Waal & Luttrell 1988), in bonnet macaques, *Macaca radiata* (Silk 1992), in Japanese macaques, *Macaca fuscata* (Schino et al. 2007), and in a social carnivore, the ring-tailed coati, *Nasua nasua* (Romero & Aureli 2008). Altogether, these data suggest that reciprocation of grooming and support in kind is common in species showing these behaviours.

Nevertheless, reciprocation in kind may not be the only reciprocal pattern at play. Services and or commodities can also be traded for other services or commodities (Hemelrijk & Ek 1991). Therefore, we studied whether grooming is interchanged for support and vice versa. We found that individuals from both macaque species preferentially support those individuals that groom them most and preferentially groom those individuals that support them most. Again, kin selection (Hamilton 1964) explained only part of it, and these correlations remained significant after controlling for relatedness. Reciprocal relations between grooming and support were reported in 36 social groups of 14 different primate species (Schino 2007), and a similar relation between allopreening and support has been reported in ravens, *Corvus corax* (Fraser & Bugnyar in press). From these results we can conclude that also the reciprocation of grooming with support or vice versa may be widespread.

Both the results on the exchange of grooming for grooming or support for support, as well as the results on the interchange of grooming for support, do not provide information on the proximate mechanism underlying these reciprocal relations. These reciprocal patterns may be explained by symmetry-based reciprocity (Brosnan & de Waal 2002).

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Symmetry-Based Reciprocity

It has been argued that in many species in which reciprocity has been found, symmetry-based reciprocity is a likely explanation. As a clear example of symmetry-based reciprocity de Waal & Luttrell (1988) refer to the blood-sharing in vampire bats, *Desmodus rotundus* (Wilkinson 1984), in which the observed reciprocity results from the symmetrical features kinship and mutual association. Note that for vampire bats, roosting places are fixed and thus that their neighbours are always the same individuals. To investigate whether the found reciprocity in our macaque groups may be based on symmetry, we studied the effect of the symmetrical features rank difference and age difference on the original correlations. We found that both age difference and rank difference did not affect the original ex- and interchange correlations, suggesting that the found reciprocity is not symmetry-based. Our study confirms similar findings in rhesus macaques (Kapsalis & Berman 1996b). However, caution is needed, since there might be other influential symmetrical features that we have not taken into account. Others (de Waal & Luttrell 1986; 1988; Schino et al. 2007) have argued that time spent in association or proximity measures are symmetrical features as well. We recognize the fact that the absolute amount of time spent in association is similar for both members of a dyad. However, in contrast to mutual association in bats, contact sitting of primates is not a fixed feature, and primates can choose whom to sit next to, thereby expressing a certain preference. Moreover, the time spent in association with an individual relative to the time spent in association with other individuals can differ dramatically from that of the other member of the dyad. Therefore, we did not use this measure as a symmetrical feature of a relation. Instead, we used contact sitting as a measure of a social bond.

To summarize, symmetrical relations cannot, or at least not fully, explain all reciprocal behaviour in our and other studies (Brosnan & de Waal 2002). Therefore, short-term attitudinal (Brosnan & de Waal 2002) or long-term emotionally mediated reciprocity (Schino et al. 2007) may determine reciprocal patterns.

Short-Term vs. Long-Term Ex- and Interchange

To distinguish between the two alternative proximate explanations of the found reciprocal relations, i.e., short-term attitudinal variation vs. long-term emotional bonds, we focused on the time frame of reciprocation (Schino et al. 2007). We investigated whether grooming was exchanged within one day, but found that not all grooming is reciprocated within the time frame of one day, and that reciprocal grooming relations are more balanced in the long run. Similar results have been

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reported for capuchin monkeys, *Cebus apella* (Schino et al. 2009), and chimpanzees (Gomes et al. 2009). Moreover, in an experimental set-up it was shown that chimpanzees are unable to develop short-term contingency in their reciprocity (Brosnan et al. 2009). In contrast, a study on orangutans, *Pongo pygmeus* (Dufour et al. 2009) showed that in an experimental set-up some individuals were able to develop contingency and to employ calculated reciprocity. Nevertheless, we found no evidence for short-term contingency in the reciprocation of grooming within both macaque species studied.

To investigate the time frame of the interchange of grooming and support, we examined the relative amount of grooming before and after a conflict of an individual towards its supporter on days this individual actually did support the subject and compared that to days on which this individual did not support the subject in a conflict. We found that grooming did not predict support later on the same day, nor did support predict grooming later on the same day. Similar results have been reported for Japanese macaques (Schino et al. 2007), and ring-tailed coatis (Romero & Aureli 2008). However, these results conflict with a previous study on long-tailed macaques (Hemelrijk 1994), in which support did depend on the grooming received on that day. Moreover, studies on chimpanzees reported that support depends on the amount of grooming received on the previous day (Koyama et al. 2006), and that food sharing depends on the amount of grooming received earlier that day (de Waal 1997). Note that short-term reciprocity is defined in different ways in all these studies. Short-term reciprocity has been operationalised within a time frame of 30 minutes (Schino et al. 2007), one day (this study; Hemelrijk 1994; de Waal 1997; Gomes et al. 2009), and the day before (Koyama et al. 2006). To make comparisons between species and studies possible a consensus is needed about what a short term is. From our study, we conclude that there is no proof of immediate or short-term reciprocation and that the mechanism of (short-term) attitudinal reciprocity does not seem plausible.

Social Bonds

Emotionally mediated reciprocity implies that the probability of giving a certain service or commodity to another individual depends on the long-term social bond the actor has with that individual (Schino et al. 2007). An observed interchange relation between grooming and some other service or commodity is then mediated by the social bond two individuals have, which is established and maintained by mutual grooming (Dunbar 1991). Therefore, an exchange relation between grooming and support is expected to be influenced by variables indicative of a social

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bond. Accordingly, relatedness and contact sitting both had a strong influence on the exchange patterns of grooming and support, and similarly reciprocated grooming (i.e., grooming received from the other individual in each dyad), relatedness and contact sitting had a strong influence on the interchange of grooming and support. Similarly, contact sitting of ravens was related to allopreening and support in a conflict (Fraser & Bugnyar in press). These results suggest that social bonds explain much of the observed ex- and interchange patterns. Moreover, when dyads with close and distant social bonds were compared, 'friends' supported each other much more often than 'non-friends'. Social bonds thus seem to predict support, much like social bonds are predictive of coalitionary support in humans (Benenson et al. 2009) and of cooperation in an experimental task in chimpanzees (Melis et al. 2006a).

Finally, 'friends' may use different decision rules in their ex- and interchange relations. From the social sciences it is known that humans do not pursue a balanced relation with their friends, whereas they do with strangers (Deutsch 1975). De Waal (1997) showed that chimpanzees are more willing to share food with individuals who had previously groomed them than with individuals who had not groomed them in the past few hours, i.e., short-term interchange or attitudinal reciprocity. This effect, however, was influenced by the relationship quality of the two individuals. Pairs of individuals that rarely groomed (i.e., 'non-friends') shared only when the receiver had previously groomed the possessor of the food, whereas for individuals that groomed at higher rates (i.e., 'friends'), the sharing depended less on recent grooming, but probably on established emotional bonds (de Waal 1997). We found, however, no evidence of differential decision rules for dyads that differed in their bond in both macaque species. The monkeys of each species in this study belonged to the same social group, and since they have the possibility to interact daily with everyone, differential decision rules for 'friends' and 'non-friends' may not be necessary. However, having differential decision rules for 'friends' and 'non-friends' may also be cognitively too complex for these monkeys. In contrast, the higher cognitive abilities of chimpanzees and the fission-fusion dynamics of chimpanzees' social life (Boesch & Boesch-Achermann 2000; Amici et al. 2008) may make differential decision rules for 'friends' and 'non-friends' both feasible and adaptive for chimpanzees.

In summary, our results indicate a relation between grooming given and received, support given and received, grooming given and support received and support given and grooming received in two macaque species. Symmetrical features between

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the actor and the recipient cannot explain these reciprocal relations, and thus symmetry-based reciprocity does not seem to be the proximate mechanism behind these relations. The reciprocal relations were not due to short-term exchange, since no balanced exchange within one day was found. Instead, a longer lasting emotional-relational feature, namely the social bond between both kin and 'friends', did influence the long-term reciprocity in behaviour substantially. Furthermore, monkeys with close social bonds ('friends') did support each other much more often than monkeys with less close social bonds ('non-friends'). Therefore, emotionally mediated bookkeeping seems the most plausible mechanism underlying the long-term reciprocal relations observed. In agreement with this theory, we would like to refrain from saying that macaques groom in order to obtain support. Rather, we conclude that support in conflicts is mediated by the strength of the social bond these macaques have.

ACKNOWLEDGEMENTS

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APPENDIX 1. ROWWISE MATRIX CORRELATIONS VS. LINEAR MIXED MODELS

When linear mixed models are used to study exchange of behaviour, e.g., grooming, the identity of the giver and the receiver are included as random effects to control for the variation between individuals in their tendency to perform and receive grooming (Gomes et al. 2009). However, no special procedure is used, comparable to the matrix permutation method used in matrix correlation software, to take the special structure of the dyadic data matrix into account. In table A1 (see below) a fictive example matrix of grooming is presented for which a linear mixed model is fitted with grooming given as response variable and grooming received as predictor variable and the identity of the giver and of the receiver as random effect variables. Note that in order to analyse this data with linear mixed models using SPSS or R, the matrix is converted into a table with 4 columns: column 1 indicates the giver identity; column 2 indicates the receiver identity. These giver and receiver identities are relative to the response variable 'GroomGiv', so column 3 (the response variable 'GroomGiv') contains the number of grooming given by the animal in column 1 to the animal in column 2; and column 4 (the predictor variable 'GroomRec') contains the number of grooming received by the animal in column 2 from the animal in column 1. So, each dyad supplies two of the total 42 data points. For instance, dyad (a,b) supplies the data point (a,b,10,25) meaning that a gave 10 to b (the response variable) and a received 25 from b (the predictor variable); and also the data point (b,a,25,10) meaning that b gave 25 to a (the response variable) and b received 10 from a (the predictor variable.) In this simple example the t-value found for the fixed effect of 'grooming received' is 3.016 ($df = 27.36$; $p = 0.005$; SPSS procedure MIXED). In contrast, Mantel's matrix correlation test, which uses Pearson's correlation coefficient, gives an r of 0.553 between this matrix and the transposed one, with a right-tailed p-value of 0.099 (based on 10,000 permutations). Using rowwise matrix correlation with Pearson's correlation coefficient yields an r_{rw} of 0.468, with a right-tailed p-value of 0.086 (based on 10,000 permutations). Finally, using rowwise matrix correlation with Kendall's correlation yields a τ_{rw} of 0.304, with a right-tailed p-value of 0.085 (based on 10,000 permutations). See de Vries (1993) for a detailed explication of rowwise correlation methods as compared to non-rowwise matrix correlation methods such as the Mantel test. As shown in Appendix B of de Vries et al. (1993), when using the rowwise correlation with Pearson's correlation coefficient the results can be overly due to one individual when this individual gives and receives (many) more acts than the other individuals.

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Therefore, and because the data in our matrices are not normally distributed, we use Kendall's rank correlation coefficient in our rowwise matrix correlation analyses.

Table A1. A fictive matrix of grooming given and received.

		receiver							Tot
		a	b	c	d	e	f	g	
giver	a	*	10	2	3	4	0	5	24
	b	25	*	20	40	10	25	15	135
	c	8	20	*	6	7	10	0	51
	d	5	30	4	*	5	3	0	47
	e	12	40	0	5	*	6	0	63
	f	10	10	7	8	9	*	10	54
	g	10	15	0	2	2	5	*	34
Tot	70	125	33	64	37	49	30	408	

APPENDIX 2: ANALYSES FOR GROOMING-TIME

Matrix Correlations of Grooming-Time and Rank

To investigate whether macaques groom in accordance with the rank of the receiver, we correlated the amount of grooming-time given with rank and found a significant negative correlation for the long-tailed macaques (Kendall's $\tau_{rw} = -0.14$, $p < 0.001$), but not for the rhesus macaques (Kendall's $\tau_{rw} = -0.10$, $p = 0.072$). Although the correlations are weak, they do suggest that long-tailed macaques groom up the hierarchy (note that the correlation is negative since high-ranking individuals have low rank numbers). However, rhesus macaques seem to groom indifferently both up and down the hierarchy.

Long-term exchanges: Grooming-time – grooming-time.**Table A2. Long-term exchanges: Grooming-time – grooming-time.**

Correlations of grooming-time given and received for long-tailed macaques and rhesus macaques, and the effect of partialling out various variables from these correlations. Bold numbers represent substantial deviations from the original correlations.

<i>Grooming-grooming</i>					
Long-tailed macaques (n = 31)			Rhesus macaques (n = 28)		
	Kendall's τ_{rw}	<i>p</i>		Kendall's τ_{rw}	<i>p</i>
Original correlation	0.39	<0.001	Original correlation	0.51	<0.001
Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>	Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>
Age difference	0.38	<0.001	Age difference	0.51	<0.001
Rank difference	0.38	<0.001	Rank difference	0.51	<0.001
Relatedness	0.35	<0.001	Relatedness	0.45	<0.001
Contact sitting	0.17	<0.001	Contact sitting	0.35	<0.001

Comparisons for Grooming-Time*Grooming for Support*

We found no significant difference in the relative number of grooming minutes before a conflict with support compared to a conflict without support (Wilcoxon signed ranks tests: ltm: $T^+ = 193$, $n = 25$, $p = 0.229$; rhm: $T^+ = 42$, $n = 16$, $p = 0.839$). In addition, we did not find a significant difference in the relative number of grooming minutes after a conflict with support compared to a conflict without support (Wilcoxon signed ranks tests: ltm: $T^+ = 160$, $n = 25$, $p = 0.790$; rhm: $T^+ = 44$, $n = 16$, $p = 0.626$).

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Differential Decision Rules for 'Friends' and 'Non-Friends'

Using Kruskal-Wallis tests, we found no significant difference in the contingency of the different types of dyad concerning grooming-time *before* a conflict with or without support (grooming-time before conflict: ltm: $\text{Chi}^2 = 4.179$, 2 df, $p = 0.124$; rhm: $\text{Chi}^2 = 0.066$, 2 df, $p = 0.968$). We did find a significant difference between the dyad types in their contingency concerning grooming *after* a conflict (with or without support) for the long-tailed macaques (grooming-time after conflict: $\text{Chi}^2 = 9.578$, 2 df, $p < 0.01$), but not for the rhesus macaques (grooming-time after conflict: $\text{Chi}^2 = 2.655$, 2 df, $p = 0.265$). However, for all dyad types of the long-tailed macaques there was no significant difference in the time of grooming after a conflict in which the groomed individual did support and did not support (Wilcoxon signed ranks tests: 'friends': $T^+ = 68$, $n = 13$, $p = 0.127$; neutral dyads: $T^+ = 163$, $n = 24$, $p = 0.726$; 'non-friends': $T^+ = 6$, $n = 5$, $p = 0.256$).

Long-term interchanges: Grooming-time - support, support - grooming-time.

Table A3. Long-term interchanges: Grooming-time - support, support - grooming-time. Correlations of grooming-time given and support received and of support given and grooming-time received for long-tailed macaques and rhesus macaques, and the effect of partialling out various variables from these correlations. Bold numbers represent substantial deviations from the original correlations.

<i>Grooming-support</i>					
Long-tailed macaques (n = 31)			Rhesus macaques (n = 28)		
	Kendall's τ_{rw}	<i>p</i>		Kendall's τ_{rw}	<i>p</i>
Original correlation	0.18	<0.001	Original correlation	0.27	<0.001
Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>	Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>
Age difference	0.18	<0.001	Age difference	0.26	<0.001
Rank difference	0.16	<0.001	Rank difference	0.26	<0.001
Relatedness	0.12	<0.001	Relatedness	0.18	<0.001
Contact sitting	0.05	0.149	Contact sitting	0.17	<0.001
Grooming received	0.08	0.023	Grooming received	0.16	<0.001
<i>Support-grooming</i>					
	Kendall's τ_{rw}	<i>p</i>		Kendall's τ_{rw}	<i>p</i>
Original correlation	0.20	<0.001	Original correlation	0.25	<0.001
Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>	Independent variable partialled out	Partial Kendall's τ_{rw}	<i>p</i>
Age difference	0.18	<0.001	Age difference	0.23	<0.001
Rank difference	0.16	<0.001	Rank difference	0.23	<0.001
Relatedness	0.11	<0.01	Relatedness	0.16	<0.001
Contact sitting	0.06	0.105	Contact sitting	0.13	<0.001
Grooming given	0.10	<0.01	Grooming given	0.13	<0.001

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Chapter 4

Generous leaders and
selfish underdogs:
Pro-sociality in despotic macaques

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“He who wishes to be obeyed
must know how to command.”
Machiavelli (1469-1527)

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ABSTRACT

Actively granting food to a companion is called pro-social behaviour and is considered to be part of altruism. Recent findings show that some non-human primates behave pro-socially. However, pro-social behaviour is not expected in despotic species, since the steep dominance hierarchy will hamper pro-sociality. We show that some despotic long-tailed macaques do grant others access to food. Moreover, their dominance hierarchy determines pro-social behaviour in an unexpected way; high-ranking individuals grant, while low-ranking individuals withhold their partner access to food. Surprisingly, pro-social behaviour is not used by subordinates to obtain benefits from dominants, but by dominants to emphasize their dominance position. Hence, Machiavellian macaques rule not through 'fear above love', but through 'be feared when needed and loved when possible'.

INTRODUCTION

Altruism remains one of the major mysteries in evolution. Although reciprocal altruism (Trivers 1971) has been found in animals (Dugatkin 1997), genuine altruism, defined as a costly act that confers benefits on non-kin regardless of reward prospects, is considered uniquely human (Fehr & Fishbacher 2003). However, pro-social preferences to deliver food to unrelated individuals at no or very low cost were also reported for the common marmoset (*Callithrix jacchus*: Burkart et al. 2007), a primate species that, similar to humans, shows a cooperative breeding system (Hrdy 2005). Consequently, it was suggested that pro-sociality may result from convergent evolution among cooperative breeders (Burkart et al. 2007). This hypothesis may not be tenable, since a recent study failed to show pro-social behaviour in another cooperatively breeding primate, the cottontop tamarin (*Saguinus oedipus*: Cronin et al. 2009). Moreover, subsequent studies also showed pro-sociality in non-cooperative breeding primates such as capuchin monkeys (*Cebus apella*, de Waal et al. 2008; Lakshminarayanan & Santos 2009) and bonobos (*Pan paniscus*, Hare & Kwetuenda, 2010). This led to the alternative suggestion that pro-sociality is an ancestral trait among primates (Lakshminarayanan & Santos 2009). However, results of chimpanzees (*Pan troglodytes*) are inconsistent, and depending on the tests used chimpanzees do not (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008) or do (Warneken et al. 2007) show pro-social behaviour. These inconsistencies suggest that pro-social behaviour may not be fully expressed among more despotic primate species. In line with these suggestions, it has been argued that human egalitarianism coevolved with pro-sociality (Fehr et al. 2008). Therefore, it is expected that despotism hampers pro-social behaviour. However, this hypothesis remains to be tested experimentally.

Here we intend to test this proposition. We examined whether long-tailed macaques (*Macaca fascicularis*) behaved pro-socially towards conspecifics, without incurring costs to self. Long-tailed macaques belong to the family of Cercopithecidae. In contrast to most other primate species, it is considered easy to detect a clear dominance hierarchy in this family of primates (Silk 1986). Furthermore, long-tailed macaques are primates that have low social tolerance and a large dominance asymmetry. Therefore, within the genus *Macaca* they are considered a despotic species with a steep linear hierarchy (Thierry 2000). Moreover, among these macaques kin relationships are important especially for females, and related individuals obtain neighbouring, but clear, dominance ranks through mutual support (van Noordwijk & van Schaik 1999). Therefore, in our experiment we distinguish kin versus non-kin. Furthermore, among these macaques there are two

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opposite ways in which dominance rank may affect pro-social behaviour: 1) Subordinates may act pro-social to those higher in rank, similar to grooming up the dominance hierarchy (Seyfarth 1977; Noë et al. 1991), with possibly either tolerance or future support as a result. 2) High-ranked individuals' generosity may be a strategy to either enhance or maintain their status (Moore 1984; de Waal 1989).

RESULTS

In this study twenty captive long-tailed macaques from the same social group participated. They were placed alone in a test compartment, located between an empty test compartment and a test compartment occupied by another macaque (figure 1). To avoid bargaining for sexual services (Gumert 2007a), partners were always of the same sex. Test-setting and apparatus were almost identical to those used in one chimpanzee study (Jensen et al. 2006). The subject macaque was given the choice between two slides, each baited with two slices of banana. By pulling on one slide, the subject would gain access to one slice of banana, while the second slice was out of reach in front of the empty test compartment (choice A). Pulling on the second slide also allowed the subject access to only one slice of banana, and in addition the second slice came within reach of the individual in the adjacent cage (choice B). As both choices involved the same cost and benefit for the subject, but the second choice also involved a benefit for the adjacent individual, we define the second choice as 'pro-social' and the first as 'a-social'. The preference for the 'pro-social' choice was compared to the control condition in which a side preference was measured when both adjacent cages were empty. In the test condition, partners were intentionally placed on the opposite side of the side preference measured in the control condition and consequently, subjects had to deviate from their initial side preference to be pro-social. Ten subjects, nine females and one male, were tested twice: both with a kin and a non-kin partner in the adjacent test compartment. Ten additional subjects, lacking same sexed kin, were tested with non-kin partners only (for a complete overview of which individuals participated and with which partners they were paired see table 1 of chapter 6).

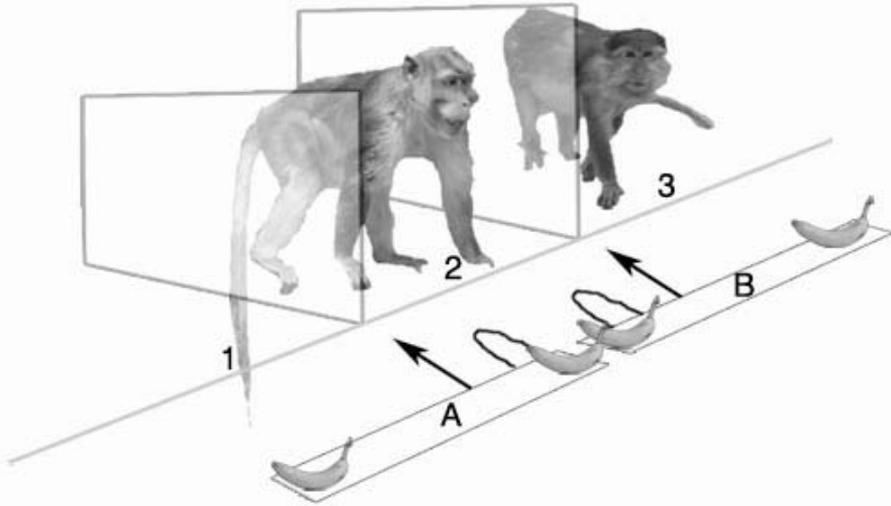


Figure 1. Drawing of two monkeys in the test setting. The drawing shows the subject in the middle compartment having the choice between either granting itself and its partner (in compartment three) access to a banana (choice B, the ‘pro-social’ choice), or granting only itself access to a banana and leaving a banana in front of an empty compartment (compartment one)(choice A, the ‘a-social’ choice).

First, our results show that five long-tailed macaques act significantly pro-socially towards kin (Chi square tests on each individual’s choices: $p < 0.05$), and one individual tends to do so ($p < 0.10$). Moreover, overall their preference for the partner side when tested with a kin partner was significantly higher than their preference for the same side in the control condition (Kin: Test vs. Control; Wilcoxon signed ranks test: $T^+ = 4$, $n=10$, $p_{\text{exact}} = 0.014$)(figure 2a). Since nine out of ten pairs concerned females, this in particular indicates that females are pro-social towards their female kin. Secondly, four out of the twenty individuals tested with a non-kin partner also acted significantly pro-social, while three were significantly the reverse of pro-social, or a-social (i.e., they withheld their partners access to food)(Chi square tests on each individual’s choices: $p < 0.05$), and two individuals tended to act a-social ($p < 0.10$). Nonetheless, no overall significant difference between the preference for the partner side in the test and the same side in the control condition was found among non-kin (Wilcoxon signed ranks test: $T^+ = 98$, $n=20$, $p_{\text{exact}} = 0.914$)(figure 2b).

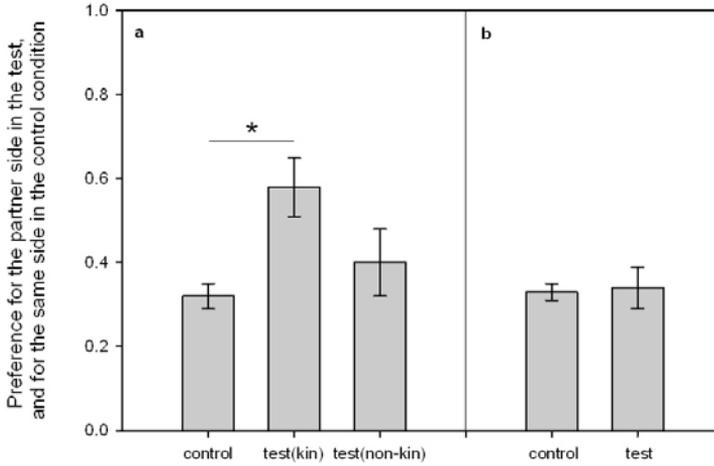


Figure 2. a: Pro-sociality and kin. Mean preference \pm s.e.m. for the partner-side of all individuals tested with their kin ($n = 10$) in the test condition, the mean preference \pm s.e.m. for the same side of the same individuals in the control condition and the mean preference \pm s.e.m. for the partner-side of the same individuals when tested with non-kin,
b: Pro-sociality and non-kin. Mean preference \pm s.e.m. for the partner-side of all individuals tested with non-kin ($n = 20$) in the test condition and the mean preference \pm s.e.m. for the same side of the same individuals in the control condition
 * indicates a difference at the $p < 0.05$ level (exact Wilcoxon signed ranks test).

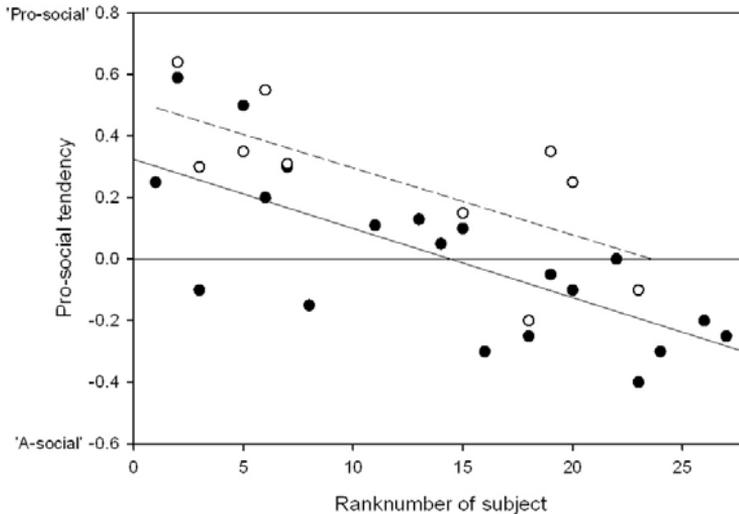


Figure 3. Pro-social tendency and rank. Pro-social tendency (difference between the preference for the partner side in the test condition and the preference for the same side in the control condition) and absolute rank number (nr 1 is the alpha male) of all subjects towards kin (open circles and dotted line) and non-kin (closed circles and full line). Lines indicate linear regressions significant at the $p < 0.05$ level.

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Consequently, the pro-social tendency towards kin partners was significantly higher than the pro-social tendency towards non-kin partners (Wilcoxon signed ranks test: $T^+ = 41$, $n = 10$, $p_{\text{exact}} = 0.031$)(figure 2a).

Among non-kin, high-ranking individuals (with a low rank number) grant their partner access to food, whereas low-ranking individuals deny their partners access to food, which is demonstrated by a significant linear regression of pro-social tendency with dominance rank ($t = -4.689$, $\beta = -0.742$, $n = 20$, $p < 0.001$)(figure 3). A similar negative linear regression of dominance rank and pro-social tendency was found within the kin-pairs ($t = -2.893$, $\beta = -0.715$, $n = 10$, $p = 0.02$)(figure 3). The effect of dominance rank may be due to either an individual's own rank position or to the rank distance with its partner. A multiple regression of pro-social tendency with both subject's rank and rank distance showed only a significant effect of the subject's rank position ($t = -2.904$, $\beta = -0.565$, $n = 20$, $p = 0.01$), yet no significant effect of rank distance ($t = 1.472$, $\beta = 0.286$, $n = 20$, $p = 0.159$). Therefore, we conclude that a subject's pro-social tendency depends on the absolute dominance rank of the subject itself.

DISCUSSION

This is, to our knowledge, the first study to show pro-sociality in a despotic monkey species. In line with the kin selection theory (Hamilton 1964) and similar to capuchin monkeys (de Waal et al. 2008), female long-tailed macaques behave pro-socially towards kin and are more pro-social towards kin than towards non-kin, reflecting the importance of their kin-relations (van Noordwijk & van Schaik 1999; but see Schaub 1996). Moreover, dominant individuals also provide benefits to non-kin others. These results suggest that pro-social behaviour is not restricted to egalitarian species, and supports the hypothesis that all anthropoid primate species may share this behaviour through common ancestry. Additional support, in the form of replication using other despotic species and comparisons with less despotic macaques, is needed. We emphasize, however, that further studies should be aware of relatedness and dominance rank as a possible interacting factor in any study of social cognitive capacities.

Machiavelli advised despotic leaders that 'it is better to be feared than loved'. Our results, however, indicate that dominant animals actually provide benefits to others, while subordinates withhold them. Moreover, the absolute dominance rank of the subject, and not its rank position relative to that of its partner, determines its pro-social behaviour, both among kin and in non-kin pairs.

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These results contrast with previous research on primates showing that subordinates give more grooming to dominants (e.g., Seyfarth 1977; Noë et al. 1991), presumably with tolerance or future support as a result. In addition, low-ranking individuals withheld their partner food. This may be part of a competitive strategy. Pro-social behaviour of only the dominants has been reported in humans too, where individuals in a dominant position behave more pro-socially than those in a subordinate position (Dovidio & Gaertner 1981; Mast & Bischof 1999). Pro-sociality of a dominant individual may be a strategy to enhance or maintain status (Moore 1984; de Waal 1989). Moreover, by being pro-social dominants may advertise their dominance, possibly convincing subordinates to accept the high-ranking individual's dominance and inhibiting rebellion of subordinates (Zahavi 2004). Therefore, this study suggests that dominant long-tailed macaques advertise their dominance position through pro-social behaviour, much like is expected in the handicap principle (Zahavi 1997). The handicap principle, however, specifically concerns behaviours that are costly for the actor, whereas in this experiment the actor has no costs. Whether long-tailed macaques would behave similarly when a cost to themselves is involved remains to be tested. Alternatively, it may be that not an individual's high dominance rank leads to its pro-social behaviour, but that the pro-social behaviour of an individual has led it to achieve such a high dominance rank. For male long-tailed macaques it has already been suggested that not only their strength, but also their social capacities influence their position within a dominance hierarchy (van Noordwijk & van Schaik 2001). In contrast to males, females remain in the same group for the rest of their life (van Noordwijk & van Schaik 1987), and have 'family ranks', since they inherit their rank from their mother (Hill & Okayasu 1996). However, family turnovers do occur (Chance et al. 1977), and pro-social behaviour of females may as well be a strategy to sustain their rank position. Nevertheless, our results indicate that dominant macaques are not just Machiavellian despots, but like benevolent leaders, also provide benefits to their subordinates.

MATERIALS AND METHODS

Ethics Statement

The experiment has been conducted according to the directives of the Dutch experiments on animals act. The experiment was approved by the Ethics Committee of Utrecht University (DEC 2007.I.08.103) and thus complies with the Dutch law. To avoid any stress, the animals were never forced to participate. Consequently, the animals that were tested, participated voluntarily. The animals were, furthermore, never food or water deprived.

Subjects and Test-setting

Ten male and ten female long-tailed macaques from a long-term, stable social group (colony of Utrecht University, The Netherlands) participated in this experiment (see table 1 chapter 6). Experiments were carried out in familiar test chambers. The test-setting consisted of three connected chambers (110 cm x 55 cm x 80 cm) that were divided by two lexan transparent screens (figure 1). The test apparatus was placed in front of the middle compartment. On the test apparatus were two handles that were connected to two separate sliding bars. Only one of these handles could be pulled per trial. At the beginning of each trial, four equally sized slices of banana simultaneously dropped on the two bars, one on each end of each bar. The monkey in the middle compartment then could pull either handle to move the bar with pieces of banana towards the compartments to grab and eat the treat from one side of the bar. The slice of banana at the other end of the bar was out of reach for the monkey in the middle compartment. However, if another monkey (kin or non-kin) was present in that outer compartment, it could take and eat the slice of banana. After the monkey(s) had taken their reward(s), the remaining banana slices were removed and a new trial was directly thereafter started. Pulling the handle that delivered the slice of banana to the other monkey too is considered as 'pro-social', while pulling the handle that delivers the banana to the front of an empty cage is termed 'a-social'. It is important to note that the monkey in the middle compartment (the test-subject) always got a piece of banana, independent of which handle he/she pulled. All subjects were already trained for a previous experiment (chapter 6) to pull in a baited bar to obtain a reward, and were equally efficient (100%) in this task. Moreover, for this previous experiment, the monkeys were also trained to be isolated in a test compartment alone or with a partner in a neighbouring compartment that was separated from it by a lexan transparent screen. Therefore, the monkeys were familiar with a partner next to them, and had learned that this partner could not enter their compartment. Several days prior to

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testing all animals got access with several animals at a time to the apparatus that was baited at the two ends of each slide, such that all animals could experience that they could pull and obtain a reward, but that the second reward was out of reach and could be taken by another individual. The two days before testing, all subjects were trained without a partner in the final test-setting (i.e., in the middle test-compartment, between two empty compartments). During this final training they got 4 trials each day in which they had to choose between the two slides that were baited on each end and after they had made their choice the other slide was blocked.

Conditions

Subjects were tested in an experimental and a control condition. Subjects were always in the middle chamber of the test setting. The subjects were first tested in the control condition, in which we determined the left/right preference of each subject without a partner. In the test condition all individuals were tested in the same way, but now with a same-sex partner sitting on the opposite side of their preferred side, as determined in the control condition. Both the control and the test condition consisted of twenty trials that, in order to retain the monkeys' motivation, were divided over two consecutive days, with ten trials on each day. The subjects did not differ significantly in the number of pro-social choices between the first ten trials and the second ten trials of the test condition (Wilcoxon signed ranks test: $T^+ = 110$, $n = 20$, $p_{\text{exact}} = 0.559$), nor in their side preference between the first ten trials and the second ten trials of the control condition (Wilcoxon signed ranks test: $T^+ = 95$, $n = 20$, $p_{\text{exact}} = 0.707$). Moreover, all animals completed all trials and were generally very motivated, since they almost always took the food (18-20 times). Consequently, there were no differences in motivation related to the dominance rank of the subjects. Furthermore, all animals generally ate the food items they retrieved or received from their partner. Aggressive behaviour was rare and, if present, directed at the experimenter. Finally, to avoid reciprocation, dyads were always novel. Ten (nine females and one male) out of the twenty subjects were counterbalanced tested with both a kin and a non-kin partner.

Measures

To measure pro-sociality, the preference for the partner-side in the test condition was compared with the preference for the same side in the control condition. Moreover, to test the pro-sociality of each individual separately, we used chi-squared tests with the amount of left and right choices in the control condition as expected values and the amount of left and right choices in the test condition as the observed values. To compare pro-social tendencies between different individuals, we calculated pro-social tendencies by subtracting from the preference for the partner-side in the test condition the preference for the same side in the control condition. A positive pro-social tendency then shows pro-social behaviour, whereas a negative pro-social tendency shows a-social behaviour, since the tested individual actually withholds a reward from its partner.

Analysis

The dominance hierarchy of the group was calculated using unidirectional submissive behaviour arranged in a socio-matrix. The dominance order most consistent with a linear hierarchy was determined with MatMan 1.1 (Landau's linearity index: $h' = 0.7204$, $p < 0.001$), indicating a significantly linear dominance hierarchy (de Vries 1995; 1998). Rank numbers were afterwards assigned with 1 for the most dominant individual and 35 for the most subordinate individual. Rank distance between a subject and its partner was calculated by subtracting the rank number of the subject from the rank number of its partner. For comparisons of preferences in the control- and test condition, and comparisons between pro-social tendencies, exact Wilcoxon signed ranks tests were used. Pro-social tendency was regressed on both dominance rank of the subject and rank distance between subject and partner. Residuals of each of these linear regression models do not differ significantly from a normal distribution. All reported P-values are two-tailed.

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Chapter 5

Benefiting ‘friends’ or dominants:
Pro-social choices depend on rank
position in long-tailed macaques
(*Macaca fascicularis*)

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“As one’s gifts increase, his friends decrease:”
Kahlil Gibran (1883-1931)

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ABSTRACT

Long-term observational studies in a number of animal species suggest that exchange patterns of social acts depend on long-term emotional bonds. Therefore, it is expected that the frequency of pro-social behaviour also depends on the strength of such a bond, e.g., friends give more to each other than non-friends. In this study we tested whether variation in relationship quality is predictive of the pro-social behaviour of long-tailed macaques in two ways: first, we related relationship quality to pro-sociality in a dyadic pro-sociality test and, second, we gave subjects the choice to give to either a 'friend' or a 'non-friend' in a triadic set-up. We show that pro-social behaviour of long-tailed macaques in general is not related to relationship quality. However, when given the choice to give to either a 'friend' or a 'non-friend', dominant long-tailed macaques preferentially give to their 'friends'. In contrast, subordinates make a more competitive choice and instead of preferentially giving to their 'friends', they avoid giving to direct competitors. Therefore, dominance rank seems to determine which of two possible social relationships, friendship or dominance, prevails in directing pro-social behaviour, and only dominants seem to confirm their 'friendships' in the short-term setting of an experiment.

INTRODUCTION

Research on reciprocal exchange patterns has changed its focus from mainly ultimate explanations, to attention for the proximate mechanism underlying exchange patterns (Brosnan & de Waal 2002). In particular, the time frame of reciprocation has been a major focus of research (Schino et al. 2007). Many of these studies show that reciprocity is not contingent on the short-term and, therefore, does not rely on a strict tit-for-tat rule (Axelrod & Hamilton 1981). Instead, these exchanges seem tolerant for short-term imbalances (exchange of grooming: capuchin monkeys, *Cebus apella*: Schino et al. 2009; chimpanzees, *Pan troglodytes*: Gomes et al. 2009; rhesus and long-tailed macaques, *Macaca mulatta* & *M. fascicularis*: chapter 3; interchange of grooming for support: Japanese macaques, *Macaca fuscata*: Schino et al. 2007; rhesus and long-tailed macaques: chapter 3; ring-tailed coatis, *Nasua nasua*: Romero & Aureli 2008; interchange of grooming for sexual access: rhesus macaques: chapter 2). The robustness of exchange patterns, irrespective of short-term imbalances, implies that regularly services are not reciprocated immediately or within a short time frame and seemingly animals are not deterred by this lack of reciprocity. Such other-regarding preferences without reciprocation have been referred to as pro-sociality.

Genuine altruism, or a costly act to benefit another, has been considered uniquely human (Fehr & Fishbacher 2003). However, pro-social behaviour, that benefits the other but does not need to invoke a cost to the actor, has also been reported for several primate and corvid species (capuchin monkeys: de Waal et al. 2008; Lakshminarayanan & Santos 2009; chimpanzees: Warneken et al. 2007; common marmosets, *Callithrix jacchus*: Burkart et al. 2007; bonobos, *Pan paniscus*: Hare & Kwetuenda 2010; long-tailed macaques: Massen et al. 2010, chapter 4; jackdaws, *Corvus monedula*: de Kort et al. 2006; ravens, *Corvus corax*: Heinrich 1988; rooks, *Corvus frugilegus*: Scheid et al. 2008). Consequently, pro-social behaviour is not limited to humans.

Since exchange patterns of services in several animal species seem robust against short-term imbalances, yet are reciprocal in the long run, these exchange patterns can be considered a consequence of long-term emotional bonds build on mutual behaviour benefiting the other. Consequently, the observed exchange patterns predict that especially individuals with close bonds will act pro-socially to one another or, at least, act more frequently pro-social than individuals with less close bonds. However, to date there are no studies reporting how within species variation in relationship quality affects the frequency of pro-social behaviour. Only one study on jackdaws (von Bayern et al. 2007) reports a similar, but reverse

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pattern; that pro-social behaviour leads to pair bonding, yet this does not show how an existing within-species variation in relationship quality relates to pro-social behaviour. From a human perspective it may seem obvious that friends are more pro-social towards each other than non-friends. However, in animals this hypothesis remains to be tested.

In this study, we tested whether variation in relationship quality is predictive of pro-social behaviour in long-tailed macaques in two ways. In the first experiment, the pro-sociality experiment, we determined with a dyadic set-up whether relationship quality was related to pro-social behaviour. In the second experiment, the choice experiment, we tested in a triadic set-up whether long-tailed macaques preferentially give to their 'friends' when given the choice between a 'friend' and a 'non-friend'. However, the pro-social behaviour of animals depends not only on the identity of the receiving partner, but also depends on the identity of the subject. Massen et al. (2010, chapter 4) report in a study on long-tailed macaques that only dominant animals provide their partners access, while subordinates withhold their partner access to food. Therefore, we controlled for dominance when analyzing the effect of relationship quality on pro-social behaviour in the pro-sociality experiment. Furthermore, in the choice experiment we also analysed the data of dominant and subordinate individuals separately. In addition, the effect of proximity of the subject to its partner(s) in the test setting was determined in both experiments.

METHODS

Subjects and Housing

The tested animals were members of a social group housed at the 'Ethologie-station' of the Utrecht University, the Netherlands that consisted of 36 individuals with males and females from all life stages. The group was formed after splitting a larger group along matriline in 1994 and has since been stable. Most animals were born in this group. The group was housed in an indoor enclosure (235 m³) attached to an outdoor compound (800 m³), with plenty of climbing and sitting facilities and was regularly provisioning with enrichment. Water and commercially available monkey chow were available at libitum. Alternately fruit, vegetables or bread were daily provided to the group half an hour after the day's testing was completed. This feeding schedule was followed regardless whether the animals participated in a test that day. The animals were never food or water deprived.

Benefiting 'Friends' or Dominants

The dominance hierarchy in the group and the friendship status among group members were analysed prior to the experiments. The dominance hierarchy was determined by analyzing unidirectional submissive behaviours ('bare teeth' and 'make room' without prior aggressive behaviour) that were observed ad libitum. Results were arranged in a socio-matrix with actors in rows and recipients in columns. The dominance order most consistent with a linear hierarchy was determined with MatMan 1.1 (linearity index: $h' = 0.7204$, $p < 0.001$), indicating a significantly linear dominance hierarchy (de Vries 1995; 1998). Rank-numbers were assigned with 1 for the most dominant individual and 36 for the least dominant individual.

To measure relationship quality, we conducted time-sample scan observations (2-4 times a day) of all independent group members (i.e., excluding infants) during the 10 months prior to testing, to assess who is sitting with whom (contact-sitting) and who is grooming whom. We ordered per individual with whom they sat most in contact (number 1) and with whom the least (number 35). Individuals with whom the subject individual sat a same proportion of time together were both given the average number, e.g., if they were 4 and 5, they were both numbered 4.5. If there were more individuals with whom the subject sat the least in contact, they all were numbered 35. The same was done for the grooming data. For each partner both numbers were added and divided by two, leading to a 'relationship quality' measure ranging between 1 (i.e., best 'friend') and 35 (i.e., the least affiliative bonds).

Subjects and their test partners were all adult or subadult monkeys (ranging in age between 3 and 21 years) that reliably could pull in a tray of the test apparatus (figure 1). In the pro-sociality experiment, we tested ten male and ten female long-tailed macaques. In the choice experiment, we tested the same animals with the exception of one subject, the alpha male, that was excluded because of a lack of male 'friends'.

For the pro-sociality experiment, pairs of a subjects and their test-partners were chosen according to their relationship quality and the subjects' dominance rank, creating a sample with as much variation in relationship quality and dominance rank as possible (relationship quality ranged from 1 to 35, with a mean of 12.2 and a standard deviation of 9.5; the subjects' dominance rank ranged from 1 (i.e., the alpha male) to 27, with a mean of 14 and a standard deviation of 8 (see table 1). To avoid reciprocation, dyads were always novel. Furthermore, to avoid bargaining for sexual services (Gumert 2007a), partners were always of the same sex. Consequently, all subjects were tested with a non-kin same-sex member of their

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group. In addition, ten (nine females and one male) out of the twenty subjects, were, counterbalanced, also tested with a same-sex kin partner (table 1).

In the choice experiment, the two partners of the subject were also chosen according to their relationship quality with the subject; one dyad with a relationship quality number as low as possible ('friends' ranged in relationship quality from 2.5 to 19.5, with a mean of 7.3 and a standard deviation of 4.5), and one partner with a relationship number as high as possible ('non-friends' ranged in relationship quality from 12.75 to 32.75, with a mean of 22.4 and a standard deviation of 4.1). Furthermore, to avoid reciprocity, combinations of subject and partner were always novel and were not tested together in the pro-sociality experiment (table 2).

Benefiting 'Friends' or Dominants

Table 1. Name, sex and dominance rank of subjects and their non-kin and kin test partners, and the relationship quality of the subjects with their test partners in the pro-sociality experiment.

Subject	Sex	Rank	Non-kin			Kin		
			Partner	Rank	R.Q.	Partner	Rank	R.Q.
Regilio	♂	1	Tabasco	12	35			
Tonko	♂	14	Burkina-faso	10	14.75			
Tabasco	♂	12	Tonko	14	6.5			
Burkina-faso	♂	10	Santiago	22	23			
Kufo	♂	27	Inlimbo	25	2.75			
Ontarijo	♂	23	Kufo	28	4.75			
Santiago	♂	22	Ontarijo	23	18.75			
Bonobo	♂	26	Just-so	8	21.75			
Just-so	♂	8	Regilio	1	32			
Inlimbo	♂	25	Ontarijo	23	4.5	Bonobo	26	5.25
Latifa	♀	19	Kraa	7	5.75	Tres-bella	20	1
Wodka	♀	2	Latifa	19	25.5	Alfa	5	26.25
Alfa	♀	5	Tres-bella	20	4.25	Tamanduwa	3	13
Tamanduwa	♀	3	Cordoba	16	4	Kraa	7	3.5
Tres-bella	♀	20	Annika	6	5.25	Freya	15	4.75
Kraa	♀	7	Rastafa	21	8	Salsaa	9	10.5
Rastafa	♀	21	Wodka	2	10.75	Tres-bella	20	5.75
Annika	♀	6	Freya	15	13.75	Alfa	5	13.75
Freya	♀	15	Cordoba	16	12.25	Rastafa	21	3.5
Cordoba	♀	16	Latifa	19	16			

Table 2. Name, sex and dominance rank of subjects and their 'friend' and 'non-friend' partners, and the relationship quality of the subject with the test partners in the choice experiment.

Subject	Sex	Rank	'Friend'			'Non-friend'		
			partner	Rank	R.Q.	partner	Rank	R.Q.
Latifa	♀	19	Alfa	5	6	Tamanduwa	3	24.5
Wodka	♀	2	Tres-bella	20	5.75	Freya	15	23.5
Alfa	♀	5	Freya	15	4.25	Rastafa	21	20.75
Tamanduwa	♀	3	Tres-bella	20	3	Rastafa	21	26
Tres-bella	♀	20	Cordoba	16	8	Salsaa	9	24.5
Kraa	♀	7	Tres-bella	20	10	Cordoba	16	23.5
Rastafa	♀	21	Annika	6	7.5	Cordoba	16	25.75
Annika	♀	6	Cordoba	16	6.25	Latifa	19	16.25
Freya	♀	15	Kraa	7	5.25	Tamanduwa	3	24.5
Cordoba	♀	16	Salsaa	9	5.25	Alfa	5	25
Tonko	♂	14	Santiago	22	7.75	Just-so	8	20
Tabasco	♂	12	Ontarijo	23	2.5	Bonobo	26	21
Burkina-faso	♂	10	Just-so	8	19.5	Bonobo	26	32.75
Kufo	♂	28	Tonko	14	3.75	Tabasco	12	22
Ontarijo	♂	23	Bonobo	26	6.75	Tonko	14	20.25
Santiago	♂	22	Inlimbo	25	18	Kufo	28	23
Bonobo	♂	26	Santiago	22	8	Kufo	28	19.5
Just-so	♂	8	Tabasco	12	8	Kufo	28	12.75
Inlimbo	♂	25	Tonko	14	3,25	Just-so	8	21

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Test-Setting

The training and testing procedure of the animals was as follows: the complete group entered from their home cage the connected test cage of 32 m³ (4 m x 4 m x 2 m). From this test cage the subject and its partner(s) entered the test compartment (110 cm x 55 cm x 80 cm)(figure 1). The test compartment was divided in three parts by two transparent lexan screens, to allow visual contact between the monkeys while keeping them physically separated. The subject was always in the middle compartment (compartment 2 in figure 1), and the partner(s) were sitting in the adjacent compartment(s) (compartment 1 and 3 in figure 1). The test apparatus that was placed in front of the middle test compartment consisted of two slides, one on the left and one on the right. All subjects had been trained to pull in a baited slide to obtain the reward. At the beginning of each trial, four equally sized slices of banana simultaneously dropped on the slides, two on each. If the monkey pulled in a slide, the other slide was blocked. After the monkey pulled in the slide, it could take the reward that was in the centre while the reward at the other side of the slide was out of reach for the subject, though could be taken by its partner on that side, if present. After the monkey(s) had taken their rewards, the remaining banana slices were removed and a new trial was started immediately. During the tests, dependent offspring were always allowed into the test compartment with their mothers. Neither subject nor test partner was tested more than once on one day.

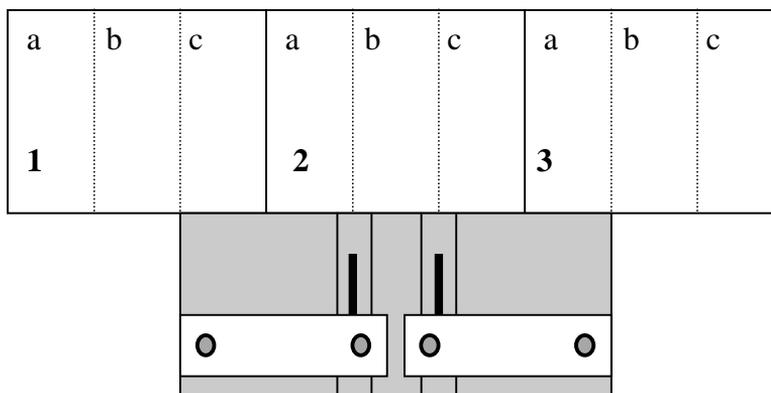


Figure 1. Schematic representation of the test-setting. On top the three different compartments (1-3) and their spatial subdivision (a-c) are represented. Below (in grey) is the test apparatus, with two different slides (white) that are connected to rails (thin black lines) and can be pulled in by the monkey in the middle compartment by pulling the bars (thick black lines). The grey circles represent slices of banana that were simultaneously dropped on both slides in the test.

Benefiting 'Friends' or Dominants

All test sessions were recorded using four CCTV system B/W cameras covering both the up-front and from-above view of the test compartments. Data were coded by I.J.A.F.L.. Coding could not be blind since subjects, their behaviour and conditions were visible.

Conditions

Pro-Sociality Experiment

Subjects were tested in an experimental and a control condition. Subjects were always in the middle compartment of the test setting. The subjects were first tested in a control condition, in which we determined the left/right preference of each subject without a partner. In the test condition all individuals were tested in the same way, but now with a same-sex partner sitting on the opposite side of their preferred side, as determined in the control condition. Partners were intentionally placed on the opposite side of the side preference measured in the control condition and consequently, subjects had to deviate from their initial side preference to be pro-social. Both the control and the test condition consisted of twenty trials that, in order to retain the monkeys' motivation, were divided over two consecutive days, with ten trials on each day. The subjects did not differ significantly in the number of pro-social choices between the first ten trials and the second ten trials of the test condition (Wilcoxon signed ranks test: $T^+ = 110$, $n = 20$, $p_{\text{exact}} = 0.559$), nor in their side preference between the first ten trials and the second ten trials of the control condition (Wilcoxon signed ranks test: $T^+ = 95$, $n = 20$, $p_{\text{exact}} = 0.707$). Moreover, all animals completed all trials and were generally very motivated, since they almost always took the food (18-20 times).

The Choice Experiment

In the choice experiment subjects were tested in one condition only. Subjects were in the middle compartment, with two partners, one in each adjacent compartment (i.e., one to the left and one to the right). The partner with whom the subject had the best relationship quality (low relationship quality number) was intentionally placed on the opposite side of the side preference measured in the control condition of the pro-sociality experiment and consequently, subjects had to deviate from their initial side preference to give to their 'friends'. In the experiment, the subjects were given 20 times the same choice that, in order to retain the monkeys' motivation, were divided over two consecutive days, with ten trials on each day. The subjects did not differ significantly in their side preference between the first ten trials and the second ten trials (Wilcoxon signed ranks test: $T^+ = 51$, $n = 19$, $p_{\text{exact}} = 0.719$). Moreover, all

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animals completed all trials and were generally very motivated, since they always took the food.

Measures

The Pro-Sociality Experiment

To measure pro-sociality, the preference for the partner-side in the test condition was compared with the preference for the same side in the control condition. To compare pro-social tendencies between different individuals, we calculated pro-social tendencies by subtracting from the preference for the partner-side in the test condition the preference for the same side in the control condition. A positive pro-social tendency then shows pro-social behaviour, whereas a negative pro-social tendency shows 'a-social' behaviour, since the tested individual actually withholds a reward from its partner.

To test for possible effect of the proximity of the subject to its partner, we measured the proportion of time the subject spend in either area a, b or c of its compartment (see figure 1). It should however be noted that the subjects were able to pull in both slides from any place within the compartment.

Finally, we measured of the subjects all affiliative (i.e., lip smacking and eye-lifting) and aggressive (i.e., open mouth threats) behaviour (Angst 1974) towards its partner, to measure whether this was predictive of its pro-social tendency.

The Choice Experiment

To measure a preference to give to a particular individual (e.g., 'friend' or 'non-friend'), we compared the proportion of choices for the corresponding slide with the subject's initial side preference, which we established in the control condition of the pro-sociality experiment.

To test for possible effects of the proximity of the subject to its partners, we measured the proportion of time the subject spend in either area a, b or c of its compartment (see figure 1).

Finally, we measured of the subjects all affiliative (i.e., lip smacking and eye-lifting) and aggressive (i.e., open mouth threats) behaviour (Angst 1974) towards its partner to establish whether this was predictive of its choice.

Data Analyses

The Pro-Sociality Experiment

Since relationship quality is a fixed measure, the pro-social tendency of the subject was regressed on the relationship quality with the partner. However, previous

analysis showed a very strong effect of the subject’s rank on its pro-social tendency (Massen et al. 2010, chapter 4). Therefore, to analyse the effect of relationship quality, we used a multiple regression in which we controlled for the rank of the subject. Residuals of each of these linear regression models do not differ significantly from a normal distribution. We used Spearman’s correlation coefficient (ρ) to assess the effect of proximity and all other behavioural measures of the subject on its pro-social tendency.

The Choice Experiment

Mean proportion of choices to give to ‘friend’ partners or to dominant partners, were compared to the subject’s initial side preference, established in the control condition of the pro-sociality experiment, using Wilcoxon signed ranks tests. Furthermore, to test the effect of the subjects’ proximity to their partners and all affiliative and aggressive behaviours of the subjects, we correlated (Spearman’s correlations) these effects with the proportion of choices.

All reported P-values are two-tailed. We consider an α between 0.10 and 0.05 as a trend and an $\alpha < 0.05$ as a significant effect.

RESULTS

The Pro-Sociality Experiment: Effect of Relationship Quality

We first tested whether the pro-social tendency of an animal was due to the quality of its relationship with its partner. We used multiple regressions, with both the rank of the subject and its relationship quality with the partner as independent variables, and the subject’s pro-social tendency as dependent variable. However, after controlling for the subject’s dominance rank, we did not find a significant effect of relationship quality on the subjects’ pro-social tendency towards their non-kin partners ($t = -0.004$, $\beta = 0.000$, 2/17 df, $p = 0.997$). In contrast, we did find a significant effect of relationship quality on the pro-social tendency of the subject within the kin-pairs ($t = 3.836$, $\beta = 0.805$, $n = 10$, $p < 0.01$). Yet, this result was in the opposite direction of what we expected, since animals were more pro-social towards related animals with which they had a worse relationship quality. This result may be a by-product of our choice of kin partners. Within the kin dyads, the subject that had the worst relationship quality with its partner was the alpha female, whereas the subject that had the best relationship quality with its partner was among the lowest ranking individuals (see table 1). Therefore, this result may reflect the finding that high-ranked individuals are pro-social, whereas low-ranked individuals are ‘a-

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social' (Massen et al. 2010, chapter 4). Accordingly, in a subsequent analysis without these two individuals the effect of relationship quality among kin disappeared ($t = -1.422$, $\beta = -0.01$, $n = 8$, $p = 0.214$).

Alternatively, it can be argued that subjects do not make a deliberate choice, but pull most often the slide on the side they are sitting. Therefore, we tested whether the pro-social tendency of an animal was due to its proximity to its partner. We first correlated pro-social tendency with the proportion of time the subjects spend in the area of their compartment closest to their partner. However, we did not find a relation between the subjects' proximity to their partner and their pro-social tendency (non-kin: Spearman's $\rho = 0.334$, $n = 20$, $p = 0.150$; kin: Spearman's $\rho = 0.226$, $n = 10$, $p = 0.530$). Moreover, we tested whether the time the subjects spend in the area of their compartment furthest away from their partner influenced their pro-social behaviour. Yet, again we did not find a relation between the subjects' distance to its partner and their pro-social tendency (non-kin: Spearman's $\rho = 0.220$, $n = 20$, $p = 0.351$; kin: Spearman's $\rho = 0.150$, $n = 10$, $p = 0.679$).

Lastly, subjects and their partner never showed any aggressive behaviour, and only four cases of affiliative behaviour were scored in the pro-sociality test. Consequently, no analyses on these behaviours have been performed.

The Choice Experiment

To test whether the long-tailed macaques preferentially choose to give to their 'friends', we compared the proportions of choices to give to the 'friend' with the subject's initial side preference, established in the control condition of the pro-sociality experiment. Subject's preference for the slide on the side of its 'friend' indeed tended to differ from the initial side (Wilcoxon signed ranks test: $T^+ = 137.5$, $n = 19$, $p_{\text{exact}} = 0.089$)(figure 2). This trend suggests that long-tailed macaques prefer to give to their 'friends' when given the choice between a 'friend' and a 'non-friend'.

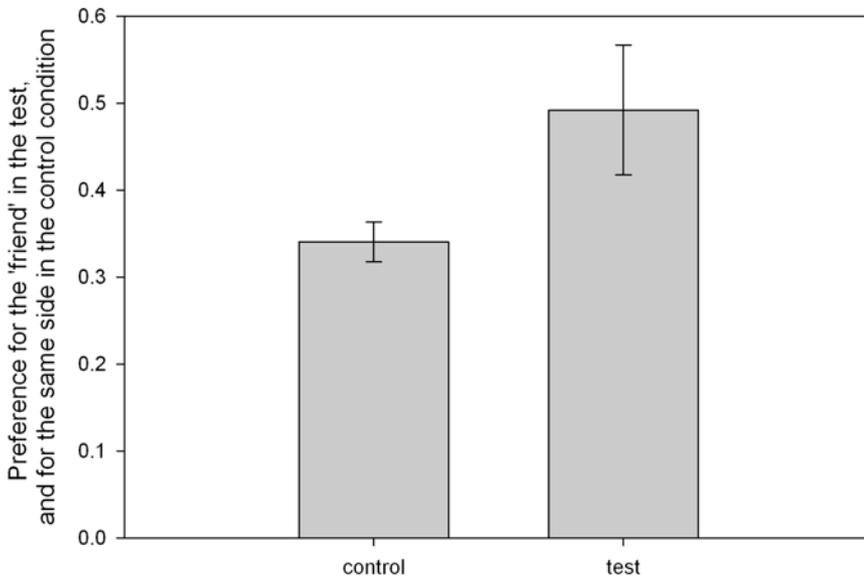


Figure 2. Mean preference \pm SEM of subjects ($n = 19$) to give to their 'friends' in the test, and the mean preference \pm SEM of the subjects for the slide on the same side in the control condition.

Since it has been shown that dominants and subordinates differ in their pro-social tendencies (Massen et al. 2010, chapter 4), we split the data into individuals that are dominant over both their partners ($n = 8$, see table 2) and individuals that are subordinate to both their partners ($n = 7$, see table 2). We found that dominant long-tailed macaques tend to prefer to benefit their 'friends', since their preference to pull in the slide on the side of their 'friends' tended to differ from their original side preference (Wilcoxon signed ranks test: $T^+ = 30.5$, $n = 8$, $p_{\text{exact}} = 0.086$) (figure 3). In contrast, subordinate individuals did not favour their friends, since their preference to pull in the slide on the side of their 'friends' did not differ from their original side preference (Wilcoxon signed ranks test: $T^+ = 16.5$, $n = 7$, $p_{\text{exact}} = 0.750$)(figure 3).

Instead of benefiting their 'friends', subjects may prefer to benefit the most dominant of their partners, since pro-social behaviour towards dominants may appease them or may result in receiving rank related benefits from these dominants in the future (Seyfarth 1977; Noë et al. 1991). Therefore, we tested the subjects' preference to give to the most dominant of their partners.

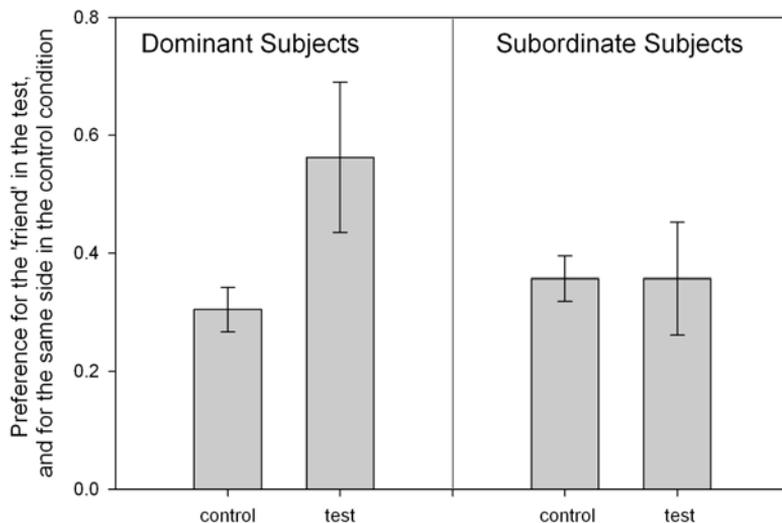


Figure 3. Mean preference \pm SEM to give to 'friends' in the test, and the mean preference \pm SEM for the slide on the same side in the control condition, for subjects that are dominant over both their partners (left, $n = 8$) and subjects that are subordinate to both their partners (right, $n = 7$).

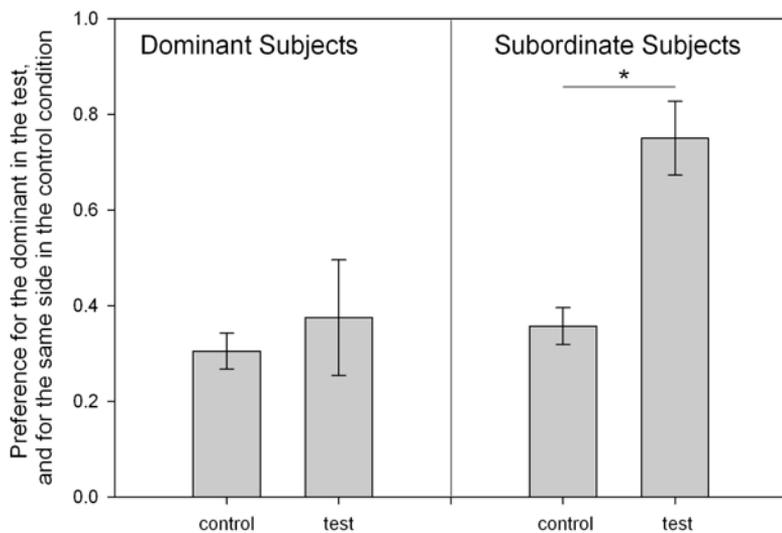


Figure 4. Mean preference \pm SEM to give to the most dominant partner in the test, and the mean preference \pm SEM for the slide on the same side in the control condition, for subjects that are dominant over both their partners (left, $n = 8$) and subjects that are subordinate to both their partners (right, $n = 7$). * $p < 0,05$.

Benefiting 'Friends' or Dominants

We found that the preference of dominant individuals to give to the most dominant of their partners did not significantly differ from their initial side preference (Wilcoxon signed ranks test: $T^+ = 23$, $n = 8$, $p_{\text{exact}} = 0.539$)(figure 4), suggesting that dominant individuals do not preferentially benefit the most dominant of their partners. In contrast, we did find a significant difference between the subordinates' preference to give to the most dominant partner and their initial side preference (Wilcoxon signed ranks test: $T^+ = 28$, $n = 7$, $p_{\text{exact}} = 0.016$)(figure 4), suggesting that subordinate individuals preferentially favour the most dominant of their partners.

Alternatively, subjects may not make a deliberate choice, but pull most often the slide on the side they are sitting. Therefore, we correlated the proportion of choices to give to each partner with the proportion of time they spend closest to that partner. However, we did not find a significant correlation between the proportion of choices for either side and the proportion of time spend in the corresponding side: i.e., when they preferentially sit on the right side of their compartment, they do not preferentially pull the right slide and vice versa (Spearman's $\rho = 0.040$, $n = 19$, $p = 0.872$).

Lastly, subjects and their partners never showed any aggressive behaviour and only three cases of affiliative behaviour were scored in the choice test. Consequently, no analyses on these behaviours have been performed.

DISCUSSION

From long-term observational studies it was expected that some animals, like humans, are more pro-social towards their 'friends' than towards their 'non-friends'. In this study we report on two experiments that test this hypothesis. While in the pro-sociality experiment we did not find an effect of relationship quality on the pro-social tendency of long-tailed macaques, in the choice experiment we did find that dominant subjects tend to prefer giving to their 'friends'.

In our first experiment, the pro-sociality experiment, we did not find an effect of relationship quality on the pro-social tendency of the long-tailed macaques. Earlier work suggested an important role for dominance rank in pro-social behaviour of long-tailed macaques (Massen et al. 2010, chapter 4): Whereas dominants benefit others, subordinates actually withhold their partners access to food. This effect may have obscured or overruled the effect of relationship quality in the pro-sociality experiment. Alternatively, strong social bonds, or 'friendships', seem to be maintained over the long term, and are tolerant to short term imbalances

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(Chapter 3). Therefore, it may be that in the short term setting of this experiment, the monkeys do not need to confirm the relationship with their partner and can let dominance effects prevail.

In the choice experiment, we found that subjects tend to prefer giving to their 'friends', yet this effect was not very strong. Again we took into account that dominance effects may have obscured or overruled the effect of relationship quality.

Therefore, we split our data in the choice experiment in individuals that are dominant over both their partners and individuals that are subordinate to both their partners. We showed that the generally more pro-social dominants tend to prefer giving to their friends. This suggests that dominants, who can afford to be pro-social in general (Massen et al. 2010, chapter 4), can express their social preferences in their pro-social behaviour. In contrast, subordinates prefer giving to the most dominant of their partner. This result is in line with previous research on primates that report that subordinates give more to dominants (Seyfarth 1977; Noë et al. 1991). Presumably this pro-social attitude towards high-ranking individuals is to gain future tolerance or support. Yet, subordinate individuals are generally not likely to behave pro-socially to their partner (Massen et al. 2010, chapter 4). Therefore, an alternative and more plausible explanation of their preference to give to the more dominant of two partners may be that this preference reflects a competitive strategy: i.e., if subordinates give to someone, they avoid giving to their direct competitors (i.e., animals close in rank to themselves). In addition, this preference shows that these subordinate long-tailed macaques are able to assess rank differences between others (i.e., third party relations), and consequently this result confirms earlier work on this species (Dasser 1987).

Alternatively, it can be argued that choices to give or to give to a particular partner are not deliberate, but merely a consequence of where the animal is sitting at the moment of the choice. However, the subject long-tailed macaques in our tests were able to pull both slides from any place within their compartment. Moreover, their proximity or distance to their partner in the pro-sociality and in the choice experiment were not predictive of their choice to give or of their choice to give to a particular partner in the two experiments. Therefore, we conclude that the choices these macaques made were not a consequence of their spatial proximity to their partners. Furthermore, their affiliative behaviour and their aggressive behaviour were also not predictive of the pro-social tendency of the subjects.

To conclude, observational studies provided the suggestion that long-tailed macaques will be more pro-social towards their 'friends' than towards their 'non-

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friends'. The two conducted experiments yielded only partially support for this hypothesis. In the pro-sociality experiment pro-sociality was not related to relationship quality. However, subjects tend to prefer giving to their 'friends' when they have the choice between a 'friend' and a 'non-friend' to give to. In particular, while dominants seem to have this preference for their 'friends', subordinates do not preferentially choose for their 'friends', but instead apply a more competitive strategy and avoid giving to close competitors. Therefore, dominance rank seems to determine which of two possible social relationships, friendship or dominance, prevails in directing pro-social behaviour, and only dominants seem to confirm their 'friendships' in the short-term setting of an experiment.

ACKNOWLEDGEMENTS

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Chapter 6

Inequity aversion and the effect of relationship quality in long-tailed macaques

Jorg J.M. Massen, Lisette M. van den Berg,
Berry M. Spruijt & Elisabeth H.M. Sterck

"Anybody can sympathize with the sufferings of a friend,
but it requires a very fine nature
to sympathize with a friend's success."

Oscar Wilde (1854-1900)

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ABSTRACT

Group-living animals may employ evolved implicit rules to maintain a balance between cooperation and competition. Inequity aversion, the aversive reaction to an unequal distribution of resources, is considered such a rule to avoid exploitation between cooperating individuals. Recent studies have revealed the presence of inequity aversion in several non-human species. However, inequity aversion may well depend on the partner's identity. While dominant individuals typically monopolize food, subordinate individuals obtain less preferred food and usually do not protest. Furthermore, 'friends' may pay less attention to equity than 'non-friends'. We first tested whether long-tailed macaques show inequity aversion. Dominant subjects express inequity aversion and its expression depends on effort. Second, we determined whether inequity aversion depends on relationship quality. However, an individual's inequity response was similar when tested with a 'friend' or a 'non-friend'. We conclude that inequity aversion exists in long-tailed macaques, but is independent of relationship quality. Furthermore, inequity aversion may not be domain specific. Lastly, inequity aversion may be an ancestral primate trait, independent of social organization.

INTRODUCTION

Cooperation exists in a myriad of varieties, though can only be evolutionary stable when the reward received by participants at least equals the effort put in. The pay-off of cooperative acts is thus important for the individuals involved. Cooperating individuals may avoid exploitation by using cognitively complex decision rules to monitor own and their co-operator's pay-off. Humans are considered highly cooperative (Fehr & Fishbacher 2003) and they prefer an equal pay-off of effort and reward in a cooperative act, and react aversive to unequal pay-offs, a preference known as Inequity Aversion (IA)(Adams 1963). Humans may react with either disadvantageous inequity aversion when they have less benefits than the other, or, less prevalent, with advantageous inequity aversion when they have more benefits than the other (Fehr & Schmidt 1999).

Until recently, IA was considered uniquely human. Yet besides humans, animals of numerous species cooperate with conspecifics. Especially species living in complex social systems with recognized individuals may have evolved a similar strategy to keep track of the balance in rewards received and given within a cooperative act. Accordingly, in their seminal paper Brosnan and de Waal (2003) found that brown capuchin monkeys (*Cebus apella*) also show IA. These monkeys refused to perform a task or rejected the reward when the monkey sitting next to them received a qualitatively better reward for the same task. These results were questioned and considered to depend on frustration effects (Dubreuil et al. 2006; Roma et al. 2006). However, when controlling for such effects, a similar reaction to inequity was still found in these capuchin monkeys, and especially performing a task in order to obtain the reward is considered crucial for IA (Brosnan & de Waal 2006; van Wolkenten et al. 2007). Moreover, IA has been reported for chimpanzees (*Pan troglodytes*; Brosnan et al. 2005) cottontop tamarins (*Saguinus oedipus*; Neiworth et al. 2009), and domestic dogs (*Canis familiaris*; Range et al. 2009a), all species known for their cooperative skills. Furthermore, when given the choice, brown capuchin monkeys (Fletcher 2008), chimpanzees (Melis et al. 2009), and cottontop tamarins (Cronin & Snowdon 2008) prefer an equitable distribution of rewards. Altogether, these studies indicate that IA in animals is not an artefact, but a rule found in at least some animal species.

The presence of IA in animals may depend on the presence of cooperation. Cooperation, however, is not a unitary phenomenon and the tendency to cooperate will vary between group members. Therefore, individuals may differ in how they employ mechanisms proposed to regulate cooperation, such as IA. First, it may depend on when animals show cooperation. Cooperation can serve many functions;

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from cooperative hunting (e.g., Boesch & Boesch-Acherman 2000) to coalitions to dethrone a dominant individual (Noë & Sluijter 1990). Second, the tendency to cooperate depends on one's own position in the group (van Schaik et al. 2004). Third, the tendency to cooperate depends on the relationship with the partner (Melis et al. 2006a). Therefore, the conditions in which IA will be found may depend on the nature of the paradigm, the position of the partners in the dominance hierarchy and partner identity.

First, we hypothesize that if IA is domain specific, only those species that cooperate to obtain food (i.e., cooperative hunting; capuchin monkeys: Rose 1997; chimpanzees: Boesch & Boesch-Acherman 2000; wolves, *Canis lupus*: Mech 1970), or at least share food (e.g., capuchin monkeys: Perry & Rose 1994; chimpanzees: Boesch & Boesch-Acherman 2000; tamarins: Feistner & Price 1999) will pass the IA tests in the food domain. IA aversion has only been tested with a food paradigm, mainly for logistic reasons. If, however, IA is not domain specific, not only species that cooperate in the food domain, but also species that cooperate in the social domain (e.g., show coalitionary support), may express IA in a food paradigm.

Second, we hypothesize that cooperation, and thus IA, may depend on an individual's social position in the group (van Schaik et al. 2004). In groups with a clear, and thus despotic, dominance hierarchy, animals often suffer an unequal distribution of food in their everyday lives, where high-ranking individuals have access to preferred food first, leaving the subordinates with less preferred food (van Schaik 1989; Sterck et al. 1997). It has been suggested that despotic species will not show IA (Neiworth et al. 2009). We, however, expect that dominants in the presence of a subordinate will show IA.

Third, we hypothesize that IA, like cooperation (Melis et al. 2006a), may also depend on the quality of the partners' relationship. In humans rules for cooperation among friends differ from those with strangers or acquaintances. The relationship between friends is characterized by concern for each other's welfare, benefiting the other when a need exists, and friends will distribute resources mainly according to differences in need, whereas strangers and acquaintances prefer equal distributions (Deutsch 1975; Clark & Mills 1979). Similarly, group-living animals can have differential bonds with group members (Aureli et al. 1997) and the closest social bonds have been compared to human friendship (Smuts 1985; Silk 2002b). Also in animals it may be in one's own interest to help a 'friend', even without a contingent return (Roberts 2005). There are some indications that quality of the participants' relationship is important in the inequity response of chimpanzees (Brosnan et al. 2005) and dogs (Range et al. 2009b). However, whether it is indeed

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the relationship quality that affects the contingency of exchange processes is still unclear and remains to be tested.

Long-tailed macaques (*Macaca fascicularis*), a highly hierarchical species (Thierry 2000), are not known to cooperatively share food. However, they do exhibit several cooperative patterns in behaviour for which IA may be beneficial. Long-tailed macaques form alliances in aggressive contexts (de Waal 1977; van Noordwijk & van Schaik 1985), trade beneficial behaviours reciprocally (grooming: Gumert & Moon-Ho 2008), interchange behaviours on a market place (mating: Gumert 2007a; b) and can behave pro-socially (Massen et al. 2010, chapter 4). Therefore, we expect long-tailed macaques to show IA when under-benefited. The present study is designed to test whether long-tailed macaques show IA and whether the response to inequity depends on the relationship quality of the dyad tested. The study consists of two experiments. In the first experiment we established whether long-tailed macaques express IA in tasks with different effort levels. In the second experiment we tested the effect of relationship quality on IA by pairing the subject with both a 'friend' and a 'non-friend'.

Experiment 1: IA in Long-Tailed Macaques

In our first experiment, we determined whether long-tailed macaques show IA and whether this depends on the effort required to obtain the food reward. Long-tailed macaques show strong contest competition at food patches and form steep linear dominance hierarchies (van Noordwijk & van Schaik 1987; Sterck & Steenbeek 1997). To enhance the chance of finding disadvantageous IA, we tested dominant individuals paired with a subordinate partner. In addition, subordinate partners may refuse a qualitative better reward when the dominant subject receives a less preferred reward, and thus show advantageous IA. Furthermore, since we expect to find no IA among 'friends', we first only tested individuals paired with a partner with whom they did not have a particularly good relationship.

The dominant individuals of these 'non-friend' non-kin dyads were tested in seven conditions. The effort level was varied: subject and its partner both did not have to work (i.e., were provisioned), or were both required to work a little, or had to work hard for their reward. The reward of the subject was either of similar (equity) or of lower (inequity) quality than the reward of its partner. Furthermore, since Adams (1963) defined inequity both in reward and effort, we tested also effort inequity. In this last condition the subject had to work hard for the less preferred reward, whereas its partner was provisioned with the more preferred reward. These seven conditions allowed us to determine the presence of disadvantageous IA for

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both effort- and reward inequity in this species. Moreover, it allowed us to determine whether subordinate individuals show advantageous IA when treated better than their dominant partners.

METHODS

Subjects and Housing

The study subjects were 12 long-tailed macaques that all lived in the same social group at the 'Ethologie-station' of the Utrecht University, the Netherlands. The social group consisted of 33 individuals with males and females from all life stages. The group was split off from a larger group in 1994 and has since been stable, and most animals were born in this group. The group was housed in an indoor enclosure (235 m³) with access to an outdoor compound (800 m³), with plenty of climbing facilities and regular provisioning of enrichment. Water and commercial monkey chow were available *ad libitum*. Alternately fruit, vegetables or bread were daily provided to the group half an hour after the day's testing was completed. This feeding schedule was followed regardless whether the animals participated in a test that day. The animals were never food or water deprived.

The dominance hierarchy in the group and the friendship status among group members were analysed prior to the experiments. The dominance hierarchy was determined by analyzing unidirectional submissive behaviours ('bare teeth' and 'make room' without prior aggressive behaviour) that were observed *ad libitum*. Results were arranged in a socio-matrix. The dominance order most consistent with a linear hierarchy was determined with MatMan 1.1 (linearity index: $h' = 0.59$, $p < 0.05$) (de Vries 1995; 1998) and the dominance hierarchy was significantly linear. Rank-numbers were assigned with 1 for the most dominant individual and 33 for the least dominant individual. Rank-difference was calculated by subtracting the rank-number of the subject from that of its partner.

To measure relationship quality, we conducted time-sample scan observations (2-4 times a day, with at least one hour between each observation) of all [independent] group members during the 10 months prior to testing, to assess who is sitting with whom (contact-sitting) and who is grooming whom. For each individual, potential friends were individuals in the upper quartile of contact sitting and grooming. Only individuals that score in the highest quartile in both contact sitting and grooming were considered friends. With these rules for friends we found 25 friends out of in total 497 non-kin dyads. All other dyads were considered non-friends.

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To test the effect of relationship quality on the inequity response, we used the data of contact sitting and grooming. We ordered relationship quality based on the degree of contact sitting and grooming per individual. The individual with whom they sat most often in contact was given number 1 and that with whom they sat least often together was given number 33. When an individual sat a same proportion of time together with two individuals, they were given the average number, e.g., if they were 4 and 5, they were both numbered 4.5. The same was done for grooming. For each partner both numbers were added and divided by two, leading to a 'relationship quality' ordering ranging between 1 and 33.

Subjects and their test partners were adult or subadult monkeys (ranging in age between 3 and 21 years) that reliably could pull in a tray of the test apparatus (figure 1). Pairs of subject and partner were chosen according to their 'friendship-status' and difference in dominance rank. A pair of subject and test partner was never kin or friends, and were furthermore chosen to have a rank difference as large as possible, in which the subject was always the dominant animal.

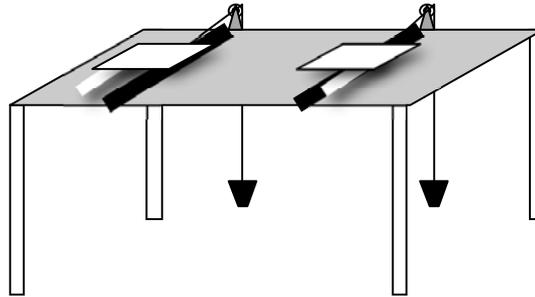


Figure 1. The test-apparatus: The white trays are on top of rails (black bar). In the provisioning conditions these trays are baited and pushed towards the animals. In the effort conditions the trays are counterweighted and the monkey has to pull the white handle to get the bait, placed on top of the tray, in range.

Based on these conditions, we selected for the first experiment five male-male pairs, five female-female pairs, two male-female pairs and two female-male pairs. The mean rank difference in the pairs was 12.4 (s.d. 7.61)(table 1). Although we tried to avoid using animals more than once in the experiment, two animals were used twice as subject, five animals twice as partner, and two animals as both partner and subject. In the analysis, multiple test results of one subject animal were averaged.

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Table 1. Abbreviation of name, and sex and age of subject and test partner, and rank difference of dyads in experiment 1.

Subject			Partner			Rank difference
Re	♂	13	Ku	♂	14	27
Wo	♀	11	In	♂	6	23
Al	♀	21	Tr	♀	7	15
Sa	♀	9	Ra	♀	14	12
Kr	♀	18	La	♀	12	12
Tb	♂	5	Fr	♀	18	3
Ju	♂	5	Sn	♂	4	14
To	♂	7	La	♀	12	5
An	♀	4	Tb	♂	5	6
Bu	♂	4	Ku	♂	14	18
Co	♀	3	Tr	♀	7	4
Wo	♀	11	Ra	♀	14	19
Sn	♂	4	In	♂	6	3
To	♂	7	Bo	♂	5	12

Test Environment

The training and testing procedure of the animals was as follows: the complete group entered from their home cage the connected test cage of 32 m³ (4 m x 4 m x 2 m). From this test cage the subject and its partner entered the test chamber (110 cm x 55 cm x 80 cm). The test chamber was divided in half by a transparent lexan screen, to allow visual contact between the two monkeys while keeping them physically separated. During the tests, dependent offspring was always allowed into the test chamber with its mother. Both subjects and partners were trained to be separated in the test chamber and to pull a tray of the apparatus (figure 1). Neither subject nor test partner was tested more than once on one day and there was always at least one day between two conditions for both subject and test partner. Both subjects and their partners participated in a series of food preference tests to determine their preference for a slice of apple over a slice of cucumber and a slice of mango over a slice of cucumber. For each comparison, each animal participated in three series of 10 trials in which both food items were presented simultaneously and the tested animal could only obtain one food item. The rewards were semi-randomly distributed over left and right. All animals preferred apple over cucumber in 80% or more of all choices, and mango over cucumber also in 80% or more of all choices. We used two different preferred food types, since a preference for a reward may decrease when this reward has been obtained frequently.

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Test Conditions

Subjects and their test partners participated in 7 test conditions, depending on the effort required in the equal or unequal reward distribution: No effort equity, no effort inequity, small effort equity, small effort inequity, large effort equity, large effort inequity and large effort reward and effort inequity (table 2). In each condition the subject and its partner sat side by side in the test chamber. A subject's initial effort level was determined at random, and the equity condition of that effort level was always tested first and followed by the inequity condition two days later. Each test session consisted of 20 trials of a single condition for each animal. Each trial was a minute apart from the previous one. Trials for the subject and its test partner alternated, started with the subject, and the interval between them was half a minute.

Table 2. Table of the seven test conditions showing the rewards offered to subject and partner (Cuc. = cucumber) and the effort needed to pull in the tray.

Condition	Reward Subject	Reward Partner	Effort Subject	Effort Partner
1. No effort - <i>Equity</i>	Cuc.	Cuc.	No	No
2. No effort - <i>Inequity</i>	Cuc.	Apple	No	No
3. Small effort - <i>Equity</i>	Cuc.	Cuc.	0.5 kg	0.5 kg
4. Small effort - <i>Inequity</i>	Cuc.	Apple	0.5 kg	0.5 kg
5. Large effort - <i>Equity</i>	Cuc.	Cuc.	2.3 kg	2.3 kg
6. Large effort - <i>Inequity</i>	Cuc.	Mango	2.3 kg	2.3 kg
7. Large effort - <i>Reward & effort inequity</i>	Cuc.	Mango	2.3 kg	No

In the 'no effort' conditions the experimenter pushed a tray with a reward to the subject and to the partner. In the 'small' and 'large effort' conditions the monkeys had to pull in the tray themselves and this tray was counterweighed with 0.5 and 2.3 kg respectively. 0.5 kg was not too hard for the monkeys to pull. However, 2.3 kg was the maximum weight our smallest individual could reliably pull. The reward distribution between the subject and its partner was either equal: equity, or unequal: inequity. The subject was always offered the cucumber, the partner, depending on the condition and the test, was offered cucumber, apple or mango. In the 'large effort' conditions an extra condition was added, in which the subject had to pull the heavy weight to obtain the less preferred reward, while the partner did not have to pull in the tray itself and the experimenter pushed the tray with the more preferred reward to it, thus creating both reward and effort inequity (table 2).

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Measures

As a measure of willingness to participate in the test, we scored whether an animal took the reward in the provisioning conditions and whether the animal successfully pulled in the tray and then took the reward in those conditions where an effort was needed (Brosnan & de Waal 2003; Brosnan et al. 2005). A refusal to accept the reward was defined as a trial in which the subject did not take the reward within 60 seconds in the provisioning conditions. A refusal to conduct the task was defined as a trial in which the subject did not pull in the tray and take the reward within 60 seconds. A stopwatch was used to determine the beginning and ending of a trial, and thus whether the reward would be taken back after the subject refused to accept or conduct the task within the 60 seconds. The delay in conducting the task or taking the reward was defined as the time it took the subject to either conduct the task or take the reward (between 0 and 60 seconds) after the reward was placed on the tray. To test for IA we compared these measures between the equity- and inequity conditions within the different effort levels (no effort, small effort and large effort).

Subjects may not immediately recognise the fact that reward distributions are unequal in the inequity conditions, but learn over time (Brosnan & de Waal 2003). Therefore, we also compared the proportion of rewards taken by the subject in the last 8 trials between equity and inequity conditions.

To test the effect of several variables on IA, we calculated an inequity response. The inequity response is defined as the proportion of rewards taken by the subject in the inequity condition minus the proportion of rewards taken by the subject in the equity condition.

All test sessions were recorded using a Sharp VL-E610 video 8 recorder, and data were coded by J.J.M.M. Coding could not be blind since subjects, their behaviour and conditions were visible. 15% of all tapes were recoded by L.M.v/d B.. Inter-observer reliability was calculated using Cohen's kappa for the proportion of rewards taken and a Pearson's correlation for the latencies. Both proportion of rewards taken and latencies were scored almost perfectly similar (Kappa = 0.995 and Spearman's correlation coefficient = 0.996, $n = 840$, $p < 0.0001$).

Data Analysis

Our data were not normally distributed; therefore, we used non-parametric tests. Since the pairs of subject and their partner in both experiments remained the same in all conditions, we used paired-sample comparisons. When Wilcoxon signed

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ranks tests were applied, we show the sum of positive ranks and the exact p-values. In this study $\alpha = 0.05$ and tests were 2-tailed.

RESULTS

Evaluating Own Effort and Reward

We first tested whether the long-tailed macaques pay attention to their own effort and reward. Therefore, we compared the proportion of rewards taken by all animals (both subjects and partners) in the equity conditions of the three different effort levels. We found an overall difference in the proportion of rewards taken (Friedman's test; $n = 19$, $\chi^2 = 15.84$, $df = 2$, $p = 0.001$)(figure 2). Post-hoc analysis showed a significant drop in the proportion of rewards taken between no- and large effort (Wilcoxon signed ranks test; $n = 19$, $T^+ = 152$, $p < 0.001$) and between small- and large effort (Wilcoxon signed ranks test; $n = 19$, $T^+ = 117.5$, $p = 0.008$). There was no significant difference in proportion of rewards taken between no- and small effort (Wilcoxon signed ranks test; $n = 19$, $T^+ = 62.5$, $p = 0.115$)(figure 2).

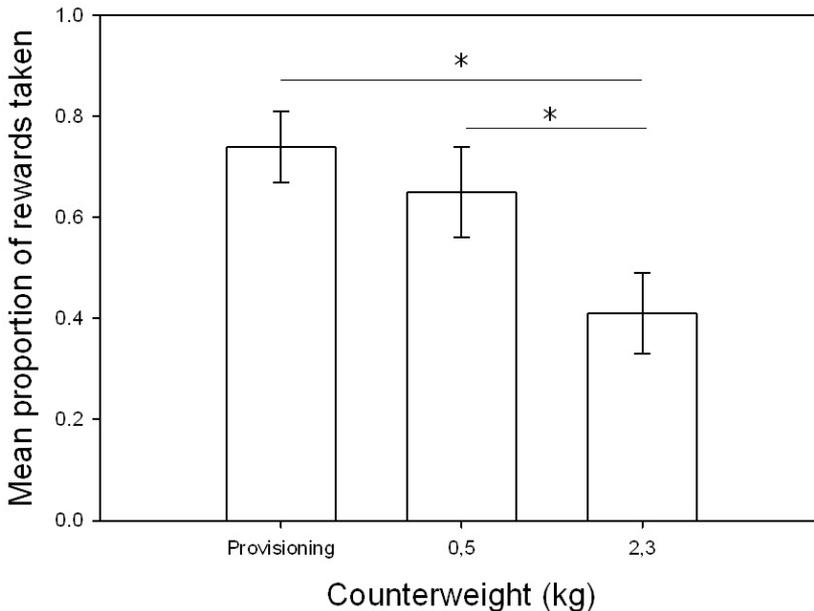


Figure 2. Mean proportion of rewards taken \pm s.e.m. by all animals (both subjects & partners)($n = 19$) in the equity conditions when provisioned, with small effort (pulling in a counterweight of 0.5 kg), and with large effort (pulling in a counterweight of 2.3 kg). * $p < 0.05$.

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Disadvantageous Inequity Aversion

To test for IA we compared the proportion of rewards taken by the subjects in the equity condition with the proportion of rewards taken in the inequity condition for the three effort-levels separately (figure 3). When the subjects were provisioned we found no significant difference in the proportion of rewards taken by the subjects between the equity and inequity condition (Wilcoxon signed ranks test; $n = 12$, $T^+ = 21$, $p = 0.719$). In the small-effort conditions, however, we did find a significant difference in the proportion of rewards taken between the equity and inequity condition (Wilcoxon signed ranks test; $n = 12$, $T^+ = 34$, $p = 0.023$). The subjects took significantly less rewards when their partners received a more preferred reward for the same effort. In the large-effort conditions, however, we found no significant difference in the proportion of rewards taken between the equity and inequity condition (Wilcoxon signed ranks test; $n = 12$, $T^+ = 8.5$, $p = 0.211$)(figure 3). Moreover, also no significant difference was found in the proportion of rewards taken between the equity and reward- and effort inequity condition (Wilcoxon signed ranks test; $n = 12$, $T^+ = 15.5$, $p = 0.250$)(figure 3). Altogether, long-tailed macaques showed disadvantageous IA in the small effort condition.

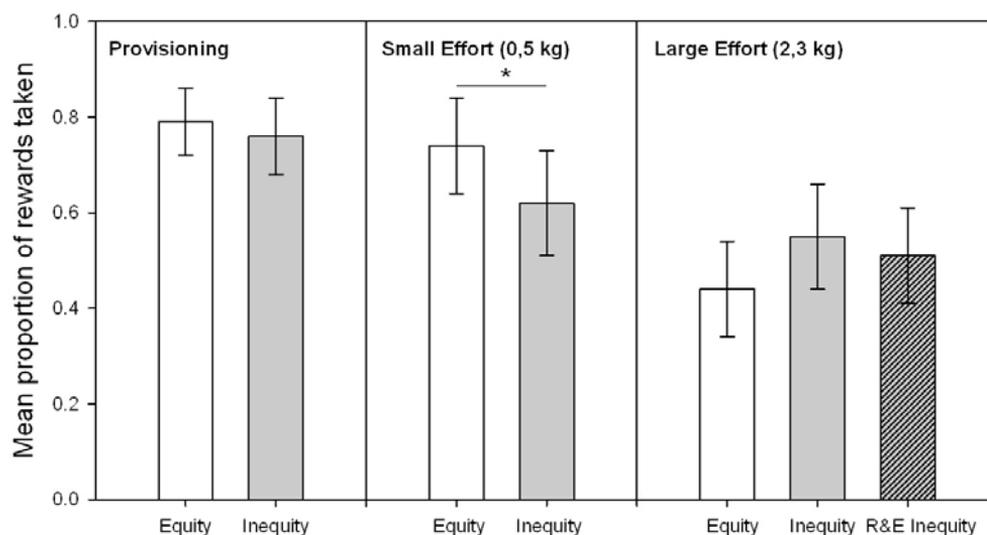


Figure 3. Mean proportion of rewards taken \pm s.e.m. by dominant subjects ($n = 12$) in the equity- (white bars), inequity- (grey bars), and reward&effort inequity (striped bars) conditions when provisioned, with small effort (pulling in a counterweight of 0.5kg), and with large effort (pulling in a counterweight of 2.3kg). * $p < 0.05$.

Advantageous Inequity Aversion

To test for advantageous IA in the subordinate partners, we compared the proportion of rewards taken by these subordinate partners in the equity conditions with the proportion of rewards taken in the inequity conditions (figure 4). We found no significant difference in the proportion of rewards taken between equity and inequity conditions when the subordinate partners were provisioned or when only a small effort was required to perform the task (Equity vs. inequity: Wilcoxon signed ranks tests: No effort: $n = 9$, $T^+ = 3$, $p = 0.156$; Small effort: $n = 9$, $T^+ = 4$, $p = 0.219$). In the large effort conditions subordinate partners took significantly more rewards when they received the more preferred reward (Wilcoxon signed ranks test: $n = 9$, $T^+ = 0$, $p = 0.008$). A similar trend was found between the reward and effort inequity condition and the equity condition in the large effort conditions (Wilcoxon signed ranks test: $n = 9$, $T^+ = 4$, $p = 0.055$)(figure 4). Altogether, we have no evidence for advantageous IA in long-tailed macaques.

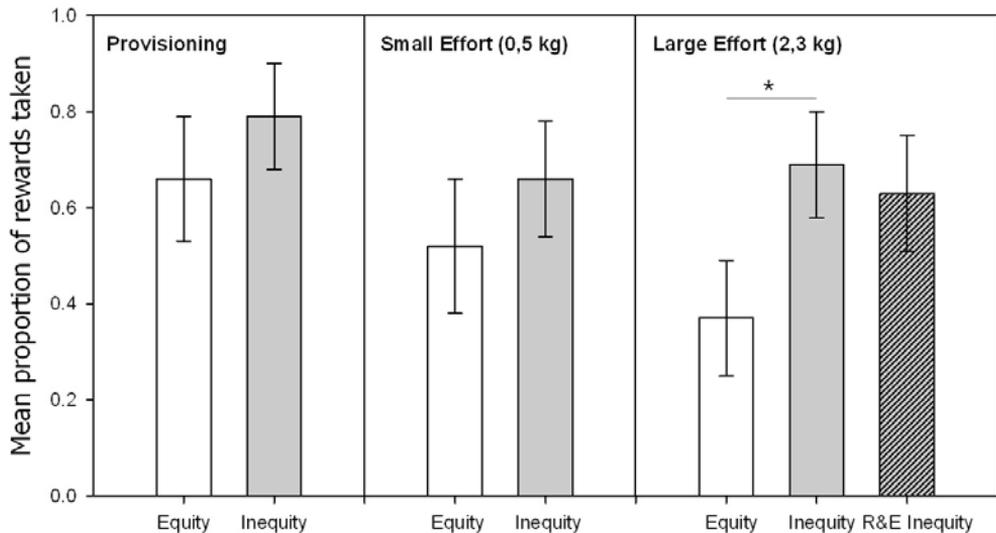


Figure 4. Mean proportion of rewards \pm s.e.m. taken by subordinate partners ($n = 9$) in the equity- (white bars), inequity- (grey bars), and reward&effort inequity (striped bars) conditions when provisioned, with small effort (pulling in a counterweight of 0.5kg), and with large effort (pulling in a counterweight of 2.3kg). * $p < 0.05$.

Rank and Relationship Quality Effects

Further analyses of the inequity response of the dominant subjects in the small-effort conditions revealed no significant effect of subject's rank (Spearman's $\rho = 0.152$, $n = 14$, $p = 0.603$), the pair's rank difference (Spearman's $\rho = 0.077$, $n = 14$, p

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= 0.794), or the pair's relationship quality (Spearman's $\rho = -0.180$, $n = 14$, $p = 0.538$) on this response.

Results (and statistics) of the analyses of the latencies were usually not significant, but were usually longer in conditions where subjects or partners were less likely to accept the reward. The results (and statistics) of the analyses of only the last 8 trials were similar to those of the proportions of rewards taken. All these results and statistics can be found in the appendix at the end of this chapter.

DISCUSSION EXPERIMENT 1

Our results show that long-tailed macaques work less for the same reward when workload increases, and at high workload work more for a more preferred reward. This indicates that long-tailed macaques pay attention to the pay-off of their own effort and reward, as is found in many mammals (Cooper & Mason 2001). This is a prerequisite necessary for IA. Moreover, our results show that in the small-effort conditions the subjects exhibit IA. In contrast, they do not show IA when provisioned. This supports the argumentation of van Wolkenten et al. (2007) that an effort to obtain a reward is required to find IA.

In the large-effort conditions, however, the long-tailed macaques showed no IA. This result might be due to the general low proportion of rewards taken in the large-effort conditions, which might create smaller variance.

Our results cannot be explained by the frustration effect (Roma et al. 2006; Silberberg et al. 2009), since, apart from the two subjects that were used as both subject and partner, none of the subjects ever received the more preferred reward for performing the task. Omitting the results of those two subjects that were used as both subject and partner, still gives a significant difference between the equity and inequity condition with small effort (Wilcoxon signed ranks test; $n = 10$, $T^+ = 26$, $p = 0.047$).

We expected an effect of rank difference and relationship quality on the response to inequity. However, we did not find such effects. Since the design of the study was to find IA, and we only tested dominant individuals with non-friend partners, variation in both rank relationship and relationship quality were rather low and, therefore, possible effects may have been obscured. To test the effect of relationship quality in more detail, we designed a second experiment.

Inequity Aversion and Relationship Quality

EXPERIMENT 2: FRIENDSHIP AND IA IN LONG-TAILED MACAQUES

In the second experiment we tested the effect of relationship quality on inequity aversion. Since friends are expected to distribute resources according to differences in need, instead of equitable distributions (Deutsch 1975; Clark & Mills 1979), it is expected that friends are more tolerant to inequity than non-friends. To determine this, we tested subjects with both a friend and with a non-friend partner. In this experiment we used the same small effort conditions as in experiment 1, since in this condition the dominant individuals expressed IA. Hence, individuals had to work a little to obtain a reward, as did their partners. Partners received either a similar (equity condition) or a more preferred (inequity condition) reward.

METHODS

Subjects

The study subjects for experiment 2 were drawn from the same social group as the ones in experiment 1. We selected thirteen individuals, and paired them with both a non-kin friend and a non-kin non-friend, yielding six male and seven female subjects with same-sex friends and non-friends. The friend dyads had a mean rank difference of 5.0 (s.d. 9.2) and the non-friends dyads had a mean rank difference of 8.3 (s.d. 7.7)(table 3). The data for friendship status and dominance hierarchy of all dyads were the same as in experiment 1.

Table 3. Abbreviation of name, and sex and age of subject, and of its friend and non-friend test partners, as well as rank difference between subject and its friends and subject and its non-friends in experiment 2.

Subject	Sex	Age	Friend	Sex	Age	Δ-rank	Non-Friend	Sex	Age	Δ-rank
Al	♀	21	Fr	♀	18	10	Tr	♀	7	15
Kr	♀	18	Ra	♀	14	14	La	♀	12	12
Wo	♀	11	Tr	♀	7	18	Ra	♀	14	19
To	♂	7	In	♂	6	11	Bu	♂	4	-4
An	♀	4	Co	♀	3	10	La	♀	12	13
Tb	♂	5	Sn	♂	4	10	Bo	♂	5	14
Sa	♀	9	Ta	♀	5	-6	Fr	♀	18	6
Ju	♂	5	Bu	♂	4	2	To	♂	7	6
Co	♀	3	Sa	♀	9	-7	Ra	♀	14	5
Ku	♂	14	In	♂	6	-4	Bo	♂	5	-3
Sn	♂	4	On	♂	5	-4	Bo	♂	5	-2
Bu	♂	4	Ju	♂	5	-5	In	♂	6	10
Ta	♀	5	Tr	♀	7	16	Ra	♀	14	17

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Test Conditions

Test environment, apparatus and measures were the same as in experiment 1. As in experiment 1, in each condition the subject and its partner sat side by side in the test chamber. Whether a subject would be tested first with its friend or non-friend was counterbalanced. The complete test with the first partner would first be finished before testing the individual with its other partner. In each dyad the equity condition was always tested first. To control for expectancy violation, the preferred reward was visible in both the equity and the inequity condition. Each test session consisted of 20 trials of a single condition for each animal. Each trial was a minute apart from the previous one. Trials alternated between partner and subject and we always started with the partner. Neither subjects nor test partners were tested more than once on one day and there was always at least one day between two conditions for both subjects and test partners.

RESULTS

Inequity Aversion

First, we tested whether we could reproduce the results from experiment 1. Although we now controlled for expectancy violation (the preferred reward was always visible), we again found that the long-tailed macaques show IA. The mean proportion of rewards taken by the subject was significantly lower in the inequity conditions compared with the equity conditions (Wilcoxon signed ranks test: $n = 13$, $T^+ = 56$, $p = 0.038$)(figure 5).

Inequity Aversion and Relationship Quality

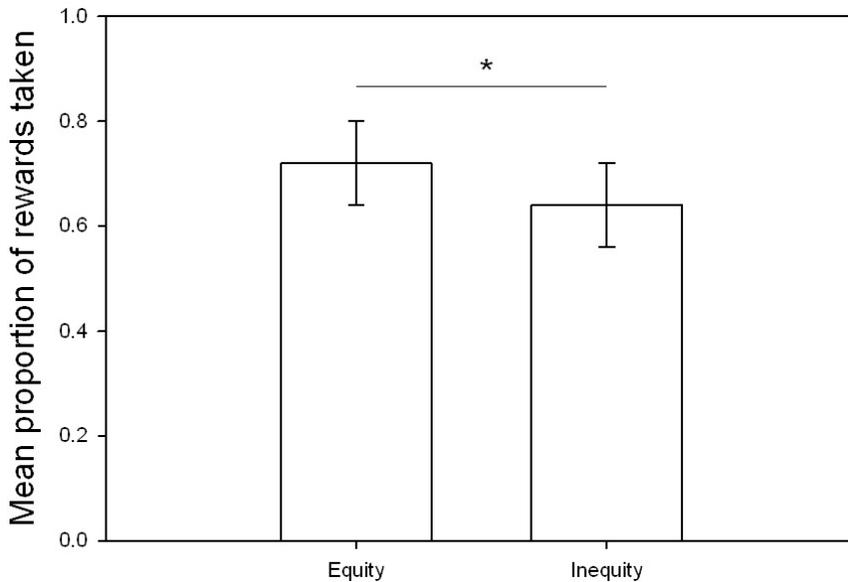


Figure 5. Mean proportion of rewards taken \pm s.e.m. by the subjects ($n = 13$) in the equity and inequity conditions. * $p < 0.05$.

Alternative Explanations

To test whether the inequity response in the small effort condition of experiment 1 was due to the violation of the monkey's expectancy, we compared the proportion of rewards taken in the equity conditions by those animals that were subject in both experiments. In experiment 2 in the equity condition the more preferred reward was always visible, while this was not the case in this condition in experiment 1. When expectancy violation is present this will result in a lower proportion of rewards taken in experiment 2 than experiment 1. However, we did not find a significant difference in the proportion of rewards taken by those animals in the equity conditions with small effort in experiment 1 and the equity condition with small effort in experiment 2 (Wilcoxon signed ranks test: $n = 11$, $T^+ = 16$, $p = 0.844$).

Inequity Aversion and Friendship

The effect of relationship quality on IA was determined by testing whether the response to inequity differs when subjects were paired with a friend compared to when paired with a non-friend. However, no significant difference in inequity response was found (Wilcoxon signed ranks test: $n = 13$, $T^+ = 29.5$, $p = 0.445$)(figure 6).

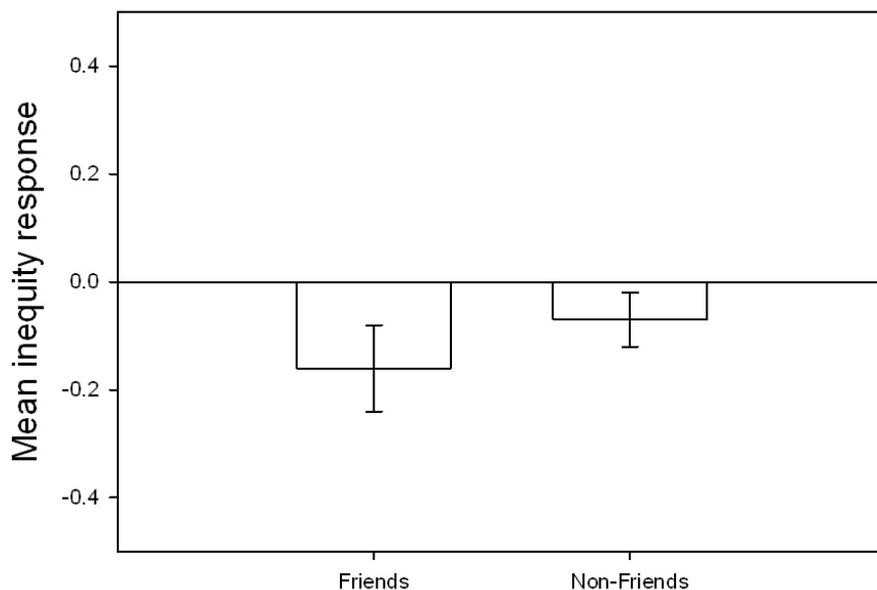


Figure 6. Mean inequity response \pm s.e.m. (calculated as: prop. of rewards taken in the inequity condition – prop. of rewards taken in the equity condition) of the subjects ($n = 13$) with friend and non-friend partner.

Results (and statistics) of the analyses of the latencies were usually not significant, but were usually longer in conditions where subjects or partners were less likely to accept the reward. The results (and statistics) of the analyses of only the last 8 trials were similar to those of the proportions of rewards taken. All these results and statistics can be found in the appendix at the end of this chapter.

DISCUSSION EXPERIMENT 2

The results of experiment 2 show again IA in long-tailed macaques. Furthermore, we show in experiment 2 that this effect cannot be explained by expectancy violation (Dubreuil et al. 2006), since we controlled for that. In addition, the results of experiment 2 show that the inequity response measured in experiment 1 also cannot be explained by expectancy violation.

Our results show no difference in inequity response between friend- and non-friend dyads. Apart from the absence of an effect of relationship quality on the inequity response, this result may also be explained by procedural unfairness, since it was the experimenter, and not the partner, that was responsible for the unequal distribution of the rewards. Alternatively, as the chimpanzees in the Brosnan et al.

Inequity Aversion and Relationship Quality

(2005) experiment, these long-tailed macaques have resided in a stable social group for a long period, and relationship quality in general may be high and variation herein low.

GENERAL DISCUSSION

IA in Long-Tailed Macaques

We hypothesized that dominant long-tailed macaques will show Inequity Aversion (IA) when treated unequally, since it contrasts with the distribution of preferred food-items in their everyday live. IA consists of two parts, first, the evaluation of one's own pay-off and, second, the comparison of this evaluation with the pay-off of another individual. We determined whether long-tailed macaques exhibited both capacities. Long-tailed macaques evaluated their own costs and benefits, similar to many other mammals (Cooper & Mason 2001). With increasing effort needed, the rate of refusals to perform the task for the same reward also increased. Moreover, long-tailed macaques perform the task more often when the reward is more preferred if a large effort was needed to perform the task. Therefore, we conclude that long-tailed macaques comply with the first condition of IA.

Moreover, dominant long-tailed macaques comply with the second condition and can show IA when their partner obtains a more preferred food item. In addition, our results indicate that an effort to obtain the reward is crucial for finding IA, since long-tailed macaques do not show IA when they are provisioned and no effort is required. This is similar to capuchin monkey studies that required an effort from their subjects (Brosnan & de Waal 2006; van Wolckenten et al. 2007) and counters the claim of absence of IA in studies that did not require an effort from their subjects (Dubreuil et al. 2006; Roma et al. 2006; Silberberg et al. 2009). Therefore, our results confirm that effort is a crucial factor for IA.

The original findings of IA (Brosnan & de Waal 2003; Brosnan et al. 2005) have been attributed to either a frustration effect (e.g., frustration since one receives a less preferred reward than on a previous trial)(Roma et al. 2006; Silberberg et al. 2009), or the violation of expectancy (e.g., frustration due to not receiving a visible preferred reward)(Dubreuil et al. 2006). We controlled for both phenomena in the design of our study and still found IA. Therefore, IA in long-tailed macaques cannot be explained by either effect. Moreover, we tested whether expectancy violation actually affected long-tailed macaques' behaviour, and found no change in their acceptance of rewards. Also capuchin monkeys do not show expectancy violation (van Wolckenten et al. 2007), but it has been found in cottontop tamarins (Neiworth

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et al. 2009). Nonetheless, also cottontop tamarins showed IA after controlling for expectancy violation. Therefore, the proposed alternative explanations cannot explain the IA found in long-tailed macaques and other species.

IA and Domain Specificity

IA in animals has been tested using a food paradigm. Thus far, IA was only tested in species that also cooperate in the food domain. When IA is domain specific, IA will only be found in these species and not in species that do not share food or cooperate to obtain food. Our study employed a similar food paradigm and showed IA in a species that does not cooperate in the food domain, yet does cooperate in the social domain (e.g., coalitionary support: de Waal 1977; van Noordwijk & van Schaik 1985). That also these animals react to an unequal distribution of food suggests that IA is not domain specific and that IA is a higher order capacity that they can employ in several contexts.

IA and Relationship Characteristics

We hypothesized an effect of the social organisation of long-tailed macaques on the expression of IA. We proposed that only dominants would express IA when paired with a subordinate, and that subordinates would not when paired with a dominant. In the present study we did find that dominants express IA, but we only tested dominant individuals and thus did not test the second part of our hypothesis.

We furthermore hypothesized an effect of relationship quality on the expression of IA. A relation between IA and relationship quality is suggested in the human literature (Clark & Mills 1979), yet was, to our knowledge, never formally tested in non-human animals. Post-hoc analyses showed that social closeness in chimpanzees may inhibit the expression of IA (Brosnan et al. 2005), and that more tolerant dogs also expressed less IA (Range et al. 2009b). In the present study, we designed our second experiment to test subjects with a friend and with a non-friend. Nevertheless, we did not find a difference in the expression of IA of individuals paired with their friend or with a non-friend. However, the variation of relationship quality in a captive group may be rather small, since all individuals interact frequently with each other and there are no strangers. Therefore, our result does not preclude that an effect of relationship quality on IA exists in other species or in long-tailed macaques for other relationships. Therefore, it would be of great interest to determine what the effect of, for example, kinship on IA may be.

The Evolution of IA

Researchers have suggested that IA is a specialized and advanced social capacity that will only be found in a limited number of species. It has been proposed that capuchin monkeys evolved specialized and advanced social capacities because of their extensive use of tools and their cooperative hunting skills (Parker & McKinney 1999; Neiworth et al. 2009). Similarly, these skills may account for IA in chimpanzees. However, both long-tailed macaques and cottontop tamarins neither habitually use tools nor cooperatively hunt, but do show IA. Consequently, IA is not uniquely linked to these skills. Alternatively, it has been suggested that assessment of inequity is a trait shared among those primates that are socially tolerant (Neiworth et al. 2009). Since long-tailed macaques are not considered particularly socially tolerant (Thierry 2000), we suggest that IA does not depend on social attitude either.

The species that show IA are from several Anthropoid primate taxa: IA is found in apes, i.e., chimpanzees (Brosnan et al. 2005), New-World monkeys, i.e., brown capuchins and cottontop tamarins (Brosnan & de Waal 2003; Neiworth et al. 2009), and Old-World monkeys (this study). Moreover, neither specialized skills nor social attitude seem to determine the presence of IA. However, IA may be limited to primate species that cooperate, but this is probably a widespread capacity among Anthropoid primates, although the context in which it is used may differ (e.g., female support of kin to obtain rank: long-tailed macaques (van Noordwijk & van Schaik 1987); female aggression against infanticidal males: Hanuman langurs, *Semnopithecus entellus* (Hrdy 1977)). Therefore, we would like to suggest that IA is present in all Anthropoid primates.

We conclude that long-tailed macaques express IA when treated unequally, and that an effort to obtain the reward is crucial for the occurrence of this behaviour. Since these macaques show IA in a food context, but do not cooperate to obtain food, IA is possibly not domain specific. Although we aimed to determine whether relationship characteristics affected IA, we did not find such an effect for 'friends', but suggest IA may depend on the dominance relationship. Furthermore, IA seems a primate trait that is present in all Anthropoid primates, independent of social organisation. Therefore, IA may be a social tool that all these primate species can employ in different contexts. Future research should focus on the social conditions that facilitate the use of inequity aversion in animals.

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ACKNOWLEDGEMENTS

We thank Inge Luyten for her help in training and testing our animals, and for collecting the data to determine the dominance hierarchy and friendship status, Han de Vries for statistical advice and Erik de Jong for his help with building the experimental apparatus. We are grateful to Sarah Brosnan, Frans de Waal, Bram Buunk, Henk de Vos and Rita Smaniotto for their comments on the experimental setup and inspiring discussion on the topic. Finally, we would like to thank Henk Westland for taking care of our study animals. This research was supported by an Evolution and Behaviour grant from the Netherlands Organization for Scientific Research (NWO). The experiments were approved by the Ethical Committee of Utrecht University (DEC 2007.I.08.103) and thus comply with the Dutch law.

APPENDIX

Graphs and Statistics of Latencies

Experiment 1

1. Latencies of all tested animals in the equity conditions of the three different effort levels:

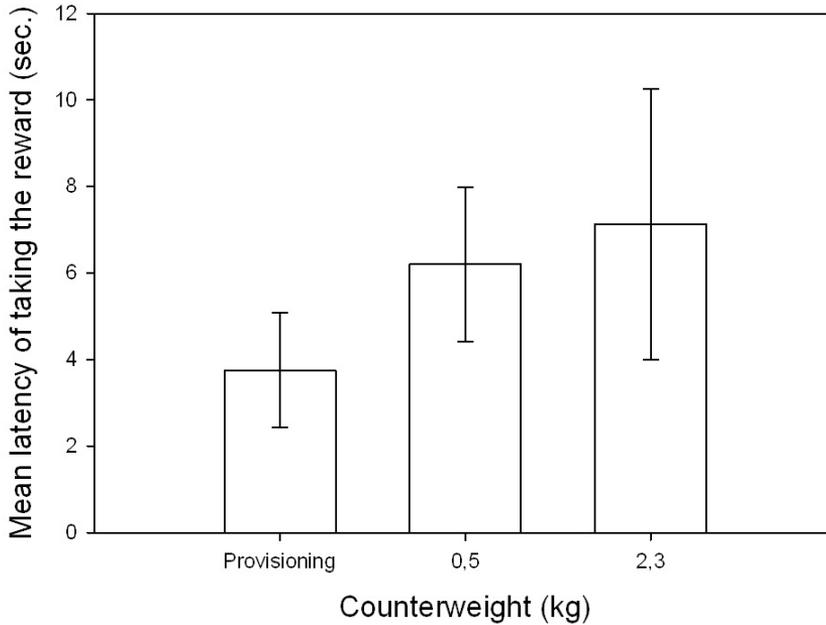


Figure A1. Mean latency \pm s.e.m. of taking the reward of all animals (both subjects & partners)(n = 19) in the equity conditions of the provisioning test, the small effort test (pulling in a counterweight of 0.5 kg), and the large effort test (pulling in a counterweight of 2.3 kg).

Statistics:

Overall: Friedman's test; n = 17, $\chi^2 = 6.118$, df = 2, p = 0.047

Post-hoc:

No vs. small effort: Wilcoxon signed ranks test; n = 17, $T^+ = 39.5$, p = 0.082

No vs. large effort: Wilcoxon signed ranks test; n = 18, $T^+ = 70$, p = 0.523

Small vs. large effort: Wilcoxon signed ranks test; n = 17, $T^+ = 63$, p = 0.540

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2. Latencies of dominant subjects in all test conditions:

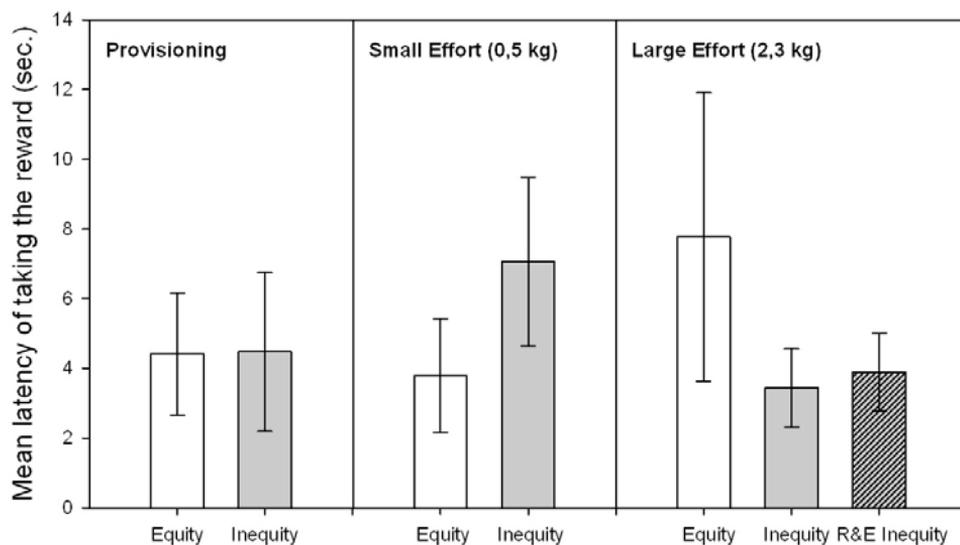


Figure A2. Mean latency \pm s.e.m. of taking the reward of dominant subjects ($n = 12$) in the equity- (white bars), inequity- (grey bars), and reward&effort inequity (striped bars) conditions of the provisioning test, the small effort test (pulling in a counterweight of 0.5 kg), and the large effort test (pulling in a counterweight of 2.3 kg).

Statistics:

Equity vs. inequity:

No effort: Wilcoxon signed ranks test; $n = 12$, $T^+ = 33$, $p = 1$

Small effort: Wilcoxon signed ranks test; $n = 11$, $T^+ = 25$, $p = 0.520$

Large effort: Wilcoxon signed ranks test; $n = 11$, $T^+ = 45$, $p = 0.320$

Large effort

+ effort inequity: Wilcoxon signed ranks test; $n = 11$, $T^+ = 30$, $p = 0.831$

Inequity Aversion and Relationship Quality

3. Latencies of subordinate partners in all test conditions:

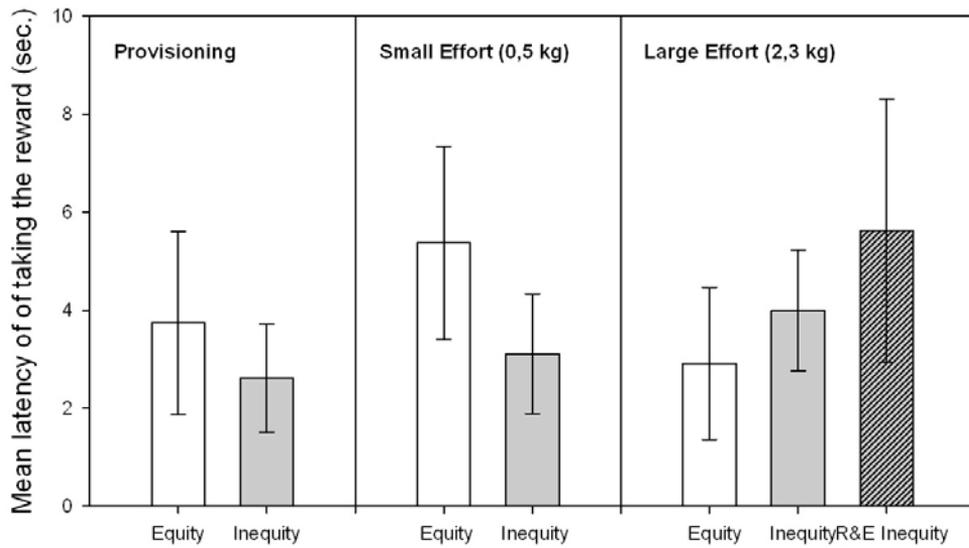


Figure A3. Mean latency \pm s.e.m. of taking the reward of subordinate partners ($n = 9$) in the equity- (white bars), inequity- (grey bars), and reward&effort inequity (striped bars) conditions of the provisioning test, the small effort test (pulling in a counterweight of 0.5 kg), and the large effort test (pulling in a counterweight of 2.3 kg).

Statistics:

Equity vs. inequity:

No effort: Wilcoxon signed ranks test; $n = 9$, $T^+ = 19$, $p = 0.469$

Small effort: Wilcoxon signed ranks test; $n = 8$, $T^+ = 22$, $p = 0.219$

Large effort: Wilcoxon signed ranks test; $n = 8$, $T^+ = 9$, $p = 0.469$

Large effort

+ effort inequity: Wilcoxon signed ranks test; $n = 8$, $T^+ = 11$, $p = 0.688$

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Experiment 2

1. Latencies of the subjects to take the rewards in the equity and inequity conditions:

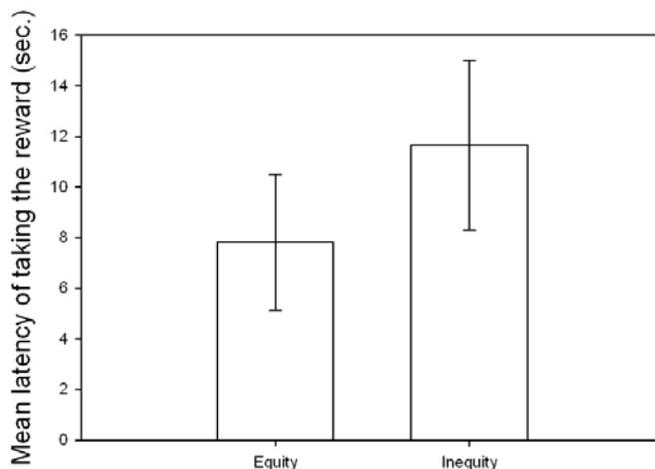


Figure A4. Mean latency \pm s.e.m. of taking the rewards by the subjects ($n = 13$) in the equity and inequity condition.

Statistics:

Equity vs. Inequity: Wilcoxon signed ranks test: $n = 12$, $T^+ = 42$, $p = 0.850$

2. Differences in the latencies of the equity condition and the inequity condition compared between friend and non-friend partners:

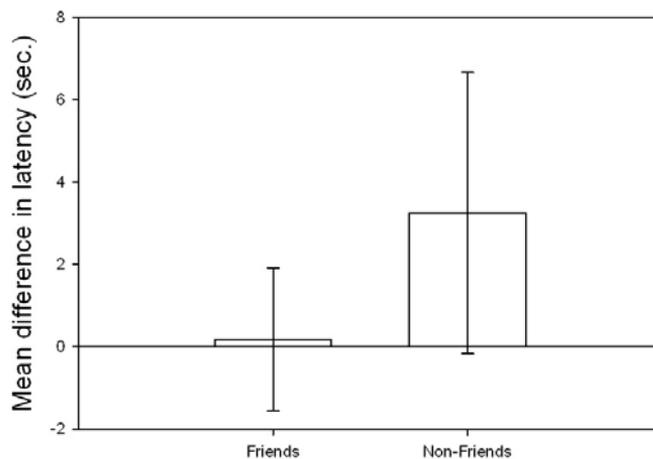


Figure A5. Mean difference in latency \pm s.e.m. between the equity and inequity condition (calculated as inequity - equity) for the subjects ($n = 13$) with either friend or non-friend partners.

Statistics:

Friends vs. Non-friends: Wilcoxon signed ranks test: $n = 12$, $T^+ = 39$, $p = 1.00$

Graphs and Statistics of the Last 8 Trials

Experiment 1

1. Proportion of rewards taken in the last 8 trials of all animals in the equity conditions of the different effort levels:

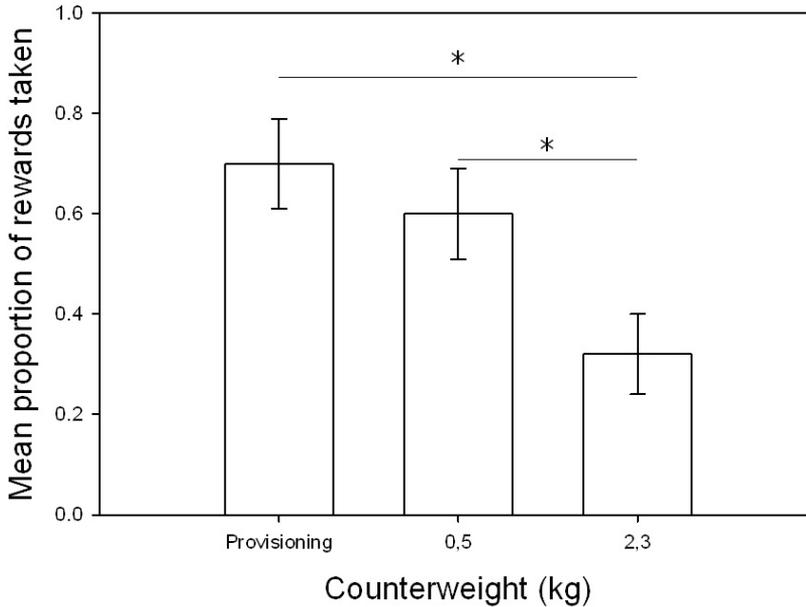


Figure A6. Mean proportion of rewards taken \pm s.e.m. by all animals (both subjects & partners) ($n = 19$) in the last 8 trials of the equity conditions of the provisioning test, the small effort test (pulling in a counterweight of 0.5 kg), and the large effort test (pulling in a counterweight of 2.3 kg). * $p < 0.05$.

Statistics:

Overall: Friedman's test; $n = 19$, $\chi^2 = 12.893$, $df = 2$, $p = 0.002$

Post-hoc:

No vs. small effort: Wilcoxon signed ranks test; $n = 19$, $T^+ = 19$, $p = 0.125$

No vs. large effort: Wilcoxon signed ranks test; $n = 19$, $T^+ = 5.5$, $p = \mathbf{0.001}$

Small vs. large effort: Wilcoxon signed ranks test; $n = 19$, $T^+ = 10$, $p = \mathbf{0.005}$

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2. Proportion of rewards taken in the last 8 trials of the dominant subjects:

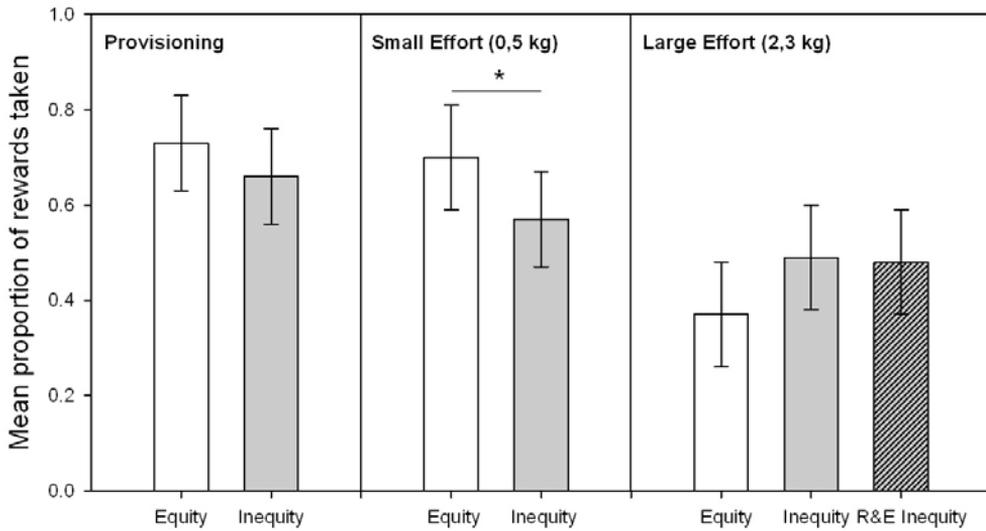


Figure A7. Mean proportion \pm s.e.m. of rewards taken by the dominant subjects ($n = 12$) during the last 8 trials in the equity- (white bars), inequity- (grey bars), and reward&effort inequity (striped bars) conditions of the provisioning test, the small effort test (pulling in a counterweight of 0.5 kg), and the large effort test (pulling in a counterweight of 2.3 kg).

Statistics:

Equity vs. inequity:

No effort: Wilcoxon signed ranks test; $n = 12$, $T^+ = 16$, $p = 0.313$

Small effort: Wilcoxon signed ranks test; $n = 12$, $T^+ = 33$, **$p = 0.039$**

Large effort: Wilcoxon signed ranks test; $n = 12$, $T^+ = 9.5$, $p = 0.273$

Large effort

+ effort inequity: Wilcoxon signed ranks test; $n = 12$, $T^+ = 13.5$, $p = 0.320$

Inequity Aversion and Relationship Quality

3. Proportion of rewards taken in the last 8 trials of the subordinate partners:

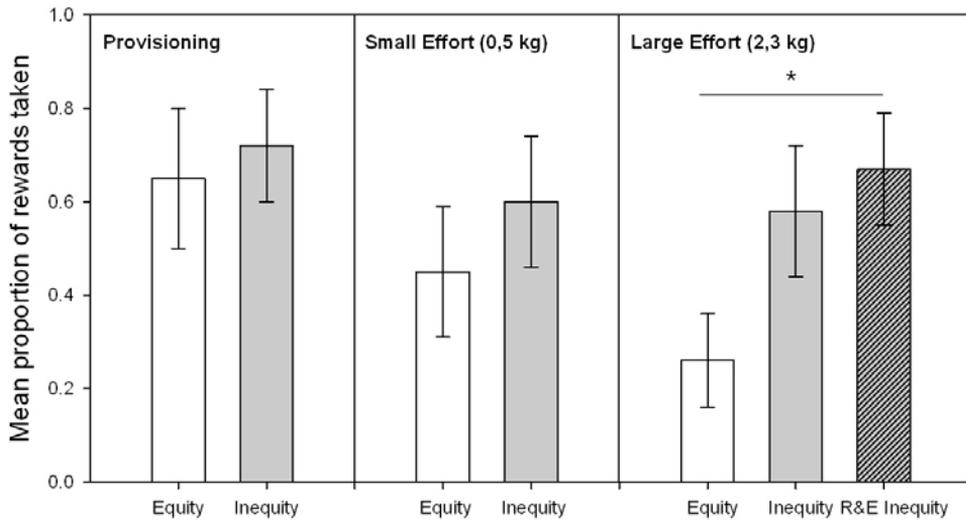


Figure A8. Mean proportion \pm s.e.m. of rewards taken by the subordinate partners ($n = 9$) during the last 8 trials in the equity- (white bars), inequity- (grey bars), and reward&effort inequity (striped bars) conditions of the provisioning test, the small effort test (pulling in a counterweight of 0.5 kg), and the large effort test (pulling in a counterweight of 2.3 kg).

Statistics:

Equity vs. inequity:

No effort: Wilcoxon signed ranks test; $n = 9$, $T^+ = 3$, $p = 0.625$

Small effort: Wilcoxon signed ranks test; $n = 9$, $T^+ = 2.5$, $p = 0.250$

Large effort: Wilcoxon signed ranks test; $n = 9$, $T^+ = 1$, $p = 0.063$

Large effort

+ effort inequity: Wilcoxon signed ranks test; $n = 9$, $T^+ = 1$, $p = \mathbf{0.031}$

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Experiment 2

1. Proportion of rewards taken by the subjects in the last 8 trials of the equity and inequity conditions:

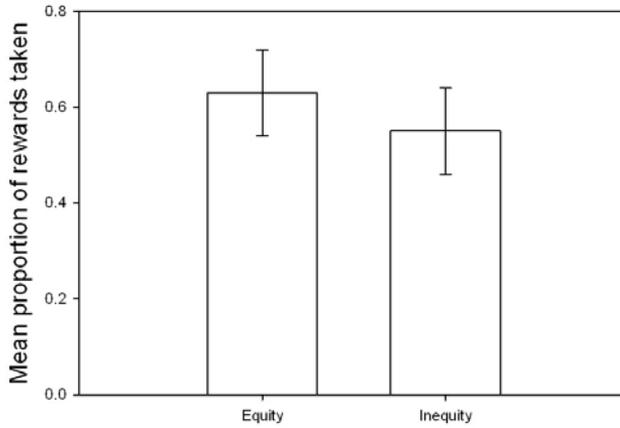


Figure A9. Mean proportion of rewards taken \pm s.e.m. by the subjects ($n = 13$) in the last 8 trials of the equity and inequity conditions.

Statistics:

Equity vs. Inequity: Wilcoxon signed ranks test: $n = 13$, $T^+ = 30.5$, $p = 0.375$

2. Inequity response during the last 8 trials of the subjects paired with either friends or non-friends:

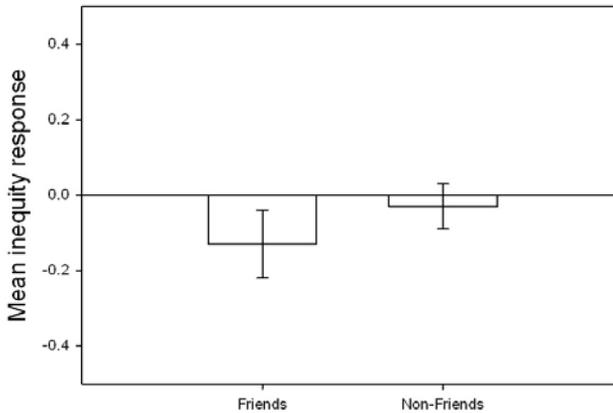


Figure A10. Mean inequity response \pm s.e.m. (calculated as: prop. of rewards taken in the inequity condition – prop. of rewards taken in the equity condition) during the last 8 trials of the subjects ($n = 13$) with friend and non-friend partners.

Statistics:

Friends vs. Non-friends: Wilcoxon signed ranks test: $n = 13$, $T^+ = 34$, $p = 0.535$

Inequity Aversion and Relationship Quality

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A review of close bonds in animals
and man: Functions and
mechanisms of friendship

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"Without friends no one would choose to live,
though he had all other goods."
Aristotle (384-322 BC)

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ABSTRACT

Both in humans and group-living animals, individuals associate and behave affiliative more with some individuals than others. Human friendships have long been acknowledged, and recently scientists studying animal behaviour have started using the term friendship for social bonds between animals. Yet, while biologists describe friends as social tools to enhance fitness, social scientists argue that human friendships are unconditional. Therefore, we investigate whether these different descriptions reflect true differences in human and animal friendships or whether they are a by-product of different research approaches: namely social scientist focussing on proximate and biologists on ultimate explanations. We first stress the importance of similar measures to determine animal and human friendship. Thereafter, we examine the ultimate benefits and proximate motivations of friendship. Moreover, we discuss the latest findings on the central-neural regulation of social bonds. We conclude that human and animal friendships are ultimately beneficial. Yet, motivations for friendship are not necessarily based on benefits and are often unconditional. Moreover, humans share with many animals a similar and highly conserved system of sociality. Therefore, we conclude that biologists and social scientist describe the same phenomenon, and the use of the term friendship for animals is justified.

Functions and Mechanisms of Friendship

INTRODUCTION

"Without friends no one would choose to live," wrote Aristotle in the 4th century BC. In humans, individuals that show relatively more affiliative behaviour to each other than other group members are called friends. Humans, however, are not the only species entertaining friends; also numerous social animals show marked preferences for particular individuals in their group (e.g. Smuts 1985; Cords 2002). These preferences have been attributed to the different values of group members for an individual (Kummer 1978), where valuable individuals will receive more affiliative behaviour than less valuable individuals. This social differentiation between group members results in different classes of group members, and those dyads that are positively engaged with each other most often are called 'good relationships'. However, it was only recently that scientists began calling non-human close social bonds friendships too. Not surprisingly, this trend started in the study of our closest living relatives, the non-human primates, and the first scientific book about friendships in baboons was written in the eighties (Smuts 1985). Nevertheless, the use of this anthropomorphic term in the study of animal behaviour took long to be accepted, and is still not accepted by everyone.

Although 'friendship' may now be partly acknowledged in animal behaviour, it seems that friendship in humans and friendship in non-human animals describe different phenomena. Therefore, the use of this term in the study of animal behaviour may not be fully justified. Whereas a human friendship in the social sciences is described as a strong commitment to mutual assistance in times of need, and a willingness to help each other without expected repayment (Davis & Todd 1985; Clark & Grote 2003), friends in biological sciences are predominantly viewed as social tools that enhance one's fitness (Kummer 1978). Here arises a contrast between 'unconditional' human friendships, and seemingly 'conditional' animal friendships. This contrast led scientist to argue that, in contrast to non-human animals, humans have evolved elaborate proximate mechanisms to regulate friendship, involving non-instrumental concern for their friends (Tooby & Cosmides 1996; de Vos et al. 2001; Smaniotto 2004). However, this apparent contrast in the concepts of friendship does not need to reflect real differences in human and non-human friendships. It may well be that these differences are a result of different research approaches, in which the social scientists mostly focus on the proximate motivations and expectations about friendship, and the biologists focus on the ultimate explanations and benefits of friendship.

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In this review we aim to explore the measures of friendship, the ultimate benefits and the proximate rules or behavioural mechanisms of both human and non-human friendships. In addition, we explore the physiological basis of close bonds in humans and animals. This will allow us to investigate whether human and non-human friendships are truly different or whether the use of the term friendship in the study of animal behaviour is also justified.

WHO ARE FRIENDS? MEASURES OF FRIENDSHIP

Two classes of affiliating individuals can be distinguished: related and unrelated individuals. Whereas affiliation among kin can be explained from an evolutionary perspective through kin selection (Hamilton 1964), i.e., helping of related individuals is helping, albeit in a diluted form, of one's own genes, kin selection cannot explain affiliation among non-kin individuals. Therefore, we suggest that friends are defined as non-kin individuals that regularly are involved in affiliative behaviour.

The methods that social scientists and biologists can employ are, at least partly, different. To identify friends in humans, social scientists can ask their subjects who their friends are. This will give a picture of the differentiation of relationships from the asked person. However, answers to these questions do not always reflect mutual friendships. For example, in a study on US schoolchildren in grades 7-12, all adolescents report to have friends, while a large set of these alleged friendships are not reported as such by the other partner (Vaquera & Kao 2008). In addition, the concept of what a friendship is differs per person. For example, a social relationship that one refers to as a friend can be interpreted as acquaintances by the other (Fischer 1982). In contrast, biologists studying friendship in non-human animals are restricted to observational methods: Measures based on behaviour in combination with knowledge on an absence of relatedness in a dyad, are used to define friendship. These different methods used to conceptualize and measure friendship in humans and non-human animals make it difficult to draw conclusions about differences between human and non-human friendships. Therefore, we suggest the use of similar measures to describe friendships of humans and other animals, such that between species comparison of friendship is possible. While questionnaires are impossible with non-human animals, observational studies can be conducted on both humans and non-human animals. Therefore, we give an overview of observational methods in defining friendships, and suggest which measures allow between species comparisons, including humans.

Functions and Mechanisms of Friendship

Relationship quality has been an important subject of study in primates. In primate research proximity and grooming preferences are the most common measures used to describe and differentiate between social relations (Silk 2002b). Both measures are easily obtained due to their relatively high frequency of occurrence and do, for example, also reflect kin relations (Chapais 2001). Here, we would like to argue that these measures are not only useful to describe primate social relations, but are also useful and objective measures of social relations of any species, including humans.

Proximity Measures

Close social bonds in animals are often defined by the amount of time two individuals spent near each other (Smuts 1985; Cords 2002). Within primate groups, these association patterns are not continuously distributed, and several dyads can easily be separated from others because of their high association patterns. Since such selectivity in association patterns is unlikely to arise by chance and close proximity reflects a certain tolerance for a given individual, researchers subsequently started to designate the label friends to such dyads (olive baboons, *Papio anubis*: Smuts 1985; rhesus macaques, *Macaca mulatta*: Manson 1994; chacma baboons, *P. urcines*: Palombit et al. 1997).

Although human friends can spend quite some time apart, typically human friendships are also characterized by frequent face-to-face contact (Hinde 1981; Baxter et al. 1997; Howes 1998). Even in contemporary Western societies, where everybody has a mobile phone and access to internet, humans report to be emotionally closest to those individuals with whom they spend the most time (Hill & Dunbar 2003). Playground proximity scores of school children also are reliable measures of what these children report themselves as their friends (e.g. Santos et al. 2008), or what teachers report as friendships (Fujisawa et al. 2005). Moreover, a meta-analysis on children's friendships (Newcomb & Bagwell 1995) showed that proximity scores were the best measures to differentiate friends from non-friends. However, it should be noted that proximity data by itself are not always easy to interpret, since the close proximity of two individuals may result from a mutual attraction to a third individual (Cords 1997). Therefore, to define friendships, it may be useful to use a second variable that describes the nature of a social relationship; e.g., affiliative body contact.

Affiliative Body Contact

Grooming in primates has long been regarded to serve a hygienic function (e.g., Hutchins & Barash 1976). However, primates groom each other much more often

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than is needed to remove parasites, and frequencies of grooming increase with group-size, suggesting it has a social function (Dunbar 1991). Furthermore, grooming of primates is often directed to a select group of group-members, and it is, therefore, suggested that grooming creates social bonds that directly affect group cohesion (Dunbar 1996). In addition, these bonds determine the degree of familiarity and predictability of each other's behaviour (Dunbar 1988). In short, grooming is an easy observable behaviour, indicative of primate friendships (Smuts 1985). Similar to primates, also the grooming of meerkats, *Suricatta suricatta* (Kutsukake & Clutton-Brock 2010), feral horses, *Equus caballus* (Sigurjonsdottir et al. 2003), and common vampire bats, *Desmodus rotundus* (Wilkinson 1986), as well as the preening of ravens, *Corvus corax* (Fraser & Bugnyar *in press*), rooks, *Corvus frugilegus*, and jackdaws, *Corvus monedula* (Emery et al. 2007), reflect valuable relationships.

Humans do not regularly groom each other, and much emphasis has been put on vocal communication in the creation and maintenance of friendships in humans. However, even with such an impressive communicative system at hand, there is also ample evidence that physical touch plays an important role in human relations. For example, humans frequently exhibit physical touch in the form of patting, petting and cuddling and, similar to animals, these affective touches are confined to the more intimate relations (Dunbar 2010) or friends (Newcomb & Bagwell 1995). Therefore, also in humans affiliative physical contact is predictive of the value of a relationship.

Alternative Measures

To describe different aspects of relations between non-human primates, Cords and Aureli (2000) suggested that three different characteristics of relationship quality can be distinguished; (1) security or consistency, the probability that the relationship will change; (2) compatibility, the tone of social interactions, depending on temperament and history; and (3) value of the partner (cf. Kummer 1978). The value of a partner depends in turn also on three factors; (1) long-lasting characteristics, such as sex, age and strength, (2) the probability of success of the partner, and (3) the partner's availability (Kummer 1978). Using principle component analyses, several studies find verification for the three separate characteristics of relationship quality in several species (chimpanzees, *Pan troglodytes*: Fraser et al. 2008a; Japanese macaques, *Macaca fuscata*: Majolo et al. 2009; ravens: Fraser & Bugnyar *in press*). These studies extract from several behavioural variables three components of relationship quality that parallel those

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described by Cords and Aureli (2000). Alternatively, low frequencies of agonistic interactions have been suggested as measures for friendship (Noë & Sluijter 1995). However, the closeness and frequent interactions of friends may lead to disagreement and conflict in frequencies comparable to non-friends (Newcomb & Bagwell 1995), or even higher (Massen *unpublished data*). For the purpose of this review, we therefore focus only on affiliative measures predictive of the value of a relationship (Cords & Aureli 2000), that are easy to observe in both humans and non-human animals, and have been shown to correlate strongly with each other, independent of the fact that one needs to be in close proximity to groom (Smuts 1985): Proximity and affiliative body contact.

Finally, to allow for within and between species comparisons, we need to take into account that species may differ in the frequency of these behaviours. Whereas an hour spent in one day with another individual may not have much significance in a highly gregarious species, it may be more than significant in a rather solitary species. Furthermore, within a species there may be differences in the frequency of close proximity and affiliative body contact, since, for example, wild populations may show these behaviours less frequently because they are more occupied with movement and searching for food in comparison to captive populations. Moreover, even within a group individuals may differ in their base-line frequencies of these affiliative behaviours. Therefore, we suggest that definitions of friendship should be based on the frequency of these affiliative behaviours of each individual separately. In addition, these measures should be relative to the frequency of these behaviours shown by the same individual towards all other group members. Lastly, friendships should be based on a mutual assessment of both 'friends' (for an example, see chapter 1), to avoid unidirectional relations that should not be classified as true friendships (Vaquera & Kao 2008).

THE BIOLOGY OF FRIENDSHIPS

Here, we review the ultimate benefits and proximate mechanisms of friendship. In his seminal paper on ethology, Tinbergen (1963) distinguished four different questions about behaviour; i.e., what is its function? (adaptation), how did it evolve? (evolution), what causes it? (causation), and how does it develop in an individual? (ontogeny). These four questions were further classified as concerning either ultimate or proximate causes; i.e., ultimate causes refer to the adaptive nature of certain behaviour and how it evolved, proximate causes refer to the mechanisms

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that elicit these behaviours and their ontogeny (Tinbergen 1963). To give a clear and relevant example of how these two causes can differ: Friends may provide much needed help to each other, resulting in a beneficial outcome (i.e., ultimate causes), however, the internal motives of friends do not need to be guided by these advantages (i.e., proximate causes). We aim to show that these causes indeed are not mutually exclusive and exist side by side, since they explain different aspects of behaviour. Therefore, we start with exploring studies on the adaptive nature of friendships and thereafter review studies on the behavioural mechanism and decision rules that may underlie the behaviour observed between friends. In addition, we examine some of the recent studies on neuronal and hormonal patterns that in turn may underlie these different decision rules.

ULTIMATE BENEFITS

To gain a better understanding of why friendships have become a component of social life and, thus, how they may have been selected for, we need to study the fitness advantages a friendship has over having no friends at all. If friendships are not a side effect of variation in proximity and affiliative behaviour, but a selected behaviour, friendships should have advantages for either the survival or the reproductive output of the participants involved (Cords 1997). Fitness is defined by an individual's survival and its reproductive success, and therefore we would like to investigate both aspects separately. However, we start by examining cooperation since that may serve to increase both aspects of fitness.

Friendship and Cooperation

Cooperation may allow its participants to achieve goals that cannot be reached alone. However, not all group members will be equally good as cooperation partners. For example, chimpanzees tend to prefer to cooperate with conspecifics experienced in the specific task at hand (Melis et al. 2006b), which obviously renders the best outcome. In addition, animals also prefer to cooperate with those individuals with whom they have better social bonds, e.g., friends (chimpanzees: Melis et al. 2006a), or show more proficient cooperation with closer bonds (spotted hyenas, *Crocuta crocuta*: Drea & Carter 2009; rooks: Seed et al. 2008). Similarly, also humans cooperate more and more proficient with their friends than with others (Majolo et al. 2006). Moreover, modelling work has shown that only cooperating with friends and not with others is an effective strategy that readily emerges and persists in a range of noisy environments (Hruschka & Heinrich 2006). Finally, for

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humans the prospect of repeated contact elicits more cooperation in a prisoner's dilemma (Gächter & Falk 2002). In sum, through cooperation, which is more frequent and proficient among friends, friends can gain multiple benefits that cannot be achieved alone.

Friendship and Survival: 'Physical and Psychological Well-being'

Friendships are defined by frequent affiliative behaviours. As we define friendship by these affiliative behaviours, we indirectly impose benefits on these friendships, since these affiliative behaviours often have beneficial properties for the receiver. For example, in primates being groomed reduces heart rates (Boccia et al. 1989; Aureli & Smucny 2000), and consequently reduces stress. Yet, these defining characteristics are not the only benefits of friendship. Macaque, *Macaca spp.*, friends also support each other more often in a conflict than non-friends (chapter 3), and this support may help obtaining access to food resources. Similarly, hyenas use their friends to gain access to carcasses (Holekamp et al. 2007).

Friendships may also affect how individuals deal with conflicts. A conflict is usually a stressful event, and reduction of this stress or its impact should be adaptive. Many primates reconcile after a conflict, and this reduces the rate of self-directed behaviours of the former opponents, which may indicate a reduction of stress (Aureli et al. 1989). In addition, friends reconcile at higher rates than non-friends (Cords & Aureli 2000). Moreover, friends have more frequent (chimpanzees: Fraser et al. 2008b) or even exclusive (rooks: Seed et al. 2007) post conflict third-party affiliation, and these third-party affiliative contacts may have a consoling (i.e., stress reducing) effect (Fraser et al. 2008b; but see Koski & Sterck 2007).

The number of supporters on each side mainly decides human conflicts, quarrels or disputes, and consequently having a lot of friends does aid in winning conflicts (Phillips & Cooney 2005). Moreover, among humans there is a causal relationship between the quantity and quality of social relations and the risk of death (House et al. 1988; Seeman et al. 2002). For example, affiliative contact with friends tends to reduce stress in women (Taylor et al. 2000).

As mentioned, Aristotle wrote that 'without friends no one would choose to live'. Indeed, loneliness and feelings indicating a lack of friends often lead to psychological depression, which in turn can lead to increased morbidity and mortality (Cacioppo et al. 1993). Alternatively, there are also studies that report that not the receiving, but giving of social support is beneficial, since giving of social support decreased own morbidity (Brown et al. 2005), and the risk of mortality

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(Brown et al. 2003). Nevertheless, this benefit can only be obtained when one has friends to give social support to.

Also in a contemporary African hunting-gatherer society, the !Kung San hunter-gatherers, friendships are probably beneficial. Based on reciprocity, these friends call upon each other in times of need. Since resources or assistance to the one in need are of much greater value than the burden that assistance places on the one that provides these, in the long-term the mutual character of assistance renders benefits for both (Weissner 1982). Consequently, within such societies, having friends reduces the risks of bad hunting/gathering years.

Finally, also human friendships affect how dyads deal with conflicts. As in other animals, friends are more concerned with and more likely to resolve disagreements or conflicts compared to non-friends (Newcomb & Bagwell 1995). In turn, reconciliation of conflicts in children and adolescents has been demonstrated to reduce cortisol levels and consequently reduce stress (Butovskaya 2008).

In sum, there are few studies examining the effect of friends on well-being. However, those that have been conducted indicate that having friends and receiving and giving social support add to both non-human animal and human physical and psychological well-being.

Friendship and Reproductive Output

Friendships may enhance reproductive output. This has been argued for male-female and for same-sex friendships. Male-female friendships have been reported to increase a male's chances in obtaining mating access in several primate species (olive baboons: Smuts 1985; rhesus macaques: chapter 2), whereas females obtain protection of these males against infanticide (chacma baboons: Palombit et al. 1997) or against non-lethal harassment to themselves or the young offspring (chacma baboons: Lemasson et al. 2008; yellow baboons, *P. cynocephalus*: Nguyen et al. 2009). Furthermore, within primates male-male alliances are more frequent among friends than among non-friends (chimpanzees: Mitani & Watts 2001; rhesus & long-tailed macaques, *M. mulatta* & *M. fascicularis*: chapter 3) and can lead to increased access to receptive females (Noë & Sluijter 1990). Moreover, chimpanzee males help their friends with mate guarding and even share matings with their friends (Watts 1998). Similar patterns have been reported for bottlenose dolphins, *Tursiops truncatus*, where male friends help each other to gain mating access to females (Conner 2007). Finally, female yellow baboons with more female friends are more likely to rear infants successfully than socially 'isolated' females (Silk et al. 2003).

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Interestingly, friendship also seems to influence the reproductive output of human females. Women in lower social-economic classes are reported to give birth to heavier babies when they have a large social network, in comparison to similar women that lack such a social network. Furthermore, women with high-quality social support also experience less often postpartum depressions (Collins et al. 1993). Moreover, social support reduces maternal stress, which in turn increases pre-school intelligence scores (Slykerman et al. 2005).

Again, there are rather few studies examining the effect of friendship on the reproductive output of both non-human animals and humans. However, the few studies that did examine this relationship show advantages of friendships in reproduction, both for animals and man.

In conclusion, we show that both human and animal friends cooperate more frequently and preferably with each other compared to non-friends. Moreover, the cooperation between both non-human and human friends is more proficient than that of non-friends. Secondly, having friends and receiving social support adds to both human's and non-human animals' physical and psychological wellbeing. Lastly, friends also have a positive effect on the reproductive output of both humans and non-human animals. Consequently, both non-human and human friendships seem to enhance fitness. However, it should be noted that this is based on a very limited number of studies, since to date there are only few studies examining the ultimate benefits of friendships. Moreover, in contrast to studies on humans, biologists mainly focus on the short-term benefits a friend provides and (apart from Silk et al. 2003) the long-term effects of having friends versus no friends remain unclear in animals. Studying the long-term effects of having friends in animals is therefore a promising field for future research.

BEHAVIOURAL MECHANISMS: PROXIMATE RULES

Friendships may benefit its participants in different ways. Friends may cooperate more readily than non-friends, thereby achieving goals that cannot be reached alone; friends may engage in exchange relations, generating reciprocal relations that benefit both; or friends may be generally more (pro-)social towards each other. However, what causes these positive fitness-effects often remains unclear and may differ between species. Therefore, a careful examination of the proximate causes of friendship is needed. Here, we examine the underlying motives of these behaviours

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and whether they differ between friends and non-friends, and between animals and humans.

Motivations to Cooperate

Individuals may employ differential rules to regulate cooperation, depending on the individual they cooperate with. For example, human friends are more concerned who of them has the largest need and do not require equity, while acquaintances and strangers do prefer an equal pay-off for all participants in cooperation (Deutsch 1975). Initially the preference for equity was considered a uniquely human capacity, yet several primate species also prefer an equal reward distribution in cooperation (brown capuchin monkeys, *Cebus apella*: Fletcher 2008; chimpanzees: Melis et al. 2009; cottontop tamarins, *Saguinus oedipus*: Cronin & Snowdon 2008). Moreover, several primate species and domestic dogs react averse when the reward distribution is unequal, thereby showing inequity aversion (brown capuchin monkeys: Brosnan & de Waal 2003; chimpanzees: Brosnan et al. 2005; cottontop tamarins: Neiwirth et al. 2009; domestic dogs, *Canis familiaris*: Range et al. 2009a; long-tailed macaques: chapter 6). There are also indications that animals do not require equity when cooperating with friends, since both chimpanzees and domestic dogs show less or no inequity aversion when paired with a conspecific to whom they are more tolerant in general (chimpanzees: Brosnan et al. 2005; domestic dogs: Range et al. 2009b). However, when tested experimentally, long-tailed macaques show inequity aversion indiscriminately of the partner they are paired with, i.e., friend or non-friend (chapter 6). Nevertheless, this study was conducted in one captive group and the variation of relationship quality in a captive group may be rather small, since all individuals interact frequently with each other and there are no strangers. Therefore, it may still be possible that some non-human animal species, similar to humans, also differentiate in their preference for equity between friends and non-friends.

Motivations of Reciprocal Altruism

The reciprocation of costly favours may be the driving mechanism of interpersonal relationships in animals, i.e., reciprocal altruism (Trivers 1971). The tit-for-tat rule, start with behaviour benefiting the other and subsequently behave as the partner did, (Axelrod & Hamilton 1981) is one of the simplest rules that result in reciprocal altruism, and has led to the suggestion that animals are economic machines that only give when a favour can be expected in return. Indeed, the cost-benefit ratio of the tit-for-tat rule of reciprocal altruism leads to ultimate benefits. However, the tit-

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for-tat rule may not be the only mechanisms of reciprocity that can evolve and is resistant to other strategies. In particular, the underlying proximate rules for reciprocity need not to be based on the expectancy of returned favours, and there may be different rules that all lead to an outcome where the cost-benefit ratio of interactions among partners may provide both with ultimate benefits. Several other proximate mechanisms, or 'decision rules', leading to reciprocal altruism have been proposed, and we will examine them one by one.

Calculated Reciprocity

A first mechanism of reciprocation is *calculated reciprocity* (de Waal & Luttrell 1988). In this type of reciprocity individuals truly keep track of the value and amount of what is given and received. However, many species seem cognitively constrained to keep track of a large number of different interactions (Stevens & Hauser 2004) or to postpone behaviour to a later moment in time. Primates, for example, are unable to wait longer than several minutes between action and reward (Ramseyer et al. 2006; Dufour et al. 2007), which has been argued to create temporal limits to possible calculated reciprocity. Not surprisingly, calculated reciprocity has to date in an experimental set-up only been shown once in orang-utans, *Pongo pygmeus* (Dufour et al. 2009), and is present in humans.

Symmetry-based Reciprocity

A second mechanism of reciprocation is *symmetry-based reciprocity* (de Waal & Luttrell 1986). Individuals are proposed to reciprocate based on symmetrical features of their relation such as age, kinship or mutual association. Since these features are symmetrical, individuals interact similarly with each other, no active scorekeeping or complex cognitive assessment is required, and reciprocity still arises (de Waal & Luttrell 1986). An example of symmetry-based reciprocity (Brosnan and de Waal 2003) may be blood-sharing in vampire bats (Wilkinson 1984), in which the observed reciprocity results from the symmetrical features kinship and mutual association: they share with their neighbours, and since these remain the same over the course of time, and all do the same, eventually reciprocity arises.

Attitudinal Reciprocity and Emotionally Mediated Reciprocity

A third mechanism of reciprocation can concern *attitudinal reciprocity* (de Waal 2000) or *emotionally mediated reciprocity* (Schino et al. 2007). Although many reciprocal relations may rely on symmetry-based reciprocity, animals can also have

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reciprocal relations with individuals that do not have symmetrical features. These interactions, however, also do not need to be cognitively too complex. Instead of keeping the balance in remembered events, individuals may base their decision to give to another individual on their attitude towards this individual, which in turn is based on (a) previous interaction(s). A distinction needs to be made on decisions based on the most recent interaction with the target individual, called *attitudinal reciprocity* (de Waal 2000), or on a general attitude towards that individual, called *emotionally mediated reciprocity* (Schino et al. 2007). Emotionally mediated reciprocity stands out as unconditional on the short term, since the act of giving is not a consequence of having received something, but is a by-product of the strength of the relation; i.e., the probability of benefiting a certain individual is high when there is a strong bond with this individual (e.g., a friendship), while it is very low when there is a weak bond with that individual. Interestingly, this ‘unconditional’ rule parallels how social scientists describe friendships (Clark & Grote 2003; Davis & Todd 1985).

In several species emotionally mediated reciprocity may be the proximate mechanism underlying exchange relations, since in these studies researchers found no proof of a short-term contingency. Animals exchange grooming (capuchin monkeys: Schino et al. 2009; chimpanzees: Gomes et al. 2009; long-tailed & rhesus macaques: chapter 3), interchange grooming for support (Japanese macaques: Schino et al. 2007; ring-tailed coati’s, *Nasua nasua*: Romero & Aureli 2008; long-tailed & rhesus macaques: chapter 3), and interchange grooming for sexual access (rhesus macaques: chapter 2) without direct reciprocation. It should be noted that, although unconditional in the short term, these exchange and interchange patterns are rather balanced in the long run. Since within these exchange relations the probability of giving depends on the strength of the relationship, and this feature is often rather symmetrical, in the long run the amount of services given and received will even out, making it an adaptive strategy.

In contrast, other studies did demonstrate short-term contingency in interchange, which may be representative of *attitudinal reciprocity* (de Waal 2000). In some species the amount of grooming received predicts whether an individual will support the individual that groomed it earlier that day (long-tailed macaques: Hemelrijk 1994; chimpanzees: Koyama et al. 2006), whether an individual will share food with the individual that groomed it earlier that day (chimpanzees: de Waal 1997; capuchin monkeys: de Waal 2000), or whether an individual will be allowed mating access (long-tailed macaques: Gumert 2007). In these studies, attitudinal

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reciprocity may be the proximate mechanism governing the observed interchange patterns.

Different Decision Rules for Different Relationships

The decision rules applied in exchange relations may differ according to the quality of the relation; e.g., friends may use different decision rules than non-friends. As mentioned before, human friends do not pursue a balanced relationship, whereas strangers do (Deutsch 1975). Also chimpanzees seem to use differential decision rules for friends and non-friends. Although in general their tendency to share food depends on the amount of grooming received earlier that day (e.g. attitudinal reciprocity), friends always get a share, independent of their previous grooming (e.g. emotionally mediated reciprocity)(de Waal 1997). However, a similar distinction in decision rules for friends and non-friends could not be demonstrated in macaques (chapter 3). Moreover, the above-described studies that show long-term, but no short-term exchange or interchange, find that *all* group members use emotionally mediated reciprocity, which also suggests that this mechanism is not restricted to friends only in these species. In contrast, in humans such unconditional exchange is only expected among friends, and not among strangers (Deutsch 1975). However, these studies are performed in captive animals that, in contrast to strangers in human society, meet and have the opportunity to interact on a daily basis with all group members, also with non-friends. Nevertheless, it is also possible that these species are cognitively constrained to have differential decision rules for friends and non-friends. In contrast, the higher cognitive abilities of chimpanzees and the fission-fusion dynamics of chimpanzees' social life (Boesch & Boesch-Achermann 2000) may make differential decision rules for 'friends' and 'non-friends' feasible and adaptive.

Humans

As mentioned earlier, human friendships are considered unconditional, and exchanges and interchanges between friends are need orientated rather than balance orientated (Deutsch 1975; Davis & Todd 1985; Clark & Grote 2003). Indeed, humans typically do not keep consciously track of benefits provided and received in social exchanges, and in everyday social interactions humans are rarely guided by pure reason alone (Fehr & Fishbacher 2004). Yet, similar to the emotionally mediated reciprocity of animals, human interactions are quite often guided by emotions (Haselhuhn & Mellers 2005). The !Kung San hunter-gatherers even have a name for such an unconditional relationship: 'hxaro'. They describe the hxaro as a

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relationship that is based on a delayed exchange of gifts. The relationship can be unbalanced over several years, but mostly eventually evens out. Furthermore, the continuous flow of gifts given and received provides both partners information about the status of the relationship (i.e. whether they are good friends)(Weissner 1982). In contrast, when interacting with strangers, humans do prefer balanced relationship (Deutsch 1975), and especially in monetary interactions with strangers, people do use reason and apply conditional and strict tit-for-tat rules (Axelrod & Hamilton 1981).

In summery, many animals and humans seem to employ ‘unconditional’ decision rules in reciprocity, and can benefit others without direct returns and without expectation of future reciprocity. Moreover, these decision rules do not seem conscious or driven by reason, but instead seem mediated by emotions. Whether animals, similar to humans, also employ different, more conditional and probably more cognitive, decision rules for non-friends and/or strangers remains unclear and may well depend on their cognitive abilities and the structure of their group life.

Pro-social Motivations

That animals can be unconditional in their interpersonal relations, suggests that they can show pro-sociality, i.e., benefiting another individual without direct reciprocation. However, genuine altruism, defined as a costly act that confers benefits on other individuals, is considered uniquely human (Fehr & Fishbacher 2003), thereby strengthening the claim that in contrast to humans, animals are economic machines. Yet, pro-social behaviour without apparent costs, or other-regarding behaviour, has recently been shown in several primate species (common marmosets, *Callithrix jacchus*: Burkart et al. 2007; capuchin monkeys: de Waal et al. 2008; Lakshminarayanan & Santos 2009; chimpanzees: Warneken et al. 2007; long-tailed macaques: Massen et al. 2010, chapter 4; bonobos, *Pan paniscus*: Hare & Kwtuenda, 2010) and also in several corvid species (ravens: Heinrich 1988; jackdaws: de Kort et al. 2006; rooks: Scheid et al. 2008). Results on pro-sociality in chimpanzees, however, are inconsistent, and several studies on chimpanzees report no pro-sociality (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008). Moreover, cottontop tamarins also did not show pro-sociality (Cronin et al. 2009). These negative findings may, however, be due to the experimental set-up, since pro-social behaviour was found for chimpanzees in a different set-up (Warneken et al. 2007). Alternatively, it could also be due to the identity of the individuals tested. For example, in long-tailed macaques, pro-social behaviour varied extensively across

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individuals. These animals' dominance hierarchy best explained this variation, i.e., high-ranking individuals were very pro-social, whereas low-ranking individuals were a-social (i.e., withheld their partners from getting access to a reward)(Massen et al. 2010, chapter 4). Presumably, the pro-social tendency of these high-ranked individuals serves as an act to enhance or maintain status (Moore 1984; de Waal 1989). Similarly, rooks actively give food to others as a costly signal of their status (Scheid et al 2008). Moreover, also humans seem to use their pro-social behaviour as a signal of their status, i.e., humans are more willing to give to another if they perceive themselves as having a higher social status as the receiver (Dovidio & Gaertner 1981; Mast & Bischof 1999). Thus, unconditional giving seems to enhance social status of an individual, and may form the mechanism of another form of reciprocity: indirect reciprocity (Alexander 1987). Indirect reciprocity predicts that generous individuals create a reputation of being helpful by benefiting those that will not return this behaviour. Consequently, others are more likely to benefit these generous or helpful individuals, since the probability of receiving something back from them is large.

While pro-social behaviour can depend on the identity of the individual, it may also depend on the identity of the receiving partner, and friends may be more pro-social towards each other than non-friends. Interestingly, however, in long-tailed macaques pro-sociality was not related to relationship quality. Yet, when given the choice between a friend and a non-friend, dominant long-tailed macaques tend to prefer giving to their friends, while subordinates prefer to give to the highest in rank of the two (chapter 5). Therefore, dominance rank also seems to determine which of the possible social relationships, friendship or dominance, prevails in directing pro-social behaviour.

Alternatively, pro-social behaviour may play an essential role in the formation of new social bonds. For example, food offers of juvenile jackdaws are an early indication of who will become their future pair-mates (de Kort et al. 2006; von Bayern et al. 2007). Similarly, in the !Kung San hunter-gatherers a gift, that can be considered a pro-social act that is costly to the giving individual, marks the invitation to start a new friendship. This offer of friendship is accepted by returning a gift, and rejected by saying that momentarily no return gifts are available (Weissner 1992).

Finally, the act of benefiting others may be rewarding and may elicit positive emotions in the giver. In humans, the act of giving is perceived as pleasurable (Steger et al. 2008), as indicated by an increased activity of the reward areas in the brain (Harbaugh et al. 2007). Similarly, the pro-social preferences of

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monkeys and apes may result from pro-social choices having more self-rewarding features than selfish choices (de Waal et al. 2008). Whether other animals also show an increased activity of reward areas in the brain during pro-social behaviour has, to our knowledge, not yet been established. However, the grooming of primates results in the release of β -endorphins, not only in the individuals that receive grooming but also in those that groom (Keverne et al. 1989). This suggests that, at least in primates, also giving can release β -endorphins and is rewarding. In conclusion, the self-rewarding aspects of giving may function as a motive to do so.

To summarise, pro-social behaviour may be widespread among animals, and not just restricted to humans. It can serve several functions, which may differ per species. Pro-sociality may serve as a costly signal of one's status, or as the initiation of a new friendship. Furthermore, some animals tend to be more pro-social towards their friends than towards their non-friends. However, the social organisation of a species may interfere with pro-social preferences towards friends, especially when relationship quality and dominance relations interact. While in a despotic species (i.e., long-tailed macaques) pro-sociality is directed by dominance rank and, less so, by friendship, it remains to be established whether relationship quality is more important in less despotic species. Finally, pro-social behaviour is pleasurable for humans, and there are some indications that it is similarly pleasurable for other animals.

To conclude this part about proximate motivations of friendship, it seems that both humans and non-human animals preferentially cooperate with their friends, engage more frequently with friends in reciprocal relations, and can behave pro-socially. Furthermore, in many instances reciprocation seems to be governed by emotions instead of cognitive reasoning, although no actual measurements of emotions are yet available. Therefore, studies indicating what emotions are important for dealing with friends, by assessing central-neural and hormonal regulation of social bonds, will be reviewed next.

NEURAL AND HORMONAL MECHANISMS OF FRIENDSHIP

That emotions play a role in the social interactions of animals and humans is commonly accepted (e.g., Trivers 1971; Aureli & Smucny 2000; Schino et al. 2007),

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yet very few studies have actually looked at what constitutes these emotions. Recent research has revealed several hormones that are involved in sociality and close social bonds. A major focus of this line of research is the vasopressin and oxytocin family of small neuropeptides, and in particular the role of these neuropeptides in the central nervous system (i.e., the brain). Oxytocin is known to regulate mother-infant bonding (Carter & Keverne 2002), whereas vasopressin is known to regulate several male-typical social behaviours, and has been traditionally viewed as a regulator of aggressive behaviour (Goodson & Bass 2001). In addition, these neuropeptides also play an important role in male-female pair bonding. Infusion of oxytocin and vasopressin in the brain in respectively female and male prairie voles (*Microtus ochrogaster*) accelerates pair bonding (Winslow et al. 1993; Williams et al. 1994). Similarly, in male rats a chronic infusion of oxytocin leads to an increase in nonsexual social interactions with a female rat (Witt et al. 1992). Compared to polygamous species (e.g. montane voles, *M. montanus*, and meadow voles, *M.s pennsylvanicus*), prairie voles have higher densities of oxytocin and vasopressin receptors in those brain regions involved in pair-bond formation (Insel & Shapiro 1992; Insel et al. 1994). Moreover, affiliative behavior can be increased in polygamous voles by inducing expression in the brain of a vasopressin receptor gene from the monogamous vole (Lim et al. 2004). In sum, in several rodent species, both oxytocin and vasopressin seem to play an important role in the formation and maintenance of affiliative social relations. It should, however, be noted that vasopressin and oxytocin are highly conserved neuropeptides. Researchers (e.g., Goodson & Bass 2001) have argued that next to their conserved morphology, the function of these neuropeptides is very likely to be conserved too. Therefore, it is expected that they are related to the formation and maintenance of affiliative social relationships in many animal species.

Indeed, vasopressin and oxytocin and their effect on social behaviour are not restricted to rodents or mammals only. Mesotocin (the avian homolog of oxytocin) also seems to promote sociality. Infusion of mesotocin in the zebra finch (*Taeniopygia guttata*) increased the time spent with large groups and familiar social partners, whereas an infusion with a mesotocin antagonist created opposing effects (Goodson et al. 2009). Similarly, the central infusion of isotocin (the fish homolog of oxytocin) in male goldfish, *Carassius auratus*, stimulated approaches to conspecifics, whereas a central infusion of vasotocin (the fish homolog of vasopressin) inhibited this response (Thompson & Walton 2004). Parallels in organization and function of these neuropeptides thus indeed seem to exist in a wide variety of vertebrates.

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Also in humans, both oxytocin and vasopressin affect social behaviour. Intranasal administration of oxytocin in humans increases trust in strangers (Kosfeld et al. 2005) and generosity in general (Zak et al. 2007), whereas intranasal administration of vasopressin has a sex-specific influence on human social communication, i.e., men react with agonistic facial motor patterns to unfamiliar men, whereas women react with affiliative facial motor patterns to unfamiliar women (Thompson et al. 2006). Furthermore, the intravenous administration of oxytocin to subjects diagnosed with autism or Asperger's disorder improved these patients' comprehension of affective speech (e.g., happy, sad) (Hollander et al. 2007). Moreover, after inhalation of oxytocin, high-functioning patients with autism spectrum disorder respond more to others, exhibit more appropriate social behaviour and show more affection (Andari et al. 2010). In addition, the urine of orphanage-reared children contains lower levels of oxytocin and vasopressin compared to family-reared children (Fries et al. 2005), and this may be related to social problems in development, in particular social attachment to others (Chisholm 1998), in orphanage-reared children. Furthermore, genetic variation in the vasopressin receptor gene is associated with pair-bonding behaviour (e.g., perceived marital problems, marital status and partner bonding) of humans (Walum et al. 2008).

The septal area of the human brain, a limbic region that controls the release of vasopressin and oxytocin and also contains receptors for both neuropeptides, seems involved in unconditional trust (Krueger et al. 2007). Using hyper-fMRI, Krueger et al. (2007) showed that when making decisions to cooperate with trustworthy individuals, the septal area was activated, while making decisions to cooperate with unfamiliar or untrustworthy individuals was associated with activation of the paracingulate cortex, an area involved in mentalizing. Furthermore, after several rounds trustworthy partners synchronized their activation of the septal area with each other, which led to perceived social attachment, but also to a decrease in activity of the 'mentalizing' paracingulate cortex. The researchers argue that this synchronization and subsequent social attachment is a cognitively less costly strategy compared to mentalizing (Krueger et al. 2007). This cognitively less costly strategy may well reflect the underlying neural mechanism accompanying what is described in behavioural biology as emotionally mediated bookkeeping (Schino et al. 2007), whereas the cognitively more costly system of the paracingulate cortex may well reflect calculated reciprocity (Brosnan & de Waal 2002). Interestingly, mentalizing, which is regulated in the paracingulate cortex, is a behavior only present in humans and in a rudimentary form in great

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apes (Povinelli & Preuss 1995) and has not been observed in monkeys (Cheney & Seyfarth 1990). Moreover, the anterior part of the prefrontal cortex, in which paracingulate cortex is located, has become enlarged and specialized during hominid evolution (Semendeferi et al. 2001), and this enlargement and specialization have been linked to the complex social interactions of humans (e.g., the social brain hypothesis: Dunbar 1998), and may aid in the more cognitive and conditional interactions with strangers. In contrast, the septal area, which may regulate emotionally mediated bookkeeping concerning non-strangers, is conserved in form and function in a wide variety of species (Font et al. 1995).

In conclusion, researchers have only just begun to reveal the underlying neural structures involved in social bonding. Many of these structures seem highly conserved and seem to have similar functions in both humans and non-human animals. Altogether, this is a very promising field for the understanding of social bonds and friendship in particular.

CONCLUSION

To summarize, we started with the question whether human and non-human animal friendships differ, and thus whether the use of this anthropomorphic term is justified in the description of non-human animals' social bonds. We acknowledged that to address this question it is of great importance that friendships are defined by the same measures and subsequently reviewed some methods of determining friendship and suggested some objective and behavioural measures of friendship that can be used in many species, including humans. Although on the proximate level human friendships are often described as unconditional (Clark & Grote 2003), both human and non-human friendships seem to have ultimate fitness benefits. Furthermore, it has been argued that, in contrast to non-human animals, humans have evolved elaborate proximate mechanisms involving non-instrumental concern for their friends (de Vos et al. 2001; Smaniotto 2004; Tooby & Cosmides 1996). However, especially these non-instrumental motives, as we showed in the part dealing with proximate mechanisms of friendship, are shared with a variety of species that actually apply these unconditional rules not only to friends, but also to other group members. It seems that social species generally interact unconditionally and that this behavioural pattern often, but not necessarily always, results in reciprocity in the long run. Most group living species interact daily with each member of their group, and very rarely with individuals of another group.

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Therefore, there seems no need for specialized cognitive bookkeeping skills and emotionally mediated 'bookkeeping' (Schino et al. 2007) seems sufficient.

Human groups, however, have become larger and larger and humans now also frequently interact with strangers (Seabright 2004). To avoid exploitation by these strangers, humans tend to apply strict tit-for-tat rules (Axelrod & Hamilton 1981) or an exchange orientation (Clark 1984) in interactions with those strangers. Therefore, we would like to argue that humans, and perhaps some other species, have evolved elaborate proximate mechanisms (probably cognitive) to keep track of what is given and received when dealing with strangers or acquaintances, e.g., calculated bookkeeping (de Waal & Luttrell 1988). With all non-strangers, humans seem to interact based on their long-term interaction history, in which emotions probably play a mediating role (Haselhuhn & Mellers 2005; Schino et al. 2007). This unconditional way of interacting with non-strangers is furthermore reflected in the fact that humans in their everyday social interactions are rarely guided by pure reason, and have limited introspective access to these processes (Fehr & Fishbacher 2004; Bargh & Williams 2006).

Finally, hormonal and neuronal patterns show a highly conserved system that enhances sociality shared among many species. Moreover, these systems seem to serve similar functions in animals and man. The only deviation of humans from most other animals in neuronal pathways is the enlargement of a brain region that may serve to interact on a more conditional and cognitive basis with strangers.

To conclude, both human and non-human friendships are ultimately beneficial, are however based on unconditional motivations that are probably mediated by emotions, and measures of neuronal and hormonal patterns show that the human physiological system of sociality is highly conserved and shared with many animals. Therefore, biologists and social scientists seem to describe a similar phenomenon when they talk about animal and human friendships, and thus applying the term friendship to animals seems justified.

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Chapter 8

Do animals have friendships or not?
Summary of the main findings

“The wicked can only have accomplices, the voluptuous have companions in debauchery, self-seekers have associates, the politic assemble the factions, the typical idler has connections, princes have courtiers.

Only the virtuous have friends.”

Voltaire (1694-1778)

Chapter 8

DO ANIMALS HAVE FRIENDSHIPS OR NOT?

In this thesis I have studied animal friendship and its underlying proximate motivations in captive macaques. In particular, the overarching hypothesis of this thesis was that friends are more tolerant towards underbenefitting than non-friends. First, using longitudinal observational data, I examined exchange relations to test whether friends are more accepting of imbalances in ongoing relationships than non-friends. Second, using an experimental design, I tested macaques for their other-regarding preferences, to examine whether macaques benefit friends more compared to non-friends. Thirdly, using a different experimental design, I tested whether friends are more tolerant towards inequity than non-friends. Finally, in a review I have put the work of others, and also my own, in perspective to gain a better understanding of what constitutes friendship in animals and humans and to determine whether the concept of friendship differs between animals and humans.

Summary of the Main Findings

The first topic of this thesis concerned exchange relations between different individuals. Primates have been reported to exchange different commodities or services on a reciprocal base (e.g. de Waal & Luttrell 1988; Hemelrijk & Ek 1991), or on a 'market place', where they trade such services with one another and the 'prices' of services are subject to supply and demand (Noë & Hammerstein 1994; Gumert 2007a). However, the underlying proximate motivations of these reciprocal relations have received little attention. Recently, several different decision rules that may lead to reciprocal relations have been suggested (see **chapter 2 & 3**). First, reciprocity may be symmetry based, where animals act based on symmetrical features of their relation such as age or kinship. Since these features are symmetrical, individuals interact similarly with each other, no active scorekeeping or complex cognitive assessment is required, and reciprocity still arises (de Waal & Luttrell 1986). Second, emotionally mediated reciprocity (Schino et al. 2007) argues that an individual's long-term history of interactions with a particular individual, mediated by emotions, directs its behaviour towards this individual. The tendency of providing benefits to another individual is then based on the long-term emotional bond with this individual and does not need to be contingent on the short-term. Third, attitudinal reciprocity (de Waal 2000) argues that individuals base their decision to give on an attitude they have of a certain individual, which in turn is based on a recent interaction. Lastly, animals may show calculated

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reciprocity (de Waal & Luttrell 1988), where they remember costs and benefits of past acts and balance their reaction.

In this thesis, I focused on the exchanges of grooming for grooming and the interchange of grooming for support in both long-tailed and rhesus macaques, and the interchange of grooming for mating access in rhesus macaques. In particular, I focused on the time frame of reciprocation in these ex- and interchanges, to distinguish between the different proposed decision rules.

The data on exchange patterns (**chapters 2 & 3**) show that all individuals in a macaque group exchange and interchange grooming, support and mating access. However, these ex- and interchanges do not rely on short-term or immediate reciprocation, but instead are best explained by long-term social relations: meaning that *emotionally mediated reciprocity* determines who exchanged with whom (Schino et al. 2007). Hence, for the macaques in my study, the decision to benefit another individual does not depend on what that individual has recently given, but instead on the strength of the long-term bond between the two individuals. For example, the probability of benefiting a certain individual is high when there is a strong bond with this individual (e.g., a friendship), while it is very low when there is a weak bond with that individual. Moreover, tolerance to an imbalance seems a general feature of the exchange relations of the studied macaques and therefore, friends do not seem to differ in that aspect from others (**chapter 3**). Since these exchanges depend on the strength of a relation, exchanges are however more frequent among friends than among non-friends, and for example, friends do support each other much more often in a conflict than non-friends (**chapter 3**).

Recently, a study showed that wild long-tailed macaques trade grooming for sex on a market place in which the amount of grooming males have to provide females to gain sexual access depends on supply, i.e., the amount of available females (Gumert 2007a). In contrast, I showed that captive rhesus macaques do not ‘pay’ for sex, nor does such a ‘price’ depend on availability (Noë & Hammerstein 1994). Also in the sexual arena, mating access is related to long-term social relations and, next to the males’ dominance hierarchy, male-female ‘friendships’ predict mating among couples (**chapter 2**). In sum, long-term emotional bonds mediate the exchange and interchange patterns of grooming, support and (in one species) mating access observed in the studied macaques. Therefore, rather than truly exchanging services, it seems that providing services for the studied macaques is a consequence of the strength of their social bonds.

In such a ‘tolerant’ or unconditional system of reciprocation, the decision to give is unlikely to be based on the expectation of future benefits, since it is not clear

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when or if your gift will be reciprocated soon or at all. In a study on chimpanzees, it was found that the decision to help another individual was indeed not based on immediate reward (Warneken et al. 2007). The chimpanzees in this study spontaneously helped both a human and a conspecific, regardless of being rewarded for it or not. Although the ultimate outcome of helping behaviour may still be reciprocation, the underlying proximate mechanism does not need to rely on the calculation of costs and benefits. Instead, natural selection may have produced psychological mechanisms that produce spontaneous helping behaviour (de Waal 2007; 2008). Yet, if individuals interact similarly and frequently with each other, both actors and recipients are benefited on average in the long run. Consequently, pro-social behaviour, behaviour benefiting the recipient, can be expected in any species that does not rely on active comparison of costs and benefits in a reciprocal relation.

In an experiment, I tested long-tailed macaques for their pro-social behaviour and found that they were capable of this behaviour (**chapter 4**). Since the exchange patterns of social behavior (**chapters 2 & 3**) were tolerant to short-term imbalances in all dyads, it could be expected that also all individuals in whatever dyad showed pro-social behaviour. However, friends are expected to differ from non-friends in the magnitude of their pro-sociality, since friends also exchange more frequently (**chapter 3**). Yet, the pro-social behaviour of the long-tailed macaques in my experiment was not determined by relationship quality. However, when given the choice, long-tailed macaques seemed to prefer giving to their friends above giving to a 'non-friend' (**chapter 5**). Yet, pro-sociality in general was determined by the rank of the subject (**chapter 4**). Only high-ranking individuals showed pro-social behaviour, while low-ranking animals even showed a-social behaviour (i.e., deliberately withholding their partners access to food). Presumably, the pro-sociality of dominants acts as a status enhancing or status maintaining strategy (Moore 1984; de Waal 1989), while subordinates prefer a more competitive strategy and withhold their partners from access to food. When given the choice between two individuals to give to, only dominants tended to prefer giving to their friends. In contrast, individuals that were subordinate to both their partners showed a significant preference to give to the most dominant of their two partners (**chapter 5**). The subordinates' preference may reflect an incentive that results in future benefits such as tolerance or support from this more dominant individual (Seyfarth 1977; Noë et al. 1991). Yet, as shown in **chapter 4**, subordinate individuals are generally not so prone on giving. Therefore I suggested that, alternatively, the

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subordinates' preference may reflect a competitive strategy in which these low-ranking animals avoid benefiting their more direct competitors (**chapter 5**).

In sum, as expected by the tolerant exchange patterns of their everyday life, long-tailed macaques are capable of pro-social behaviour. This pro-social behaviour is however, strongly influenced by the subject's dominance rank: dominants are pro-social and subordinates are a-social. The pro-social tendencies of long-tailed macaques in general do not depend on relationship quality, yet, dominant individuals do tend to prefer giving to their friends. In contrast subordinates prefer giving to their most dominant partner instead of their friend. Therefore, dominance rank also seems to determine which of the possible social relationships, friendship or dominance, prevails in directing pro-social behaviour.

Another assumption of emotionally mediated reciprocity is a certain tolerance for an imbalance within what is given and received. Such a tolerance could be expressed by showing less or no inequity aversion when treated unequally. Furthermore, in humans it is also expected that such a tolerance is larger for friends than for non-friends (Deutsch 1975). I showed that long-tailed macaques do express inequity aversion when treated unequal (**chapter 6**). However, they did not differentiate between friends and non-friends in their expression of inequity aversion, and consequently, at least within this experiment, are not more tolerant to inequity aversion when paired with a friend. Yet, all individuals in this captive group interact frequently with each other and there are no strangers. Consequently, variation of relationship quality in this group may be rather small. Alternatively, the partners did not cause inequity in this experiment, but instead the experimenter. Therefore, the aversive attitude of the subjects may not be directed at their partners, but to the experimenter, and whether the partner is a friend or a non-friend is consequently insignificant. Additionally, the differentiation in the expression of inequity aversion has been extensively described in the social sciences (Deutsch 1975), yet, to my knowledge, has not yet been tested experimentally in any other animal species or in humans. Therefore, this remains an interesting topic.

In the final part of this thesis (**chapter 7**) I examined whether biologists and social scientists describe the same phenomenon when they write about non-human and human friendships. Biologists often describe friends as social tools (Kummer 1978) and social scientists rather refer to unconditional relationships (Clark & Mills 1979; Davis & Todd 1985). Therefore, an apparent contrast in the concept of friendship between the social sciences and the life sciences arose. Moreover, this contrast led scientist to argue that, in contrast to non-human animals, humans have evolved elaborate proximate mechanisms to regulate friendship, involving non-instrumental

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concern for their friends, where no return benefits are required or expected from friends (Tooby & Cosmides 1996; de Vos et al. 2001; Smaniotto 2004). However, this contrast may be merely a result of different research designs and different explanatory levels: i.e., social scientists focus on the proximate motivations of friendship, whereas biologists focus on the ultimate benefits of friendship. Therefore, in the review I first examined measures used to describe friendship and propose the use of similar and objective measures in the description of both human and non-human friendships. Secondly, I examined the ultimate benefits of both human and non-human friendships, and show that both human and non-human friendships are ultimately beneficial and thus adaptive. Thirdly, I examined the proximate motivations for friendships in humans and other animals. I show that, although beneficial in the long run, the motivations for friendship in both humans and other animals do not need to be based on the prospect of future benefits. Instead, these motivations seem mainly unconditional and are probably mediated by emotions. Lastly, I explored the latest studies on the hormonal and neuronal regulation of social attachment in the brain. These studies seem to confirm a role of emotions in social behaviour among friends, with particular interest to the neuropeptides oxytocin and vasopressin. Moreover, these neuropeptides and some of the neuronal pathways are highly conserved among a wide variety of species, and seem to serve similar functions in animals and man. Therefore, I conclude that biologists and social scientists seem to describe a similar phenomenon when they refer to animal and human friendships, and thus applying the human term friendship to animals seems justified.

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Chapter 9

Conclusion:
The nature of social interactions
with friends, acquaintances and
strangers

“We cannot tell the precise moment when friendship formed. As in filling a vessel drop by drop, there is at last a drop which makes it run over; so in a series of kindness there is at last one which makes the hart run over.”

Samuel Johnson (1709-1784)

Chapter 9

THE NATURE OF SOCIAL INTERACTIONS WITH FRIENDS, ACQUAINTANCES AND STRANGERS

From Humans to Animals...

Friendship in humans is as old as the written word and probably dates back even further. One of the earliest known literary works in history, i.e., 'The Epic of Gilgamesh' (\pm 2150-2000 BC), describes in great depth the friendship between two of the main characters in this Babylonian poem. Moreover, friendships are found among all cultures, and friendship has been sanctified by most major religions. While human friendship has been widely acknowledged, scientists have been very cautious to apply the term friendship to non-human animals. It lasted up to 1985 before the first scientific book on friendship in animals was written (Smuts 1985). Although many scientists to date still disapprove the use of this anthropomorphic term in animal biology, the body of scientific work on animal friendships has been growing ever since. Always keen on an evolutionary perspective, these biologists mainly focused on the adaptive value of friendships and, in doing so, found that friendships in several primate species are indeed adaptive (*for a review see Silk 2002*). For example, although friends may help each other, it was argued that this is adaptive since they will receive a return benefit in the future. This economic view of a friendship, however, strongly contrasts with the unconditional view of human friendship among social scientists. For example, Clark and Mills (1979) suggest that friends use other behavioural guidelines than strangers or acquaintances when providing help to each other, in which the relationship between friends is characterized by concern for each other's welfare and benefiting the other when a need exists. This seeming antagonism in the concept of friendship used by social scientists and biologists has been fuel for the critics of non-human friendship. It led them to suggest that friendships of humans and of non-human animals are different: e.g., in contrast to animals, humans have evolved elaborate proximate mechanisms involving non-instrumental concern for their friends (de Vos et al. 2001; Smaniotta 2004; Tooby & Cosmides 1996). Consequently, biologists should refrain from adopting the term friendship in their description of animal social relations. Yet, it may also be that these differential concepts of friendship are a result of different research approaches. Whereas social scientists mainly focus on proximate motivations and expectations about friendship, biologists have mostly focused on ultimate explanations, i.e., on the fitness benefits a friend may provide. Therefore, it may also be possible that these different explanations are not mutually exclusive and exist side by side, since they explain different aspects of the same

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phenomena. However, as long as social scientists and biologists use different measures and approaches in the study of friendship, it remains impossible to draw the conclusion that friendships of humans and non-human animals are truly different. Consequently, a heightened need for studies that cross-apply concepts, measures and research methods from both disciplines exists. This thesis was a first attempt to fulfill this need.

I explored social interactions between macaques with different relationship qualities. I demonstrated that on the long run all these macaques have reciprocal exchange relations, regardless of their relationship quality. However, relationship quality is predictive of the extent of these exchange relations and friends, for example, exchange much more and more frequent than non-friends. Because of their reciprocal nature, these exchange patterns are ultimately beneficial for their participants and consequently these social relations are adaptive, thereby confirming other work on primate friendships (Silk 2002). This adaptive nature, however, contrasts with the general view of friendship in humans. For example, C.S. Lewis (1898-1963) wrote: “Friendship is unnecessary, like philosophy, like art... It has no survival value; rather is one of those things that give value to survival.” Yet, in **chapter 7** I review several studies that show that also human friendships have fitness benefits and are ultimately adaptive. The next question then is whether interactions within these human and non-human friendships are also motivated by these benefits? For example, do benefits received from friends create obligations?

To answer these questions, one needs to investigate the proximate mechanism underlying the observed exchange relations. Therefore, I examined the time frame of reciprocation of the observed exchange relations. I showed that macaques do not reciprocate immediately or within the time frame of one day. Similar findings were reported for various other animal species. Consequently, these animals are tolerant for short-term imbalances in their exchange relations, and decisions about whether or not to provide any benefit do not rely on what is recently received. Instead, these decisions seem mediated by the long-term social bond these animals have with each other, which in turn is probably regulated through emotions (i.e., *emotionally mediated reciprocity*: Schino et al. 2007). Emotions also seem to play a mediating role in the interaction of human friends and acquaintances (Haselhuhn & Mellers 2005), and in everyday life, human social interactions are rarely guided by pure reason alone, which is reflected in the limited introspective access to these processes in humans (Fehr & Fishbacher 2004). Consequently, it seems that instead of a conscious mechanism that calculates costs and benefits, natural selection may have produced psychological mechanisms that

produces spontaneous helping behaviour, although these still benefit actors and recipients on average in the long run (de Waal 2007; 2008), and are consequently very efficient. In **chapter 5** I show that in an experimental design, the long-tailed macaques indeed are capable of spontaneous helping behaviour. In contrast to what was suggested by social scientists (de Vos et al. 2001; Smaniotta 2004; Tooby & Cosmides 1996), humans are probably not the only species that have evolved elaborate proximate mechanisms involving non-instrumental concern for their friends. In addition, studies on hormonal and neuronal patterns (reviewed in chapter 7) show the existence of a highly conserved system of such unconditional sociality, in which the neuropeptides oxytocin and vasopressin play a major role, that is shared among a large variety of vertebrates, and that probably serves similar functions in animals and man.

For humans it has been argued that only friends interact with each other governed by a non-instrumental concern, whereas with strangers humans may pursue a balanced relationship (Deutsch 1975). Interestingly, the macaques in my study did not differentiate in their decision rules between friends and non-friends, and all exchange relations seemed to be mediated by the long-term emotional bond of its participants. Therefore, it seems that this unconditional exchange pattern is a general pattern in these macaques. Yet, these macaques and many other group living animals interact on a daily base with each group member. In contrast, interactions with conspecifics other than their group members are rare and mostly of an aggressive nature. Therefore, these animals mainly interact with conspecifics with which they have some sort of emotional bond ('good' or 'bad'), and consequently elaborate cognitive mechanisms to keep track of the amount and value of benefits provided and received are probably superfluous. In contrast, an emotional assessment of appropriate behaviour seems sufficient to guide behaviour.

...and Back to Humans Again.

Humans not only interact with friends and acquaintances, but also interact frequently with strangers. As mentioned before, many species lack frequent interactions with strangers and thus have no need for elaborate cognitive mechanisms to deal with that. Therefore, of great interest are species that do have interactions with strangers or at least interact with several individuals on a rather infrequent base; i.e., species that show fission-fusion dynamics such as chimpanzees, hyenas, dolphins and elephants, or semi-solitary species such as orang-utans. It has been suggested that emotionally mediating interactions within these species may not be sufficient for all relations, since there is not enough emotional experience

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with each individual they meet (Aureli et al. 2008). Consequently, for these species there may be a need for different ways to interact with others depending on the frequency and patterns of spatial and temporal separations (Barrett et al. 2003). Therefore, I would like to argue that humans, and perhaps some other species, have evolved elaborate proximate mechanisms (probably cognitive) to keep track of what is given and received when dealing with strangers, e.g., calculated bookkeeping (de Waal & Luttrell 1988).

A brain study in humans confirms that decisions to cooperate with familiar individuals are accompanied with activation of brain areas related to emotional assessments, whereas decisions to cooperate with unfamiliar individuals are accompanied by brain activation of the more cortical and cognitive brain areas (Kreuger et al. 2007). Whether other animals, such as those who's social life is characterized by fission-fusion dynamics, also employ differential decision rules and have differential brain processing for friends, acquaintances and strangers remains unknown. Yet, the way chimpanzees share food unconditionally with their friends, though base their decision to share on a previous interaction with others (de Waal 1997), and the finding that orang-utans are capable of calculated bookkeeping (Dufour et al. 2009), seems a first indication that some animals may be able to employ differential, and also more cognitively complex, decision rules. Therefore, in my opinion, whether animals employ different decision rules to friends and strangers and are capable of cognitively complex decision rules when dealing with strangers is a very interesting research question that should inspire future research on social interactions and cooperation in non-human animals in particular.

To conclude, interactions with friends and well-known individuals are mediated by a fast, old, emotional system that is shared among humans and non-human animals. In humans, and possibly some other species, the newer, cortically mediated, decision processes that allow for conscious, cognitively complex, evaluations of costs and benefits when dealing with strangers, complement this emotional system.

Chapter 9

Nederlandse samenvatting en conclusie

Je hebt iemand nodig

Stil en oprecht

Die als het erop aankomt

Voor je bidt en voor je vecht

Pas als je iemand hebt

Die met je lacht en met je grient

Dan pas kun je zeggen

Ik heb een vriend

Toon Hermans (1916-2000)

DE AARD VAN SOCIALE INTERACTIES MET VRIENDEN, KENNISSEN EN VREEMDEN.

Van mensen naar dieren.....

Vriendschap bij mensen is zo oud als het geschreven woord en bestaat hoogstwaarschijnlijk nog veel langer. Een van de vroegst bekende literaire werken, het “Gilgameshepos” (± 2150-2000 v. Chr.), beschrijft met veel diepgang de vriendschap tussen twee van de hoofdrolspelers uit dit Babylonische gedicht. Vriendschappen vind je bovendien in alle culturen en de meeste grote religies zien vriendschap als een gewijde relatie. Terwijl vriendschap bij mensen overal als iets wezenlijks wordt erkend, zijn wetenschappers toch erg voorzichtig geweest de term ‘vriendschap’ ook bij dieren toe te passen. Het heeft tot 1985 geduurd voordat het eerste wetenschappelijke boek over vriendschap bij dieren werd geschreven (Smuts 1985). Ondanks dat veel wetenschappers vandaag de dag het gebruik van deze antropomorfistische term nog steeds niet goedkeuren binnen de biologie der dieren, is sindsdien de hoeveelheid wetenschappelijk werk aan dierenvriendschappen gestaag gegroeid. Aangezien biologen graag vanuit een evolutionair perspectief naar dingen kijken, heeft dit werk zich vooral geconcentreerd rondom de adaptieve waarde van vriendschap, en deze biologen vonden dat vriendschap bij verschillende soorten primaten inderdaad voordelen met zich meebrengt (*voor een overzicht zie Silk 2002*). Bijvoorbeeld: ondanks dat de ene vriend de ander helpt is dat toch voordelig voor hen beiden, omdat de dienst geretourneerd kan worden, waardoor ze allebei uiteindelijk iets krijgen. Zulk een economische kijk op vriendschap staat in groot contrast met de onvoorwaardelijke kijk op vriendschap tussen mensen binnen de sociale wetenschappen. Clark en Mills (1979) bijvoorbeeld suggereren dat vrienden ander gedragsregels hanteren dan vreemden of kennissen. Bovendien zou de relatie tussen vrienden gekenmerkt zijn door zorg voor elkaars welzijn en de ander helpen als die in nood is. Deze schijnbare tegenstelling over het concept vriendschap tussen sociale wetenschappers en biologen was als olie op het vuur voor de criticasters omtrent vriendschap bij dieren. Het heeft er toe geleid dat ze zelfs de suggestie wekten dat vriendschappen tussen mensen en vriendschappen tussen dieren andere fenomenen waren, bijv. dat in tegenstelling tot andere dieren, alleen bij mensen complexe motivationele mechanismen zijn geëvolueerd die in staat zijn tot niet-instrumentele zorg voor vrienden (de Vos et al. 2001; Smaniotto 2004; Tooby & Cosmides 1996). Als gevolg daarvan zouden biologen moeten afzien van het gebruik van de term ‘vriendschap’ bij het beschrijven van sociale relaties onder dieren. Echter, het zou ook zo kunnen zijn dat de verschillende concepten van

vriendschap slechts een resultaat zijn van verschillende manieren van onderzoek. Waar sociale wetenschappers zich vooral concentreren op de directe motivaties en verwachtingen van vriendschap, concentreren biologen zich vooral op evolutionaire verklaringen, d.w.z. op de *'fitness'* voordelen die een vriend kan bezorgen. Aangezien deze verschillende verklaringen verschillende aspecten van hetzelfde fenomeen verklaren, zou het ook mogelijk kunnen zijn dat ze elkaar niet uitsluiten. Zolang sociale wetenschappers en biologen echter verschillende maten en methoden blijven gebruiken voor hun studies naar vriendschap bij mensen en dieren, blijft het onmogelijk om de conclusie te trekken dat vriendschappen bij mensen en vriendschappen bij andere dieren daadwerkelijk anders zijn. Daarom bestaat er ook een grote vraag naar studies die concepten, maten en methoden uit beide disciplines combineren. Dit proefschrift is een eerste poging om aan die vraag te voldoen.

Ik heb sociale interacties van makaken met verschillende kwaliteiten van hun relaties onderzocht. Ik heb aangetoond dat op de lange termijn deze makaken wederkerige uitwisselingsrelaties hebben, onafhankelijk van de kwaliteit van hun relatie. Echter, de kwaliteit van de relatie is voorspellend voor de omvang van zulke uitwisselingsrelaties en vrienden wisselen bijvoorbeeld veel meer en veel vaker dingen met elkaar uit dan niet-vrienden. Aangezien deze uitwisselingen wederkerig zijn, zijn ze uiteindelijk voordelig voor elke participant en als gevolg daarvan zijn deze sociale relaties adaptief, en bevestigen ze ander werk aan vriendschap bij primaten dat ook laat zien dat vriendschap adaptief is (Silk 2002). Deze adaptieve aard staat echter in contrast met de algemene blik op vriendschap bij mensen. C.S. Lewis (1898-1963) schreef bijvoorbeeld: "Vriendschap is onnodig, zoals filosofie, zoals kunst.....Het heeft geen overlevingswaarde; Maar is eerder zo iets dat waarde geeft aan overleven." Echter in dit proefschrift geef ik een overzicht van meerdere studies die laten zien dat ook vriendschappen van mensen *fitness* voordelen opleveren en uiteindelijk adaptief zijn. De volgende vraag die dan gesteld kan worden is of interacties tussen vrienden bij zowel mensen als dieren ook gemotiveerd worden door die voordelen? Bijvoorbeeld, als je iets van een vriend krijgt, moet je dan ook persé iets teruggeven?

Om zulke vragen te beantwoorden, moet men de directe motivationele mechanismen die ten grondslag liggen aan de geobserveerde uitwisselingsrelaties onderzoeken. Daarom heb ik de tijdspanne van retournering binnen uitwisselingsrelaties onderzocht. Ik heb aangetoond dat makaken elkaar niet meteen teruggeven wat ze gekregen hebben, noch dat dit binnen een dag gebeurt. Vergelijkbare resultaten zijn ook voor andere soorten gerapporteerd. Daarom lijkt

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het erop dat deze dieren binnen een korte termijn tolerant zijn ten opzichte van een ongebalanceerde relatie, en dat de keuze om iemand wel of niet iets te geven niet afhankelijk is van wat recentelijk ontvangen is. In plaats daarvan lijken deze keuzes gebaseerd te zijn op de sociale band die deze dieren met elkaar hebben op de lange termijn, wat waarschijnlijk vervolgens weer door emoties wordt bemiddeld (d.w.z. *emotionally mediated reciprocity*: Schino et al. 2007). Emoties lijken bij mensen ook een bemiddelende rol te spelen bij interacties tussen vrienden en kennissen (Haselhuhn & Mellers 2005), en in het dagelijks leven worden humane sociale interacties bijna nooit door slechts pure logica gestuurd. Dit is terug te zien in de gelimiteerde introspectieve toegang die mensen hebben tot zulke processen (Fehr & Fishbacher 2004). Daarom lijkt het erop dat in plaats van een bewust mechanisme dat kosten en baten berekent, natuurlijke selectie een psychologisch mechanisme heeft gegenereerd dat zorgt voor spontaan hulpgedrag, maar dat desondanks zowel de gever als de ontvanger bevoordeelt op de lange termijn (de Waal 2007; 2008), en dus erg efficiënt is. In dit proefschrift laat ik middels een experiment zien dat java-ape inderdaad in staat zijn tot spontaan hulpgedrag. Contrasterend met suggesties van sociale wetenschappers (de Vos et al. 2001; Smaniotta 2004; Tooby & Cosmides 1996), lijkt het er dus op dat de mens niet de enige soort is bij wie complexe motivationele mechanismen die in staat zijn tot niet-instrumentele zorg voor vrienden zijn geëvolueerd. Daarbij laten studies naar hormonale en neurale patronen het bestaan zien van een evolutionair zeer geconserveerd systeem dat onvoorwaardelijk sociale interacties reguleert. Binnen dat systeem spelen de neuropeptiden oxytocine en vasopressine een belangrijke rol. Bovendien wordt dit systeem gedeeld met een grote variëteit aan vertebraten en lijkt het eenzelfde functie te hebben bij zowel dieren als mensen.

Over mensen werd er geschreven dat alleen vrienden op een niet-instrumentele manier zorg voor elkaar dragen en dat vreemden daarentegen een gebalanceerde relatie nastreven (Deutch 1975). Het is dan ook interessant dat de makaken in mijn studie geen onderscheid maakten in hun gedragsregels tussen vrienden en niet-vrienden, en dat alle uitwisselingsrelaties door de emotionele band van de participanten op de lange termijn leken te worden gereguleerd. Het lijkt er daarom op dat zulke onvoorwaardelijke uitwisselingsrelaties een algemeen patroon vormen bij deze makaken. Echter, deze makaken en vele andere dieren die in groepen leven, gaan dagelijks met elke groepsgenoot om. Interacties met soortgenoten buiten de groep zijn daarentegen zeldzaam en vaak van een agressieve aard. Daaruit volgt dat deze dieren over het algemeen alleen omgaan met soortgenoten met wie ze een bepaalde emotionele band hebben ('goed' of 'slecht'),

en daarom zijn complexe cognitieve mechanismen om de hoeveelheid en waarde van wat is gegeven en wat is gekregen bij te houden, waarschijnlijk overbodig. Een emotionele beoordeling van gepast gedrag lijkt daarentegen voldoende om hun gedrag te sturen.

SAMENVATTING

Hebben dieren vriendschappen of niet?

Voor dit proefschrift heb ik bij makaken in gevangenschap vriendschappen en de onderliggende motivaties voor vriendschap bestudeerd. De allesomvattende hypothese van dit proefschrift is dat ongelijk bedeed worden onder vrienden eerder geaccepteerd wordt dan onder niet-vrienden. Om dat te onderzoeken heb ik vriendschap gedefinieerd als die dieren die relatief gezien het meest bij elkaar zitten en elkaar het meest vlooiën. Vervolgens heb ik allereerst, middels langdurige observatiestudies, gekeken naar uitwisselingsrelaties om te testen of vrienden toleranter zijn waar het ongebalanceerde relaties betreft dan niet vrienden. Ten tweede heb ik, middels experimentele gedragstesten, onderzocht of makaken hun vrienden meer bevoordelen dan hun niet vrienden. Ten derde heb ik, door middel van een andere experimentele set-up, getest of vrienden toleranter zijn ten opzichte van een ongelijke behandeling dan niet vrienden. Tot besluit heb ik in een overzicht mijn eigen werk en dat van anderen in perspectief gezet om een duidelijker beeld te krijgen van wat een vriendschap inhoudt bij zowel dieren als mensen, en om te kijken of vriendschappen bij dieren van een andere orde zijn dan vriendschappen tussen mensen.

Samenvatting van de belangrijkste bevindingen.

Het eerste onderwerp in dit proefschrift betreft de mate waarin verschillende individuen diensten met elkaar uitwisselen (uitwisselingsrelaties). Over primaten is bekend dat ze verschillende goederen en diensten met elkaar uitwisselen op basis van wederkerigheid (bijv. de Waal & Luttrell 1988; Hemelrijk & Ek 1991) of aan de hand van een 'marktwerking', waarbij deze diensten worden geruild met elkaar en waarbij de 'prijs' afhangt van vraag en aanbod (Noë & Hammerstein 1994; Gumert 2007a). Desalniettemin hebben de onderliggende motivaties van deze wederkerige relaties weinig aandacht gekregen. Recentelijk zijn verschillende perspectieven op het maken van keuzes hieromtrent ('keuzeregels') voorgesteld die alle op hun eigen manier tot wederkerige relaties kunnen leiden (zie **hoofdstuk 2 & 3**). Allereerst kunnen wederkerige relaties gebaseerd zijn op symmetrie, waarbij dieren handelen op basis van de symmetrische kenmerken van hun relatie zoals leeftijd of

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verwantschap (*'symmetry based reciprocity'*). Aangezien deze kenmerken symmetrisch zijn gaan individuen op eenzelfde manier met elkaar om, is actief boekhouden of een complexe cognitieve beoordeling niet nodig, en ontstaat alsnog een wederkerige relatie (de Waal & Luttrell 1986). Als tweede mechanisme gaat *'emotionally mediated reciprocity'* (door emoties bemiddelde wederkerigheid)(Schino et al. 2007) ervan uit dat een individu's lange termijn historie van interacties met een bepaald individu, bemiddeld door emoties, het gedrag ten opzichte van dit individu stuurt. De tendens om iemand anders te bevoordelen is dan gebaseerd op de emotionele band op de lange termijn met dat individu en hoeft niet uitgebalanceerd (d.w.z. ieder heeft evenveel gegeven als gekregen) te zijn op de korte termijn. Als derde mechanisme gaat *'attitudinal reciprocity'* (wederkerigheid gebaseerd op een attitude) ervan uit dat individuen hun keuze om te geven baseren op de houding die ze hebben t.o.v. een bepaald individu. Deze houding is op zichzelf weer gebaseerd op een recente interactie. Het laatste mechanisme is *'calculated reciprocity'* (berekende wederkerigheid)(de Waal & Luttrell 1988), waarbij de kosten en baten van voorbije interacties onthouden worden, waarop een uitgebalanceerde reactie volgt.

In dit proefschrift heb ik me geconcentreerd op de uitwisseling van elkaar vlooien, en de uitwisseling van vlooien met steun in een conflict bij zowel java- als resusapen. Bovendien heb ik bij de resusapen gekeken naar de uitwisseling van vlooien met paringen. Daarbij heb ik me in het bijzonder geconcentreerd op de tijdspanne van wederkerigheid in deze uitwisselingen, om zo de verschillende keuzeregels van elkaar te kunnen onderscheiden.

De data van uitwisselingspatronen (**hoofdstuk 2 & 3**) laten zien dat alle individuen in een makakengroep het vlooien met elkaar uitwisselen, vlooien met steun in een conflict uitwisselen, en vlooien met paringen uitwisselen. Deze uitwisselingen hangen echter niet af van korte termijn wederkerigheid of directe wederkerigheid en zijn juist beter te verklaren door sociale relaties op de lange termijn. Dit betekent dat wederkerigheid door emoties wordt bemiddeld en op die manier wordt bepaald wie met wie iets uitwisselt (Schino et al. 2007). Dus, voor de makaken die ik heb bestudeerd hangt de keuze om iemand iets te geven niet af van wat diegene recentelijk aan hen heeft gegeven, maar in plaats daarvan hangt die keuze af van de sterkte van de emotionele band die ze met elkaar op de lange termijn hebben. Bijvoorbeeld, de kans dat twee dieren elkaar bevoordelen is groot wanneer deze dieren een sterke band met elkaar hebben (bijv. een vriendschap), echter deze kans is klein wanneer deze dieren een zwakke band met elkaar hebben. Bovendien zijn alle makaken tolerant ten opzichte van ongelijkheid in hun

uitwisselingsrelaties en accepteren ze op korte termijn een ongebalanceerde relatie. Deze tolerantie is een algemeen kenmerk bij deze makaken en beperkt zich dus niet alleen tot vrienden (**hoofdstuk 3**). Omdat de uitwisselingen echter afhangen van de sterkte van een relatie, komen uitwisselingen veel vaker voor tussen vrienden t.o.v. niet vrienden, en steunen vrienden elkaar bijv. vaker dan niet vrienden (**hoofdstuk 3**)

Een studie aan wilde java-apen liet recentelijk zien dat deze makaken het elkaar vlooien ruilen voor seks op een 'marktplaats', waarbij de vlooitijd die de mannetjes moeten 'betalen' om met een vrouwtje te paren afhangt van het aanbod, d.w.z. de hoeveelheid beschikbare vrouwtjes (Gumert 2007a). Ik laat echter zien dat resusapen in gevangenschap niet hoeven te 'betalen' voor seks, noch dat de 'prijs' afhangt van beschikbaarheid (Noë & Hammerstein 1994). Ook in de seksuele arena blijkt dat seksuele toegang tot een vrouwtje gerelateerd is aan emotionele banden op de lange termijn en dat naast de mannelijke dominantiehiërarchie, man-vrouw vriendschappen kunnen voorspellen wie er met wie zal paren (**hoofdstuk 2**). Samenvattend: bij de twee soorten makaken die ik heb bestudeerd bemiddelen emotionele banden op de lange termijn de uitwisselingspatronen van vlooien, steun in een conflict en (bij één soort) seksuele toegang. In plaats van te stellen dat ze deze diensten met elkaar uitwisselen, lijkt het er daarom meer op dat binnen de bestudeerde makaken het bewijzen van een dienst aan elkaar een consequentie is van de sterkte van hun sociale band.

In zulk een 'tolerant' of onvoorwaardelijk systeem van wederkerigheid is het onwaarschijnlijk dat de keuze om iemand iets te geven gebaseerd is op de verwachting van toekomstige voordelen aangezien het niet duidelijk is of je gift snel of überhaupt wordt geretourneerd. Op vergelijkbare wijze werd in een studie aan chimpansees gevonden dat de keuze om iemand te helpen voor chimpansees niet afhangt van een directe beloning (Warneken et al. 2007). De chimpansees in deze studie hielpen spontaan zowel een mens als een soortgenoot, of ze er nu voor beloond werden of niet. Ondanks dat de uiteindelijke uitkomst van hulpgedrag misschien toch wederkerigheid kan zijn, hoeft de onderliggende directe motivatie niet gebaseerd te zijn op een calculatie van de kosten en de baten. In plaats daarvan kan het ook zo zijn dat natuurlijke selectie psychologische mechanismen heeft gegenereerd welke spontaan hulpgedrag veroorzaken (de Waal 2007; 2008). Als individuen echter gelijkwaardig en met regelmaat met elkaar omgaan zullen op de lange termijn gemiddeld genomen zowel de gever als de nemer er voordeel bij hebben. Daarom kan men pro-sociaal gedrag, d.w.z. gedrag dat de ontvanger

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bevoordeelt, verwachten bij elke soort waarin wederkerige relaties niet gebaseerd zijn op een actieve vergelijking van kosten en baten.

Ik heb middels een experiment getest of java-apen in staat zijn om pro-sociaal gedrag te vertonen. De heersende gedachte tot op heden was dat despotische soorten zoals java-apen hiertoe niet in staat zouden zijn, juist vanwege hun stricte dominantiehiërarchie. In mijn experiment konden de apen kiezen om of alleen zichzelf, of om naast zichzelf ook een ander de toegang tot een stukje banaan te verschaffen. De uitkomst van dit experiment laat zien dat ook sommige despotische java-apen anderen bevoordelen en dus tot pro-sociaal gedrag in staat zijn (**hoofdstuk 4**). Binnen elk tweetal binnen de groepen die ik bestudeert heb heerst op de korte termijn tolerantie t.a.v. ongelijkheid in hun uitwisselingspatronen, d.w.z. dat op de korte termijn de hoeveelheid die gegeven en gekregen is niet in balans hoeft te zijn (**hoofdstuk 2 & 3**). Daarom zou men kunnen verwachten dat ook alle tweetallen pro-sociaal gedrag ten opzichte van elkaar vertonen. Van vrienden wordt echter verwacht dat ze verschillen van niet-vrienden in de omvang van hun pro-sociaal gedrag, aangezien ze ook veel vaker diensten met elkaar uitwisselen (**hoofdstuk 3**). Desalniettemin wordt het pro-sociaal gedrag van de java-apen in mijn experiment niet bepaald door de kwaliteit van de relatie. Wanneer de java-apen echter de keus hadden leek het er wel op dat ze liever aan hun vrienden geven dan aan hun niet-vrienden (**hoofdstuk 5**). In zijn algemeenheid wordt pro-sociaal gedrag echter bepaald door de dominantierang van het subject (**hoofdstuk 4**). Alleen de dieren die een hoge rang hebben vertonen pro-sociaal gedrag, terwijl de dieren met een lage rang zelfs a-sociaal gedrag vertonen (d.w.z., zij beletten hun partners met opzet de toegang tot voedsel). Het pro-sociale gedrag van de dominanten dient waarschijnlijk als een strategie om hun status te vergroten of te behouden (Moore 1984; de Waal 1989), terwijl de subordinate dieren een meer competitieve strategie prefereren en daarmee hun partners (concurrenten) de toegang tot voedsel beletten. Echter, wanneer de dieren de keuze hebben tussen twee partners om een beloning aan te geven, blijken alleen de dominanten liever aan hun vrienden te geven. Dieren die subordinaat aan beide partners zijn hebben daarentegen een significante voorkeur om aan de meest dominante van de twee partners een beloning te geven (**hoofdstuk 5**). Deze voorkeur van de subordinaten zou een drijfveer voor toekomstige voordelen, zoals tolerantie en steun in een conflict van dit dominantere individu, kunnen weerspiegelen (Seyfarth 1977; Noë et al. 1991). Subordinaten zijn echter in het algemeen niet snel geneigd te geven, zoals ik laat zien in **hoofdstuk 4**. Daarom poneer ik een alternatieve verklaring, namelijk dat de voorkeur van de subordinaten een competitieve strategie weerspiegelt waarbij deze laaggeplaatste

dieren vermijden iets te geven aan hun meest directe concurrent (**hoofdstuk 5**). Samenvattend: java-apen zijn zoals verwacht werd n.a.v. de tolerante uitwisselingspatronen in hun dagelijks leven, in staat tot pro-sociaal gedrag. Dit pro-sociale gedrag wordt echter sterk beïnvloed door de dominantierang van het desbetreffende dier. Dominante dieren zijn pro-sociaal en subordinate dieren zijn a-sociaal. In zijn algemeenheid lijken pro-sociale tendensen niet af te hangen van de kwaliteit van de relatie, echter dominante dieren lijken er een voorkeur aan te geven om aan hun vrienden te geven. Daartegenover hebben subordinaten een voorkeur om aan de meest dominante van twee partners te geven i.p.v. aan hun vriend. Daarom lijkt het er dus op dat dominantierang bepaalt welk van de mogelijke sociale relaties, vriendschap of dominantie, de overhand heeft in het vertonen van pro-sociaal gedrag.

Een andere aanname van wederkerigheid, bemiddeld door emoties, is dat er een bepaalde tolerantie bestaat voor ongelijkheid in wat is gegeven en wat is gekregen. Zulk een tolerantie zou zich kunnen uiten in een minder aversieve of helemaal geen aversieve reactie als men oneerlijk bedeed wordt. Verder is het zo dat bij mensen verwacht wordt dat zulk een tolerantie groter is bij vrienden dan bij niet-vrienden (Deutsch 1975). Ik heb laten zien dat java-apen 'boos' worden, d.w.z. aversief reageren, als ze oneerlijk bedeed worden (**hoofdstuk 6**). De java-apen laten echter geen verschillende reacties zien wanneer ze met vrienden of met niet-vrienden getest worden. Daarom lijkt het erop, in ieder geval in dit experiment, dat vrienden niet toleranter zijn t.a.v. ongelijkheid dan niet-vrienden. De dieren uit deze groep in gevangenschap gaan echter zeer frequent met elkaar om. Daaruit zou kunnen volgen dat de variatie in de kwaliteit van relaties in deze groep nogal klein is. Een andere verklaring zou kunnen zijn dat het niet de partner was die de ongelijkheid veroorzaakte maar de experimentator. Daarom zou het zo kunnen zijn dat de 'boze' reactie van de geteste dieren niet naar de partner is gericht, maar juist naar de experimentator, en dat het dus niet belangrijk is of de partner nu een vriend of niet is. Bovendien is zulk een differentiatie in de uiting van aversie voor ongelijkheid - ondanks dat het uitgebreid beschreven is in de sociale wetenschappen (Deutsch 1975) - nog nooit experimenteel getest op andere diersoorten, inclusief de mens. Dit blijft daarom een interessant vraagstuk.

In het laatste deel van mijn proefschrift (**hoofdstuk 7**) heb ik onderzocht of biologen en sociale wetenschappers hetzelfde fenomeen beschrijven als ze het hebben over vriendschappen tussen dieren en tussen mensen. Biologen omschrijven vrienden vaak als sociaal gereedschap (Kummer 1978), terwijl sociale wetenschappers het liever over onvoorwaardelijke relaties hebben (Clark & Mills

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1979; Davis & Todd 1985). Er lijkt zich daarom een duidelijk contrast tussen biologen en sociale wetenschappers voor te doen betreffende het concept vriendschap. Dit contrast heeft er bovendien toe geleid dat wetenschappers suggereerden dat er alleen bij mensen zich ingewikkelde motivationele mechanismen om vriendschap te reguleren hebben geëvolueerd; d.w.z. mechanismen die gepaard gaan met een niet-instrumentele zorg voor de ander, waarbij er geen wederkerigheid nodig is of wordt verwacht (Tooby & Cosmides 1996; de Vos et al. 2001; Smaniotta 2004). Het zou echter ook zo kunnen zijn dat dit contrast slechts een gevolg is van verschillende onderzoeksontwerpen en van verschillende niveaus van verklaring, d.w.z. sociale wetenschappers concentreren zich op de directe motivatie van vriendschap, terwijl biologen zich concentreren op de evolutionaire voordelen van vriendschap. Daarom heb ik me in dit hoofdstuk als eerste geconcentreerd op de maten die gebruikt worden om vriendschappen te beschrijven en stel ik enkele vergelijkbare en objectieve maten voor om zowel vriendschappen tussen mensen als tussen dieren te omschrijven: de frequentie van nabijheid en vriendelijke aanrakingen (bijv. vlooiën). Ten tweede heb ik de evolutionaire voordelen van vriendschap tussen zowel mensen als dieren onderzocht en laat ik zien dat zowel vriendschappen tussen mensen als vriendschappen tussen dieren evolutionair voordelig zijn en dus ook adaptief. Als derde heb ik de directe motivaties voor vriendschappen tussen zowel dieren als mensen onderzocht. Ondanks dat die vriendschappen evolutionair voordelig zijn, laat ik zien dat de motivaties voor vriendschap bij zowel mensen als bij dieren niet gebaseerd zijn op deze toekomstige voordelen. In plaats daarvan lijken deze motivaties vooral onvoorwaardelijk en worden ze waarschijnlijk bemiddeld door emoties. Als laatste heb ik de nieuwste studies over de hormonale en neurale regulatie van sociale verbinding verkend. Deze studies lijken een rol voor emoties in het sociale gedrag van vrienden te bevestigen, waarbij een speciale rol blijkt weggelegd voor de neuropeptiden oxytocine en vasopressine. Daarbij komt dat deze neuropeptiden en sommige van de neurale paden al heel lang bestaan, ze worden gedeeld met een grote variëteit aan dieren, en dat ze waarschijnlijk een vergelijkbare functie hebben bij zowel mensen als andere dieren. Het lijkt er dus op dat vriendschappen bij mensen en dieren hormonaal en neuraal op eenzelfde manier gereguleerd worden. Daarom kom ik uiteindelijk tot de conclusie dat biologen en sociale wetenschappers een vergelijkbaar fenomeen beschrijven wanneer ze het over vriendschappen tussen mensen of tussen dieren hebben, en dat dus het gebruik van de term vriendschap in het geval van dieren onderling gerechtvaardigd is.

CONCLUSIE

...Van dieren weer terug naar mensen.

Mensen gaan niet alleen om met vrienden en kennissen, maar hebben vrij regelmatig ook interacties met vreemden. Zoals al eerder genoemd is, ontbreekt het vele soorten aan frequente interacties met vreemden en hebben deze soorten dus geen noodzaak voor ingewikkelde cognitieve mechanismen om daarmee om te gaan. Daarom zijn juist soorten die wel interacties met vreemden hebben - of op z'n minst nogal infrequente contacten met sommige individuen hebben - erg interessant: d.w.z. soorten die *'fission-fusion dynamics'* laten zien zoals chimpansees, hyena's, dolfinen en olifanten, of semi-solitaire soorten zoals orangutans. Er wordt gesuggereerd dat de bemiddeling van emoties bij interacties van deze soorten niet afdoende is voor alle relaties, omdat er niet genoeg emotionele ervaring is met elk individu dat ze tegenkomen (Aureli et al. 2008). Als gevolg daarvan hebben deze soorten behoefte aan andere manieren om om te gaan met anderen, afhankelijk van de frequentie en patronen van ruimtelijke en tijdelijke afscheidingen (Barret et al. 2003). Daarom zou ik willen stellen dat bij mensen en misschien sommige andere diersoorten zich ingewikkelde motivationele (waarschijnlijk cognitieve) mechanismen hebben geëvolueerd om bij te houden wat ze hebben gegeven aan en wat ze hebben gekregen van vreemden, bijvoorbeeld *'calculated bookkeeping'* (berekendend boekhouden)(de Waal & Luttrell 1988).

Een hersenstudie aan mensen bevestigt dat keuzes om samen te werken met bekende individuen gepaard gaan met activiteit in hersengebieden die gerelateerd zijn aan emotionele beoordelingen, terwijl keuzes om samen te werken met onbekende individuen gepaard gaan met activiteit van de meer corticale en cognitieve hersengebieden (Kreuger et al. 2007). Het blijft echter de vraag of andere dieren, zoals die soorten waarvan het sociale leven gekenmerkt wordt door *'fission-fusion dynamics'*, ook verschillende keuzeregels hanteren en verschillende hersenprocessen gebruiken bij vrienden, kennissen en vreemden. Echter de manier waarop chimpansees hun voedsel onvoorwaardelijk met vrienden delen, terwijl ze bij anderen de keuze om te delen laten afhangen van voorgaande interacties (de Waal 1997), en de ontdekking dat orangutans in staat zijn tot berekendend boekhouden (Dufour et al. 2009), lijkt een eerste indicatie dat sommige dieren misschien wel in staat zijn om verschillende, en ook cognitief complexere, keuzeregels toe te passen. Daarom is de onderzoeksvraag of dieren verschillende keuzeregels toepassen voor vrienden en vreemden, en of ze wanneer ze met vreemden te maken hebben ook in staat zijn om cognitief complexere keuzeregels te hanteren, volgens mij heel erg interessant en zou deze vraag toekomstig onderzoek

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naar sociale interacties en samenwerking, bij niet-menselijke dieren in het bijzonder, moeten stimuleren.

Concluderend: Interacties met vrienden en bekenden worden bemiddeld door een snel, (evolutionair gezien) oud, emotioneel systeem dat door mensen en verschillende dieren gedeeld wordt. Bij mensen en misschien sommige andere soorten wordt dit emotionele systeem aangevuld met nieuwere, corticaal gereguleerde, keuzeprocessen die bewuste, cognitief complexe, evaluaties van kosten en baten toelaten in de omgang met onbekenden.

Appendices

Appendix 1: Group composition of the rhesus macaque group at the BPRC

Robbedoes α ♂ (20-05-1995)

[Dona]

Mona α ♀	(01-07-1996)	
Lisa ♀	(30-05-2003)	
Da ♀	(29-05-2007)	
Anna ♀	(12-06-2008)	
Verf ♀	(01-06-2004)	
Qbert ♂	(02-05-2008)	
Bea ♀	(15-05-2009)	
Kwast ♂	(15-05-2005)	(Back cover: Middle)
Vinci ♂	(08-06-2007)	
Acryl ♀	(06-07-2008)	
[Gouda]		
Jam ♂	(24-06-2003)	
Saravi ♀	(05-05-2001)	
Fassa ♀	(06-06-2005)	
Kimsie ♂	(07-07-2006)	(Front cover: Top)
Rudi ♂	(21-06-2007)	(Front cover: Bottom)
Huub ♂	(04-06-2008)	
Latex ♀	(05-06-2009)	
Priegel ♀	(11-06-2002)	
Okki ♂	(23-05-2005)	
Taptoe ♀	(06-06-2006)	
Jetix ♀	(23-05-2007)	
Isabel ♀	(16-06-2008)	
Nanny ♀	(15-05-2009)	

[Oogje]

Nala ♀	(12-05-2000)	‡ (12-01-2007)
Timon ♂	(14-06-2001)	‡ (06-07-2007)

Staat ♀	(03-12-1988)	‡ (12-01-2007)
Emoe ♀	(01-07-1996)	
Girl ♀	(25-07-2005)	
Judith ♀	(27-05-2008)	
Wouter ♂	(29-05-2009)	
Cosmo ♂	(17-07-2007)	

Wenk ♀	(03-12-1988)	‡ (16-02-2009)
Natasha ♀	(01-07-1996)	
Kaas ♂	(02-05-2001)	
Ham ♂	(14-04-2004)	
Choco ♂	(14-05-2005)	
Venz ♂	(06-06-2006)	
Ugg ♂	(29-05-2008)	
Bout ♂	(13-05-2002)	
Yota ♀	(11-07-2004)	
Snars ♂	(15-06-2007)	
Olivier ♂	(14-04-2009)	

Epha ♀	(03-12-1988)	
Moer ♂	(23-05-2002)	
Zier ♂	(05-06-2003)	
Dremel ♂	(07-07-2004)	
Tang ♀	(04-07-2005)	

Appendix 2: Group composition of the long-tailed macaque group at the 'Ethologie station'.

Regilio α ♂ (19-01-1995)		
<hr/>		
[Felix]	Alfa ♀ (24-03-1987)	
	Kraa ♀ (26-09-1990)	
	Wodka α ♀ (11-04-1097)	
	Ekzekwo ♂ (13-11-2001)	
	Tamanduwa ♀ (20-03-2003)	
	Nirgendwo ♂ (11-08-2008)	
	Tonko ♂ (12-08-2001)	(Back cover: Top)
	Annika ♀ (10-11-2004)	
	Rijstevlaa ♀ (04-08-2008)	
	Aviko ♂ (17-12-2007)	‡ (21-09-2009)
	Milka ♀ (28-06-2009)	
[Yabaa]	Caya ♀ (03-04-1998)	
	Tabasco ♂ (17-06-03)	
	Suraya ♀ (16-06-2000)	
	Burkina-faso ♂ (24-05-2004)	
	Vivaa ♀ (28-12-1995)	
	Salsaa ♀ (17-09-1999)	
	Justso ♂ (08-06-2003)	(Back cover: Bottom)
	Plopsa ♀ (06-07-2008)	
	Kufo ♂ (08-08-1994)	‡ (06-07-2009)
<hr/>		
	Cordoba ♀ (13-04-2005)	
	Metellica ♀ (02-06-2009)	
<hr/>		
Freya ♀ (25-01-1990)		
	Rastafa ♀ (18-11-1994)	
	Latifa ♀ (08-03-1996)	
	Tres-bella ♀ (28-01-2001)	
	Toronto ♂ (28-02-2007)	‡ (22-09-2009)
	Risotto ♂ (09-12-2008)	
	Vodafo ♂ (29-01-2004)	‡ (06-07-2009)
<hr/>		
Roza ♀ (07-01-1982)		
	Jura ♀ (13-12-1994)	
	Oh-ja ♀ (13-08-2002)	
	Hengeloo ♂ (11-03-2008)	‡ (20-09-2008)
	Ontarijo ♂ (28-09-2003)	
<hr/>		
Hoeba ♀ (12-09-1988)		‡ (11-01-2009)
	Geisha ♀ (14-12-1996)	
	Mega ♀ (19-02-2002)	
	Santiago ♂ (05-01-2004)	
	Winnebago ♂ (18-11-2005)	‡ (22-09-2009)
[Beha]	Inlimbo ♂ (07-02-2002)	
	Bonobo ♂ (01-11-2003)	

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Curriculum Vitae



I, Jorg Johannes Maria Massen, was born on Friday the 13th of March 1981 in Sittard, The Netherlands. I spent my childhood years in Buchten, a small village in the beautiful province of Limburg. I attended the gymnasium of 'het College' (later 'Serviam College' / 'Trevianum') in Sittard, where I attained my high school diploma in 1999. During my childhood I always had a great fascination for animals, and therefore decided to study either Veterinarian Sciences or Biology. Fate (a lottery for admission to Veterinarian Sciences) decided for me and in

September 1999 I started to study Biology. During my undergraduate years I became more and more interested in Behavioural Ecology. Therefore, in 2003 I started my first internship at the Netherlands Institute of Ecology (NIOO) studying the begging behaviour of young blue tits. I spend eight months roaming the Dutch National Park 'de Hoogge Veluwe' and scanning videotapes in Heteren under the supervision of Tobias Limbourg and Kate Lessels. It was there that Liesbeth Sterck told me about possibilities for internships in Indonesia. And by the end of 2003 I found myself in the rainforest of Central Kalimantan, studying the development of feeding competence in wild orang-utans. Under the supervision of Serge Wich I spend eight wonderful months in Indonesia and back in the Netherlands Liesbeth Sterck helped me to write my Master's thesis. In November 2004 I then graduated from Utrecht University with a Master in Biology.

Unfortunately the job market for Behavioural Biologists is not too big. After working as a waiter for half a year, I started a Master in Science Communication. However, during this master I applied for a PhD project at Utrecht University on friendship in macaques. Since then I have been studying both rhesus and long-tailed macaques using both observational and experimental approaches. This thesis is the results of those years.

Next, I hope to study cooperation in ravens, which are sometimes referred to as the feathered apes, at the University of Vienna.