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# Social grooming in Barbary macaques

Ph.D. Thesis

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## Annotation

Social grooming is one of the most common forms of affiliative behaviour among socially living animals and has been in the centre of interest from the early beginnings of primatology. Social grooming is a behaviour in which social animals, clean or maintain one another's body and many studies focused on investigating the function of grooming behaviour. This thesis consists of general introduction and three studies that investigate social grooming in a population of semi-free ranging Barbary macaques from Gibraltar. The studies are based on original data and the results provide an interesting and new insight into the grooming behaviour in Barbary macaques. The first study focused on grooming patterns among females and we found that grooming was directed up the hierarchy, was affected by friendship and kinship. In the second study we tested the effect of maternal status on grooming among females and results showed that mothers gave less grooming but did not receive more grooming from other females. On the basis of these results we proposed that the observed patterns would be better explained by time constraints posed on mothers, rather than by grooming for infant handling exchange. In the last study we investigated the relationship between grooming and sexual activity between males and females. Our data showed that males as well as females preferred for mating activities those individuals that groom them most.

**Declaration [in Czech]**

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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## List of papers and author's contribution

The thesis is based on the following papers:

I. Lhota S, Roubová V, Gregorová V, Konečná M. Not just payment for mating: patterns of grooming and sexual activity in Barbary macaques *(Macaca sylvanus)*.
*manuscript*

*Veronika Roubová collected half of the behavioural data, prepared the data for analysis and contributed to the writing of the manuscript together with the co-authors.*

II. Roubová V, Lhota S, Wallner B, Konečná M. Time constraints rather than attraction to infants may explain the effect of maternal status on grooming among Barbary macaque *(Macaca sylvanus)* females.
*manuscript*

*Veronika Roubová collected half of the behavioural data, prepared the data for analysis and contributed to the writing of the manuscript together with the co-authors.*

III. Roubová V, Konečná M, Šmilauer P, Wallner B (2015). Whom to Groom and for What? Patterns of Grooming in Female Barbary Macaques *(Macaca sylvanus)*. PLoS ONE 10(2): e0117298. https://doi.org/10.1371/journal.pone.0117298; IF=2,806

*Veronika Roubová participated on study design preparation, collected half of the behavioural data, evaluated and analysed the data, and wrote manuscript with the help of co-authors.*

## Content

# CHAPTER I.

## General Introduction

## 1. Description of grooming behaviour

Social grooming is a behaviour in which social animals (including humans), clean or maintain one another's body or appearance. It is one of the most common forms of affiliative behaviour among socially living animals and involves gentle touches as well as stroking, scratching or massaging with removing the ectoparasites or old skin. Grooming moves are very rhythmic, and the plucking often involves pinching and pulling of the skin that can at times be quite painful (Dunbar 2010).

Social grooming, or allo-grooming (the grooming of others), is a widespread activity throughout the animal kingdom, but especially in primates plays a particularly important role in social bonding which, in turn, has a major impact on an individual's lifetime reproductive fitness (Dunbar 2010). Strong social bonds among individuals can affect ability to survive via coalitionary support (Schino 2007, Borgeaud and Bshary 2015) or tolerance over limited sources (Ventura et al. 2006, Yu et al. 2013), can increase infant survival (Lazaro-Perea et al. 2004) or health outcomes (Silk et al. 2003a). Grooming is a regularly performed behaviour in a variety of socially living species including rodents (Boles 1960, Ferkin and Leonard 2004), felids (Eckstein and Hart 2000), primates (Schino 2001, Clutton-Brock 2009, Molesti and Majolo 2017), ruminants (Hart et al. 1992, Hart and Hart 1992, Mooring et al. 2000), horses (Feh and de Mazières 1993) meerkats (Kutsukake and Clutton-Brock 2010), birds (Radford and Du Plessis 2008) or bats (Carter and Lauren 2015) which all form social bonds through grooming behaviour. Additionally, we can also observe inter-specific grooming between taxonomically unrelated groups of vertebrates as in the case of capybaras *(Hydrochoerus hydrochaeris)* and wattled jacanas *(Jacana jacana)*, horses *(Equus caballus)* and cattle egrets *(Bubulcus ibis)* (Sazima and Sazima 2010, Tomazzoni et al. 2005), or in sambars *(Rusa unicolor)* groomed by rhesus macaques *(Macaca mulatta)* (Vasava et al. 2013).

In different species, grooming is performed by a different manner. Birds use their beaks, felids groom by licking, whereas horses used mainly their teeth. In anthropoid primates precision grip (point finger – thumb grip) evolved which made grooming more precise and grooming movement became more complex. At the beginning, infant monkeys and apes are worse groomers until their precision grip has developed properly. This is usually after a completed myelinisation at the age of 6–8 months (Altmann, 1980). Infants "experimental grooming movements" can more remind slapping than careful grooming movements. Moreover, according to Dunbar (2010) manual grooming characteristic to monkeys and apes is much less common even among the prosimian (Strepsirrhine) primates, whose precision grip is much less efficient. On the other hand, many prosimians possess a dental comb which is a specially adapted lower incisor row that is used like grooming tool in both self and social grooming.

Grooming might sometimes serve a species-specific function. It can be a question of survival in some species compared to others. For vampire bats, for example, social grooming is crucial, since it is necessary for them to maintain food-sharing relationships in order to sustain their unique regurgitated food sharing behaviour. In primates, who mostly live in social groups, researchers observe intraspecific as well as interspecific social grooming interactions that can differ in its intensity and in its aim. Interspecific grooming behaviour can be observed in species who form mixed-species groups like tamarins (Heymann and Sicchar Valdez 1988, Bicca-Marques and Garber 2003, Peres 1993), Cercopithecus monkeys (Cords 1990), or in lemurs (Freed 2006) or in species who are forced to share the same enclosure in zoological gardens. It could be supposed that more social grooming interactions should be probably observed between individuals of the same species, inside the same troop or among kins due to currently expected functions of the social grooming.

The literature review shows that the majority of the grooming studies are focused on primate taxa. Therefore, grooming has been labelled as the most commonly studied primate social behaviour at all (Schino 2001). It is one of the most common forms of affiliative behaviour mainly among primate species such as macaques, baboons, or chimpanzees. The fact that social grooming in some species may occupy up to 20% of the daily time budget and is conserved despite the other demands (that could be seemingly more important e.g. increased foraging requirements), suggests that it has a great biological importance for the involved individuals (Henzi and Barrett

1999). However, it is necessary to mention that there are numerous primate species that allogroom rarely or not at all (e.g. *Tarsius* or *Daubentonia madagascarienis*) (Sparks 1967, Dunbar 1991). In general, the social grooming seems to be less common in New World than in the Old-World monkeys. This pattern could be possibly caused by different socio-ecological adaptations among species (Old world monkeys form larger and more complex social groups). According to Dunbar (1991) there is a necessity in larger group to adopt behavioural strategies designed to support the cohesion of such groups (Dunbar 1991) and such a strategy can be the grooming. Life style (terrestrial or arboreal) or fur length were also proposed as other possible factors influencing the amount of grooming, however these factors did not explain the grooming patterns fully (Dunbar 1991). Therefore, other studies tried to reveal the factors affecting the amount and distribution of social grooming across the species and potentially shed light on the principles governing primate social structures (Schino 2001).

Most of the studies, however, focuses on intraspecific grooming distribution. Within the group, grooming interactions are influenced by many factors such as kinship (Cords and Nikitopoulos 2015, Städele et al. 2016), dominance (Schino et al. 2007), affiliative behaviour (Koski et al. 2007), age (Kanngiesser et al. 2011) or sex of individuals involved (Kulik et al. 2015). These factors I will discuss later in a chapter: Grooming partner choice.

## 2. Grooming function

Social grooming has been in the centre of interests from the early beginnings of primatology. Different studies suggested, grooming may have a different meaning for animals involved.

### 2.1 Hygienic function

The hygiene is accepted to be the evolutionary origin of allogrooming behaviour in primates (Barton 1985). In last years this function has received little interest from researchers compared to the lastly proposed social function (Dunbar 1991) that have been studied extensively (see below, chapter: Grooming function). The supposed aim of hygienic function is removing parasites, old skin, dust, or cleaning the wounds (Goosen 1987) with possible benefits for thermoregulation (McFarland et al. 2016) when fur improved its thermoregulatory ability after the grooming session.

Hygienic function of social grooming predicts, that the amount of the grooming should be positively correlated with the body size of the groomee (larger body means higher parasite load) and that the inaccessible body sites should be groomed more (Saunders 1987, Barton 1985, Perez and Vea 1999, Reichard and Sommer 1994). This was supported by Perez and Vea (1999) who confirmed that inaccessible sites received more social grooming than predicted by their actual surface area. Similarly, Tanaka and Takefushi (1993) found that most (98.9 %) of what Japanese macaques picked up and ate during grooming were the eggs of lice. Hence, social grooming is supposed to have a hygienic function and eliminate the load by the external parasites (Tanaka and Takefushi 1993).

Although, previously mentioned studies suggest hygienic function, Dunbar (1991) found that frequencies of social grooming of free-living catarrhine primates correlate with group size rather than with body size. This was later interpreted as an evidence for the social function of grooming and against the purely hygienic function. According to Dunbar (1991) it is possible to found important differences between platyrrhine and catarrhine species where in platyrrhines body weight correlates better with grooming time than does group size (for catarrhines the reverse is true). These results seem to suggest that in platyrrhines the hygienic function of grooming is relatively more important than the social function. However, this conclusion seems to be inconsistent with that found by Perry (1996) and O'brien (1993) who claimed based on their results that grooming in capuchins has more than purely hygienic function. Also, Sanchez-Villagra et al. (1998) showed that in red Howler monkeys data collected for social grooming supported both: grooming for hygiene and for better social relationships. According to Perez and Vea (1999) or Reichard and Sommer (1994) the importance of hygienic function hypothesis should be easily verified by grooming preference for a particular body site. The sites that are inaccessible for self-grooming should receive more grooming than predicted by their actual surface area which is due to the fact that given individuals are not able to remove parasites from these places on their own. This has been supported in white-crowned mangabeys *(Cercocebus torquatus lunulatus)* (Perez and Vea 1999) and gibbons *(Hylobates lar)* (Reichard and Sommer 1994).

However, a potentially problematic factor that can influence distribution of social grooming over different body areas is the effect of social hierarchy when lower-ranking individuals tend to avoid a frontal eye contact (regarded as a threat) with higher-ranking individuals and preferentially groom dorsal and caudal parts of the body (Franz 1999, Boccia et al. 1982). This could bias the results in favour of the hygienic function hypothesis based on site preferences. Moreover, Dunbar (2011) pointed out to the fact that wild primates do not suffer from high external parasitic load as might be expected and that the amount of time devoted to social grooming in primates far exceeds that minimally required to keep the fur clean.

Based on the current literature, at least old-world monkeys seem to use grooming mostly for social purposes. Otherwise, it does not mean that it still does not serve also the hygienic function and in some cases, it could even overweight the social function in some species.

## 2.2 Calming effect

The hypothesis of tension reduction predicts that affiliative social interactions such as grooming alleviate psychological stress. This was firstly proposed by Terry (1970). Tension was described as an animal's internal state derived from conflict situation (Schino et al. 1988) or from approach/presence of dominant or potentially dangerous individual (Aureli and Schaffner, 2002). The calming effect of positive social interactions was confirmed in humans as well as in other animal species (Thorsteinsson and James 1999 - humans, Rosal et al. 2004 - humans, Schino et al. 1988 – long-tailed macaques, Aureli and Yates 2010 – crested black macaques, Feh and de Mazières 1993 – horses).

The social grooming can be seen as a tool how to re-establish the previous state and reduce psychological tension (Aureli et al. 1999, Shutt et al. 2007). The tension reduction can be the important mechanisms that may contribute to the group cohesion and facilitate reconciliation or bond formation. Several studies have been looking on physiological reactions to grooming interactions among the groomer and groomee. According to

Keverne et al. (1989) being groomed results in the releasing of Beta-endorphins that have calming effect on a given individual. Beta-endorphins are opioid agonists and acts on receptors to promote feelings of relaxation and pain reduction (Royston 2013, Stefano et al. 2000) and are very sensitive to persistent low level of muscular or emotional stress which also explain psychological release in humans during exercise (Howlett et al. 1984). In contrast, Aureli et al. (1999) or Feh and de Mazières (1993) found stress release due to grooming by showing a reduction in heart rate in groomed individuals with use of a stethoscope. Stress reduction can be also positively associated with immunity and improved recovery of T-helper and T-suppressor cells (Gust et al. 1996). This was supported by Yee et al. (2008) who found in rat that social affiliation positively correlates with lower levels of mammary tumor development and longer lifespan. Similar evidence is further supported by studies using behavioural stress indicators such as self-scratching and self-grooming (Aureli, 1997). Schino et al. (1988) found that after grooming, long-tailed macaques *(Macaca fascicularis)* display decreased level of aggressive interactions. The reduction of stress among individuals and the increase of tolerance can be taken as a support for the prediction that grooming others is more or less beneficial. Moreover, several studies also provided evidence that grooming is beneficial not only for groomer but also for groomee (Aureli and Yates 2010, Shutt et al. 2007). This could be tied with lower possibility to be attacked by the individuals who are groomed.

In conclusion, physiological as well as behavioural data usually confirm that animals exhibit stress reduction and relaxation during and/or after the grooming session which probably have a great importance for wellbeing and group dynamics in socially living species.

## 2.3 Social cohesion

It is presumed that individuals have relationships with their social partners and that these relationships can exist outside of particular interactions. It seems that the social grooming plays a particularly important role in social bonding (Dunbar 2010) and increase group cohesion especially in primates (Sparks 1967, Kummer 1978).

Intensive close social relationships among primates can be roughly analogous to human friendships (Silk 2002b). In human friend cohesions, it is possible to observe strong social bonds or stability and the same pattern can be found in non-human primate grooming networks (Guan et al. 2013). In primates, strong social bonds exist mainly between individuals inside one social group. Social bonds provide benefits such as higher reproductive success or higher inter group competition success (e.g. Xiang et al. 2014, Qi et al. 2017). Thus, grooming can be seen as an affiliative act which increases group cohesion (Guan et al. 2013). Moreover, it has been shown that the time primates invest in grooming increases with group size (Manson et al. 2004). This can be probably explained by the fact that with increasing number of cooperative individuals it is necessary to increase the time individuals need to interact with each member to maintain the cohesion. However, because bonds between individuals need to be maintained, sociality will be limited by time constraints (Lehmann et al. 2007). Thus, when the group is too large, individuals do not have enough time to groom all possible social partners and group cohesion is expected to decrease. This was confirmed by Dunbar (2010) who found that grooming time was influenced by group size and that the group size has its maximal number to be stable. This number is species specific and is likely influenced by neocortex size (Lehmann et al. 2007) and the cognitive abilities of a given species.

It is also known that the probability of support in aggressive interaction is positively correlated with the amount of time two individuals spend with grooming each other (Dunbar 1980, Datta 1983) and that grooming provides basis for inter-individual alliances. Social grooming is also used as a means for conflict resolution and reconciliation in some species (Henzi and Barrett 1999, Aureli et al. 1989, Cords 1997, Preuschoft and van Schaik 2000). There is strong positive correlation between quality of relationship (measured by grooming interactions) and the tendency to reconcile in several primate species (Aureli 1997, Das et al. 1998 or Palagi et al. 2008). Individuals which groom more have a stronger tendency to reconciliate. In some species this relationship has been found only for females and not for males (Cooper et al. 2005) or was not find at all (Matheson 1999). However, Matheson (1999) admit that the possible reason why affiliation was not detected in his study of rhesus macaques *(Macaca mulatta)* is due to the used methodology. It has been shown that social cohesion and stability can play a vital role in females' lives and their reproductive success (Silk et al. 2006a).

In summary, previous studies have documented that positive social relationships among group living individuals can reach far behind the directly observable interactions and that the grooming is an indispensable social interaction serving important functions to maintenance of social group.

## 3. The social market

Cooperation is crucial for survival and social success of many social animals including humans (Barclay 2016, Noë 2017). In biological markets, firstly proposed by Noë and Hammerstein (1994), two classes of traders cooperate and exchange commodities to fulfil their mutual benefits. In other words, one individual offers in exchange something that is demanded by the other and both of them benefit from this. Nevertheless, if a given individual wants to cooperate with another it must possess something which is demanded.

In early times of biology, ability to exchange different commodities was attributed only to humans as was published by Smith (1776) who mentioned that exchanging is common to all men, and not to be found in animals, literally: "nobody ever saw a dog make a fair and deliberate exchange of one bone for another with another dog" (Smith 1776). Nevertheless, biologists could observe a different act of exchanging between individuals in animal kingdom. The authors who firstly described clear exchanging between animals and who on its base proposed the label "biological markets" were Noë and Hammerstein (1994, 1995). Scientists then started to describe biological markets in wide range of species e.g.: in primates (Wei et al. 2013, Fruteau et al. 2009, Löttker et al. 2007), bats (Carter and Wilkinson 2013), meerkats (Kutsukake and Clutton-Brock 2008, 2010) or wrasses (Adam 2010) and in wide range of situations e.g.: in mating markets (Wincenciak et al. 2015, Massen et al. 2012, Metz et al. 2007), cleaner mutualism (Adam 2010), cooperative breeders (Kutsukake and Clutton-Brock 2008), grooming in primates (Balasubramaniam 2011, Barrett et al. 1999), nutrient exchange (Werner and Kiers 2015), or plants animal mutualism (Song and Feldman 2013).

As a biological market can be labelled interactions between organisms in which one can recognise different classes of “traders” that exchange commodities, such as goods (e.g. food, shelter, gametes) or services (e.g. warning calls, protection, pollination) (Noë and Hammerstein 1995, Hammerstein and Noë 2016). One of these different classes of “traders” is the one that offers some kind of benefits - seller (food, shelter, gametes, infants, protection, grooming etc.) and the second that looks for these benefits - client. Biological market models are dynamic, where individuals’ decisions vary across time according to local circumstances (current availability of commodities). Biological markets also explain and make predictions about why individuals desire to associate with particular partners and how they attract them. Noë and Hammerstein (1994, 1995) proposed that biological market runs under few assumptions: **1)** individuals control resources or can provide a service to others, these constitute commodities that can be exchanged but not taken by force (it cannot be stolen), **2)** trading partners are chosen from a range of individuals by a system of outbidding competition, where the aim is a maximal profit (partner with the best offer is winner), **3)** supply and demand determine the value of exchanged commodities among individuals - the value of commodities is variable depending on circumstances and its availability.

In summary, the principles of biological markets can be found in context of e.g. mating systems, cooperation among conspecifics or mutualisms between members of different species. Otherwise, the ability to demonstrate biological markets depends on various factors such as availability of different traders or variable circumstances.

## 4. Grooming as a commodity on biological market

In primate biological market one of the most studied traded commodities is grooming. Grooming is considered as an important exchange commodity and can be traded for the same-kind service – for reciprocal grooming (Schino and Aureli 2008, Muroyama 1991), or for different-kind services or commodities including: infant handling (Muroyama 1994, Gumert 2007, Yu et al. 2013, Wei et al. 2013, Tiddi et al. 2010), mating opportunity (Gumert 2007, Sonnweber et al. 2015), coalitionary support (Henzi and Barrett 1999, Ventura et al. 2006), or tolerance over food resources (de Waal 1997, Borgeaud and Bshary 2015).

## 4.1 Reciprocal grooming

When no other services are available for the exchange, grooming is predicted to be approximately reciprocated within a dyad (Wei et al. 2012). In principle, individuals then reciprocate grooming solely for the benefits that grooming itself offers (parasite removal, release of β-endorphins/reduction of tension, coalition formation, see chapter: Grooming function).

Barrett et al. (1999) proposed that grooming is a tradable commodity and individuals within a primate group are traders who compete with each other in the marketplace exchanging grooming for itself (reciprocal traders) or for other goods (interchange traders). It is proposed that duration of grooming bouts offered and returned is usually asymmetrical within dyads which is probably caused by a different market power of participating individuals (Katsu et al. 2013). Such a power can be differentiated by individual's dominance status, by mutual kinship or relationship quality. However, Schino et al. (2003) mentioned that primate interindividual relationships seem more likely to be characterized by a variable mixture of reciprocation and interchange, and disentangling such complex web is not a trivial task. This means that the amount of received grooming can be reciprocated by the different ration of grooming and other type of benefits or solely by e.g. tolerance over the food source. The question is if we are able to fully capture all interchanges between a given individuals. Several studies reported that individuals groomed preferentially those individuals that groomed them the most but that the grooming relationship was rather asymmetrical (Schino and Aureli 2008, Xia et al. 2012).

The reciprocation can also partly depend on cognitive abilities of a given individuals to remember their counterparts and amount of interactions with them (Barrett et al. 2003). There is ongoing debate over whether primates keep track of previous interactions and, if so, whether they can do it over extended periods of time, or whether they are constrained to exchange grooming within a single encounter. The time lag between giving and receiving of services and resources is one of the crucial aspects of reciprocity (Gomes et al. 2009). Several authors suggested that non-human primates do not have cognitive abilities that would enable them to reciprocate acts on a long-term basis (Barret et al. 1999, Barrett and Henzi 2002, Payne et al. 2003, Stevens and Hauser 2004). This could be a case of chacma baboons *(Papio cynocephalus ursinus)* or blue monkeys *(Cercopithecus mitis)*, which reciprocated grooming rather on short term basis (Barrett et al. 2002, Pazol and Cords 2005). In contrast, other studies suggested that reciprocation can be observed rather in a longer time frame (Manson et al. 2004 - data for white-faced capuchins, *Cebus capucinus*, and bonnet macaques, *Macaca radiata*, Schino et al. 2007 - Japanese macaques, *Macaca fuscata*, Gomes et al. 2009 – chimpanzees, *Pan troglodytes verus*). Gomes et al. (2009) also suggested that grooming was reciprocated more symmetrically when measured on a long-term, rather than on an immediate or short-term basis. These authors also noted that it is unknown, whether different results of studies were caused due to exploring only limited time frames for reciprocation which then could lead to false conclusions on the time lag between giving and receiving, or if these results are due to the real species differences. Also, Sánchez-Amaro and Amici (2015) claimed that determining the real time frame over which exchanges take place is clearly a hard task, especially in primates, where species significantly differ in terms of ecology, demography and social structure.

In summary, grooming reciprocation is frequently observed behaviour among primates with more or less species-specific differences. We can usually find that it has an asymmetrical distribution between individuals involved and that it is influenced by animal cognitive abilities. It will probably need other studies to fully understand underlying principles of reciprocation.

## 4.2 Exchange for infant handling

In the most of primate species the mother is the main handler and caretaker of her infant (Nicolson 1987). However, in some species, other group members participate often in infant care (Barrett et al 1999, Kümmerli and Martin 2008, Silk 1999). It has been frequently observed that mothers with infants are very attractive social partners, suggesting that individuals exchange grooming for the access to an infant (Barrett et al. 1999). Exchange between grooming and infant handling has been observed in many primate species: e.g. in chacma baboons (Henzi and Barrett, 2002), long-tailed macaques (Gumert 2007), spider monkeys (Slater et al. 2007) sooty mangabeys (Fruteau et al. 2011), or golden-snub nosed monkeys (Wei et al. 2013).

Many authors claim that especially new-born infants are extremely attractive to other group members, particularly to adult and adolescent/subadult female primates (Silk et al. 2003b, Silk 1999, Manson 1999) or juveniles (Cords et al. 2010), who usually approach a mother, groom her and then touch, hold or groom her infant. It is not only females who are interested to infants. Males can also carry and interact with infants and in some species this behaviour is typical in the context of male-male social bonding processes (Kümmerli and Martin 2008, Bauer et al. 2014, Kalbitz et al. 2017). According to mating effort hypothesis (Seyfarth 1978) males who spent the highest percentage of the time with infants achieved the highest mating frequencies compared to other males (Zhao 1996; Menard et al. 2001) and they increase their future mating success with the infants' mothers. Some authors can also see male-infant interaction as a paternal investment (Ostner et al. 2013).

Females' interest in new-borns is well known but there is still a debate about the exact explanation of infant handling by females. Firstly, from observation of some species it is assumed that alloparental care may have been favoured by kin selection, where alloparents typically care for closely related infants (Owens and Owens 1984, Johnson et al. 1980, Silk 1999) to help their mothers with infant raising when alloparents would simultaneously increase their own inclusive fitness (e.g. Rabenold 1985, Curry 1988). This could be seen in marmosets and tamarins where high dispersal costs and saturated habitats create poor breeding chances and therefore older offspring often remain in their natal groups and care for their younger siblings (Lazaro-Perea et al. 2004). Moreover, Kümmerli and Martin (2008) found that female Barbary macaques preferred to interact with related mothers and their infants. Secondly, alloparental care may be a means to obtain the alloparent's own parenting skills and increase their own future reproductive success by gaining experience with infant care (Paul et al. 1996). This was supported by Fairbanks (1990) who found that females who had more experience in caretaking and carrying infants as juveniles were more likely to rear their first live-born infant successfully. In contrast, Silk (1999) found that older experienced females were as interested in infants as were subadult females without any infant raising experience which provide only little support for the learning to mother hypothesis. Lastly, it is possible to find cases when alloparents harm entrusted infants thus the alloparenting may be seen as a form of reproductive competition (Silk 1980, Maestripieri 1994). Mothers can also benefit from alloparental care for their infants as they can increase their foraging efficiency and self-carrying possibilities (Silk et al. 2003b, Vogel 1984).

The amount of time when other females can approach, and touch infants depends on restrictiveness of maternal style. In some species, such as Asian colobines, infants are frequently held and carried by other group members (Stanford 1992). In contrast, in some macaques, baboons, vervets, or mangabeys, mothers are much more restrictive of their infants (Tiddi et al. 2010, Gumert 2007). Mostly in these species, where mothers tend prevent other females to access their infants, the allomothers can exchange grooming for infant handling. This was also probably the reason why most of "infant-handling for grooming studies" were made on species with restrictive maternal style which was supported by Gumert (2007) in long-tailed macaques, Henzi and Barrett (2002) in chacma baboons, or Fruteau et al. (2011) in vervet monkeys and mangabeys. However, we can find evidence that biological trade of grooming and infant handling exists also in primates with more permissive maternal style (Muroyama 1994, Yu et al. 2013, Wei et al. 2013).

In summary, infants are very attractive to most of the group members. Handlers as well as mothers can profit from infant handling in a various way. The amount of infant handling time usually depends on restrictiveness of its mother which can differ among the species.

### 4.3 Exchange for mating opportunities

Grooming can be also exchange for mating opportunities. Specifically, in species in which males cannot coerce females to mate, males may attempt to interchange grooming for mating opportunity, particularly when females are receptive and mating opportunities are more likely to arise (Barelli et al. 2011).

The value of mating can differ between both sexes and males and females may often have different sexual interests (Johnstone et al. 1996, Baldwin and Baldwin 1997). Therefore, it is expected that males and females express more or less different behavioural strategies in mating context. In humans as well as in other primates, various behavioural patterns have been reported between sexual partners before or after mating (Hughes and Kruger 2011, Nishida 1997). In primates, mating is often associated with other social behaviours, such as grooming (Sonnweber et al. 2015), and these behaviours can be species or sex specific.

Grooming in mating context can occur before or after sexual interaction. The majority of studies has been focused on **grooming before the sexual interaction**. For males, social grooming interaction was proposed as a male's strategy to gain tolerance from a female and increase his probability to engage in sexual activity with her (Barrett and Henzi 2001). Gumert (2007) claimed that male must invest some level of effort to gain sexual access to a female whose will to cooperate in mating is largely based on the male's ability to perform or show something that will attract her. Grooming can have this effect and it can increase the likelihood that female would prefer to mate with her male groomer over other males (Gumert 2007). For females, we know very little about function of grooming before mating. Females may groom males to maintain long-term social relationships. These bonds could be profitable for females and their offsprings because males could later protect their offspring and though reduce the risks of infanticide and infant mortality (Palombit 2000).

In case of the **grooming after the sexual interaction**, Sonnweber et al. (2015) mentioned that females may benefit from grooming males to increase protection or to gain additional mating. Whereas males may profit from grooming females after ejaculatory copulation by keeping them from mating with another male (form of male mate-guarding) and thus potentially decreasing sperm competition. Li and Zhao (2007) proposed that female's grooming after copulation can be also a form of female mate-guarding when female try to prevent other females from conception (so reduce the number of competitors for their own offsprings) or try to gain own offspring protection by males (although they do not have to be necessarily their fathers in some cases) (Palombit et al. 1997). For example, male and female in snub-nosed monkeys (*Rhinopithecus roxellana*) tend to groom after copulations, where females initiate more post-mating grooming bouts than males (Li and Zhao 2007). Sonnweber et al. (2015) found that males and females in Barbary macaques adjust grooming initiations depending on copulation type, with males initiating grooming after copulations with ejaculation and females after non-ejaculatory mating.

In general, many circumstances can influence grooming for mating strategies and female interest can extremely differ from those of males. Grooming partner choice can be also skewed by other factors such as dominance status of given individuals, age, or accessibility of demanded grooming partners. As one can notice grooming can be exchanged for the wide variety of commodities or benefits and the value of mentioned commodities or benefits differ in dependence on the current state of social market.

### 4.4 Exchange for coalitionary support and tolerance over food resources

Grooming can be profitable in many ways and if two animals experienced a reduction in anxiety after they groomed one another, they might be more likely to groom each other again in the future, tolerate each other near food resources or form coalitions (Molesti et al. 2015).

At first, exchange of grooming and support in fights among primates was seen only as a side-effect of correlations with other variables (Hemelrijk 1994). Soon, it was found that grooming is often directed up the hierarchy and that the dominant individuals can possess some valuable commodities. These findings support Seyfarth's (1977) hypothesis that grooming can be exchanged for different benefits and that these benefits can be rank related. In such a case, higher ranking animals may be preferential grooming partners, because they provide more efficient agonistic support, and also tolerance from them is more important than the one from subordinate animals. Lately, Seyfarth and Cheney (1984) tried to support the assumption with the finding that vervet monkeys attend to a vocal solicitation for aid longer if they had recently engaged in grooming with the solicitor. Hemelrijk (1994) studied interchange of support for being groomed by giving individuals an opportunity to support others under three conditions: **1)** after being groomed by the other, **2)** after grooming the other and **3)** without prior grooming. She found that females provided agonistic support to other females significantly more often if they had received grooming from them than if they had not groomed each other.

Nowadays, it is widely accepted that grooming-coalitionary support reciprocation truly exists (Schino 2007, Koyama et al. 2006, Schino et al. 2007). Nevertheless, given a low rate of coalitionary support occurrence it can hardly be considered as an ideal candidate behaviour for investigating reciprocity (Tiddi et al. 2011). As emphasized by other authors, grooming could be more simply exchanged for tolerance over food resources than for coalitionary support (Sánchez-Amaro and Amici 2015, Mitani 2006, Ventura et al. 2006) and tolerance may represent an important (though often overlooked) currency that primates routinely exchange and may also have important fitness consequences (Tiddi et al. 2011). It is also possible that when the food resources are more abundant and scattered the competition over the food will be smaller though the grooming amount will decrease, or grooming will be exchanged for other commodities.

## 5. Grooming partner choice

Social grooming can be exchanged for different commodities dependent on their availability and momentary demand. Some commodities can be acquired from almost every individual such as grooming, but some can be gained only from specific group members e.g. mothers, individuals of opposite sex or dominant individuals. What individual wants or is able to get/give in exchange for grooming thus guides his/her choice of grooming partners.

Traditionally, grooming has been considered to be an altruistic behaviour that is costly to the groomer (e.g. lost time and energy) and beneficial to the recipient - groomee (e.g. parasite removal or stress reduction) (Henzi and Barrett, 1999). The time and energy spend with grooming could be devoted to foraging, vigilance or finding a mate. Therefore, individuals are expected to select a groomee who will be worth investing in, who may reciprocate the service and/or provide alternative benefits. The literature offers several theories explaining observed patterns of grooming partner choice in primates and explaining, how the partner choice enhances individual fitness in both female (Silk et al. 2003a, Silk et al. 2010) and male primates (Schülke et al. 2010).

### 5.1 Kinship

Nowadays, we can find lots of studies were kins are preferred over the non-relative individuals during the grooming or other interactions (Silk 2002a, Schino and Aureli 2008, Johnson et al. 2013). In early times of ethology, however, such a behaviour wreaked havoc during the interpretation of mutualistic relationships. There was no expectation that among animals can be found behaviour that is costly to actors and beneficial to recipients and that such a behaviour can be differently distributed among individuals.

The first explanation has been suggested by Hamilton (1964). He set the Hamilton's rule ($rB > C$, where $r$ is coefficient of relatedness, $B$ is benefit of recipient, $C$ is cost of actor) providing an explanation for the evolution of altruism via kin selection. Kin selection may influence social interactions in a way that acts to increase an individual's inclusive fitness. Moreover, it can shape the evolution of social organization, reproductive strategies, or social behaviour.

The support for this theory has been provided by Schino and Aureli (2008) who in their meta-analysis found that in 22 different primate species grooming is directed preferentially to related individuals and are more frequent among the maternal relatives. The ability to distinguish relatives probably shapes altruistic behaviour in primates. There was a general assumption that primates could better recognize their maternal kin over their paternal kin (Silk 2002a). This was explained by the fact that subadult animals usually stayed around their mothers even some time after the weaning, so they could meet and coexist with her new infant, their sibling.

Early association may also provide an efficient mechanism to learn to recognize maternal kin, but not for identifying paternal kin (Schino 2001). Paternal kins even do not have to meet each other on regular basis as mothers can be from a different hierarchical level or even from neighbouring groups. Moreover, there may be considerable uncertainty about paternity in the most of primate species. Many species are polygynandrous - females mate with multiple males, but even in monogamous species (gibbons, titis) or one-male groups (patas, blue monkeys) females can mate with non-resident/outgroup males (Palombit 1994, Reichard 1995). Nevertheless, there is necessity to avoid inbreeding to maximize reproductive success and therefore it is desirable to distinguish close relatives (Alberts 1999). More recent studies reported the ability of primates to recognize also paternal siblings (Widdig et al. 2001, Silk et al. 2006b, Charpentier et al. 2006) and several possible mechanisms have been proposed how primates can distinguish paternal relatives, such as via olfactory (Smith and Abbott 1998 – scent marks, Wedekind and Furi 1997 - MHC), visual (Parr et al. 2010) or even behavioural cues (Widdig et al. 2001). According to some studies (Widdig et al. 2006), females support and groom maternal half-sisters significantly more often than paternal half-sisters or non-kin regardless of the costs associated with such interventions. Widdig et al. (2006) also found clear evidence for paternal kin discrimination in their study but admitted that patterns of social activity among paternal kins were quite complex and other studies were necessary to fully understand this subject.

In summary, kinship seems to have a broad impact on primate's social life and discrimination over the close relatives can play an important role in life success of a given individuals. Maternal relatives seem to be better recognized and preferred over the paternal relatives.

### 5.2 Dominance hierarchy

Another factor affecting distribution of grooming is dominance hierarchy. In social living animals, competition over resources inevitably exists and to avoid potentially dangerous encounters and injuries the social hierarchy evolved in many species. Dominant-subordinate relationship is then possible to define as a dyadic relationship that is characterized by an asymmetric distribution of power (Preuschoft and van Schaik 2000).

Grooming of high-ranking individuals can lead to acquiring benefits such as tolerance over food sources (Ventura et al. 2006, Borgeaud and Bshary, 2015) or agonistic support during conflict between individuals (Schino et al. 2007, Scihno 2007). Given that grooming with high ranking individuals is thus more profitable that grooming with low ranking partner. Moreover, dominant individuals can become a valuable "commodity" on itself. Individuals then can compete for access to the dominant partner by raising the price they are willing to pay (Frank and Silk 2009). Tiddi et al. (2012) proposed that high ranking females experience the least competition for preferred partners. On the other hand, middle-ranking females have fewer opportunities to access higher-ranking grooming partners because they are out-competed by higher-ranking females. Thus, it can be predicted that middle-ranking females would direct most of their grooming to other middle-ranking females. For the same reason, low-ranking females are limited to direct most of the grooming to other low-ranking females. The result of this mechanism is that females direct their grooming up the dominance hierarchy and that most grooming occurs between females of adjacent ranks (Singh et al. 2006, Tiddi et al. 2012), exactly as hypothesized by Seyfarth (1977) in his model for social grooming.

It was found that in socially living cercopithecoid primates, grooming distribution is in general greatly influenced by dominance status (Gumert 2007, Schino 2007, Ventura et al. 2006). Grooming is usually directed up the hierarchy (Schino 2001, Schino 2007, Nakamichi and Shazawa 2003, Gumert and Ho 2008). In contrast, recent reviews suggested that grooming asymmetries could change with social system and ecological conditions and should reflect asymmetries in services provided by different group members (Lazaro-Perea et al. 2004). For example, an absolutely opposite trend in grooming distribution (more grooming directed down the social hierarchy) was found in many studies of New world monkeys (Lazaro-Perea et al. 2004, Parr et al. 1997). Lazaro-Perea et al. (2004) suggested that, in cooperatively breeding systems, breeding females may use grooming as a payment for helper females to stay in the group. Such a situation could be better explained by the model proposed by Henzi and Barrett (1999) who suggested that grooming is a currency that is exchanged between group members. They predicted that grooming should be reciprocated within a dyad when no other services are being exchanged. However, when different partners within the dyad offer different services, the amount of grooming given should decrease as the other services offered increase. When dominant individuals have less to offer to subordinate ones (when there is a low level of resource competition), grooming asymmetry between dominant and subordinate decreases.

In summary, dominance status is an important factor for socially living animals and influences the choice of social partners. However, grooming distribution is also influenced by the social system, ecological conditions, relatedness, friendship etc. which make the situation more complex and sometimes it is very difficult to distinguish the power of individual factors.

## 5.3 Relationship quality

Quality of social relationship between group members can broadly influenced distribution of grooming. Good social relationship between group members may provide fitness benefits such as better access to food, protection from enemies or predators, reduced risk of infanticide, or better access to mating opportunities (van Schaik and Horstermann 1994, van Schaik and Janson 2000, Silk et al. 2003b, Shülke et al. 2010). Health consequences and reproductive advantages suggest that quality of social relationship has adaptive benefits (Brent et al. 2014). Despite these facts, relationship quality seems to be still underestimated and understudied factor.

The first who identified relationship quality as an important factor influencing the life of socially living animals was Kummer (1978) and soon after also Hinde (1979). Later, the relationship quality was considered analogous to human friendship (Silk 2002b). Kummer (1978) and Hinde (1979) measured the power of the relationship by frequency of observed behaviour (e.g. grooming, reconciliation). In a similar manner, the relationship quality was described in many other studies (Palombit et al. 1997, Silk et al. 2010, Moscovice et al. 2010). In some authors, the most popular method for measuring relationship quality is grooming between individuals (e.g. Silk et al. 2006a, McFarland and Majolo 2011). Nevertheless, in studies where grooming is one of the observed variables different measures as coalitionary support (Silk et al. 2004), approach (Cooper et al., 2005), mutual contact (Call et al. 1999), mutual contact and proximity (Cords 1997) or the combination of these behaviours (Palombit et al. 1997, Koski et al. 2007, Majolo et al. 2010, McFarland and Majolo 2011) were used to measure the quality of social relationship.

Cords and Aureli (2000) suggested that social relationships are likely to be asymmetrical in a dyad, because two partners are not equally valuable to a given individual and that a social relationship is very likely to be asymmetrical in a dyad. They also described relationship quality by three main components: value, security and compatibility. Where **value** is what the subject gains from her or his relationship with a partner, which depends on what the partner can offer (grooming, tolerance around food etc.); **security** is the probability that the relationship with the partner will not change over time; and **compatibility** is the general tenor of social interactions in a dyad. Cords and Aureli (2000) demonstrated their "three-component concept" on reconciliation tendencies between dyads. The reconciliation tendency with more valuable partner is higher than with less valuable partner. When social partners are valuable, unsecure relationships are in greater need for repair after aggressive conflict because their stability is more endangered. Moreover, the reconciliation between individuals who more often interact in non-antagonistic ways, may be easier because, they usually interact in affiliative manner, and so it is familiar to both of them. Assessment of relationship quality between individuals suggested by Cords and Aureli (2000) is very complex and due to its quite difficult evaluation and necessity for a complex dataset this framework was followed only by few authors (McFarland and Majolo 2011, Rebecchini et al. 2011, Majolo et al. 2010, Fraser and Bugnyar 2010, Fraser et al. 2008).

In summary, quality of social relationship is not equally distributed, that is why some dyads interact in affiliative way more often than others (Cords 1997). Strong relationships (friendship, bonds) are advantageous in several ways: e.g. male allies can improve their competitive ability and reproductive success, females with the strongest and most enduring bonds experience less stress, higher infant survival, or live longer. Good social relationship obviously has an important influence on individual's fitness.

## 6. Barbary macaques

Macaques are medium-sized primates belong to the family *Cercopithecidae*. They are the most geographically widespread primate genus (Thierry et al. 2000) and inhabit the wide variety of habitats that spread from west Morocco to Japan.

Barbary macaques is the only primate species that can be found north of the Sahara Desert in Africa and the only species of the genus "Macaca" that lives outside of Asia (Butynski et al. 2008). There is also population of Barbary macaques living in Gibraltar that is, however, supposed to be non-native (Fooden 2007). The Barbary macaques inhabit places between 400 and 2300 meters above the sea level and they can be found in a mixed cedar-oak (*Cedrus atlantica, Quercus ilex*) and oak only forests (*Quercus faginea, Quercus afores*), shrubs, grassland and rocky places (Fooden 2007). This species inhabits the Rif, the Middle and High Atlas Mountains in Morocco and parts of the Tellian Atlas in Algeria (Menard and Vallet 1993; Scheffrahn et al. 1993). Barbary macaques are categorized as a granivorous and folivorous species with occasional eating of lichens, mushrooms, or insects (Thierry 2000; Menard 2002). Like other macaques, they typically form multimale/multifemale troops with a strong matrilineal hierarchy where the sex ration is skewed in favour of females. Females stay in their natal group and form matrilineal sub-groups with their relatives (Thierry 2000, 2007). The troop typically consist of 40 individuals on average. Macaques have a promiscuous mating system, breed once per year and usually have one infant (Thierry, 2007). The mating season starts in November (Rowe, 1996) and lasts for the next few months.

It was found, that macaque's species differ in a degree of aggressive/affiliative interactions. These differences were broadly described by Thierry (1990, 2000, 2007) who divided macaques into a 4-grade scale. The grade 1 was described as the most despotic (e.g. *M. fuscata, M. mulatta*), the less despotic species can be found in grade 2 (*M. fascicularis, M. nemestrina*) and the most tolerant species are in grade 3 (e.g. *M. sylvanus, silenus*) and grade 4 (e.g. *M. nigra, M. maura*). Through the grades the power of aggressive interactions decreases and the amount of affiliative behaviours increase (from grade 1 to grade 4). The steepest dominance gradient and the most asymmetrical interactions can be found in species from grade 1 where grooming is directed mainly up the hierarchy and individuals tend to interact mainly with kins. On the other hand, in egalitarian macaque species Thierry (1990) found that dominance has a less influence on the distribution of grooming and that individuals interact in a more relaxed manner.

Barbary macaques are geographically and phylogenetically separated from the other macaque species (Liedigk et al. 2014). They are classified as a relatively egalitarian species and it is supposed that social interactions between individuals should be more symmetrical than in the species from grade one who are the most studied species. They are known for intensive infant handling by other group members (especially males), females are more permissive to infant handling in comparison to species from despotic groups (Maestripieri 1995).

The most of previously published studies focused on grooming in macaque species were done on species from grade 1 (e.g. *M. fuscata, M. mulatta*). However, less studies observed species from grade 2 (*M. fascicularis, M. nemestrina*) and the most tolerant species from grade 4 (e.g. *M. nigra, M. maura*). Researches focused on behaviour of the species from grade 3 (e.g. *M. sylvanus, silenus*) are very scarce. Barbary macaques (from grade 3), in comparison with some other macaque species, are quite unique in some traits (e.g. very sexually active females, intensive infant handling by other group members, strictly seasonal breeding). That make them very attractive species for testing hypotheses focused on grooming functions or grooming preferences and their general validity through the genus *Macaca*.

## 7. References

Adam TC (2010). Competition encourages cooperation: client fish receive higher-quality service when cleaner fish compete. Animal Behaviour 79(6), 1183-1189.

Albert SC (1999). Paternal kin discrimination in wild baboons. Proceedings of The Royal Socciety B 266, 1501-1506.

Altmann J (1980). Baboon mothers and infants. Cambridge: Harvard University Press.

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

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

Aureli F, Preston SD, de Waal FBM (1999). Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): A pilot study. Journal of Comparative Psychology 113, 59–65.

Aureli F, Schaffner CM (2002). Relationship assessment through emotional mediation. Behaviour 139, 393-420.

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

Balasubramaniam K, Berman C, Ogawa H, Li J (2011). Using biological markets principles to examine patterns of grooming exchange in *Macaca thibetana*. American Journal of Primatology 73, 1269-1279.

Baldwin JD, Baldwin JI (1997). Gender differences in sexual interest. Archives of Sexual Behavior 26, 181–210.

Barclay P (2016). Biological markets and the effects of partner choice on cooperation and friendship. Current Opinion in Psychology 7, 33–38.

Barelli C, Reichard UH, Mundry R (2011). Is grooming used as a commodity in wild white-handed gibbons, *Hylobates lar*? Animal Behaviour 82(4), 801–809.

Barrett L, Henzi SP, Weingrill T, Lycett JE, Hill RA (1999). Market forces predict grooming reciprocity in female baboons. Proceeding of The Royal Socciety B 266, 665–670.

Barrett L, Henzi P (2001). The utility of grooming in baboons troop. In Noë R, Van Hooff J, Hammerstein P (eds.), Economics in Nature: Social dilemmas, mate choice and biological markets. Cambridge University Press: Cambridge pp 119-145.

Barrett L, Henzi SP (2002). Constraints on relationship formation among female primates. Behaviour 139, 263–289

Barrett L, Gaynori D, Henzi SP (2002). A dynamic interaction between aggression and grooming reciprocity in female chacma baboons. Animal Behaviour 63, 1047–1053.

Barrett L, Henzi P, Dunbar R (2003). Primate cognition: from 'what now?' to 'what if?', Trends in cognitive sciences 7(11), 494-497.

Barton R (1985). Grooming site preferences in primates and their functional implications. International Journal of Primatology 6, 519-532.

Bauer B, Sheeran LK, Matheson MD, Li JH, Wagner SR (2014). Male Tibetan macaques' (*Macaca thibetana*) choice of infant bridging partners. Zoological Research 35, 222–230.

Bicca-Marques JC, Garber PA (2003). Experimental field study of the relative costs and benefits to wild tamarins (*Saguinus imperator* and *S. fuscicollis*) of exploiting contestable food patches as single- and mixed-species troops. American Journal of Primatology 60, 139–153.

Boccia ML, Rockwood B, Novack M (1982). The influence of behavioural context and social characteristics on the physical aspects of social grooming in rhesus monkeys. International Journal of Primatology 3, 91-108.

Borgeaud C, Bshary R (2015). Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in experimentally induced conflicts. Current Biology 25, 3011–3016.

Brent LJ, Chang SW, Gariépy J, Platt ML (2014). The neuroethology of friendship. Annals of New York Academy of Science 1316, 1-17.

Butynski TM, Cortes J, Waters S, Fa J et al. (2008). *Macaca sylvanus*. The IUCN Red List of Threatened Species 2008: e.T12561A3359140.

Call J, Aureli F, de Wall FBM (1999). Reconciliation patterns among stumptailed macaques: a multivariate approach. Animal Behaviour 58, 165–172.

Carter GG, Wilkinson GS (2013). Does food sharing in vampire bats demonstrate reciprocity? Communicative & Integrative Biology 6.

Carter GG, Lauren L (2015). "Social grooming in bats: Are Vampire bats exceptional?". PLOS ONE 10(10): e0138430.

Charpentier M, Peignot P, Hossaert-McKey M, Wickings EJ (2006). Kin recognition in juvenile mandrills (*Mandrillus sphinx*). Animal Behaviour 73(1), 37-45.

Clutton-Brock T (2009). Cooperation between non-kin in animal societies. Nature 462, 51-57.

Cooper MA, Bernstein IS, Hemelrijk CK (2005). Reconciliation and relationship quality in Assamese macaques (*Macaca assamensis*). American Journal of Primatology 65, 269–282.

Cords M (1990). Mixed-species association of East African guenons: general patterns or specific examples? American Journal of Primatology 21, 101–114.

Cords M (1997). Friendships, alliances, reciprocity and repair. In Whiten A, Byrne RW (eds.), Machiavellian intelligence II. Cambridge University Press: London pp 24–49.

Cords M, Aureli F (2000). Reconciliation and relationship qualities. In Aureli F, de Waal FBM (eds.), Natural conflict resolution. University of California Press: Berkeley pp 177–198.

Cords M, Sheehan MJ, Ekernas LS (2010). Sex and age differences in juvenile social priorities in female philopatric, nondespotic Blue monkeys. American Journal of Primatology 72, 193–205.

Cords M, Nikitopoulos E (2015). Maternal kin bias in affiliative behavior among wild adult female blue monkeys. American Journal of Primatology 77, 109–123.

Curry RL (1988). Influence of kinship on helping behavior in Galapagos mockingbirds. Behavioral Ecology and Sociobiology 22, 141-152.

Datta S (1983). Relative power and the acquisition of rank. In Hinde R (ed.), Primate social relationships. Blackwell: Oxford pp 91–103.

Das M, Penke Z, van Hooff JARAM (1998). Postconflict affiliation and stress-related behavior of Long-tailed macaque aggressors. International Journal of Primatology 19(1), 53-71.

De Waal FBM (1997). The Chimpanzee's service economy: Food for grooming. Evolution and Human Behavior 18(6), 375-386.

Dunbar RIM (1980). Determinants and evolutionary consequences of dominance among female gelada baboons. Behaviour Ecology and Sociobiology 7, 253–265.

Dunbar RIM (1991). Functional significance of social grooming in primates. Folia Primatologica 57(3), 121-131.

Dunbar RIM (2010). The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. Neuroscience and Biobehavioral Reviews 34, 260–268.

Dunbar RIM (2011). Evolutionary basis of the social brain. In Decety J, Cacioppo J (eds.), Oxford handbook of social neuroscience. Oxford University Press: Oxford pp 28–38.

Eckstein RA, Hart BL (2000). The organization and control of grooming in cats. Applied Animal Behaviour Science 68(2), 131-140

Fairbanks LA (1990). Reciprocal benefits of allomothering for female vervet monkeys. Animal Behaviour 9, 425–441.

Feh C, de Mazières J (1993). Grooming at a preferred site reduces heart rate in horses. Animal Behaviour 46(6), 1191-1194.

Ferkin MH, Leonard ST (2004). Self-grooming by rodents in social and sexual contexts. Acta Zoologica Sinica 51(5), 772 – 779.

Fooden J (2007). Systematic review of the Barbary macaque, *Macaca sylvanus* (Linnaeus, 1758). Zoology, New series 113.

Frank RE, Silk JB (2009). Grooming exchange between mothers and nonmothers: the price of natal attraction in wild baboons (*Papio anubis*). Behaviour 146, 889-906.

Franz C (1999). Allogrooming behavior and grooming site preferences in captive Bonobos (*Pan paniscus*): Association with female dominance. International Journal of Primatology 20, 525-546.

Fraser ON, Schino G, Aureli F (2008). Components of relationship quality in chimpanzees. Ethology 114, 834–843.

Fraser ON, Bugnyar T (2010). The quality of social relationships in ravens. Animal Behaviour 79, 927–933.

Freed BZ (2006) Polyspecific associations of crowned lemurs and Sanford's lemurs in Madagascar. In Gould L, Sauther ML (eds.) Lemurs: ecology and adaptation. Springer: New York pp 111–131.

Fruteau C, Voelkl B, van Damme E, Noë R (2009). Supply and demand determine the market value of food providers in wild vervet monkeys. PNAS 106(29), 12007-12012.

Fruteau C, van de Waal E, van Damme E, Noë R, (2011). Infant access and handling in sooty mangabeys and vervet monkeys, Animal Behaviour 81(1), 153-161.

Gomes CM, Mundry R, Boesch C (2009). Long-term reciprocation of grooming in wild West African chimpanzees. Proceeding of The Royal Socciety B 276, 699–706.

Goosen C (1987). Social grooming in primates. In Mitchell G, Erwin J, (eds.), Comparative primate biology, behavior, cognition, and motivation. Alan R. Liss: New York pp 107-131.

Guan Z, Huang B, Ning W, Ni Q, Sun G, Jiang X (2013). Significance of grooming behavior in two polygynous groups of western black crested gibbons: Implications for understanding social relationships among immigrant and resident group members. American Journal of Primatology 75, 1165-1173.

Gumert MD (2007). Grooming and infant handling interchange in *Macaca fascicularis*: The relationship between infant supply and grooming payment. International Journal of Primatology 28, 1059–1074.

Gust DA, Gordon TP, Wilson ME, Brodie AR, Ahmed-Ansari A, McClure HM (1996). Group formation of female pigtail macaques (Macaca nemestrina). American Journal of Primatology 39, 263-273.

Hamilton WD (1964). "The genetical evolution of social behaviour. II". Journal of Theoretical Biology **7**(1), 17–52.

Hammerstein P, Noë R (2016). Biological trade and markets. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 371 (1687).

Hart BL, Hart LA (1992). Reciprocal allogrooming in impala, *Aepyceros melampus*. Animal Behaviour 44(6), 1073-1083.

Hart BL, Hart LA, Mooring MS, Olubayo R (1992). Biological basis of grooming behaviour in antelope: the body-size, vigilance and habitat principles. Animal Behaviour 44(4), 615-631.

Hemelrijk CK (1994). Support for being groomed in long-tailed macaques, *Macaca fascicularis*. Animal Behaviour 48(2), 479-481.

Henzi SP, Barrett L (1999). The value of grooming to female primates. Primates 40, 47–59.

Henzi SP, Barrett L (2002). Infants as a commodity in a baboon market. Animal Behaviour 63, 1–7.

Heymann EW, Sicchar Valdez LA (1988). Interspecific social grooming in a mixed troop of Tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Platyrrhini: Callitrichidae), in an outdoor enclosure. Folia Primatologica 50, 221-225.

Hinde RA (1979) Towards understanding relationships. London: Academic Press.

Howlett TA, Tomlin S, Ngahfoong L, Rees LH et al. (1984). Release of b-endorphin and met-enkephalin during exercise in normal women in response to training. British Medical Journal 288, 295–307.

Hughes SM, Kruger DJ (2011). Sex differences in post-coital behaviors in long- and short-term mating: an evolutionary perspective. Journal of Sex Research 48, 496–505.

Johnson C, Koerner C, Estrin M, Duoos D (1980). Alloparental care and kinship in captive social groups of vervet monkeys (Cercopithecus aethiops sabaeus). Primates 21(3), 406–415.

Johnson ET, Snyder-Mackler N, Beehner JC, Bergman TJ (2013). Kinship and dominance rank influence the strength of social bonds in female geladas *(Theropithecus gelada)*. International Journal of Primatology, DOI 10.1007/s10764-013-9733-5.

Johnstone RA, Reynolds JD, Deutsch JC (1996). Mutual mate choice and sex differences in choosiness. Evolution 50, 1382–1391.

Kalbitz J, Schülke O, Ostner J (2017). Triadic male-infant-male interaction serves in bond maintenance in male Assamese macaques. PLoS ONE 12(10): e0183981.

Kanngiesser P, Sueur C, Riedl K, Grossmann J, Call J (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. American Journal of Primatology 73, 758–767.

Katsu N, Yamada K, Nakamichi M (2013). Social relationships of nulliparous young adult females beyond the ordinary age of the first birth in a free-ranging troop of Japanese macaques (*Macaca fuscata*). Primates 54(1), 7-11.

Keverne EB, Martensz N, Tuite B (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. Psychoneuroendocrinology 14, 155–161.

Koski SE, Koops K, Sterck EHM (2007). Reconciliation, relationship quality, and postconflict anxiety: testing the integrated hypothesis in captive chimpanzees. American Journal of Primatology 69, 158–172.

Koyama NF, Caws C, Aureli F (2006). Interchange of grooming and agonistic support in chimpanzees. International Journal of Primatology 27, 1293-1309.

Kulik L, Amici F, Langos D, Widdig A (2015). Sex differences in the development of social relationships in Rhesus macaques (*Macaca mulatta*). International Journal of Primatology 36, 353–376.

Kummer H (1978). On the value of social relationships to nonhuman primates: A heuristic scheme. Social Science Information 17, 687–705.

Kümmerli R, Martin RD (2008). Patterns of infant handling and relatedness in Barbary macaques (*Macaca sylvanus*) on Gibraltar. Primates 49, 271–282.

Kutsukake N, Clutton-Brock TH (2008). The number of subordinates moderates intrasexual competition among males in cooperatively breeding meerkats. Proceedings of the Royal Socciety B, Biological Sciences 275, 209-216.

Kutsukake N, Clutton-Brock TH (2010). Grooming and the value of social relationships in cooperatively breeding meerkats. Animal Behaviour 79, 271-279.

Lazaro-Perea C, de Fátima Arruda M, Snowdon CT (2004). Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. Animal Behaviour 67(4), 627-636.

Lehmann J, Korstjens AH, Dunbar RIM (2007). Group size, grooming and social cohesion in primates. Animal Behaviour 74(6), 1617-1629.

Li BG, Zhao DP (2007). Copulation behavior within one-male groups of wild Rhinopithecus roxellana in the Qinling Mountains of China. Primates 48, 190–196.

Liedigk R, Roos C, Brameier M, Zinner D (2014). Mitogenomics of the Old World monkey tribe Papionini. BMC evolutionary biology 14, 176.

Löttker P, Huck M, Zinner DP, Heymann EW (2007). Grooming relationships between breeding females and adult group members in cooperatively breeding moustached tamarins (Saguinus mystax). American Journal of Primatology 69, 1-14.

Maestripieri D (1994). Social structure, infant handling, and mother styles in group-living Old World monkeys. International Journal of Primatology 15, 531–553.

Maestripieri D (1995). Maternal responsiveness to infant distress calls in Stumptail macaques. Folia Primatologica 64, 201–206.

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

Manson JH (1999). Infant handling in wild *Cebus capucinus*: testing bonds between females? Animal Behaviour 57, 911-921.

Manson JH, Navarette CD, Silk JB, Perry S (2004). Time-matched grooming in female primates? New analyses from two species. Animal Behaviour 67, 493-500.

Massen JJ, van Der Berg LM, Spruijt BM, Sterck EH (2012). Inequity aversion in relation to effort and relationship quality in long-tailed Macaques (*Macaca fascicularis*). American Journal of Primatology 74, 145-156.

Matheson MD (1999). Social contact following severe aggression in Rhesus macaques (Macaca mulatta): A New Test of the Consolation Hypothesis. International Journal of Primatology 20(6), 961-975.

McFarland R, Majolo B (2011). Exploring the components, asymmetry and distribution of relationship quality in wild Barbary macaques (*Macaca sylvanus*). PLoS ONE 6(12): e28826.

McFarland R, Henzi SP, Barrett L, Wanigaratne A et al. (2016). Thermal consequences of increased pelt loft infer an additional utilitarian function for grooming. American Journal of Primatology 78, 456–461.

Menard N, Vallet D (1993). Population dynamics of Macaca sylvanus in Algeria: an 8-year study. American Journal of Primatology 30, 101-118.

Menard N, von Segesser F, Scheffrahn W, Pastorini J et al (2001). Is male-infant caretaking related to paternity and/or mating activities in wild Barbary macaques (*Macaca sylvanus*)? Comptes rendus de l'Académie des sciences Série III, Sciences de la vie 324, 601.

Menard N (2002). Ecological plasticity of Barbary macaques (*Macaca sylvanus*). Evolutionary Anthropology 1, 95–100.

Metz M, Klump G, Friedl T (2007). Temporal changes in demand for and supply of nests in red bishops (*Euplectes orix*): dynamics of a biological market. Behavioral Ecology and Sociobiology 61, 1369-1381.

Mitani JC (2006). Reciprocal exchange in chimpanzees and other primates. In van Schaik CP, Kappeler PM (eds.), Cooperation in primates and humans: evolution and mechanisms. Springer Verlag: Berlin pp 107–119.

Molesti S, Majolo B, Wright J (2015). No short-term contingency between grooming and food tolerance in Barbary macaques (*Macaca sylvanus*). Ethology 121, 372-382.

Molesti S, Majolo B (2017). Evidence of direct reciprocity, but not of indirect and generalized reciprocity, in the grooming exchanges of wild Barbary macaques (*Macaca sylvanus*). American Journal of Primatology 79: e22679.

Mooring MS, Benjamin JE, Harte CR, Herzog NB (2000). Testing the interspecific body size principle in ungulates: the smaller they come, the harder they groom. Animal Behaviour 60, 35-45.

Moscovice L, DiFiore A, Crockford C, Kitchen DM, et al. (2010). Hedging their bets? Male and female chacma baboons form friendships based on likelihood of paternity. Animal Behaviour 79: 1007–15.

Muroyama Y (1991). Mutual reciprocity of grooming in female Japanese macaques (*Macaca fuscata*). Behaviour 119, 161-170.

Muroyama Y (1994). Exchange of grooming for allomothering in female Patas monkeys. Behaviour 128, 103-119.

Nakamichi M, Shazawa Y (2003). Distribution of grooming among adult females in a large, free-ranging Japanese macaques. International Journal of Primatology 24(3), 607-625.

Nicolson NA (1987). Infants, mothers and other females. In Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds.), Primate Societies. University of Chicago Press: Chicago pp 330–342.

Nishida T (1997). Sexual behavior of adult male chimpanzees of the Mahale Mountains national park, Tanzania. Primates 38, 379–398

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

Noë R, Hammerstein P (1995). Biological markets. Trends in Ecology and Evolution 10(8), 336-339.

Noë R (2017). Local mating markets in humans and non-human animals. Behavioral Ecology and Sociobiology 71, 148.

O'Brien TG (1993). Allogrooming behaviour among adult female Wedge-capped capuchin monkeys. Animal Behaviour 46, 499-510.

Ostner J, Vigilant L, Bhagavatula J, Franza M, Schülke O (2013). Stable heterosexual associations in a promiscuous primate. Animal Behaviour 86, 623–631.

Owens M, Owens D (1984). Helping behaviour in brown hyenas. Nature 308, 843–845.

Palagi E, Antonacci D, Norscia I (2008). Peacemaking on treetops: first evidence of reconciliation from a wild prosimian (*Propithecus verreauxi*). Animal Behaviour 76(3), 737-747.

Palombit RA (1994). Dynamic pair bonds in Hylobatids: implications regarding monogamous social systems. Behaviour 128, 65-101.

Palombit RA, Cheney DL, Seyfarth RM (1997). The adaptive value of “friendships” to female baboons: experimental and observational evidence. Animal Behaviour 54(3), 599–614.

Palombit RA (2000). Infanticide and the evolution of male - female bonds in animals. In van Schaik CP, Janson CH (eds.), Infanticide by Males and Its Implications. Cambridge University Press: Cambridge pp 239-268.

Parr L, Matheson M, Bernstein IS, De Waal F (1997). Grooming down the hierarchy: allogrooming in captive brown capuchin monkeys, Cebus apella. Animal Behaviour 54(2), 361-367.

Parr LA, Heintz M, Lonsdorf E, Wroblewski E (2010). Visual kin recognition in nonhuman primates: (*Pan troglodytes* and *Macaca mulatta*): Inbreeding avoidance or male distinctiveness? Journal of Comparative Psychology 124(4), 343-350.

Paul A, Kuester J, Arnemann J (1996). The sociobiology of male–infant interactions in Barbary macaques, *Macaca sylvanus*. Animal Behaviour 51(1), 155-170.

Payne H, Lawes MJ, Henzi PS (2003). Competition and the exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). Behaviour 160, 453–471.

Pazol K, Cords M (2005). Seasonal variation in feeding behavior, competition and female social relationships in a forest dwelling guenon, the blue monkey (*Cercopithecus mitis stuhlmanni*), in the Kakamega Forest, Kenya. Behavioral Ecology and Sociobiology 58, 566–577.

Peres CA (1993) Anti-predation benefits in a mixed-species group of Amazonian tamarins. Folia Primatologica 61, 61–76.

Perry S (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. American Journal of Primatology 40(2), 167-182.

Preuschoft S, van Schaik CP (2000). Dominance and communication. In Aureli F, de Waal F (eds.), Natural conflict resolution. University of California press: London pp 77-103.

Qi XG, Huang K, Fang G, Grueter CC et al. (2017). Male cooperation for breeding opportunities contributes to the evolution of multilevel societies. Proceeding of The Royal Socciety of B 284, 20171480.

Rabenold KN (1985). Cooperation in breeding by nonreproductive wrens: Kinship, reciprocity, and demography. Behavioral Ecology and Sociobiology 17, 1-17.

Radford AN, Du Plessis MA (2008). Dual function of allopreening in the cooperatively breeding green woodhoopoe Pheoniculus purpureus. Behavioral Ecology and Sociobiology 61, 221–230.

Rebecchini L, Schaffner C, Aureli F (2011). Risk is a component of social relationships in spider monkeys. Ethology 117, 691–699.

Reichard U, Sommer V (1994). Grooming site preferences in wild white-handed gibbons (*Hylobates lar*). Primates 35(3), 369-374.

Reichard U (1995). Extra-pair Copulations in a Monogamous Gibbon (*Hylobates lar*). Ethology 100, 99-112.

Rosal MC, King J, Ma Y, Reed GW (2004). Stress, social support, and cortisol: Inverse associations? Behavioral Medicine 30, 11–21.

Rowe N (1996). The Pictorial Guide to the Living Primates. Pogonia Press, Charlestown.

Royston D (2013). Physiology and Pharmacology for Anesthesia: Foundations and Clinical Application: Expert Consult - Online and Print. Elsevier.

Sánchez-Amaro A, Amici F (2015). Are primates out of the market? Animal Behaviour 110, 51-60.

Saunders CD (1987). Grooming quality in relation to tick density and reciprocity between partners. American Journalof Primatology 12, 369A.

Sazima I, Sazima C (2010). Brazilian cleaner birds: update and brief reappraisal. Biota Neotropica 10(1), 327-331.

Scheffrahn W, Menard N, Vallet D, Gaci B (1993). Ecology, demography, and population genetics of Barbary macaques in Algeria. Primates 34(3), 381- 394.

Schino G, Scucchi S, Maestripieri D, Turillazzi PG (1988). Allogrooming as tension reduction mechanism: A behavioural approach. American Journal of Primatology 16, 43-50.

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

Schino G, Ventura R, Troisi A (2003). Grooming among female Japanese macaques: distinguishing between reciprocation and interchange. Behavioral Ecology 14(6), 887–891.

Schino G (2007). Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. Behavioral Ecology 18(1), 115–120.

Schino G, di Sorrentino EP, Tiddi B (2007). Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame reciprocation. Journal of Comparative Psychology 121(2), 181-188.

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

Schülke O, Bhagavatula J, Vigilant L, Ostner J (2010). Social bonds enhance reproductive success in male macaques. Current Biology 20(24), 2207-2210.

Seyfarth RM (1977). A model of social grooming among adult female monkeys. Journal of Theoretical Biology 65, 671–698.

Seyfarth RM (1978). Social relationships among adult male and female baboons. I. Behaviour during sexual consortship. Behaviour 204–226.

Seyfarth RM, Cheney DL (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. Nature 308, 541–543.

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

Silk JB (1980). Kidnapping and female competition in captive Bonnet macaques. Primates 21, 100–110.

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

Silk JB (2002a). Kin selection in primate groups. International Journal of Primatology 23(4), 849-875.

Silk JB (2002b). Females, food, family, and friendship. Evolutionary Anthropology 11, 85–87.

Silk JB, Alberts SC, Altmann J (2003a). Social bonds of female baboons enhance infant survival. Science 302, 1231–1234.

Silk JB, Rendall D, Cheney DL, Seyfarth RM (2003b). Natal attraction in adult female baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. Ethology 109, 627-644.

Silk JB, Alberts, SC, Altmann J (2004). Patterns of coalition formation by adult female baboons in Amboseli, Kenya. Animal Behaviour 67(3), 573-582.

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

Silk JB, Alberts SC, Altmann J (2006b). Social relationships among adult female baboons (*Papio cynocephalus*) II. variation in the quality and stability of social bonds. Behavioral Ecology and Sociobiology 61, 197–204.

Silk JB, Beehner JC, Bergman TJ, Crockford C et al. (2010). Strong and consistent social bonds enhance the longevity of female baboons. Current Biology 20(15), 1359-1361.

Singh M, Krishna BA, Singh M (2006). Dominance hierarchy and social grooming in female lion-tailed macaques (*Macaca silenus*) in the Western Ghats, India. Journal of Biosciences 31(3), 369-377.

Slater KY, Schaffner CM, Aureli F (2007). Embraces for infant handling in spider monkeys: evidence for a biological market? Animal Behaviour 74(3), 455-461.

Smith A (1776). Of the principle which gives occasion to the division of labour. In Soares SM (ed.), An Inquiry into the Nature and Causes of the Wealth of Nations. MetaLibri Digital Library: Laussane pp 15-17.

Smith TE, Abbott DH (1998). Behavioral discrimination between circumgenital odor from peri-ovulatory dominant and anovulatory female common marmosets (*Callithrix jacchus*). American Journal of Primatology 46, 265–284.

Song Z, Feldman MW (2013). Plant-animal mutualism in biological markets: Evolutionary and ecological dynamics driven by non-hgeritable phenotypic variance. Theoretical Population Biology 88, 20-30.

Sonnweber RS, Massen JJM, Fitch WT (2015). Post-copulatory grooming: a conditional mating strategy? Behavioral Ecology and Sociobiology 69, 1749.

Sparks J (1967). Allogrooming in primates: a review. In Morris D (ed.), Primate ethology. Weidenfeld & Nicholson: London pp 148–175.

Städele V, Pines M, Swedell L, Vigilant L (2016). The ties that bind: Maternal kin bias in a multilevel primate society despite natal dispersal by both sexes. American Journal of Primatology 78, 731–744.

Stanford C (1992). The costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*). Behavioral Ecology and Sociobiology 30, 29-34.

Stefano G, Goumon Y, Casares F, Cadet P et al. (2000). Endogenous morphine. Trends in Neurosciences 23, 436–442.

Stevens JR, Hauser MD (2004). Why be nice? Psychological constraints on the evolution of cooperation. Trends in Cognitive Sciences 8, 60–65.

Terry RL (1970). Primate grooming as a tension reduction mechanism. Journal of Psychology 76, 129-136.

Thierry B (1990). Feedback loop between kinship and dominance: the macaque model. Journal of Theoretical Biology 145, 511–521.

Thierry B (2000). Covariation of conflict management patterns across macaque species. In Aureli F, de Waal FBM (eds.), Natural Conflict Resolution. University of California press: Berkeley pp 106-128.

Thierry B, Bynum EL, Baker S, Kinnaird MF et al. (2000). The social repertoire of Sulawesi macaques. Primate Research 16, 203-226.

Thierry B (2007). The Macaques. A double-layered social organization. In Campbell CJ, Fuentes A, Mackinnin KC, Panger M, Bearder SK (eds.), Primate in Perspective. Oxford University Press: New York pp 224-239.

Thorsteinsson EB, James JE (1999). A meta-analysis of the effects of experimental manipulations of social support during laboratory stress. Psychology & Health 14, 869–886.

Tiddi B, Aureli F, Schino G (2010). Grooming for infant handling in tufted capuchin monkeys: a reappraisal of the primate infant market. Animal Behaviour 79(5), 1115-1123.

Tiddi B, Aureli F, di Sorrentino EP, Janson CH, Schino G (2011). Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. Behavioral Ecology 22, 663-669.

Tiddi B, Aureli F, Schino G (2012). Grooming up the hierarchy: the exchange of grooming and rank-related benefits in a New world primate. PLoS ONE 7(5).

Tomazzoni AC, Pedó E, Hartz SM (2005). Feeding associations between capybaras *Hydrochoerus hydrochaeris* (*Linnaeus*) (*Mammalia, Hydrochaeridae*) and birds in the Lami Biological Reserve, Porto Alegre, Rio Grande do Sul, Brazil. Revista Brasileira de Zoologia 22(3), 713-716.

van Schaik CP, Horstermann M (1994). Predation risk and the number of adult males in a primate group: a comparative test. Behavioral Ecology and Sociobiology 35, 261–272.

van Schaik CP, Janson CH (2000). Infanticide by males and its implications. London: Cambridge University Press.

Vasava AG, Mahato S, Navaneethan M, Dashahre A (2013). Grooming of sambar (*Rusa unicolor*) by Rhesus macaque (*Macaca mulatta*) in Sariska Tiger Reserve, Rajasthan, India. Current science 1014 (3), 296-298.

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

Vogel C (1984). Patterns of infant transfer within two groups of common langurs (*Presbytis entellus*) near Jodhpur: Testing hypotheses concerning the benefits and risks. In Roonwal ML, Mohnot SM, Rathore NS (eds.), Current Primate Researches. Jodhpur University Press: Jodhpur pp 361–379.

Wedekind C, Furi S (1997). Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? Proceeding of The Royal Socciety B 264, 1471-1479.

Werner GDA, Kiers ET (2015). Partner selection in the mycorrhizal mutualism. New Phytologist 205, 1437-1442.

Wei W, Qi XG, Guo ST, Zhao DP et al. (2012). Market powers predict reciprocal grooming in Golden Snub-nosed Monkeys (*Rhinopithecus roxellana*). PLoS ONE 7: e36802.

Wei W, Qi XG, Garber PA, Guo ST, Zhang P, Li B (2013) Supply and demand determine the market value of access to infants in the Golden Snub-Nosed monkey (*Rhinopithecus roxellana*). PLoS ONE 8(6): e65962.

Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB (2001). Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. PNAS 98, 13769–13773.

Widdig A, Streich WJ, Nürnberg P, Croucher PJP et al. (2006). Paternal kin bias in the agonistic interventions of adult female rhesus macaques (*Macaca mulatta*). Behavioral Ecology and Sociobiology 61(2), 205-214.

Wincenciak J, Fincher CL, Fisher CI, Hahn AC et al. (2015). Mate choice, mate preference, and biological markets: The relationship between partner choice and health preference is modulated by women's own attractiveness. Evolution and Human Behavior 36(4), 274-278.

Xia D, Li J, Garber PA, Sun L, Zhu Y, Sun B (2012). Grooming reciprocity in female tibetan macaques, *Macaca thibetana*. American Journal of Primatology 74(6), 569-579.

Xiang ZF, Yang BH, Yang Y, Hui Y et al. (2014). Males collectively defend their one-male units against bachelor males in a multi-level primate society. American Journal of Primatology 76, 609–617.

Yee JR, Cavigelli SA, Delgado B, McClintock MK (2008). Reciprocal affiliation among adolescent rats during a mild group stressor predicts mammary tumors and lifespan. Psychosomatic Medicine 70(9), 1050–1059.

Yu Y, Xiang ZF, Yao H, Grueter CC, Li M (2013). Female Snub-nosed monkeys exchange grooming for sex and infant handling. PLoS ONE 8(9): e74822.

Zhao QK (1996). Male-infant-male interactions in Tibetan macaques. Primates 37, 135–143.

# CHAPTER II.

## Not just payment for mating: patterns of grooming and sexual activity in Barbary macaques *(Macaca sylvanus)*.

manuscript

# Not just payment for mating: patterns of grooming and sexual activity in Barbary macaques (*Macaca sylvanus*)

**Short title:** Grooming and mating in Barbary macaques

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## ABSTRACT

Grooming in primates is often explained as a “currency” that can be exchanged for other “services” or “commodities”, such as reciprocal grooming, coalitionary support, infant handling, tolerance around food sources, active food sharing, or mating opportunities. Previous studies in primate grooming-for-sex exchange tend to view the males as the demanding class, while females supply mating opportunities. In this study, we have examined the broad context of the grooming-for-mating interchange in Barbary macaques in Gibraltar. Our data show that Barbary macaque males groom females with whom they were mating more frequently and for longer periods of time, and the relationship between grooming and mating remains significant regardless of the context, either sexual or non-sexual. In addition, the females also groomed males with whom they were mating more frequently and for longer periods of time. In both sexes, grooming was observed to be far more frequent and longer in the sexual, compared to the non-sexual context. We did not find any difference between grooming behavior in the presexual and postsexual context. The simple model, which would describe Barbary macaque males as the sex that uses grooming as payment for mating, cannot fully explain the observed behavioral patterns. It rather appears that the significant correlation between grooming and mating in this species is mediated through longer-lasting behavioral bonds between two individuals, and that both sexes benefit from, and invest in, this social bond.

**Keywords**: grooming, sexual activity, mating, male-female relationship, exchange

## RESEARCH HIGHLIGHTS

Grooming and mating are exchanged over long and short timescales in Barbary macaques; long-term relationships between sexes underlie the patterns.

Female and male grooming behaviors are similar; 'payment for sex' hypothesis cannot explain the former.

### Tweetable Summary

Both sexes initiate grooming before and after sexual activity in Barbary macaques.

## INTRODUCTION

Social grooming is one of the most common forms of affiliative behavior among various animals, and one which has been particularly frequently observed and studied in primates (Sparks, 1967; Dunbar, 1991; Schino, 2001). There is a widely accepted view that grooming in many, if not most primates serves a dual function of being both hygienic and social (Dunbar, 1991). The hygienic function lies in removal of dirt, dead skin and ectoparasites, and maintaining the pelage in good condition and in a functional state (Sparks, 1967; McFarland et al., 2016). However, there is less consensus among authors as to the social function of grooming (Cooper & Bernstein, 2000; Lehmann, Korstjens, & Dunbar, 2007; Dunbar, 2010; Guan et al., 2013).

One hypothesis to explain the social function of grooming is the model of the biological market (Noë & Hammerstein, 1994). This model considers grooming as a “currency” that can be exchanged for other “services” or “commodities”. The hypothesis of behavioral exchange is consistent with the idea of the dual function of grooming, which is valuable *per se* due its hygienic function, yet can be also used as a social tool to obtain other benefits. In primates, these commodities may include reciprocal grooming (Schino & Aureli, 2008), coalitionary support (Ventura, Majolo, Koyama, Hardie, & Schino, 2006; Schino, di Sorrentino, & Tiddi 2007), infant handling (Muroyama, 1994; Gumert 2007a; Yu, Xiang, Yao, Grueter & Li, 2013), tolerance around food sources (Borgeaud & Bshary 2015), active food sharing (de Waal, 1997), or mating opportunities (Gumert, 2007b).

While the idea of such behavioral exchange dates back several decades, the model of the biological market makes it much more specific by introducing the concept of market forces, based on supply and demand laws, as an underlying principle of the exchange. Besides applying the key concept of supply and demand, the biological market model also clarifies the role of dominance rank in shaping the patterns of the exchange. While the previous model proposed by Seyfarth (1977) stressed the role of competition for grooming partners as an important mechanism leading to patterns of hierarchical and adjacent rank-based grooming (Schino, 2001), the biological market model considered grooming as a free market commodity (Noë & Hammerstein, 1994). Instead of by coercion, competition is resolved by outbidding, i.e. by offering a higher price. The higher-ranking partners, who offer more valuable services, such as tolerance or possibly coalitionary support, receive more grooming. Furthermore, they also pay less when trading grooming for other benefits, such as mating or infant handling, as demonstrated by Gumert (2007a; 2007b) in long-tailed macaques (*Macaca fascicularis*).

While studies that simply considered behavioral exchange of grooming for other benefits showed relatively consistent results, the more specific concept of market forces highlighted numerous inconsistencies among them. These discrepancies have been hotly debated in a series of papers (Sánchez-Amaro & Amici, 2015; Dunayer & Berman, 2016; Kaburu & Newton-Fischer, 2016; Sánchez-Amaro & Amici, 2016). It is becoming apparent that broad patterns showing exchange of grooming for other benefits may actually combine several different behavioral mechanisms, which operate on different time scales and are underlain by different behavioral and cognitive mechanisms. For example, grooming-for-grooming exchange (reciprocity) in chacma baboons (*Papio ursinus*) has been documented on the level of single interactions (grooming bouts), which suggests existence of cognitive mechanisms that "calculate" both partners' contributions (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999). In contrast, Massen et al. (2012) argue for a different underlying mechanism of grooming-for-mating exchange in rhesus macaques (*Macaca mulata*), which instead operates on relatively long time scales, and is based in formation of longer-term social relationships or bonds.

The relationship between grooming and sexual behavior has been demonstrated by several studies in primates. In chimpanzees (*Pan troglodytes*, Hemelrijk, van Laere, & Van Hooff, 1992) and Hamadryas baboons (*Papio hamadryas*, Colmenares, Zaragoza, & Hernández-Lloreda, 2002), females' sexual swellings reflect the higher chance of conception (Nunn, 1999), and in these species the males groom the swollen females more than non-swollen females. In contrast, there is no such correlation in long-tailed macaques, where sexual swelling in females does not seem to reflect their fertility (Gumert, 2007b). In chimpanzees (Hemelrijk et al., 1992), bonnet macaques (*Macaca radiata*, Kurup, 1988) and long-tailed macaques (Gumert, 2007b), grooming is often followed by copulation, and males more frequently groom females they then mount. In addition to showing the relationship between grooming and mating, the study by Gumert (2007b) on long-tailed macaques also provided clear evidence that market forces are involved in observed patterns. He showed that the amount of grooming given by the male to the female in the mating context depended on the number of fertile females available; in other words, it reflected the supply of the commodity grooming was being traded for.

Several studies on other macaque species have found results that may be seen as contradictory with Gumert's (2007b) findings on long-tailed macaques. For example, although Massen et al. (2012) found a correlation between grooming and mating in captive rhesus macaques, even for grooming interactions that preceded and followed the mating season, there was no such correlation for grooming during the female's fertile days. In fact, the authors did not observe any grooming in mating contexts in this study. Similarly, Cooper and Bernstein (2000) did not observe any clear grooming-for-mating interchange in their study on grooming in Assamese macaques (*Macaca assamensis*).

Previous studies in primate grooming-for-sex exchange tend to view the males as the demanding class, while females supply mating opportunities (Massen et al., 2012; Gumert, 2007b). This reflects the long-recognized (since Darwin, 1871) fact that the typical male reproductive strategy is to maximize mating opportunities, while the typical female reproductive strategy is to choose the best sire for her offspring. However, this may be an oversimplification; studies have found that there can also be value in multiple copulations for females, especially when mating opportunities are limited (Sommer, 1989) or in cases where mating serves to confuse paternity of the future offspring (Nunn, 1999). Barbary macaque females, for example, have been described as highly sexually assertive, taking an active role in initiation of sexual contact with multiple males and mating ca. every 30 minutes during their fertile days (Kuester & Paul, 1992). In addition, more than two commodities of value to females may be traded during the grooming-for-mating exchange, such as tolerance, protection, and paternalistic behavior toward the female's future offspring (Sonnweber, Massen, & Fitch, 2015). Together, these findings make it difficult to assign the two sexes to simple roles of a supplying and demanding class. Furthermore, both being groomed as well as being a groomer may be intrinsically rewarding; studies have found animals to actively seek the opportunity to groom, sometimes even engaging individuals of a different species or inanimate objects. Positive short-term physiological impacts of being a groomer have also been demonstrated (Falk, 1958; Aureli & Yates, 2010; Russel & Phelps, 2013).

Finally, and perhaps most importantly, previous studies of the grooming-for-mating interchange have often strictly focused on predictions of the grooming-for-mating market model, ignoring broader aspects of behavior which are less easily explained. For example, observations show that grooming occurs not only before, but also after mating (Barbary macaques, Sonnweber et al., 2015); that the grooming preferences of mating partners are observed even outside the mating context, and even after cessation of the mating season (rhesus macaques, Massen et al., 2012); and that both sexes may be actively involved in grooming within the context of mating (Barbary macaques, Sonnweber et al., 2015). Together, these observations suggest that the biological market model, which is based on the narrow assumption that males are the demanding sex that instigate the grooming for mating exchange, provides a rather incomplete description and interpretation of the behavioral mechanisms involved in grooming and mating interactions.

In this study, we have examined the broad context of the grooming-for-mating interchange in free ranging Barbary macaques. We tested the relationship between grooming and mating during the mating season in both immediate (sexual) and non-immediate (non-sexual) context. Within the immediate sexual context we considered trends in both pre-sexual and post-sexual grooming. We analyzed grooming behavior, as well as effect of rank on this behavior, in both sexes. Based on a simple grooming-for-mating hypothesis, where males employ grooming as a currency to pay females for mating opportunities, we expected the grooming-for-mating interchange to be detectable only in mating contexts and, more specifically, before sexual activity. Based on this hypothesis, we also expected that this pattern would be shown only for grooming interactions initiated by males, not for those instigated by females. Similarly, the effect of dominance on grooming behavior should differ between sexes and should be more apparent in males as they are the sex that initiates grooming trades. Deviations from this basic pattern would suggest that there is a more complex mechanism involved in the grooming-for-mating behavioral interchange.

## METHODS

### Ethical statement

This study was fully observational, non-invasive, and adhered to the legal requirements of Gibraltar. Approval to conduct the study was granted by the Animal Care Appointee of the Gibraltar Ornithological and Natural History Society (GONHS). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

## Study subjects

The study was conducted in the Apes' Den troop of Barbary macaques (*Macaca sylvanus)* living in Upper Rock Natural Reserve, Gibraltar. This group is provisioned daily by the Gibraltar Ornithological and Natural History Society (GONHS) and visited by tourists. At the beginning of the study the group included 17 adult females (age from 3 to 26 years; mean = 11.2) and 6 adult males (age from 7 to 18 years; mean = 10.5) (age data provided by GONHS) and up to 15 juveniles and infants. During the second season, 3 new males (2 sub adult and 1 young adult male; age data not available) immigrated into the troop and 7 infants were born. All adult macaques were individually recognized and well-habituated to the presence of human observers (for more details on the study site and subjects see Konečná, Weiss, Lhota, & Wallner, 2012).

## Behavioral data collection

Behavioral observations were collected during two study periods (season 1: November 2007 to February 2008; season 2: October 2008 to February 2009) that corresponded with two mating seasons. All focal animals (17 females and 9 males) were observed using two methods of data collection at the same time: focal individual continuous sampling (30 minutes focal period) and focal instantaneous sampling (in 2 minutes intervals) (Altmann, 1974). Data collection was equally distributed among individuals within each day (from 8:00 to 18:00) and across the entire season. Behaviors were recorded according to an ethogram, which included over 50 items selected from previous studies (Dolhinow, 1978; Berman, Ionica, Dorner, & Li, 2004). Two observers (MK and VR), experienced in the using of the behavioral ethogram, collected all data used in this analysis. Before beginning data collection, the two observers reached 93% reliability in simultaneous observations of a given individual. All behaviors analyzed in this study are listed in Table 1. While focal animal sampling leads to fewer observed interactions, it provides a less biased representation of interactions than other techniques (such as ad libitum or all occurrence sampling), which could bias the data toward more visible, central or dominant individuals (Altmann, 1974). Avoiding this bias is especially important when observing sexual activity.

### Grooming behavior

Observers recorded the start and end time of grooming behavior, direction of the interaction, and identity of the social partner. The grooming interaction was considered terminated if it stopped for 20 seconds or more. If grooming was reciprocated (the previous groomer became the groomee or vice versa) this new grooming interaction was not included in the data analysis. Interactions terminated by a third party (another animal, tourist, etc.) were also excluded.

### Sexual behavior

Following previous studies (Gumert, 2007b), three types of sexual behavior were recorded and analyzed in this study: copulation, genital inspection and present (for definitions see Table 1). Hereafter, we refer to these behaviors broadly as sexual activity.

Table 1: List of behaviors and their definitions used for analyses.

| | |
|---|---|
| **Grooming** | An animal grooms the hair of the other, watching the groomed place on the other's body and using its fingers or mouth. It may or not pick up particles. |
| **Displacement** | One animal in any way (threat, attack or target approach) drives away another individual from a location or resource (place, shade, food, partner). |
| **Copulation** | An animal mounts the other with sexual intention; activity is quite long and complete and is not only indicative (as in mount behavior). |
| **Genital inspection** | Olfactory/visual/manual examination of another individual's genital area. |
| **Present** | Body is stretched, hindquarters are elevated toward the partner, and the upper part of the body is crouched. May or may not be connected with other gestures. |

### Dominance hierarchy

The separate dominance hierarchy among 17 females and 9 males was assessed on the basis of dyadic displacement interactions between pairs of observed individuals. Sociometric matrices were assembled using the displacement interactions to compute the dominance hierarchy during each season. This approach is based on a documented pattern of acceptance of subordinate positions by displaced individuals (Hinde, 1978). A linearity index, h′(computed in MatMan 1.1.4; Noldus 2003) (de Vries, Netto, & Hanegraaf, 1993), was used to assess linearity of the dominance hierarchy. All hierarchies were linear, and outcomes of interactions were highly consistent with the existing hierarchies (for details see Konečná et al. 2012). Individuals were then ranked based on their normalized David's score (NDS) (Gammell, de Vries, Jennings, Carlin, & Hayden, 2003).

## Data analysis

### Preparation of datasets

We aggregated all grooming and sexual interactions recorded over the study period to ask whether the frequency of sexual activity within a particular dyad could predict grooming behavior over the long term, and if this depends on the sex of the groomer. In this model we did not consider if and how grooming was related to sexual interactions in a given observation.

Second, we explored the data in more detail to ask if grooming is exchanged in a more immediate, or short-term time frame. We only included grooming interactions with information on which behaviors occurred during 3 instantaneous samples before and after that particular grooming interaction (approx. 6 min before/after). This method results in a 12-minute total sexual time frame of observation and is within ranges used in previous studies (15min: Colmenares et al., 2002; 10 min: Gumert, 2007b; 5 min: Tiddi, Aureli, Schino & Voelkl, 2011). We differentiated grooming interactions as non-sexual (no sexual activity occurred before or after the grooming) and as two types of sexual grooming: pre-sexual (grooming occurred before sexual interaction) and post-sexual (grooming occurred after sexual interaction). If the grooming occurred before and continued after a sexual interaction, we classified it as both pre- and post-sexual. We asked if non-sexual, as well as sexual grooming behavior is related to the sexual interactions of a given dyad. We also explored whether patterns of grooming interaction differ in relation to sexual context and asked if grooming activity is higher before (pre-sexual), after (post-sexual) or outside of (non-sexual) sexual interactions.

### Statistical analysis

We analyzed the data using linear mixed effect models (LMMs) using the package nlme (Pinheiro, Bates, DebRoy, & Sarkar, 2018) in R 3.3.1. Grooming as a response variable was represented either as grooming rate (the sum of grooming acts when X grooms Y divided by the total time of observation of the two individuals) or grooming time (the sum of grooming time when X grooms Y divided by the total time of observation of the two individuals). All grooming data were log transformed to increase homogeneity. In models based on time-sequenced interactions, the number of grooming interactions in sexual (pre- or post-sexual) and non-sexual contexts were divided by the amount of time the individuals spent in a given context (defined by 6 minutes before or after sexual activity). The identity of individual male and female macaques was always included as a random factor.

First, we ran models based on our complete dataset (for the list of models see Table 2). Next, we split each dataset into two subsets on the basis of groomer sex, resulting in datasets that included either grooming initiated by males or grooming initiated by females. We followed this approach despite having sex as one of the fixed factors in the complete models for two reasons: our relatively small sample size (especially number of males), and to enable direct comparison with previous studies that generally only include grooming interactions initiated by one sex (e.g. Gumert, 2007b).

With all datasets, we first fit the full model with grooming rate or grooming time as a response, sexual activity rate, sex of the groomer (for models including grooming initiated by both sexes), season, male and female ranks as fixed variables, and macaque identity as a random factor. The final model selection was performed using the drop1 function, and variables were included in the final model on the basis of their LRT and p-value (to be able to evaluate possible trends, variables with $p < 0.1$ were included). The significance of individual variables in the final model was then tested using the confint function.

Table 2. List of questions and characteristics of the corresponding models based on complete datasets:

| Main question | Dataset | Responses | Fixed variables |
|---|---|---|---|
| Is grooming predicted by sexual activity over the long term? | all interactions | Grooming rate or time | sexual activity rate, sex of the groomer, season, male rank, female rank |
| Is grooming in sexual contexts predicted by sexual activity? | time-sequenced interactions | Grooming rate or time in sexual contexts | sexual activity rate, sex of the groomer, season, male rank, female rank |
| Is grooming in non-sexual contexts predicted by sexual activity? | time-sequenced interactions | Grooming rate or time in non-sexual contexts | sexual activity rate, sex of the groomer, season, male rank, female rank |
| Does grooming occur more before-, after-, or outside sexual interactions? | time-sequenced interactions | Grooming rate or time | context of interaction (pre-, post- or non-sexual), sex of the groomer, season, male rank, female rank |

Note: Male and female identity was always included as a random factor.

## RESULTS

### Descriptive results

**Grooming.** We collected ca. 900 hours of focal observation data, with a mean of 15.42 (±0.38 SD) hours/individual in season 1 and a mean of 13.42 (±1.12 SD) hours/ individual in season 2. We recorded 954 grooming interactions among males and females (461 in season 1 and 493 in season 2) from which 435 (45.6%) of grooming interactions were initiated by females (180 in season 1 and 255 in season 2) and 519 (54.4%) were initiated by males (281 in season 1 and 238 in season 2). When the groomer was female, the number of grooming interactions/female ranged from 12 to 73, with an average of 25.59 interactions. When the groomer was male, the number of grooming interactions ranged from 4 to 111, with an average of 57.67 interactions.

The total number of grooming interactions that could be classified according to context (pre- and post-sexual; non-sexual) was 359. The total number of sexual grooming interactions was 242, while 117 occurred in non-sexual contexts. Within sexual grooming interactions, the number of pre-sexual grooming interactions initiated by females ranged from 1 to 7, with an average 2.41 interactions/female. The number of pre-sexual grooming interactions initiated by males ranged from 1 to 16, with an average of 5.11 interactions/male. The number of post-sexual grooming interactions initiated by females ranged from 1 to 12, with an average 5.53 interactions/female. The number of post-sexual grooming interactions initiated by males ranged from 1 to 22, with an average of 12.56 interactions/male.

**Sexual activity.** We recorded 1295 sexual interactions among males and females (564 in season 1 and 731 in season 2) from which 386 were copulations (171 in season 1 and 215 in season 2). The number of sexual interactions/female in season 1 ranged from 2 to 71, with an average 33.2/female, and in season 2 ranged from 13 to 111 with an average 43 interactions/female. The number of sexual interactions/male in season 1 ranged from 49 to 128, with an average 94 interactions/male, and in season 2 ranged from 46 to 153 with an average 81.2 interactions/male.

## Results of LMMs

The results of the LMMs were very similar with either grooming rate or grooming time as response variables. Thus, we present only results of models based on grooming rate (for results based on grooming time see Supplementary material S1).

## Is grooming predicted by sexual activity over the long term?

The only predictor of grooming rate selected for in the final model was sexual activity. The more sexual activity that occurred within a given dyad, the more often that pair groomed each other. This was the case in both a model based on the complete dataset, as well as in models with interactions initiated by a male or a female only (Table 3).

Table 3. Results of LMMs testing the effect of selected variables on grooming rate.

| Model | Selected predictors | Estimate | SE | 95% CI | |
|---|---|---|---|---|---|
| Complete | sexual activity | **6.614** | **0.496** | **5.615** | **7.588** |
| Male initiated | sexual activity | **5.833** | **0.675** | **4.476** | **7.157** |
| Female initiated | sexual activity | **7.460** | **0.660** | **6.151** | **8.745** |

Variables with values in bold had significant effects on grooming rate, based on their 95% CI.

**Is grooming in non-sexual contexts predicted by sexual activity?**

Sexual activity was the only predictor selected for in the final models of grooming rate in nonsexual contexts. Higher sexual activity in a given dyad predicted a higher rate of grooming interactions between those individuals outside of the sexual context, and this effect was independent of the sex of the groomer (Table 4).

Table 4. Results of LMMs testing the effect of selected variables on grooming rate in non-sexual context.

| Model | Selected predictors | Estimate | SE | 95% CI | |
|---|---|---|---|---|---|
| Complete | sexual activity | **1.566** | **0.350** | **0.871** | **2.255** |
| Male initiated | sexual activity | **2.074** | **0.493** | **1.066** | **3.059** |
| Female initiated | sexual activity | **1.159** | **0.467** | **0.241** | **2.075** |

Variables with values in bold had significant effects on grooming rate based on their 95% CI.

**Is grooming in sexual contexts predicted by sexual activity within a particular dyad?**

Sexual activity was selected as a predictor for grooming rate in sexual context. Higher rates of sexual activity in a given dyad was related to higher rates of grooming interactions in sexual contexts. Moreover, in models of grooming interactions initiated by females, high-ranking females groomed less often in sexual contexts than low-ranking females (Table 5).

Table 5. Results of LMMs testing the effect of selected variables on grooming rate in sexual context.

| Model | Selected predictors | Estimate | SE | 95% CI | |
|---|---|---|---|---|---|
| Complete | sexual activity | **7.716** | **0.756** | **6.228** | **9.191** |
| Male initiated | sexual activity | **8.819** | **1.038** | **6.782** | **10.853** |
| Female initiated | sexual activity | **7.248** | **1.121** | **5.047** | **9.428** |
| | female rank | **-0.479** | **0.239** | **-0.951** | **-0.008** |

Variables with values in bold had a significant effect on grooming rate based on their 95% CI.

**Does grooming occur more often before, after, or outside of sexual interactions?**

Context, rank of groomer, and season were selected as predictors of grooming rate. Individuals groomed each other more often in pre- as well as post- sexual contexts as compared to non-sexual contexts. High-ranking individuals groomed others less often then subordinates. There was a trend for grooming interactions to be slightly more frequent in season 2. The same three predictors were selected in a model based on female-initiated interactions, but only context was selected in a model based on male-initiated interactions. In sum, both males and females groomed more often in pre- and post- sexual contexts as compared to non-sexual context. Additionally, high-ranking females groomed less than lower-ranking females, and females generally groomed more often in season 2 than season 1 (Table 6).

Table 6. Results of LMMs testing the effect of selected variables on grooming rate.

| Model | Selected predictors | Estimate | SE | 95% CI | |
|---|---|---|---|---|---|
| Complete | context (post) | **4.447** | **0.076** | **4.297** | **4.594** |
| | context (pre) | **4.261** | **0.091** | **4.082** | **4.438** |
| | groomer rank | **-0.102** | **0.046** | **-0.192** | **-0.013** |
| | season (2) | 0.135 | 0.074 | -0.010 | 0.282 |
| Male initiated | context (post) | **4.404** | **0.109** | **4.186** | **4.617** |
| | context (pre) | **4.184** | **0.109** | **3.922** | **4.440** |
| Female initiated | context (post) | **4.463** | **0.104** | **4.263** | **4.672** |
| | context (pre) | **4.308** | **0.124** | **4.069** | **4.554** |
| | female rank | **-0.150** | **0.060** | **-0.266** | **-0.023** |
| | season (2) | **0.268** | **0.106** | **0.052** | **0.471** |

Variables with values in bold had significant effects on grooming rate based on their 95% CI.

## DISCUSSION

In accordance with the hypothesis of grooming-for-mating exchange, our data show that free-ranging Barbary macaque males groom their mating partners more frequently and for longer periods of time than other females with whom they are not mating. The same result was shown in previous studies on long-tailed macaques (Gumert, 2007b), bonnett macaques (Kurup, 1988), rhesus macaques (Massen et al., 2012), and common chimpanzees (Hemelrijk et al., 1992). In contrast, Cooper and Bernstein (2000) did not find such a pattern in their study on the Assamese macaques. Gumert (2007b) argued that Cooper and Bernstein (2000) did not consider the specific context of grooming, which may have obscured the pattern of behavioral exchange; however, in our study the relationship between grooming and mating remains significant regardless of context. Interestingly, we found the same pattern for the opposite sex; females also groomed males with whom they had longer-term sexual activity more frequently and for longer periods of time. This cannot easily be explained by a simple hypothesis that consider only males, and not females, as the sex that pays for mating.

Although the relationship between grooming and mating in our study remained significant regardless of context, grooming was far more frequent and longer in the sexual, compared to the non-sexual context. This corresponds to the result of Gumert (2007b), who found that males groomed females for significantly longer periods of time in sexual contexts. In our case, however, the same relationship also applied to females grooming males. In a study of captive rhesus macaques, the relationship between grooming and mating was documented in relation to a dyad's mating history, but not during the specific days when females were sexually active; furthermore, grooming did not occur in the immediate context of mating (Massen et al., 2012). Therefore, some studies (including our own) highlight the importance of temporal associations between grooming and mating and suggest that grooming-for-mating exchanges do not follow a universal pattern among the primates and can vary even within macaque genera.

Cooper and Bernstein (2000) explain their finding that grooming does not relate to mating in Assamese macaques by the fact that the species is a single-mount ejaculator; this means that males cannot shorten the interval between consecutive mounts by grooming the female. Furthermore, the Assamese macaque males in their study could use coercion to gain matings. However, studies that failed to find the immediate exchange of grooming for mating have focused predominantly on multiple-mount-ejaculating species (rhesus macaque, Massen et al., 2012) as well as a predominantly single-mount-ejaculating species (Barbary macaque, this study), while the study that proved the exchange (long-tailed macaque, Gumert, 2007b) referred to a species in which both single-mount-ejaculation and multiple-mount-ejaculation regularly occur (Shively, Clarke, Schapiro & Mitchell, 1982). Moreover, in rhesus and Barbary macaques, the coercive tactics on the part of the males occur exceptionally or not at all (Kuester & Paul, 1992; Massen et al., 2012), yet the grooming-for-mating exchanged was not demonstrated. However, one of the differences between the species that have been studied is the fact that only the long-tailed macaques can reproduce year-round (Kavanagh & Laursen, 1984). Therefore, there may be fewer female simultaneously in estrus in this species as compared to rhesus or Barbary macaques, which can strengthen the grooming-for-mating market forces. Finally, all of the cited studies used different methods of collecting and analyzing the data, which can influence the results. Although this has been perceived as a weakness of current studies examining the biological market in primates (Sánchez-Amaro & Amici, 2015), it can also be argued that the leading behavioral principles should be highly robust and should be detectable using various experimental and analytical approaches.

The effect of the dominance rank on the observed grooming patterns was found to be similar for both sexes. In several analyses, the higher-ranking individuals invested less in grooming as compared to lower-ranking animals. The effect of dominance was detected more often in tests that involved females, as compared to those that involved males. The effect of rank is predicted to occur in the sex that uses grooming as a "currency" in biological market; therefore, our study counters the idea that it is specifically males who are paying females for sex by grooming them. Rather, it seems that both sexes invest similarly in grooming and mating interactions. In previous studies, female Barbary macaques have been described as sexually assertive; they mate frequently and indiscriminately with a large number of males, often initiate mating interactions (Taub, 1980; Small, 1990), and rarely reject a male (Kuester & Paul, 1992). A model in which males use grooming as a "currency" to pay females for mating may therefore not apply for this species.

We did not find any difference in grooming behavior between the pre-sexual and post-sexual contexts, which contradicts the hypothesis of direct grooming-for-mating exchange. If grooming serves as a payment for sex, the post-sex payment tactic would be prone to cheating and therefore evolutionary unstable. The fact that pre-grooming behavior resembles post-grooming interactions strongly suggests that the mechanism that is responsible for the correlation between grooming and mating is a longer-lasting social bond between males and females. The sexual context can be viewed as an opportunity to strengthen this social bond, which can in turn result in more mating and/or other benefit over the longer term. Grooming in sexual contexts can help to solidify this social bond. The females (or both partners) are then more likely to choose their mating partner based on the previous history of their interaction, rather than on the behavior immediately preceding the mating. This has also been found in rhesus monkey colonies: long-term relationships between males and females are good predictors of mating frequency, and the only significant predictor of paternity success. These relationships are already formed at the beginning of the mating season, and they persist even after the mating season ends (Massen et al., 2012).

According to Sonnweber et al. (2015), the function of grooming in the post-sexual context could differ between the two sexes. For the male, it can represent a mate-guarding strategy. This is in accordance with findings by Kuester and Paul (1992), in which female Barbary macaques tended to initiate interactions with other males soon after mating. On the other hand, for the female, the post-mating grooming can help to establish a bond that could discourage future harassment of the female and her offspring, and/or promote paternal behaviors. Therefore, both sexes may be motivated to groom their partner after sexual interaction. As the magnitude of these benefits cannot be quantified, there is no specific prediction as to which of the sexes should invest more or less into the post-mating grooming. In our case, there were no pronounced differences between the sexes except that females spent more time grooming males in general contexts than vice versa.

As the specific motivations of each sex during the grooming and mating interactions probably differ, it is likely that we would find more differences between males and females if we observe their behavior in more detail and/or if we take into account additional variables. For example, Sonnweber et al. (2015) reported that males were more likely to groom females after copulations with ejaculation, while females did so more often after copulations without ejaculation. Furthermore, lactating females started post-copulatory grooming more readily than males.

In the Kuester and Paul's (1992) study, Barbary macaque males actually groomed females 3 times more often than females groomed males. Likewise, it was mainly males who stayed close to females after mating, followed them during locomotion, and tried to mate with them repeatedly. The authors of this study, however, only observed females during the last seven days of their conceptual estrus, when copulations likely to be most valuable to males. During this limited time frame, males probably invest more into interactions with females as compared to the rest of the mating season, during which females remain sexually active but chances of conception are much lower.

In conclusion, the simple model of the biological market, which would describe Barbary macaque males as the sex that uses grooming as payment for mating, cannot fully explain the observed behavioral patterns. Rather, it appears that the significant correlation between grooming and mating in this species is mediated through longer-lasting behavioral bonds between individuals, and that both sexes benefit from and invest in this social bond.

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## REFERENCESS

Altmann, J. (1974). Observational study of behavior: Sampling methods. Behaviour, 49, 227–267. DOI: 10.1163/156853974X00534

Aureli, F., & Yates K. (2010). Distress prevention by grooming others in crested black macaques. *Biology Letters, 6*, 27-29. DOI: 10.1098/rsbl.2009.0513

Barrett, L., Henzi1, S.P., Weingrill, T., Lycett, J.E., & Hill, R.A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceeding of the Royal Society of London B, 266*, 665-670. DOI: 10.1098/rspb.1999.0687

Berman, C.M., Ionica, C.S., Dorner, M., & Li, J. 2004. Postconflict affiliation between former opponents in *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology, 27*(3), 827-854. DOI: 10.1007/s10764-006-9039-y

Borgeaud, C., & Christèle, R. (2015). Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in experimentally induced conflicts. *Current Biology*, *25*(22), 3011 – 3016. DOI: 10.1016/j.cub.2015.10.016

Colmenares, F., Zaragoza, F., & Hernández-Lloreda, M. V. (2002). Grooming and Coercion in One-Male Units of Hamadryas Baboons: Market Forces or Relationship Constraints? *Behaviour*, *139*(11), 1525–1553. DOI: 10.1163/15685390260514753

Cooper, M.A., & Bernstein, I.S. (2000). Social Grooming in Assamese Macaques (*Macaca assamensis*). *American Journal of Primatology, 50*, 77–85. DOI: 10.1002/(SICI)1098-2345(200001)50:1<77::AID-AJP7>3.0.CO;2-R

Darwin, C. (1871). The descent of man, and selection in relation to sex. London: John Murray.

de Vries, H., Netto, W.J., & Hanegraaf, P.L.H. (1993). MatMan: a program for the analysis

of sociometric matrices and behavioural transition matrices. *Behaviour, 125*(3-4), 157-175. DOI: 10.1163/156853993X00218

de Waal, F.B.M. (1997). The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior, 18*, 375–386. DOI: 10.1016/S1090-5138(97)00085-8

Dolhinow, P. (1978). A behavior repertoire for the Indian langur monkey (*Presbytis entellus*). *Primates, 19*(3), 449–472. DOI: 10.1007/BF02373308

Dunayer, E.S., & Berman, C.M. (2016). Biological markets: theory, interpretation, and proximate perspectives. A response to Sánchez-Amaro and Amici (2015). *Animal Behaviour, 121*, 131-136. DOI: 10.1016/ j.anbehav.2016.08.018

Dunbar, R.I.M. (1991). Functional significance of social grooming in primates. *Folia Primatologica, 57*, 121–131. DOI: 10.1159/000156574

Dunbar, R.I.M. (2010). The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews, 34*(2), 260-268. DOI: 10.1016/j.neubiorev.2008.07.001.

Falk, J.L. (1958). The grooming behavior of the chimpanzee as a reinforcer. *Journal of the Experimental Analysis of Behavior, 1*(1), 83–85. DOI: 10.1901/jeab.1958.1-83

Gammell, M.P., de Vries, H., Jennings, D.J., Carlin, C.M., & Hayden, T.J. (2003). David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Animal Behaviour*, *66*(3), 601–605.

Guan, Z.H., Huang, B., Ning, W.H., Ni, Q.Y., Sun, G.Z., & Jiang, X.L. (2013). Significance of grooming behavior in two polygynous groups of western black crested gibbons: Implications for understanding social relationships among immigrant and resident group members. *American Journal of Primatology, 75*(12), 1165–1173. DOI: 10.1002/ajp.22178

Gumert, M.D. (2007a). Grooming and Infant Handling Interchange in *Macaca fascicularis*: The relationship between infant supply and grooming payment. *International Journal of Primatology, 28*, 1059–1074. DOI: 10.1007/s10764-007-9202-0

Gumert, M.D. (2007b). Payment for sex in a macaque mating market. *Animal Behaviour*, *74*(6), 1655–1667. DOI: 10.1016/j.anbehav.2007.03.009

Hemelrijk, C.K., van Laere, G.J., & Van Hooff, J.A.R.A. (1992). Sexual exchange relationships in captive chimpanzees? *Behavioral Ecology and Sociobiology*, *30*(3-4), 269–275. DOI: 10.1007/BF00166712

Hinde, R.A. (1978). Dominance and role—two concepts with dual meanings. *Journal of Social and Biological Structures*, *1*(1), 27-38. DOI: 10.1016/0140-1750(78)90016-7

Kaburu, S.S.K., & Newton-Fischer, N.E. (2016). Markets misinterpreted? A comment on Sánchez-Amaro and Amici (2015). *Animal Behaviour, 119*. DOI: 10.1016/j.anbehav.2016.02.011

Kavanagh, M., & Laursen, E. (1984). Breeding seasonality among long-tailed macaques, *Macaca fascicularis*, in Peninsular Malaysia. *International Journal of Primatology, 5*(1), 17-29. DOI: 10.1007/BF02735145

Konečná, M., Weiss, A., Lhota, S., & Wallner, B. (2012). Personality in Barbary macaques *(Macaca sylvanus)*: Temporal stability and social rank. *Journal of Research in Personality, 46*(5), 581-590. DOI: 10.1016/j.jrp.2012.06.004.

Kuester, J., & Paul, A. (1992). Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca Sylvanus). Behaviour, 120*, 192-216. DOI: 10.1163/156853992X00606

Kurup, G.U. (1988). The grooming patterns in bonnet macaques. *Annals of the New York Academy of Sciences, 525*, 414–416. DOI: 10.1111/j.1749-6632.1988.tb38629.x

Lehmann, J., Korstjens, A.H., & Dunbar, R.I.M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour, 74*(6), 1617-1629. DOI: 10.1016/j.anbehav.2006.10.025

Massen, J. J. M., Overduin-de Vries, A. M., de Vos-Rouweler, A. J. M., Spruijt, B. M., Doxiadis, G. G. M., & Sterck, E. H. M. (2012). Male mating tactics in captive rhesus macaques (*Macaca mulatta*): The influence of dominance, markets, and relationship quality. *International Journal of Primatology*, *33*(1), 73–92. DOI: 10.1007/s10764-011-9552-5

McFarland, R., Henzi, S.P., Barrett, L., Wanigaratne, A., Coetzee, E., Fuller, A., Hetem, R.S., Mitchell, D., & Maloney S.K. (2016). Thermal consequences of increased pelt loft infer an additional utilitarian function for grooming. *American Journal of Primatology 78*, 456–461. DOI: 10.1002/ajp.22519

Muroyama, Y. (1994). Exchange of grooming for allomothering in female patas monkeys. *Behaviour 128*, 103-119. DOI: 10.1163/156853994X00064

Noë, R., & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, *35*(1), 1–11. DOI: 10.1007/BF00167053

Nunn, C. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour*, *58*(2), 229–246. DOI: 10.1006/anbe.1999.1159

Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team (2018). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137

Russell, Y.I., & Phelps, S. (2013). How do you measure pleasure? A discussion about intrinsic costs and benefits in primate allogrooming. *Biology & Philosophy, 28*(6), 1005-1020. DOI: 10.1007/s10539-013-9372-4

Sánchez-Amaro, A., & Amici, F. (2015). Are primates out of the market? *Animal Behaviour, 110*, 51-60. DOI: 10.1016/j.anbehav.2015.09.020.

Sánchez-Amaro, A., & Amici, F. (2016). Markets carefully interpreted: a reply to Kaburu and Newton-Fisher (2016). *Animal Behaviour, 119*. DOI: 10.1016/j.anbehav.2016.06.022.

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour, 62*, 265–271. DOI: 10.1006/anbe.2001.1750

Schino, G., di Sorrentino, E.P., & Tiddi, B. (2007). Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame of reciprocation. *Journal of Comparative Psychology, 121*(2), 181–188. DOI: 10.1037/0735-7036.121.2.181

Schino, G., & Aureli, F. (2008). Grooming reciprocation among female primates: a meta-analysis. *Biology letters, 4*, 9-11. DOI: 10.1098/rsbl.2007.0506

Seyfarth, R.M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology, 65*, 671–698. DOI: 10.1016/0022-5193(77)90015-7

Shively, C., Clarke, S., Schapiro, S., & Mitchell, G. (1982). Patterns of sexual behavior in male macaques. *American Journal of Primatology, 2*(4), 373-384. DOI: 10.1002/ajp.1350020406

Small, M.F. (1990). Alloparental behaviour in Barbary macaques, *Macaca sylvanus*. *Animal Behaviour, 39*(2), 297-306. DOI: 10.1016/S0003-3472(05)80874-7

Sommer V. (1989). Sexual harassment in langur monkeys *(Presbytis entellus)*: competition for ova, sperm, and nurture? Ethology 80, 205–217. DOI: 10.1111/j.1439-0310.1989.tb00740.x

Sonnweber, R. S., Massen, J. J. M., & Fitch, W. T. (2015). Post-copulatory grooming: a conditional mating strategy? *Behavioral Ecology and Sociobiology*, *69*(11), 1749–1759. DOI: 10.1007/s00265-015-1987-9

Sparks, J. (1967). Allogrooming in primates: a review. In: Morris, D. (Ed.), Primate Ethology. Weidenfeld & Nicholson, London, pp. 148–175.

Taub, D. (1980). Female choice and mating strategies among wild Barbary macaques *(Macaca sylvanus)*. In: Lindburg, D. (Ed.), The macaques: studies in ecology, behaviour, and evolution. New York, NY: Van Nostrand Reinhold Company, pp. 287-367.

Tiddi, B., Aureli, F., Schino, G., & Voelkl, B. (2011). Social relationships between adult females and the alpha male in wild tufted capuchin monkeys. *American Journal of Primatology, 73*(8), 812–20. DOI: 10.1002/ajp.20939

Ventura, R., Majolo, B., Koyama, N. F., Hardie, S., & Schino, G. (2006), Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology, 68*, 1138–1149. DOI: 10.1002/ajp.20314

Yu, Y., Xiang, Z.F., Yao, H., Grueter, C.C., & Li, M. (2013) Female Snub-Nosed Monkeys Exchange Grooming for Sex and Infant Handling. *PLOS ONE, 8*(9). DOI: 10.1371/journal.pone.0074822

## Supplementary material S1. Results of LMMs based on grooming time as a response.

### Is grooming predicted by sexual activity?

The only predictor of grooming time selected for in the final model was sexual activity. The more sexual activity that occurred within a given dyad, the longer they groomed each other. This was true for a model based on the complete dataset, a dataset that included male-initiated interactions only, and a dataset with female-initiated interactions only. Sex of the groomer was also selected as a predictor of grooming time, with females generally grooming males longer than vice versa. Rank of the female was selected as a predictor in a model based on male-initiated interactions only, subsequently showing a nonsignificant trend that males groomed longer higher ranking females compared to low ranking ones in final model (Table S1).

Table S1. Results of LMMs testing the effect of selected variables on grooming time.

| Model | Selected predictors | Estimate | SE | 95% CI | |
|---|---|---|---|---|---|
| Complete | sexual activity | **7.741** | **0.628** | **6.482** | **8.970** |
| | groomer sex (M) | **-0.419** | **0.213** | **-0.836** | **-0.002** |
| Male inic. only | sexual activity | **8.334** | **0.837** | **6.662** | **9.957** |
| | female rank | 0.396 | 0.225 | -0.046 | 0.843 |
| Female inic. only | sexual activity | **6.860** | **0.874** | **5.095** | **8.574** |

Variables with values in bold had significant effects on grooming time based on their 95% CI.

**Is grooming in non-sexual contexts predicted by sexual activity?**

Sexual activity was the only predictor selected for in the final models of grooming time in non-sexual contexts. Higher sexual activity in a given dyad predicted longer durations of grooming interactions outside of sexual contexts, independent of sex of the groomer (Table S2).

Table S2. Results of LMMs testing the effect of selected variables on grooming time in non-sexual contexts.

| Model | Selected predictors | Estimate | SE | 95% CI | |
|---|---|---|---|---|---|
| Complete | sexual activity | **1.796** | **0.409** | **0.986** | **2.601** |
| Male initiated | sexual activity | **2.419** | **0.578** | **1.241** | **3.568** |
| Female initiated | sexual activity | **1.302** | **0.538** | **0.245** | **2.360** |

Variables with values in bold had significant effects on grooming time based on their 95% CI.

**Is grooming in sexual contexts predicted by sexual activity?**

Sexual activity was selected as a predictor for grooming time in sexual contexts. Higher rates of sexual activity in a given dyad was related to longer durations of grooming interactions in sexual contexts. Additionally, rank was selected as a predictor in a model based on grooming initiated by males, with high-ranking males grooming for longer periods of time than low ranking ones. (Table S3).

Table S3. Results of LMMs testing the effect of selected variables on grooming time in sexual contexts.

| Model | Selected predictors | Estimate | SE | 95% CI | |
|---|---|---|---|---|---|
| Complete | sexual activity | **8.368** | **0.818** | **6.756** | **9.964** |
| Male initiated | sexual activity | **9.714** | **1.125** | **7.495** | **11.898** |
| | male rank | **0.629** | **0.278** | **0.093** | **1.172** |
| Female initiated | sexual activity | **7.009** | **1.157** | **4.697** | **9.288** |

Variables with values in bold had significant effects on grooming time based on their 95% CI.

## Does grooming occur more often before-, after-, or outside of sexual interactions?

Context, rank of groomee, and season were selected as predictors of grooming time in a model based on the complete dataset. Individuals groomed each other for longer in pre- as well as post- sexual contexts as compared to non-sexual contexts. High-ranking individuals were groomed by others for longer durations than low-ranking individuals. In a model based on male-initiated grooming interactions, males groomed for longer in pre- as well as post- sexual contexts compared to non-sexual ones. Moreover, high-ranking males groomed for longer than low-ranking males. For interactions initiated by females, only context was selected as a predictor: females groomed longer in pre- as well as post- sexual contexts (Table S4).

Table S4. Results of LMMs testing the effect of selected variables on grooming time.

| Model | Selected predictors | Estimate | SE | 95% CI | |
|---|---|---|---|---|---|
| Complete | context (post) | **4.529** | **0.170** | **4.192** | **4.860** |
| | context (pre) | **4.512** | **0.204** | **4.112** | **4.910** |
| | groomee rank | **0.215** | **0.095** | **0.027** | **0.407** |
| | season (2) | 0.284 | 0.161 | -0.042 | 0.597 |
| Male initiated | context (post) | **4.592** | **0.239** | **4.111** | **5.054** |
| | context (pre) | **4.582** | **0.287** | **4.010** | **5.136** |
| | male rank | **0.353** | **0.147** | **0.068** | **0.636** |
| Female initiated | context (post) | **4.473** | **0.233** | **4.018** | **4.933** |
| | context (pre) | **4.399** | **0.278** | **3.855** | **4.946** |

Variables with values in bold had significant effects on grooming time based on their 95% CI.

# CHAPTER III.

## Time constraints rather than attraction to infants may explain the effect of maternal status on grooming among Barbary macaque *(Macaca sylvanus)* females.

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# Time constraints rather than attraction to infants may explain the effect of maternal status on grooming among Barbary macaque (*Macaca sylvanus*) females

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## Abstract

Grooming and infant handling could be considered exchangeable commodities in the biological market model. In species with strict allomothering, where mothers often resist the attempts of other females to inspect or take away their infants, allomothers may exchange grooming for infant handling. The grooming-infant-handling exchange is less understood in primates with less restrictive allomothering, such as Barbary macaques. We have examined data on 17 semi-free ranging Barbary macaque females. The 'infant attractivity' hypothesis posits that grooming should be more evenly distributed between pairs of non-mothers than between mothers and non-mothers. Moreover, we expected that mothers would receive more and give less grooming to other females as compared to non-mothers, and that non-mothers who groom mothers would spend more time with infant handling. Using matrix correlations and linear mixed effect models (LMM), we found that mothers gave less grooming but did not receive more grooming from other females. We propose that the observed patterns can be better explained by time constraints posed on mothers, rather than by grooming for infant handling exchange. Biological market forces may not be fully applicable to behaviour in species with permissive allomothering styles and/or high seasonality of births.

**Key words:** grooming, exchange, reciprocity, mother-infant interactions, *Macaca sylvanus*, allomothering

## Introduction

Many primates spend considerable amounts of time carefully inspecting and cleaning the fur of other individuals. This behaviour, termed allogrooming (Schino 2006) (hereafter ‘grooming’), is one of the most common forms of affiliative behaviour among many primates including macaques, baboons, and chimpanzees, while some other primate species groom rarely or not at all (Sparks 1967; Dunbar 1991; Schino 2001). Grooming in some species may occupy up to 20% of the daily time budget, and is consistently performed even when other demands, such as foraging, require increased effort. This suggests that grooming is of great significance for the animals involved (Henzi and Barrett 1999; Dunbar and Sharman 1984).

Grooming probably arose to keep fur in good hygienic condition by removing parasites, old skin, or dust (Goosen 1987), as well as to increase possible benefits to thermoregulation (McFarland et al. 2015). However, it also serves important fundamental social functions such as appeasing other individuals, maintaining relationships and increasing group cohesion (Sparks 1967; Kummer 1968). Currently, this array of social functions served by grooming is often modelled as an exchange between “commodities” or “services” on a biological market (Noë and Hammerstein 1994). This economic approach focuses on the ultimate fitness-related outcome of social grooming, rather than on its proximate behavioural and physiological benefits. In a biological market, grooming can be traded for same-kind service, for reciprocal grooming (Schino and Aureli 2008), or for different-kind services or commodities that may include sex (Gumert 2007), coalitionary support (Henzi and Barrett 1999), and sharing of food resources (de Waal 1997).

Another commodity thought to be exchanged for grooming in the biological market model is infant handling (Henzi and Barrtett 2002; Frank and Silk 2009; Fruteau et al. 2011; Scheid and Noë 2005; Muroyama 1994; Gumert 2007; Yu et al. 2013; Wei et al. 2013; Tiddi et al. 2010). Primate females are strongly attracted to other females’ infants, especially new-borns, which makes mothers more attractive social partners than females without offspring (Hrdy 1976). This tendency for non-mothers to interact with other females’ infants varies in intensity across primate species. For example, non-mother group members are regularly involved in carrying infants and provisioning them with resources in marmosets (da Silva Mota et al. 2006); similarly, langur mothers will allow other individuals to hold infants for long periods of time (Stanford 1992). However, the communal breeding system in marmosets and other species represents a rather special case and will not be further considered here; for a study on grooming exchange in this type of social system, see Lazaro-Perea et al. (2004).

Various functional hypotheses have been proposed to explain why infants are attractive to non-mothers (Silk et al. 2003). Infant-non-mother interactions may help establish and maintain social contact with the infant and/or its mother (Small 1990). These interactions may also serve to improve the caretaker's (non-mother's) parenting skills (Riedman 1982; Fairbanks 1990; Paul and Kuester 1996), thus increasing the survival of caretakers' own future offspring (Mann and Smuts 1998). Mothers might also benefit from alloparental care for their infants as they can maximize their foraging efficiency and self-care (Vogel 1984), and all parties can benefit if efforts to provision and protect the young increase the size and competitive power of the group (Kokko et al. 2001; Silk et al. 2003).

However, infant handling by allomothers is not without risk. The allomother usually provides lower-quality care to the infant; for example, they may physically harm the infant, avoid/be unable to breastfeed, and refuse to return the infant to their mother (Hrdy 1976). In general, it seems that allomothers are often the party that gains most benefit, while mothers and infants bear most risk from infant handling. Perhaps because of these risks, mothers often resist the attempts of other females to inspect or take away their infants. For example, female chacma baboons are only permitted to interact with the others' infants when they are with their own mothers (Henzi and Barrtett 2002). However, allomothers may be able to increase access to infant handling if they provide an additional service, such as grooming, as an exchange commodity to other females.

Several studies have provided support to the idea of grooming-for-infant-handling exchange in primates. Henzi and Barrett (2002) found that non-mother chacma baboons are more likely to initiate interactions with mothers than vice versa; grooming is generally unidirectional from non-mothers to mothers; and mothers are more tolerant of other females' efforts to handle their infants if they are groomed first. Moreover, the proportion of grooming provided by a female was greater if their partner had an infant than if they did not. In long-tailed macaques, grooming tended to promote an exchange with infant handling (Gumert 2007). In addition, for both macaques and baboons, the supply of available infants is positively related to the duration of grooming by allomothers (Henzi and Barrett 2002; Gumert 2007).

The value of infant handling in the biological market can be influenced by differences in maternal style across species. If the mother allows other females easy access to infants, investment in grooming may become superfluous. Most previous studies focused on the possible exchange of grooming for infant handling have been conducted on species characterized by restrictive maternal styles, in which mothers do not easily allow other females access to their infants. These include baboons, vervets, mangabeys, capuchin monkeys and long-tailed macaques (Henzi and Barrtett 2002; Frank and Silk 2009; Fruteau et al. 2011; Scheid and Noë 2005; Tiddi et al. 2010; Gumert 2007). Our understanding of exchange of grooming for infant handling in primates with less restrictive maternal styles remains less understood, although studies on patas monkey (Muroyama 1994) and golden snub-nosed monkeys (Yu et al. 2013; Wei et al. 2013) found evidence for the exchange even in these allomothering-permissive species.

In this study, we examined the grooming interactions of mother – non-mother dyads in a population of semi-free ranging Barbary macaques, a species with both allomothering-permissive maternal style and high seasonality of births. Barbary macaques have been classified as a tolerant macaque species with a high degree of affiliative interactions among group members (Thierry 1990), including very frequent interactions with infants (Small 1990). Both males and females are allowed to handle infants from a very young age (Kuběnová et al. 2017). If, in spite of this more permissive allomothering and high birth seasonality, the grooming-for-infant-handling exchange occurs and brings benefits to Barbary macaque females, we expected that mothers would receive more grooming from other females and give less grooming to other females relative to non-mothers. In other words, we predicted that grooming between mothers and non-mothers would be less balanced/reciprocal than grooming between non-mothers.

We also expected that non-mothers who engaged in more grooming behaviour with mothers would spend more time with infant handling. Such relationships would demonstrate that the trade occurs, and that it brings benefit to both parties by increasing time being groomed or increasing time with infants.

## Materials and methods

### Study subjects

Subjects of this study were 17 semi free-ranging adult (aged 3–26 years; mean age 11.2 years) female Barbary macaques living in Gibraltar. Over two seasons of data collection, 6 and 7 females, respectively, had infants that aged 0-6 months during the study period. The group also consisted of up to nine adult males and up to 15 juveniles (Konečná et al. 2012). The study group was regularly provisioned and visited by the public.

### Behavioural data collection and analysis

Behavioural observations were made between November 2007 and February 2008 (season 1, hereafter referred to as "S1") and between October 2008 and February 2009 (season 2, hereafter referred to as "S2"). Focal continuous and focal instantaneous sampling methods were used for data collection, with adult females being the focal subjects (Altmann 1974). Behaviours were recorded according to an ethogram that was prepared based on previous studies (Dolhinow 1978; Berman et al. 2004); for details see Konečná et al. (2012). Behaviours used in this study are listed in Table 1. We collected an average of 14.6 (±0.46 SD) hours of observation per female per season; data collection per female was equally distributed within each day and season. In total we observed 1,514 grooming episodes. For each episode, the following details of the grooming behaviour were recorded: start and end time of the episode (to the nearest second), direction of the interaction, and identity of the social partner. The grooming episode was considered terminated if it stopped for at least 20 seconds.

The data collection was designed mainly to study individual variation in behaviour (Konečná et al. 2012) and thus focal individual observation was used rather than *ad libitum* sampling of grooming and infant handling sequences. Focal observations of individuals are less prone to sampling bias of particular (more visible, dominant) individuals (Altmann 1974). However, we do not possess data on full grooming-infant handling sequences, as we always followed one focal individual (adult female) who could be either groomer or the groomee, mother or allomother. We thus cannot test predictions of the biological market model that are based on studying behavioural sequences (Henzi and Barrtett 2002; Frank and Silk 2009; Fruteau et al. 2011; Gumert 2007). We have, however, been able to use our data to ask if an exchange of grooming for infant handling exists and translates to the time the females spend grooming and handling infants.

Social dominance hierarchy among females was computed using dyadic displacement interactions between pairs of females. Linearity of the dominance hierarchy was evaluated by the linearity index h′ in MatMan 1.1.4 (Noldus 2003) (de Vries et al. 1993). Subjects were ranked based on their normalized David's score (NDS) (de Vries et al. 2006; Gammell et al. 2003) computed on the basis of the Dyadic Dominance Index corrected for chance $D_{ij}$ (de Vries 1998). Dominance hierarchy characteristics are described in Roubová et al. (2015). We assessed friendship based on the amount of time females spent in mutual body contact (see Table 1 for definition), as this metric has also been used in other studies (Call et al. 1999; Cords 2002). Maternal kinship information was based on local management records. Females were categorized as mothers (M) if they gave birth to an infant during the preceding birth season, and as non-mothers (NM) if they did not give birth that year. No infants died over the course of our study.

## Statistical analyses

To test reciprocity of grooming behaviour among mothers and non-mothers, we computed correlations of matrices using MatMan 1.1.4 (Noldus 2003) (de Vries et al. 1993). We created 8 matrices for each of two response variables, grooming rate and total grooming time, for a total of 16 matrices. For each response variable, we first separated datasets by season (S1, S2), and within these created matrices of interactions among non-mothers only and among non-mother – mother pairs. To assess reciprocity, we used the Kr test, and to compare the strength of the reciprocity we used Spearman's ρ (Hemelrijk 1990; de Vries et al. 1993).

We tested the effect of maternal status on grooming episodes (rate and time) using linear mixed effect models (LMM) with identity of the groomer and groomee as random factors. We also included all dependent variables that had a significant effect on grooming episodes in our previous study as dependent fixed factors to control for their effect (Konečná et al. 2012). These included maternal kinship, relative rank, friendship, grooming received, aggression received, and season (see Table 1 for definitions). All grooming data were log transformed, and the estimated effect sizes (regression coefficient estimates) of predictor variables were deemed significant if the 95% CI of the estimate did not overlap zero. The interpretations of the estimated effect sizes ($b_i$) and the upper and lower confidence limits are based on an exponential function (given that the response variables were log-transformed): an increase in a continuous predictor value of one unit predicts that the response will change $\exp(b_i)$ times; in the case of categorical predictors (which all had only two states in our data set), $\exp(b_i)$ shows how many times larger the mean response value for the particular predictor state is than the mean of observations for the other state; for more details see (Konečná et al. 2012). LMMs were implemented in the lme4 package (Bates et al. 2014) in R 3.0.2 (R Core Team 2013).

We ran two linear models (LMs) to test if time spent with infant handling by non-mothers was predicted by rate and/or time of grooming the infant's mother. Our response variable for both models was time spent with infant handling, and the predictors were either the initiated grooming rate or the initiated grooming time. We created separate models because grooming rate and grooming time among females were strongly collinear (S1 $r = 0.89$, $p<0.001$, $N = 17$; S2 $r = 0.83$, $p<0.001$, $N = 17$ (Roubová et al. 2015)), and we wanted to explore potential effects of both variables. We also included season and rank of the groomer (=non-mother) as covariates in each LM.

Table 1: Variables used in LMM and their definitions

| Variable | Type | Definition |
|---|---|---|
| Grooming initiated | R, C | grooming rate and time initiated by the groomer with a given groomee |
| Maternal status of groomer | P, D | mothers and non-mothers |
| Maternal status of groomee | P, D | mothers and non-mothers |
| Kinship | P, D | kinship category between groomer and groomee: kin, non-kin |
| Relative rank | P, D | relative rank of groomer to groomee: dominant, subordinate |
| Friendship | P, C | measured as the ratio of time spent in contact by a given pair of individuals divided by the average time the focal individual spent in contact with other group members |
| Grooming received | P, C | grooming rate or time received by the groomer from a given groomee |
| Aggression received | P, C | rate of aggression received by a groomer from a given groomee |
| Season | P, D | season 1, season 2 |

P – predictor, R – response, C – continuous, D – discrete variable

## Results

### Summary of grooming behaviour

We recorded 1,514 grooming interactions among females (S1 N = 911; S2 N = 603). The number of grooming interactions per female ranged from 69 to 298, with an average of 160.2 interactions per female. We observed 101 grooming interactions between mothers, 597 grooming interactions between non-mothers, and 816 grooming interactions between non-mothers and mothers.

Table 2 shows the average grooming rate and duration when grooming was initiated by mothers vs. non-mothers in a given season. The data illustrate that mothers groom other females (non-mothers as well as other mothers, and also males) less frequently and for shorter durations than non-mothers. Mothers and non-mothers did not differ in grooming interactions with juveniles. However, mothers handle infants far more often and for longer periods of time compared to non-mothers.

We further compared females who had an infant in only one of the two seasons (N=5). Rate of grooming initiated by these females was almost 4 times higher in seasons when they were classified as non-mothers (N = 365) relative to seasons in which they had their own infant (N = 95). However, females received almost equal numbers of grooming interactions, irrespective of their status as mothers or non-mothers (N = 279 and N = 223, respectively).

Table 2. Average grooming rate and grooming time (per hour of observation) non-mothers and mothers initiated with different categories of group members in given season.

| | | season 1 | | | |
|---|---|---|---|---|---|
| groomer | | non-mothers | | mothers | |
| grooming | | rate | time | rate | time |
| groomee | mothers | 1.96 | 4.96 | 0.74 | 1.53 |
| | non-mothers | 2.52 | 6.77 | 0.87 | 2.40 |
| | males | 0.29 | 0.89 | 0.15 | 0.29 |
| | juveniles | 1.59 | 2.88 | 1.60 | 2.99 |
| | infants | 0.16 | 0.13 | 3.89 | 7.38 |
| | | | | | |
| | | season 2 | | | |
| groomer | | non-mothers | | mothers | |
| grooming | | rate | time | rate | time |
| groomee | mothers | 1.14 | 3.38 | 0.34 | 1.43 |
| | non-mothers | 1.33 | 5.54 | 0.93 | 2.96 |
| | males | 0.60 | 1.51 | 0.52 | 1.06 |
| | juveniles | 1.09 | 2.63 | 1.10 | 1.70 |
| | infants | 0.06 | 0.05 | 3.19 | 8.54 |

## Grooming reciprocity

The matrix correlations of grooming rate revealed that grooming was significantly reciprocal among non-mothers (S1: Kr test, Kr=176, $\tau_{rw}$=0.55, p<0.001; S2: Kr test, Kr=108, $\tau_{rw}$=0.57, p<0.001) as well as among mother – non-mother dyads (S1: Kr test, Kr=276, $\tau_{rw}$=0.37, p<0.001; S2: Kr test, Kr=534, $\tau_{rw}$=0.52, p<0.001). However, the strength of the correlation was weaker for the mother – non-mother dyads as compared to non-mother dyads only (S1: M-NM ρ=0.39, NM-NM ρ=0.63; S2: M-NM ρ=0.58, NM-NM ρ=0.64).

The results for grooming time followed a similar pattern to those of grooming rate. Grooming was significantly reciprocated in terms of duration between non-mother dyads (S1: Kr test, Kr=121, $\tau_{rw}$=0.43, p<0.001; S2: Kr test, Kr=93, $\tau_{rw}$=0.48, p<0.001) as well as mother – non-mother dyads (S1: Kr test, Kr=378, $\tau_{rw}$=0.30, p<0.001; S2: Kr test, Kr=635, $\tau_{rw}$=0.64, p<0.001). The strength of the relationship was again weaker among mother – non-mother dyads, but only in the first season (S1: M-NM ρ=0.36, NM-NM ρ=0.50; S2: M-NM ρ=0.69, NM-NM ρ=0.54).

## Grooming distribution among females

We found a significant influence of groomer maternal status on grooming rate and duration. Non-mothers groomed other females more frequently and for longer time than mothers. On average the rate of grooming initiated by non-mothers was 62 % higher than that of mothers. On the other hand, groomee maternal status did not affect grooming behaviour. As in our previous study (Roubová et al. 2015), grooming rates were significantly related to kinship, relative rank, friendship, grooming received, aggression received, and season (Table 3; Table 4).

Table 3: Results of LMMs testing the relationships between grooming rate and the following variables: groomer and groomee maternal status, kinship, relative rank, friendship, grooming received, aggression received and season.

| Fixed effects | Estimate | SE | 95% CI | |
|---|---|---|---|---|
| Kinship (no) | **-0.720** | **0.295** | **-1.306** | **-0.144** |
| Relative rank (s) | **0.578** | **0.197** | **0.184** | **1.005** |
| Friendship | **0.411** | **0.044** | **0.324** | **0.498** |
| Grooming received | **1.418** | **0.368** | **0.697** | **2.131** |
| Aggression received | **2.394** | **0.464** | **1.503** | **3.314** |
| Groomer status (NM) | **0.487** | **0.178** | **0.135** | **0.831** |
| Groomee status (NM) | -0.289 | 0.201 | -0.677 | 0.102 |
| Season (2) | **-0.303** | **0.151** | **-0.597** | **-0.008** |

Variables with values in bold had a significant effect on the grooming rate based on 95% CI.

Table 4: Results of LMMs testing the relationships between grooming time and the following variables: groomer and groomee maternal status, kinship, relative rank, friendship, grooming received, aggression received and season.

| Fixed effects | Estimate | SE | 95% conf. int. | |
|---|---|---|---|---|
| Kinship (no) | **-0.828** | **0.388** | **-1.602** | **-0.068** |
| Relative rank (s) | **0.923** | **0.276** | **0.365** | **1.526** |
| Friendship | **0.546** | **0.055** | **0.437** | **0.653** |
| Grooming received | **0.222** | **0.113** | **0.001** | **0.443** |
| Aggression received | **3.057** | **0.619** | **1.858** | **4.272** |
| Groomer status (NM) | **0.571** | **0.252** | **0.063** | **1.065** |
| Groomee status (NM) | -0.312 | 0.273 | -0.840 | 0.219 |
| Season (2) | **-0.593** | **0.201** | **-0.984** | **-0.201** |

Variables with values in bold had a significant effect on the grooming rate based on 95% CI.

### Grooming by non-mothers and time spent with infant handling

We found a significant effect of the initiated grooming rate, but not of the initiated grooming time, on duration of infant handling by non-mothers.

Non-mothers who groomed mothers often, but not necessarily for longer, spent more time with the infant handling. Season and non-mother rank were not significant predictors of this relationship.

Table 5. Results of LMs testing the effect of grooming rate and time initiated by non-mothers on their time spent in contact with infants.

| | Estimate | SE | p |
|---|---|---|---|
| season (2) | 0.054 | 0.551 | 0.923 |
| rank | 0.374 | 0.249 | 0.152 |
| **grooming rate** | **0.897** | **0.334** | **0.016** |
| season (2) | -0.472 | 0.632 | 0.465 |
| rank | 0.368 | 0.290 | 0.221 |
| grooming time | 0.053 | 0.053 | 0.333 |

## Discussion

The results of this study indicate that infant attractivity cannot fully explain the observed patterns of grooming in Barbary macaques. This suggests that grooming is not necessarily traded for infant handling in this species, contrary to conclusions of other studies focusing on different monkey species (Henzi and Barrtett 2002; Frank and Silk 2009; Fruteau et al. 2011; Scheid and Noe 2005; Muroyama 1994; Gumert 2007; Yu et al. 2013; Wei et al. 2013; Tiddi et al. 2010).

We found that grooming between non-mothers is more balanced, or reciprocated, than grooming between mothers and non-mothers, although the results were less clear in the second season. Such a pattern could have emerged for multiple reasons. For example, non-mothers may preferentially invest their time grooming mothers (which would be indicative of grooming-for-infant-handling exchange). Alternatively, they may groom all females equally, but receive unequal grooming in return from mothers, as compared to other non-mothers. As we detail in the following paragraphs, results of the LMM suggest that the latter explanation is more likely the case.

### Barbary macaque mothers do not receive more grooming

According to the results of our LMM, Barbary macaque mothers and non-mothers are equally likely to be groomed by other females. This contrasts with the findings of other studies. For example, the proportion of olive baboon, tufted capuchin monkey, and golden snub-nosed monkey mothers groomed by other adult females was higher than expected from their availability (Frank and Silk 2009; Tiddi et al. 2010; Wei et al. 2013). Wei et al. (2013) also found that mothers were groomed by non-mothers for longer durations during the 6-month period after giving birth compared to the 6-month period before giving birth, and that non-mothers groomed mothers for longer than mothers groomed non-mothers. A similar pattern was also found for sooty mangabey and vervet mothers (Fruteau et al. 2011) or for tufted capuchin monkeys (Tiddi et al. 2010).

Our findings, however, suggest that in Barbary macaques maternal status may not significantly impact the amount of social attention (exemplified by grooming) received from other females. The effect of being a mother on receiving more grooming may differ among species, and possibly even among populations, and could be altered by factors such as species-specific maternal styles, population-specific reproductive parameters that influence availability of infants in the group (such as average birth interval or birth seasonality), and also the age of infants considered in the study.

Primate species differ in their maternal styles, from very restrictive to very tolerant or permissive mothers. Restrictive mothers allow very limited infant handling on the other hand permissive mothers allow alloparenting by other group members to various degrees (Maestripieri 1994). Such differences in maternal style, and thus variation in access to infants, may have species-specific consequences to the grooming for infant handling trade.

For example, in golden snub-nosed monkeys (a species permissive to allomothering), mothers may receive more grooming from other females while separated from their infant, which means that infant handling is not directly involved in the interaction (Xi et al. 2008). In contrast, Moor macaque mothers (a species with relaxed dominance relations among females but not high levels of allomothering) received more grooming when accompanied by their infants (Matsumura 1997). Both of these studies included groups with comparable numbers of infants per female (about half of the females were accompanied by infants) and included infants of similar age (0-12 months by Xi et al. (2008) and 0-18 months by Matsumura (1997)). Therefore, differences in maternal style remain the most likely explanation for differences between these two studies. Also, Fruteau et al. (2011) found that grooming episodes preceding infant handling were longer than episodes of grooming without infant handling. This result was found in both sooty mangabeys and vervet monkeys, two species with more restrictive behaviours in relation to infant handling by allomothers. These results further support the hypothesis that allomothering-restrictive species may use grooming as a social tool to access infants.

The number of infants available at a given time in a group, and the ratio of infants to allomothers have been considered important predictors of infant-handling value on the exchange market. Several studies have documented that, with increasing numbers of infants, their value decreases and females stop trading grooming for infant handling (Henzi and Barret 2002).

Moreover, the relative value of grooming and infant handling in the primate biological market is usually not specified. Frank and Silk (2009) noted that in olive baboons, access to infants may not be such a valuable commodity compared to grooming. Females thus do not compete for infant handling with increased grooming effort, and do not groom mothers longer than non-mothers. The idea that low demand for infant handling may impose a limited “carrying capacity” for a group’s infant handling is illustrated by vervet monkeys (Fruteau et al. 2011): in this species, females groomed mothers and non-mothers for equal durations after a second infant was born into their group, possibly due to the larger number of infants per female and therefore lower competition among females for infant handling (Fruteau et al. 2011).

Such a scenario may be even more applicable to species with less restrictive mothers, such as Barbary macaques, in which access to infants is relatively easy to obtain not only from mothers, but also from other allomothers. Barbary macaques are also seasonal breeders, and most infants are born within a few months of each other. The number of concurrentlyavailable infants at one time can be relatively high – for example, 0.4 infants were available per adult female in our study. However, it is also important to note that males and juveniles act as allomothers in Barbary macaques. Kümmerli and Martin (2008) reported that males actually spent more time in dyadic handling of infants then non-mother females. Thus, for Barbary macaques and other permissive species, the infant-female ratio might not be the best indicator of difficulty to access infants; competition with all potential alloparents still leaves some potential for scramble competition for infant handling in Barbary macaques.

The age range of infants included in this study was rather broad. In general, younger infants tend to be more attractive to other females, and their value in the biological market decreases with age (Tiddi et al. 2010; Frutau et al. 2011). Focusing only on infants in the most attractive age category might lead to more conclusive results; however, previous studies found evidence for grooming in exchange for infant handling across infants of various ages (up to 3 –3.5 months (Henzi and Barrett 2002; Frank and Silk 2009; Fruteau et al. 2011); up to 6 months (Slater et al. 2007; Wei et al. 2013); up to 12 months (Gumert 2007; Xi et al. 2008; Matsumura 1997)). Thus, the age limit of 6 months in our study is not exceptional compared to previous studies. Additionally, infant handling by Barbary macaque males has been observed even after infants reach 6 months of age, although at a decreased rate (Deag 1980). Detailed study on attractiveness of infants of various ages to allomothers in Barbary macaques is still lacking, and therefore the impact of infant age on their "market value" in relation to exchange for grooming remains untested.

### Non-mothers, who spend more time in contact with infants, did not groom mothers for longer durations, but did so more frequently.

One finding in our study suggests that a subtle trade of grooming for infant handling may indeed occur in Barbary macaque females. We find that non-mothers who groom mothers more often also spend more time with infant handling. However, this result is only supported when we consider rate of grooming, and not significant in relation to grooming duration. Such a result was previously reported for tufted capuchin monkeys, another species with relatively permissive allomothering (Tiddi et al. 2010).

Given that, overall, mothers do not receive more grooming than non-mothers, such a result may suggest that some non-mothers are more social in general, interacting with both other non-mothers as well as mothers, rather than biasing their grooming investment only toward mothers with infants. Also, given that a statistically significant association was found only in relation to grooming rate and not grooming time, it is possible that the non-mothers who aim to interact with infants groom mothers only as long as is necessary to obtain access to infants. Therefore, mothers may not benefit by receiving more grooming time compared to non-mothers.

This result can be expected only when mothers are not highly restrictive, when infant availability is high, and/or when infant attractiveness is low, as might have been the case in our study. In contrast, Fruteau et al. (2011) found that grooming episodes preceding infant handling were longer than episodes of grooming reciprocation without infant handling in sooty mangabeys and vervet monkeys, two species where mothers are more restrictive to allomothering. These results were found when infants were studied during the first 2 months of life, when they are most attractive to allomothers.

It has been argued that grooming time, rather than grooming rate, may be a better measure of benefit to mothers. Frequent but short grooming may just be a signal showing benign interest of an allomother in a mother's infant (Tiddi et al. 2010). On the other hand, a study on embracing in spider monkeys found that even brief interactions that serve a signal rather than service function may still be subjected to effects of the biological market (Slater et al. 2007).

Overall, our data suggest that biological market forces may not explain grooming behaviour of Barbary macaque mothers, although we cannot conclude if this is due to permissive maternal style, seasonality of births (and therefore high infant availability), or the wide age range of infants in our study. However, our next result – that Barbary macaque mothers give less grooming to other females compared to non-mothers – might offer an alternative explanation of what drives patterns of grooming interactions.

### Barbary macaque mothers give less grooming

Barbary macaque females were 4 times less likely to groom other females when they were mothers, as compared to seasons in which they did not have their own infant. This result qualitatively agrees with most previous studies showing that mothers are much less likely to initiate grooming episodes, and less likely to reciprocate grooming, than non-mothers. However, given that our previous results do not support grooming for infant handling exchange, we need to look for an explanation outside of the concept of the biological market.

Mothers can be occupied with caring for their infants and therefore have less time to interact actively with other females. In our study group, mothers spent on average 7.0±2.64 and 8.5±2.28 minutes per hour (mean±SD) grooming infants in seasons 1 and 2, respectively. This was much longer than the time non-mothers spent grooming infants (S1: 0.12±0.17 minutes per hour, S2: 0.05±0.10 minutes per hour). At the same time, the mothers spent less time grooming all categories of adult macaques, including other mothers, non-mothers and males, which suggests that there is a time constraint imposed on the total time that mothers spend grooming other animals.

On the other hand, passive receipt of grooming by other females interferes less with maternal behaviour, because infants can still be cradled or nursed by the mother while she is being groomed. Therefore, the time females spend being groomed may not be affected by their maternal status.

This ‘time constraint’ hypothesis may be complementary, rather than contradictory to the hypothesis of ‘infant attractivity’. Indeed, this framework has been applied to describe findings from other systems, such as those discussed previously in olive baboons; Frank and Silk (2009) considered that time constraints may explain differences in the duration of grooming bouts in this species, with baboon mothers, on average, grooming for shorter periods of time, while non-mothers did not groom for longer durations. This time constraint on mothers may also explain why there was less grooming-for-infant-handling exchange in mother-mother dyads in chacma baboons that was not compensated for by reciprocal infant handling (Henzi and Barrett 2002); mothers may have been preoccupied with handling their own infants during this complex four-party interaction.

The time constraint hypothesis also yields additional predictions for grooming behaviour among females during the birth season, including more grooming bouts between females without infants (even when infants are present in the group) compared to mother – non-mother grooming dyads, and even less frequent bouts in mother – mother grooming dyads. Indeed, in our study we observed only 101 grooming interactions among mothers, 597 grooming interactions among non-mothers, and 816 grooming interactions among non-mothers and mothers, which suggests that grooming among mothers happens least frequently.

An interesting question is why other females continue grooming mothers at the same rate, even when they receive less grooming in return. Our result suggests that the grooming pattern among Barbary macaque females cannot be fully explained by grooming reciprocity. Additional mechanisms are likely involved, which may include trading of commodities or maintaining group cohesion. We cannot, however, distinguish between these explanations with our data.

Overall, our data suggest that mothers groom less than non-mothers, but probably not for reasons related to attractiveness of the grooming partner. Instead, they are likely more occupied by infant care. More studies of other species, and using comparable methodology, will help to shed more light on this issue. In particular, we call for future studies that simultaneously investigate grooming among group members, infant interactions, and activity budgets of mothers across a wide range of species to fully understand how motherhood constrains social interactions in primate females.

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## Compliance with Ethical Standards

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## References

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267

Bates D, Maechler M, Bolker B, Walker S (2014) Package Lme4: Linear mixed-effects models using Eigen and S4. Technical Report in: J Stat Softw 67:1-101

Berman CM, Ionica CS, Li J (2004) Dominance style among *Macaca thibetana* on Mt. Huangshan, China. Int J Primatol 25:1283–1312

Call J, Aureli F, de Waal FB (1999) Reconciliation patterns among stumptailed macaques: a multivariate approach. Anim Behav 58:165–172

Cords M (2002) Friendship among adult female Blue monkeys (*Cercopithecis mitis*). Behaviour 139:291–314

da Silva Mota MT, Franci CR, DE Sousa MBC (2006) Hormonal changes related to paternal and alloparental care in common marmosets (*Callithrix jacchus*). Horm Behav 49(3):293-302

de Vries H (1998) Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim Behav 55:827–843

de Vries H, Netto WJ, Hanegraaf PLH (1993) MatMan: A program for the analysis of sociometric matrices and Behavioral transition matrices. Behaviour 125:157–175

de Vries H, Stevens JMG, Vervaecke H (2006) Measuring and testing the steepness of dominance hierarchies. Anim Behav 71:585–592

de Waal FBM (1997) The chimpanzee’s service economy: food for grooming. Evol Hum Behav 18:375–386

Deag JM (1980) Interactions between males and unweaned Barbary macaques: testing the agonistic buffering hypothesis. Behaviour 75:54-80

Dolhinow P (1978) A behavior repertoire for the Indian langur monkey (*Presbytis entellus*). Primates 19:449–472

Dunbar RIM (1991) Functional significance of social grooming in primates. Folia Primatol 57:121–131

Dunbar RIM, Sharman M (1984) Is social grooming altruistic? Tierpsychol 64:163-173

Fairbanks LA (1990) Reciprocal benefits of allomothering for female vervet monkeys. Anim Behav 40(3):553-562

Frank RE, Silk JB (2009) Grooming exchange between mothers and non-mothers: the price of natal attraction in wild baboons (*Papio anubis*). Behaviour 146:889–906

Fruteau C, van de Waal E, van Dammea E, Noë R (2011) Infant access and handling in sooty mangabeys and vervet monkeys. Anim Behav 81:153–161

Gammell MP, de Vries H, Jennings DJ, Carlin CM, Hayden TJ (2003) David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. Anim Behav 66:601–605

Goosen C (1987) Social grooming in primates. Comp Primatol Biol 2:107-131

Gumert MD (2007) Grooming and Infant Handling Interchange in *Macaca fascicularis*: The Relationship Between Infant Supply and Grooming Payment. Int J Primatol 28:1059–1074

Hemelrijk CK (1990) Models of, and tests for, reciprocity, unidirectionality and other social-interaction patterns at a group level. Anim Behav 39:1013-1029

Henzi SP, Barrett L (1999) The value of grooming to female primates. Primates 40:47–59

Henzi SP, Barrett L (2002) Infants as a commodity in a baboon market. Anim Behav 63:1–7

Hrdy SB (1976) Care and exploitation of nonhuman primates by conspecifics other than mother. In: Rosenblatt JS, Hinde RA, Shaw EA, Beer C (ed) Advances in the Study of Behavior Vol 6. Academic Press, New York, pp 101-156

Kokko H, Johnston RA, Clutton-Brock TH (2001) The evolution of cooperative breeding through group augmentation. Proc R Soc Lond 268:187-196

Konečná M, Weiss A, Lhota S, Wallner B (2012) Personality in Barbary macaques (*Macaca sylvanus*): Temporal stability and social rank. J Res Pers 46:581–590

Kuběnová B, Konečná M, Majolo B, Smilauer P, Ostner J, Schülke O (2017) Triadic awareness predicts partner choice in male-infant-male interactions in Barbary macaques. Anim Cogn 20:221-232

Kummer H (1968) Social organization of hamadryas baboons. Chicago, IL: University of Chicago Press

Kümmerli R, Martin RD (2008) Patterns of infant handling and relatedness in Barbary macaques (*Macaca sylvanus*) on Gibraltar. Primates 49:271–282

Lazaro-Perea C, Arruda MDF, Snowdon C (2004) Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. Anim Behav 67(4):627-636

Maestripieri D (1994) Social structure, infant handling, and mothering styles in group-living Old World monkeys. Int J Primatol, 15:531-553

Mann J, Smuts BB (1998) Natal attraction: allomaternal care and mother–infant separations in wild bottlenose dolphins. Anim Behav 55:1097–1113

Matsumura S (1997) Mothers in wild group of Moor macaques (*Macaca maurus*) are more attractive to other group members when holding their infants. Folia Primatol 68:77-85

McFarland R, Henzi SP, Barrett L, Wanigaratne A, Coetzee E, Fuller A, Hetem RS, Mitchell D, Maloney SK (2016) Thermal consequences of increased pelt loft infer an additional utilitarian function for grooming. Am J primatol 78:456-461

Muroyama Y (1994) Exchange of grooming for allomothering in female patas monkeys. Behaviour 128:103-119

Noë R, Hammerstein P (1994) Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. Behav Ecol Sociobiol 35:1-11

Paul A, Kuester J (1996) Differential reproduction in male and female Barbary macaques. In: Fa JE, Lindburg DG (ed) Evolution and Ecology of Macaque Societies, Cambridge, Cambridge University Press, pp 293–317

Qi XG, Li BG, Ji WH (2008) Reproductive parameters of wild female *Rhinopithecus roxellana*. Am J Primatol 70:311–319

Riedman ML (1982) The evolution of alloparental care and adoption on mammals and birds. Q Rev Biol 57:405-435

Roubová V, Konečná M, Šmilauer P, Wallner B (2015) Whom to Groom and for What? Patterns of Grooming in Female Barbary Macaques (*Macaca sylvanus).* PLoS ONE 10(2):e0117298

Scheid C, Noë R (2005) Talk: Baby market in vervet monkeys. Primate Rep 72:84

Schino G (2001) Grooming, competition and social rank among female primates: a meta-analysis. Anim Behav 62:266-271

Schino G (2006) Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. Behav Ecol 18:115–120

Schino G, Aureli F (2008) Grooming reciprocation among female primates: a meta-analysis. Biol Lett 4:9–11

Slater KY, Schaffner CM, Aureli F (2007) Embraces for infant handling in spider monkeys: Evidence for a biological market? Anim Behav 74:455–461

Small MF (1990) Alloparental Behav in Barbary macaques, *Macaca sylvanus*. Anim Behav 39(2):297-306

Silk JB, Rendall D, Cheney DL, Seyfarth RM (2003) Natal attraction in adult female baboons (*Papio cynocephalus ursinus*). Ethology 109:627–644

Sparks J (1967) Allogrooming in Primates: a Review. In: Morris D (ed) Primate Ethology, London, pp 148-175

Stanford C (1992) The costs and benefits of allomothering in wild capped langurs (Presbytis pileata). Behav Ecol Sociobiol 30:29-34

Thierry B (1990) Feedback loop between kinship and dominance: the macaque model. J Theor Biol 145:511–521

Tiddi B, Aureli F, Schino G (2010) Grooming for infant handling in tufted capuchin monkeys: a reappraisal of the primate infant market. Anim Behav 79(5):1115-1123

Vogel C (1984) Patterns of infant transfer within two groups of common langurs (*Presbytis entellus*) near Jodphur: testing hypotheses concerning the benefits and risks. In: Roonwal ML, Mohnot SM, Rathore NS (ed), Current Primate Researches, Jodphur University Press, Jodphur, pp 361–379

Wei W, Qi X, Garber PA, Guo S, Zhang P, Li B (2013) Supply and Demand Determine the Market Value of Access to Infants in the Golden Snub-Nosed Monkey (*Rhinopithecus roxellana*). PLoS ONE 8(6):e65962

Xi W, Li B, Zhao D, Jo W, Zhang P (2008) Benefits to female helpers in wild *Rhinopithecus roxellana*. Int J Primatol 29:593-600

Yu Y, Xiang Z-F, Yao H, Grueter CC, Li M (2013) Female Snub-Nosed Monkeys Exchange Grooming for Sex and Infant Handling. PLoS ONE 8(9):e74822

# CHAPTER IV.

## Whom to Groom and for What? Patterns of Grooming in Female Barbary Macaques *(Macaca sylvanus)*.

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RESEARCH ARTICLE

# Whom to Groom and for What? Patterns of Grooming in Female Barbary Macaques (*Macaca sylvanus*)

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## Abstract

Grooming is one of the most conspicuous social interactions among nonhuman primates. The selection of grooming partners can provide important clues about factors relevant for the distribution of grooming within a social group. We analyzed grooming behavior among 17 semi-free ranging female Barbary macaques (*Macaca sylvanus*). We tested whether grooming is related to kinship, rank and friendship. Furthermore, we tested whether grooming is reciprocated or exchanged for rank related benefits (i.e. lower aggression and increased tolerance whilst feeding). We found that in general grooming was reciprocally exchanged, directed up the hierarchy and at the same time affected by friendship and kinship. Grooming was more frequent among individuals with higher friendship values as well as amongst related individuals. We also divided our data set on the basis of rank difference and tested if different power asymmetries between individuals affected the tendency to exchange grooming for rank related benefits and grooming reciprocation. In support of our initial hypothesis our results show that the reciprocation of grooming was a significant predictor of grooming interactions between individuals of similar rank, but not between those individuals more distantly separated in the social hierarchy. However, we did not find any evidence for grooming being exchanged for rank related benefits in either data set. Our results, together with previously published studies, illustrate the behavioral flexibility of macaques. It is clear that multiple studies of the same species are necessary to gather the data required for the solid comparative studies needed to shed light on patterns of grooming behavior in primates.

## Introduction

Grooming behavior involves the careful inspection and subsequent cleaning of other individuals' fur and may occupy up to 20% of the daily time budget in non-human primates [1]. Moreover grooming is not compromised in the face of other demands that may appear more

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important (e.g. increased foraging) [1], which suggests that it is of significant importance for the individuals involved. Unsurprisingly, grooming has been recognized as a fundamental aspect of primate sociality.

Traditionally grooming has been considered to be an altruistic behavior that is costly to the groomer (e.g. lost time and energy) and beneficial to the recipient (e.g. parasite removal or stress reduction) [1]. The time and energy devoted to grooming could otherwise be devoted to foraging, vigilance or finding a mate. Therefore individuals are expected to select a groomee who will be worth investing in, who may reciprocate the service and/or provide alternative benefits. Several theories have been suggested to explain the observed patterns of grooming in primates. For example, an explanation based on kin selection theory [2] would predict that there is selection for individuals to groom their own kin in preference to non-relatives in order to increase their own indirect fitness. Relatives benefit from reciprocal grooming exchange or the exchange of other benefits as well as non-relatives. However, the potential cost of non-reciprocation is lower to the groomer when the recipient is related. Although it has been shown that kinship has an effect on the grooming distribution within groups of primates, it is obviously not the only factor determining this behavior [3]. An alternative explanation is based on reciprocal altruism [4] and predicts that a groomer will favor a partner who is likely to reciprocate the investment. Reciprocal altruism is predicted to result in patterns of grooming reciprocation among individuals, with grooming being exchanged reciprocally. The concept of exchange has been broadened by biological market theory [5], which allows individuals to trade grooming not only reciprocally but also for other benefits. Some of these benefits can be provided mainly by high ranking individuals (e.g., tolerance around food or lower aggression) and thus exchange for these rank related benefits may explain the common pattern of grooming up the social hierarchy [1,6].

Strong positive social relationships (sometimes referred to as “friendship” or “high relationship quality” [7,8]) have been discussed as an important factor in explaining patterns of interactions in primate social groups [8–12]. Cords and Aureli [12] introduced a complex approach designed to measure social relationships. These authors defined three components relating to the quality of the relationship between individuals: value, security and compatibility. Only recently has this theoretical proposal been tested empirically, although it remains for such tests to be carried out using a standardized approach. In this study we adopted the concept of friendship defined as a way how to differentiate the strength of social interactions based on positive interactions [8]. Although the two terms (friendship and relationship quality) are related, and have sometimes been used interchangeably, friendship is defined more loosely and its measurement is usually based on one or a few behaviors [7,8].

Silk et al. [11] suggested that social bonds play a vital role in females’ lives, and the ability to establish and maintain strong social bonds (e.g., through grooming) may have important fitness consequences for baboon females. Despite recognizing the importance of grooming only a limited number of studies have tested the effect of social bonds on other behaviors empirically. One exception to this is the field of reconciliation, where a number of studies have reported a positive correlation between friendship or relationship quality and the probability of post conflict reconciliation (see e.g., [7,12,13]). However, it is obvious that primates living in social groups do not interact in the same way with all group-mates. Furthermore, the probability of a given behavioral interaction (e.g., grooming) occurring between two individuals is strongly influenced by the characteristics of each partner and the quality of their mutual relationship [8,11,13,14]. For example, individuals spend more time grooming their favorite partner in comparison to less favored ones (for review see [1]). It is also predicted that a generally high level of social tolerance in a particular group or species may decrease the need for subordinate females to achieve tolerant relationships via grooming-tolerance exchanges with dominant females [1]. As such the grooming partners chosen by females may be selected according to friendship rather than social rank. The tendency for individuals to select grooming partners with which they had good social relationships has been found in several macaque species (*Macaca assamensis* [13], *M. arctoides* [7]). This trend is expected to be more common in species with a more tolerant social style (see below) [15]. Barbary macaques are considered to be tolerant and as such we expect that friendship will play an important role in partner selection for grooming interactions.

Patterns of grooming interactions and their driving factors are not expected to be the same across different species of primates. Several characteristics of social hierarchy, particularly dominance steepness, vary among species and may have important consequences for grooming interactions [1]. Dominance steepness represents a measure of power difference between adjacently ranked individuals and it has been used to characterize species of macaques along a despotic-tolerant gradient [16]. In groups of despotic species (e.g. rhesus macaques) with steeper dominance hierarchies individuals are expected to exchange grooming for rank related benefits more often than individuals in groups of tolerant species (e.g., Barbary macaques) [1]. In tolerant species it is possible that the power differential among individuals is so low that grooming reciprocation among individuals will prevail over the exchange of other commodities. Interactions among individuals from despotic species should also be more dependent on rank and kinship than those of more tolerant species, where friendship among group mates may be more than or equally as important as rank and kinship [16]. Moreover, even within a single species, the exchange of grooming for rank related benefits is expected to be more frequent between individuals with higher rank difference than between individuals closer in rank, who will be more likely to groom reciprocally [1]. A number of problems make testing this prediction difficult, resulting in a paucity of relevant studies. Firstly, we still do not have relevant data for all species of interest, although the number of species on which data is available is slowly increasing. Second, for most species we have to rely on data from a single group. This is especially troubling for primates as this order is known for its wide behavioral flexibility, often related to ecological and social conditions [17]. These conditions may results in different levels of competition, which in turn influence the steepness of dominance hierarchies and therefore grooming

**Table 1. List of behaviors and their definitions used for analyses.**

| | **Behaviors recorded using focal continuous sampling** |
|---|---|
| Approach | An animal comes into proximity of one or more individuals, stays in proximity for at least 5 sec. and the approach is not motivated by another obvious reason such as food. |
| Displacement | One animal in any way drives away another from some kind of resource (place, shadow, food, partner) and then stays in place, the displacing individual may or may not use the resource. |
| Groom | An animal grooms the hair of another; it watches the groomed spot on the other's body. It may, use its fingers or mouth to pick up some particles. The identity of groomer and groomee as well as the duration of the grooming episode was recorded. |
| Aggression | This category included all aggressive interactions between given individuals e.g., silent threat, hand threat, chase, attack and bite. |
| Behaviors recorded using instantaneous sampling | |
| Contact | Two or more animals are touching with any part of the body. Not engaged in any other defined behavior such as an embrace or grooming etc. |
| Proximity | Two or more animals are within a stretched arm's length of each other but are not in physical contact. |
| Co-provisioning | Two animals simultaneously use one food source. They may be in physical contact or proximity. |

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patterns, similarly group size and adult sex ratio have also been shown to affect grooming patterns [17,18].

Macaques are a suitable group for testing the predictions of inter- and intra-species variation in grooming patterns. The number of species studied has been growing and for some species (e.g., Japanese macaques, *Macaca fuscata*) data from different groups and populations are available. This well-studied species is highly variable with regards to social behavior, and serves as a reminder that data from several groups per species is important for detailed comparative studies (Table 1 in [17,19]). Despite the importance of replication for behavioral studies, the data used in most meta-analyses [3,17,20,21] are derived from only one or two groups per species. This is even more conspicuous when considering socially tolerant species which are less well studied in comparison to their despotic relatives. Therefore, from a comparative perspective it is important not only when studying different species but also different populations within each species. Only a rich and diverse database of studies enables robust tests of the proposed hypotheses.

Grooming in Barbary macaques has been studied from various perspectives [22–25]. In this study we investigated the pattern of grooming in semi-free-ranging female Barbary macaques living in one social group. We investigated the main predictors of grooming interactions on the level of dyads, including: i) characteristics of the pair (kinship, relative rank, friendship), ii) previously proposed exchange commodities such as grooming received and, iii) potential rank-related benefits (lower aggression received and higher tolerance during co-feeding). Moreover, we tested whether grooming interactions among females close in rank showed a different pattern and relationship with the proposed predictors than grooming interactions among females more distant in rank. This study is the first to test the hypothesis that pair based characteristics and exchange commodities in Barbary macaques may have different effect on grooming interactions according to the difference in rank between grooming partners.

## Methods

### Ethical statement

This study was fully observational and non-invasive and adhered to the legal requirements of Gibraltar. Approval to conduct the study was granted by the Animal Care Appointee of the Gibraltar Ornithological and Natural History Society (GOHNS) (no permission IDs were given).

### Study subjects

The study was conducted in the Apes' Den troop of Barbary macaques living in the Apes' Den in the Upper Rock Natural Reserve, Gibraltar. This group is semi-free ranging, provisioned daily by the Gibraltar Ornithological and Natural History Society (GONHS), and visited by tourists. The study included all 17 adult females (age $\geq$ 3 years) present in the troop at the beginning of the study (age of females ranged from 3 to 26 years; mean 11.2 years, age data provided by GONHS). The troop also included six adult males and up to 15 juveniles and infants. Three new immigrant males (two sub-adult and one young adult male) joined the troop in the second part of the study. All adult subjects were individually recognized and well-habituated to the presence of human observers (for more details on study site and subjects see [26]). Maternal kin relationships were obtained from the GONHS database. The kinship data were included in the analyses as kin (mother-daughter and sister-sister dyads) and non-kin.

## Behavioral data collection

Behavioral observations were collected during two study periods that overlapped with two mating seasons: between November 2007 and February 2008 referred to hereafter as season 1 and between October 2008 and February 2009, referred to hereafter as season 2. Females were observed using two methods of data collection at the same time: focal continuous sampling (30min focal period) and focal instantaneous sampling [27] (focusing on the same individual at 2 min intervals). Behaviors were recorded according to an ethogram that consisted over 50 items, this ethogram was prepared on the basis of previous studies in non-human primates [28,29]. Behaviors analyzed in this study are listed in Table 1 together with the data collection methods. Data collection was distributed equally for each individual both throughout the day (from 8:00 to 18:00) as well as throughout the entire study. Females were observed once in a given day at most (and on average 2.1 (SD ±0.05) and 1.6 (SD ±0.08) times per week in season 1 and season 2 respectively). Behavioral observations were made by two observers (MK and VR) who were trained in data collection and the use of the behavioral ethogram in advance of data collection. The reliability of simultaneous observations of a given individual by the two observers reached 93% before the beginning of the data collection. For all of the following analyses only interactions among females were analyzed. For the grooming behavior the start and end time, direction of the interaction and identity of the social partner were recorded. The grooming act was considered terminated if it stopped for $\geq$20s.

## Dominance hierarchy

The social dominance hierarchy among 17 females was assessed on the basis of dyadic displacement interactions between pairs of observed individuals. Displacement interactions have been used to assess dominance hierarchy in wide range of species (elephants [30]; fowl [31]; macaques [32]) and are based on the clear observed acceptance of a subordinate position by the displaced individual (which is not always the case in aggressive interactions) [33]. The displacement interactions were entered into two sociometric matrices, separated by season. The linearity of the dominance hierarchy was assessed by the linearity index h′ in MatMan 1.1.4 (Noldus 2003) [34]. Subjects were subsequently ranked based on their normalized David's score (NDS) [35,36] computed on the basis of the Dyadic Dominance Index corrected for chance (Dij) [37]. The NDS is a method of ranking individuals that also takes the relative strengths of the opponents into account and serves as a basis for computing the hierarchical steepness measured as the absolute values of regression slopes in plots between NDS and the order of individuals [35].

## Friendship measurement

Several measures of social relationship strength or friendship based on different behavioral characteristics and spatial proximity measures have been used in previous studies including grooming [11], approach interactions [13], mutual contact [7], or mutual contact and proximity [8]. Given that grooming was our behavior of interest we cannot use the measurement of friendship based on grooming data for our analysis. First we computed 4 different friendship measurements for each dyad based on four behaviors: time spent in body contact, time spent in proximity (within 2m), approaches and grooming. All 4 were positively correlated (see Table S5 Table and S6 Table). Body contact represents more intimate spatial relationship then proximity and is less time dependent on grooming behavior then approach (in other words an approach always has to occur before grooming can be performed but the two individuals do not have to be in body contact before and/or after grooming). We therefore chose to assess the friendship on the basis of the time females spent in mutual body contact (see Table 1 for definition) as it was also used in previous studies [7,8]. The friendship that individual A has with individual B was computed as the amount of time individual A spends in contact with individual B divided by the average amount of time individual A spends in contact with all other females. This resulted in an asymmetrical description of the relationship within a given dyad as the relationship that A has with B does not have to be equal to that of B to A. We favor this friendship assessment because it has been shown that asymmetry is an important predictor in social interactions [9]. The matrix of friendship values is provided in S8 Table and S9 Table.

## Data analysis

Linear mixed effect models (LMM) were used to test the effect of kinship, rank and friendship on grooming interactions. Grooming was represented by two measurements: grooming rate (the sum of grooming acts when A grooms B divided by the total time of observation of the two individuals) and grooming time (the sum of grooming time when A grooms B divided by the total time of observation of the two individuals). These two variables were positively correlated in our study (Spearman, season1 $r = 0.89$, $p<0.001$, season2 $r = 0.83$, $p<0.001$, $N = 17$), however some previous studies have shown different results for grooming rate and time, thus we computed models for both. The grooming data were log transformed to increase the homogeneity of their variances. The dataset for each model comprised two lines per dyad (i.e., A-B and B-A) and in total included 272 lines for each season. All the LMMs analyses were run in **R 3.0.2** (R Core Team, 2013) using the lme4 package [38]. When presenting model results, we show the estimated effect sizes (regression coefficient estimates) and their 95% confidence intervals. In this way, we can falsify null hypotheses (typically rejecting them at $\alpha = 0.05$ when a confidence interval does not cover a zero value), and we also obtain biologically more interesting information about the size of each effect, finally we can also quantify the reliability of such an effect size estimate [39]. Given the fact that the response variables were log-transformed, we can quantitatively interpret the estimated effect sizes ($b_i$) by saying that the expected response variable value increases $exp(b_i)$-times (if the resulting value is $< 1$, then the change represents decrease) when the predictor value increases by one unit. In the case of categorical predictors (which all had only two states in our data set), $exp(b_i)$ shows how many times larger the mean response value for the particular predictor state is than the mean of observations for the other (reference) state. This interpretation using the exponential function can also be applied to the end points of the estimated confidence intervals.

The models tested the effects of the following variables on initiated grooming rate or grooming time. **Rank**—represented the dominance relationship of the groomer relative to the groomee coded as two states: dominant and subordinate. **Rank distance**—represented by the absolute value of the rank distance between the groomer and groomee (based on the David`s score). **Kinship**—represented the maternal kin relationship between the groomer and groomee coded as two states: kin and non-kin. **Friendship**—measured as the time spent in contact by a given pair of individuals relative to average time spent in contact with other group members, entered as a continuous variable. **Co-provisioning**—measured as the percentage of time spent by individuals in a given dyad using one food source. **Grooming received**—grooming rate or time received by the groomer from a given groomee. **Aggression received**—rate of aggression received by a groomer from a given groomee. **Season**—coded as two states: season 1 and season 2, corresponding to the two study periods. **Age difference**—the absolute value of age difference between the groomer and the groomee. This last variable was added to control for dyad similarity based on age. The identities of the groomer and groomee were used as crossed random factors in the models.

In order to assess the differences in grooming patterns of individuals closer in rank compared to those of individuals that were distant in rank, we divided our data into two subsets based on rank distance: a) a dataset with grooming interactions among females who have higher rank distance than the total sample average rank distance and b) a dataset with grooming interaction among females who have smaller than average rank distance. Again we tested the effect of the same variables on grooming rate and grooming time. This yielded four additional models. For each model we checked homoscedasticity and distribution of residuals using regression diagnostic plots. The significance of all our models was assessed by comparison with corresponding null models.

## Results

### Grooming behavior

We collected a mean of 15.5 (±0.27 SD) hours of focal observation data per female in season 1 and 13.6 (±0.65 SD) hours per female in season 2. We recorded 1,362 grooming interactions among females (842 in season 1 and 520 in season 2). Females were involved in an average of 0.17 (±0.48 SD) grooming interactions per hour and for an average of 0.79 (±1.74 SD) minutes per hour. The number of grooming interactions per female ranged from 69 to 298 with an average of 160.2 interactions. Data provided in S1, S2, S3 and S4 Tables.

### Dominance hierarchy

The resulting dominance hierarchies were based on 495 (with 21 unknown dyads) and 395 (with 35 unknown dyads) interactions in season 1 and season 2 respectively. The dominance hierarchies were significantly linear (season 1: $h' = 0.78$, $p < 0.001$; season 2: $h' = 0.63$, $p < 0.001$) and the direction of interactions was highly consistent with the resulting rank order (directional consistency index [40] in season 1 DCI = 0.97; in season 2 DCI = 0.99). No rank changes were identified within each season, but there were several changes in rank order of particular individuals (by up to three positions) between the two seasons. The values of the hierarchical steepness gradient were 0.50 in season 1 and 0.40 in season 2. Both linearity and steepness values are comparable with a previous study of a different group of Barbary macaques; $h' = 0.60$, steepness = 0.48 [22].

### Grooming pattern (results of LMMs)

**Grooming distribution among all females.** Grooming rates were significantly related to kinship, relative rank, friendship, grooming received and aggression received (Table 2).

Females groomed their kin more often than non-kin. The model predicted that in the absence of maternal kinship between the grooming partners the grooming rate is 1% to 71% lower when compared to grooming among maternal kin dyads. Females directed grooming up the hierarchy (i.e., most often the groomers were of lower dominance rank than groomees). The model predicted that when a groomer is subordinate to a groomee the rate of grooming is 16% to 184% higher than when the groomer is dominant to the groomee. Friendship was also a significant predictor of grooming and females groomed their higher quality partners more often than low quality social partners. The model predicted that an increase of 1 in the friendship value will lead to an increase in grooming rate of 37% to 64%.

The results also show that females exchange grooming for grooming with their partners as they more often groom females who groomed them back. The model predicted that an increase of 0.1 in grooming rate received is related to an increase of 5% to 22% in grooming rate initiated. Aggression received was also related to grooming rate although, contradictory to our hypotheses, this was in a positive direction, in other words those groomers who initiated more

Table 2. Results of LMMs testing grooming rate and grooming time and their relationship to kinship, rank distance, relative rank, friendship, grooming received, co-provisioning, aggression received and season.

| | Grooming rate | | | | Grooming time | | | |
|---|---|---|---|---|---|---|---|---|
| Fixed effects | Estimate | SE | 95% confidence interval | | Estimate | SE | 95% confidence interval | |
| Age difference | 0.002 | 0.014 | -0.026 | 0.030 | 0.004 | 0.019 | -0.034 | 0.040 |
| Kinship (no) | **-0.608** | **0.306** | **-1.222** | **-0.012** | -0.645 | 0.402 | -1.451 | 0.140 |
| Rank distance | -0.073 | 0.048 | -0.167 | 0.026 | -0.102 | 0.064 | -0.226 | 0.028 |
| Relative rank (s) | **0.587** | **0.214** | **0.148** | **1.045** | **0.929** | **0.292** | **0.330** | **1.554** |
| Friendship | **0.405** | **0.045** | **0.317** | **0.493** | **0.531** | **0.056** | **0.421** | **0.640** |
| Groom received | **1.229** | **0.038** | **0.496** | **1.959** | 0.159 | 0.115 | -0.063 | 0.383 |
| Co-provisioning | 0.140 | 0.141 | -0.134 | 0.415 | 0.213 | 0.187 | -0.149 | 0.577 |
| Aggression received | **2.156** | **0.488** | **1.210** | **3.117** | **2.775** | **0.644** | **1.520** | **4.041** |
| Season (2) | **-0.363** | **0.152** | **-0.658** | **-0.063** | **-0.686** | **0.203** | **-1.079** | **-0.289** |

Variables with values in bold had significant effect on grooming rate or grooming time based on CI.

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grooming received more aggression from that given partner. The model predicted that an increase of 0.1 in aggression is related to an increase from 13% up to 37% in grooming rate.

The season had also a significant effect on grooming, with females grooming less often during the second season. Neither relative rank distance among grooming partners nor time spent co-provisioning were related to grooming distribution in this or any of the following models.

The results were slightly different for the model based on grooming time (Table 2). Kinship was not a significant predictor and females did not groom their relatives for a longer time than their non-relatives. The amount of grooming received was also not a significant predictor in this model suggesting that the exchange of grooming among females is mainly based on frequency and not time. Relative rank, friendship and aggression received were significant predictors of the grooming time pattern. Thus females groom longer a) partners dominant to

Table 3. Results of LMMs testing grooming rate and grooming time and their relationship to kinship, rank distance, relative rank, friendship, grooming received, co-provisioning, aggression received and season among females with low rank distance.

| | Grooming rate | | | | Grooming time | | | |
|---|---|---|---|---|---|---|---|---|
| Fixed effects | Estimate | SE | 95% confidence interval | | Estimate | SE | 95% confidence interval | |
| Age difference | -0.002 | 0.020 | -0.040 | 0.035 | -0.003 | 0.025 | -0.052 | 0.046 |
| Kinship (no) | -0.446 | 0.350 | -1.159 | 0.227 | -0.532 | 0.452 | -1.453 | 0.343 |
| Rank distance | -0.031 | 0.146 | -0.318 | 0.252 | -0.042 | 0.188 | -0.413 | 0.322 |
| Relative rank (s) | 0.423 | 0.243 | -0.043 | 0.892 | **0.766** | **0.317** | **0.159** | **1.381** |
| Friendship | **0.397** | **0.055** | **0.291** | **0.503** | **0.503** | **0.066** | **0.374** | **0.631** |
| Groom received | **1.243** | **0.417** | **0.429** | **2.052** | 0.211 | 0.136 | -0.052 | 0.478 |
| Co-provisioning | 0.094 | 0.163 | -0.220 | 0.408 | 0.158 | 0.212 | -0.253 | 0.567 |
| Aggression received | **2.283** | **0.576** | **1.161** | **3.450** | **2.888** | **0.744** | **1.426** | **4.410** |
| Season (2) | -0.233 | 0.219 | -0.655 | 0.194 | -0.504 | 0.286 | -1.058 | 0.053 |

Variables with values in bold had significant effect on grooming rate or grooming time based on CI.

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themselves, b) partners with which they have a better relationship and c) partners who target them with aggression.

**Comparison of grooming distribution among females close in rank and distant in rank.** Results of the LMMs based on the two separate data sets showed that grooming received was a significant predictor in grooming among females close in rank but not in grooming among females distant in rank. Females close in rank thus exchanged grooming reciprocally and females distant in rank did not (Table 3, Table 4). This was the case for grooming rate models but not for grooming time models (Table 3, Table 4). Moreover the aggression received by an individual was related to grooming distribution (both rate and time) among females close in rank but not among females distant in rank. Kinship was a significant predictor in grooming interactions among females distant in rank but not among females close in rank, although the direction of the relationship was similar. Relative rank was also a significant predictor in most of the models, thus females close as well distant in rank usually groomed females dominant to themselves more often and for longer periods of time. Finally friendship was also a significant predictor of grooming rate and grooming time in both datasets. Thus females close as well as distant in rank groomed more often and for longer time their friends. Our results thus suggest that grooming interactions among females close in rank and females distant in rank are not always affected by our predictor variables in the same way.

## Discussion

Our study determines the effects of three main factors on grooming interactions in female Barbary macaques, namely kinship, relative rank, and friendship. It also shows that the main reward for grooming is reciprocation, but no evidence was found for exchange of rank-related benefits (i.e. lower aggression and higher tolerance while feeding). In addition to these general patterns, we detected differences between pairs of individuals that were particularly close or distant in rank.

Of the factors studied here the effect of kinship and rank on grooming behavior has already been demonstrated (for reviews see [3,10,20,21]). However, the significance of kinship and rank in respect to other factors and social structure is not clear. For example, in their recent meta-analysis, Schino & Aureli [3] conclude that although kinship plays some role in grooming interactions among primates its importance is much lower than previously thought, particularly in relation to grooming reciprocation. Our data are compatible with this conclusion: the effect sizes suggested that although kinship is a significant predictor of grooming in some cases it was not an overriding factor in our models. A more complex scenario for rank-dependent effect has been suggested by Thierry [15]. This scenario suggests that the effect of dominance rank and kinship on social interactions should be of limited importance, perhaps negligible, in species with a tolerant social style (e.g. Sulawesi macaques), compared to those with a more despotic style (e.g. rhesus macaques). However, our results, as well as several previous studies, demonstrate that the effects of kinship (*M. sylvanus*, [22]) and/or rank (*M. thibetana*, [41]) is nevertheless recognizable and significant even in tolerant macaque species. This suggests that the behavioral patterns along the tolerance-despotism species range should indeed be seen as a continuum with inter-species overlaps rather than entirely distinct modes [15].

The third factor, friendship, was previously demonstrated to influence positive social interactions e.g. reconciliation [13] and this was confirmed by our analyses. Under this scheme females groom other females with whom they had a better relationship more frequently and for longer time periods. Although well-known and acknowledged, this factor has rarely been tested in one model together with the other factors, such as kinship and rank, to show its effect on

**Table 4. Results of LMMs testing grooming rate and grooming time and their relationship to kinship, rank distance, relative rank, friendship, grooming received, co-provisioning, aggression received and season among females with high rank distance.**

| | Grooming rate | | | | Grooming time | | | |
|---|---|---|---|---|---|---|---|---|
| **Fixed effects** | **Estimate** | **SE** | **95% confidence interval** | | **Estimate** | **SE** | **95% confidence interval** | |
| Age difference | -0.023 | 0.018 | -0.058 | 0.013 | -0.023 | 0.026 | -0.072 | 0.027 |
| Kinship (no) | **-2.105** | **0.790** | **-3.614** | **-0.571** | **-2.824** | **1.002** | **-4.743** | **-0.885** |
| Rank distance | -0.067 | 0.096 | -0.251 | 0.117 | -0.136 | 0.136 | -0.394 | 0.122 |
| Relative rank (s) | **1.485** | **0.352** | **0.807** | **2.155** | **2.097** | **0.519** | **1.107** | **3.077** |
| Friendship | **0.359** | **0.092** | **0.183** | **0.543** | **0.549** | **0.118** | **0.314** | **0.781** |
| Groom received | 3.567 | 1.864 | -0.049 | 7.159 | 0.099 | 0.233 | -0.353 | 0.546 |
| Co-provisioning | 0.544 | 0.334 | -0.106 | 1.186 | 0.819 | 0.443 | -0.045 | 1.668 |
| Aggression received | 1.800 | 1.093 | -0.290 | 3.921 | 2.342 | 1.498 | -0.516 | 5.309 |
| Season (2) | **-0.454** | **0.212** | **-0.865** | **-0.044** | **-0.858** | **0.289** | **-1.416** | **-0.301** |

Variables with values in bold had significant effect on grooming rate or grooming time based on CI.

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grooming patterns. Our design proves that even after including the effect of rank and kinship, friendship remains a significant behavioral factor affecting the grooming distribution.

## Absence of rank related benefits

As mentioned above the significant relationship between grooming and rank was not surprising. The tendency of females to prefer a dominant grooming partner is usually explained by social market theory, where low ranking females have more to gain from high ranking individuals than vice versa [1,6]. As has been previously proposed and tested, subordinate females may exchange grooming for agonistic support from dominant individuals [21], their tolerance [1], or for access to desirable or scarce resources [42]. We did not find any potentially rank related benefits included in our models (decreased aggression received and higher tolerance during co-provisioning) to be related to grooming patterns. While slightly surprising, these results correspond to several studies reporting a lower tendency to exchange grooming for rank related benefits in other macaque species [42–45]. A possible theoretical background for such an observation may be provided by the prediction of Henzi and Barret [1]. They proposed that the pattern of grooming interactions is affected by the power differential between individuals, where a lower steepness of dominance hierarchy may lead to a lower demand for rank related benefits. In such a case, grooming would be exchanged for grooming, rather than for any other benefits. Based on their recent study of Assamese macaques (*Macaca assamensis*), Macdonald and colleagues [45] also suggested that in the absence of competition there is no need to exchange rank related benefits among females. However, this explanation does not seem to fit our observations. The group under study was provisioned by local management with food in a single small patch that could be monopolized by several individuals. We thus expect the motivation of subordinates to exchange their grooming for tolerance while using this food resource to be high. Considering the condition of our study group, (i.e., high levels of stress due to tourism and unavoidable contact with human visitors), stress factors may provide an alternative explanation for the lack of exchange for rank related benefits. Balasubramaniam et al. [46] showed that stressful conditions may lead to a more intensive demand for grooming per se than to agonistic support or other potential rank related benefits. This view is based on the perception of grooming as a stress-reducing and relaxing mechanism [47,48]. We therefore suppose that stress factors (including the clumped provisioning of food) may have led to a higher demand for grooming interactions as a positive stress-reducing behavior.

Environmental conditions together with the more tolerant social system of Barbary macaques might explain the absence of exchange for potential rank related benefits. If this was the case we would also expect infrequent grooming up the hierarchy, but this remains present among females in our focal group. Moreover, exchange for rank related benefits has recently been documented in another study of Barbary macaques [22], although surprisingly this study did not find an effect of rank on grooming interactions. One possible explanation is that there are other rank related benefits that were not included in our model. One of such benefit is agonistic support. The incidence of agonistic support was very rare in our study group and thus impossible to analyze (only 29 instances in two seasons, and 52% of them were among the members of the largest matriline). However the significant relationship between grooming and agonistic support in general has been hard to find in previous studies [1] and as concluded by Shino [21] the relationship is rather weak, and given publication bias, probably overestimated.

We suggest that another relevant rank related benefit may be access to mates. Although competition among females for mates has been usually overlooked [49] it can represent a potentially important factor in a) Barbary macaques in general, as they breed seasonally and have partly synchronized ovulatory cycles [50], and in b) our study group in particular where adult sex ratio was skewed (1M:2.8F). Thus females may compete for access to males to gain mates. This can be motivated by the possibility of sperm depletion or by limitation of future resource competition, both factors previously reported for primates (reviewed in [49]). However, tolerance during mating was not tested in our models. Further studies comparing data from mating and non-mating seasons in the same group may shed more light on the role of mating competition on grooming interactions among females, and help to investigate the role of tolerance while mating as another potential rank related benefit for females.

## Relationship between aggression and grooming

An interesting and contradictory result of our study is the positive relationship between aggression received and grooming given. While lower aggression has been considered as one of the potential benefits to be gained via grooming interactions [51], in our study group females received more aggression from females whom they groomed more. For Barbary macaques this phenomenon is not atypical since it has been recently reported elsewhere [22,25]. The explanations suggested by these studies include grooming being used to appease aggressive individuals and its use in post-conflict reconciliation. Such situations might represent an opportunity for a former aggressor to coerce a victim by demanding grooming, with subordinates being more prone to succumb to such behavior when the power difference is high [25]. However our data did not provide much support for either of these views. In our focal group aggression was positively related to grooming only in dyads close in rank, but not in the dyads distant in rank. This observation is difficult to reconcile with the suggestion that higher rank distance should actually result in a situation where subordinates are highly motivated to appease or succumb to coercion, a pattern contradictory to our observations. It has also been suggested that the levels of aggression will be even higher without grooming and that individuals do in fact exchange grooming for reduced aggression [22]. However, this idea can only be tested using detailed behavioral time-sequence analysis or an experimental setup. Moreover our result showing that grooming is generally reciprocated also, in our opinion, does not fit with these explanations, e.g., if there is a motivation on the side of the aggressor to coerce a subordinate individual via aggression to grooming, we would not expect that he/she would also reciprocally groom the former victim. While these causal relationships are difficult to test we suggest an alternative and simpler hypothesis. We suppose that the higher incidence of grooming and aggression might be explained simply by the spatial and temporal associations of individuals, which determines the probability of interactions among individuals. In other words, this conclusion is based on the observation that individuals spending more time together grooming each other also have a higher probability of getting into a conflict. Furthermore, spending more time in close association is more typical for individuals close in rank compared to those distant in rank. Thus our results for the two data sets fit this explanation well.

### Grooming rate vs. grooming time

In our data we found several differences in models based on grooming rate compared to those based on grooming time. These differences suggest that individuals reciprocate grooming more on the basis of rate rather than time. In other words, individuals in a given dyad groom each other at the same rate but not necessarily for the same duration of time. This finding is unfortunately difficult to compare to other studies, as they usually use either time or rate as an exclusive parameter in their analyses (but see [41]) or do not discuss the differences. We may hypothesize that individuals can control or track the rate of interactions (make decisions on whether to approach a given individual or not) better than the duration of interaction. Moreover, the duration can also be influenced by other factors such as the decision by the groomee or actions of other individuals (e.g., fights, alarm calls etc.). We also assume that tracking time investment is more cognitively demanding then keeping track of frequency. However, regardless of the real causes for these differences, the usage of either frequencies or time of grooming may be another source of variation between studies, and measurements should therefore be well defined in such behavioral studies.

Finally it should be noted that statistical analysis of grooming data involves several limitations and potential issues of the reliability of the fitted models. First, the grooming interactions are not evenly distributed across all group members and thus the resulting dataset includes many zeroes. This is a natural consequence of the fact that individuals groom others selectively and thus some dyads groom each other more often than others and some do not engage in grooming at all. Second, some combinations of predictors included in our model are rare or even non-existent e.g., females distant in rank are more often unrelated than related. This again is an inevitable consequence of the nepotistic hierarchies and matriline system of macaques. These data characteristics may limit the power and possibly even the reliability of the tests but are also impossible to avoid.

## Conclusions

Our study tested the hypothesis that grooming is exchanged for different commodities in relation to rank difference among tolerant Barbary macaque females. We found that individuals in general, and specifically those close in rank, mainly exchange grooming reciprocally. Our results thus support the hypothesis that in tolerant species reciprocal grooming will prevail over exchange of grooming for rank related benefits. However, females still directed grooming up the hierarchy and thus further studies are needed to reveal if other rank-related benefits can explain this pattern. We also suggest that the relationship between aggression and grooming is more complex than previously thought. The prediction that grooming serves to reduce the aggression received from ones grooming partner has not been supported in Barbary macaques.

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## Supporting Information

**S1 Table. Grooming rate (per hour of observation) in season 1.**
(XLS)

**S2 Table. Grooming rate (per hour of observation) in season 2.**
(XLS)

**S3 Table. Grooming time (minutes per hour of observation) in season 1.**
(XLS)

**S4 Table. Grooming time (minutes per hour of observation) in season 2.**
(XLS)

**S5 Table. Correlations among friendship measurements based on contact, proximity, approach and grooming (season 1).**
(XLS)

**S6 Table. Correlations among friendship measurements based on contact, proximity, approach and grooming (season 2).**
(XLS)

**S7 Table. Friendship matrix based on time spent in contact (data season 1).**
(XLS)

**S8 Table. Friendship matrix based on time spent in contact (data season 2).**
(XLS)

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## Author Contributions

Conceived and designed the experiments: VR MK BW. Performed the experiments: VR MK. Analyzed the data: VR MK PS. Contributed reagents/materials/analysis tools: PS BW. Wrote the paper: VR MK PS BW.

## References

1. Henzi SP, Barrett L (1999) The value of grooming to female primates. Primates 40: 47–59. doi: 10.1007/BF02557701 PMID: 23179531
2. Hamilton W (1964) The genetical evolution of social behaviour, I & II. J Theor Biol 7: 1–52. PMID: 5875341
3. Schino G, Aureli F (2010) The relative roles of kinship and reciprocity in explaining primate altruism. Ecol Lett 13: 45–50. doi: 10.1111/j.1461-0248.2009.01396.x PMID: 19840082
4. Trivers R (1971) Evolution of reciprocal altruism. Q Rev Biol 46: 35–57.
5. Noë R, Hammerstain P (1995) Biological markets. Trends Ecol Evol 10: 336–339. PMID: 21237061
6. Seyfarth RM (1977) A model of social grooming among adult female monkeys. J Theor Biol 65: 671–698. PMID: 406485
7. Call J, Aureli F, de Waal FB (1999) Reconciliation patterns among stumptailed macaques: a multivariate approach. Anim Behav 58: 165–172. PMID: 10413553
8. Cords M (2002) Friendship among adult female Blue monkeys (*Cercopithecis mitis*). Behaviour 139: 291–314.

9. McFarland R, Majolo B (2011) Exploring the components, asymmetry and distribution of relationship quality in wild Barbary macaques (*Macaca sylvanus*). PLoS One 6: e28826. doi: 10.1371/journal.pone.0028826 PMID: 22194923
10. Schino G, Aureli F (2008) Grooming reciprocation among female primates: a meta-analysis. Biol Lett 4: 9–11. PMID: 17999942
11. Silk J, Altmann J, Alberts S (2006) Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. Behav Ecol Sociobiol 61: 183–195.
12. Cords M, Aureli F (2000) Reconciliation and relationship qualities. In: Aureli F, de Waal FBM, editors. Natural Conflict Resolution. University of California Press. pp. 177–198.
13. Cooper MA, Berntein IS, Hemelrijk CK (2005) Reconciliation and relationship quality in Assamese macaques (*Macaca assamensis*). Am J Primatol 65: 269–282. PMID: 15772987
14. Castles DL, Aureli F, Waal FBM (1996) Variation in conciliatory tendency and relationship quality across groups of pigtail macaques. Anim Behav 52: 389–403.
15. Thierry B (2000) Covariation of conflict management patterns across macaque species. In: Aureli F, de Waal FBM, editors. Natural Conflict Resolution. Berkeley: University of California Press. pp. 106–128.
16. Thierry B, Iwaniuk AN, Pellis SM (2000) The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus Macaca). Ethology 106: 713–728.
17. Schino G, Aureli F (2008) Trade-offs in primate grooming reciprocation: testing behavioural flexibility and correlated evolution. Biol J Linn Soc 95: 439–446.
18. Hemelrijk CK, Luteijn M (1998) Philopatry, male presence and grooming reciprocation among female primates: a comparative perspective. Behav Ecol Sociobiol 42: 207–215.
19. Zhang P, Watanabe K (2014) Intraspecies variation in dominance style of *Macaca fuscata*. Primates 55: 69–79. PMID: 23797620
20. Schino G (2001) Grooming, competition and social rank among female primates: a meta-analysis. Anim Behav 62: 265–271.
21. Schino G (2006) Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. Behav Ecol 18: 115–120.
22. Carne C, Wiper S, Semple S (2011) Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. Am J Primatol 73: 1127–1133. doi: 10.1002/ajp.20979 PMID: 21769908
23. Shutt K, MacLarnon A, Heistermann M, Semple S (2007) Grooming in Barbary macaques: better to give than to receive? Biol Lett 3: 231–233. PMID: 17327200
24. Semple S, Harrison C, Lehmann J (2013) Grooming and anxiety in Barbary macaques. Ethology 119: 779–785.
25. McFarland R, Majolo B (2011) Grooming coercion and the post-conflict trading of social services in wild Barbary macaques. PLoS One 6: e26893. doi: 10.1371/journal.pone.0026893 PMID: 22046398
26. Konečná M, Weiss A, Lhota S, Wallner B (2012) Personality in Barbary macaques (*Macaca sylvanus*): Temporal stability and social rank. J Res Pers 46: 581–590.
27. Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49: 227–267. PMID: 4597405
28. Dolhinow P (1978) A behavior repertoire for the Indian langur monkey (*Presbytis entellus*). Primates 19: 449–472.
29. Berman CM, Ionica CS, Li J (2004) Dominance style among *Macaca thibetana* on Mt. Huangshan, China. Int J Primatol 25: 1283–1312.
30. Archie E, Morrison T, Foley C, Moss C, Alberts S (2006) Dominance rank relationships among wild female African elephants, *Loxodonta africana*. Anim Behav 71: 117–127.
31. Bayly KL, Evans CS, Taylor A (2006) Measuring social structure: a comparison of eight dominance indices. Behav Processes 73: 1–12. PMID: 16527432
32. Ostner J, Heistermann M, Schülke O (2008) Dominance, aggression and physiological stress in wild male Assamese macaques (*Macaca assamensis*). Horm Behav 54: 613–619. doi: 10.1016/j.yhbeh.2008.05.020 PMID: 18625235
33. Hinde R (1978) Dominance and role- two concepts with dual meanings. J Soc Biol Syst 1: 27–38.
34. De Vries H, Netto WJ, Hanegraaf PLH (1993) MatMan: A program for the analysis of sociometric matrices and behavioural transition matrices. Behaviour 125: 157–175.
35. De Vries H, Stevens JMG, Vervaecke H (2006) Measuring and testing the steepness of dominance hierarchies. Anim Behav 71: 585–592.

**36.** Gammell MP, De Vries H, Jennings DJ, Carlin CM, Hayden TJ (2003) David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. Anim Behav 66: 601–605.

**37.** De Vries H (1998) Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim Behav: 827–843. PMID: 9632471

**38.** Bates D, Maechler M, Bolker B, Walker S (2014) lme4: 1.0–6., Linear mixed-effects models using Eigen and S4. R package version Http://CRAN.R-project.org/package = lme4.

**39.** Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol Rev 82: 591–605. PMID: 17944619

**40.** Van Hooff JARAM, Wensing JA (1987) Dominance and its behavioral measures in a captive wolf pack. In: Frank H, editor. Man and Wolf. Dordrecht: DRW Junk Publishers. pp. 219–252.

**41.** Xia D, Li J, Garber PA, Sun L, Zhu Y (2012) Grooming reciprocity in female Tibetan macaques *Macaca thibetana*. Am J Primatol 74: 569–579. doi: 10.1002/ajp.21985 PMID: 22539271

**42.** Gumert MD (2007) Grooming and infant handling interchange in *Macaca fascicularis*: The relationship between infant supply and grooming payment. Int J Primatol 28: 1059–1074.

**43.** Schino G, di Sorrentino EP, Tiddi B (2007) Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame reciprocation. J Comp Psychol 121: 181–188. PMID: 17516796

**44.** Ventura R, Majolo B, Koyama N, Hardie S, Schino G (2006) Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. Am J Primatol 68: 1138–1149. PMID: 17096423

**45.** Macdonald S, Schülke O, Ostner J (2013) The absence of grooming for rank-related benefits in female Assamese macaques (*Macaca assamensis*). Int J Primatol 34: 571–584.

**46.** Balasubramaniam KN, Berman CM, Ogawa H, Li J (2011) Using biological markets principles to examine patterns of grooming exchange in *Macaca thibetana*. Am J Primatol 73: 1269–1279. doi: 10.1002/ajp.20999 PMID: 21922505

**47.** Boccia ML, Reite M, Laudenslager M (1989) On the physiology of grooming in a pigtail macaque. Physiol Behav 45: 667–670. PMID: 2756061

**48.** Aureli F, Preston S, de Waal FBM (1999) Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. J Comp Psychol 113: 59–65. PMID: 10098269

**49.** Stockley P, Bro-Jorgensen J (2011) Female competition and its evolutionary consequences in mammals. Biol Rev 86: 341–366. doi: 10.1111/j.1469-185X.2010.00149.x PMID: 20636474

**50.** Küster J, Paul A (1984) Female reproductive characteristics in semi-free-ranging Barbary macaques (*Macaca sylvanus* L. 1758). Folia Primatol 43: 69–83. PMID: 6519600

**51.** Schino G, Ventura R, Troisi A (2005) Grooming and aggression in captive Japanese macaques. Primates 46: 207–209. PMID: 15688120

# CHAPTER V.

## Summary of the results

## Summary of the results

This thesis is focused on grooming interactions between individuals of Barbary macaques in Gibraltar. The findings are based on three studies and can be summarized as follows:

**I.** In our first study we examined the context of grooming for mating interchange. We found that males groomed females with whom they were mating more frequently and for longer periods of time. Our results also showed that the relationship between grooming and mating was significant in all context – sexual and non-sexual. The same was found for females – they groomed males with whom they were mating more frequently and for longer periods of time. In both sexes grooming was more frequent and longer in the sexual in contrast to non-sexual context. We did not find any differences between presexual and postsexual grooming interactions. We summarised that significant correlation between grooming and mating was mediated through long-lasting bonds between individuals, and that both sexes could benefit from these social bonds.

**II.** In our second study we focused on grooming and infant handling interchange. The most of similar studies were done on primates with restrictive allomothering where mothers often resist the attempts of other females to inspect or take away their infants. In contrast, Barbary macaques belong to the species characterized with less restrictive allomothering where grooming – infant handling exchange is less understood. We expected that mothers would receive more and give less grooming to other females than non-mothers, and that non-mothers who groom mothers would spend more time with infant handling. Our data showed that mothers gave less grooming but did not receive more grooming from other females. We proposed that this could be explained by time constraint posed on mothers rather than by grooming for infant handling exchange.

**III.** In our third study we focused on the mechanism of the grooming partner selection. We tested whether grooming is related to kinship, rank and friendship. Furthermore, we also tested whether grooming is reciprocated or exchanged for rank related benefits (i.e. lower aggression and increased tolerance during feeding). In general, we could say that grooming was reciprocally exchanged and directed up the hierarchy. Moreover, grooming was more frequent among individuals with higher friendship values as well as among relatives. Our results also showed that the reciprocation of grooming was a significant predictor of grooming interactions between individuals of similar rank. However, we did not find any evidence for grooming being exchanged for rank related benefits.

# APENDIX

Curriculum Vitae

# Curriculum Vitae

## Education

| | |
|---|---|
| 2011 – now | doctoral studies: Department of Zoology, Faculty of Science, University of South Bohemia, Czech Republic (Doctoral thesis: Social grooming in Barbary macaques.) |
| 2007 – 2011 | master studies: Department of Zoology, Faculty of Science, University of South Bohemia, Czech Republic (Master thesis: Grooming in female Barbary macaques: Role of dominance, kinship and relationship quality.) |
| 2004 – 2007 | bachelor studies: Faculty of Science, University of South Bohemia, Czech Republic (Bachelor thesis: Personality of common voles: Behaviour in the new environment.) |
| 2000 – 2004 | Grammar School, Pilsen |

## Experience/fieldwork

| | |
|---|---|
| 6/2014 | DNA extraction from hair of Przewalsky horses and laboratory processing – cooperation with Dr. Yoshan Moodley, Konrad Lorenz Institute of Ethology, University of Veterinary Medicine Vienna, Department of Integrative Biology and Evolution |
| 2014 – 2015 | Molecular analysis, Hospital Na Homolce, Prague, cooperation with RNDr. Emanuel Žďárský, CSc. |
| 2013 – 2015 | Molecular analysis, Laboratory of Archaeobotany and Paleoecology, cooperation with doc. PhDr. Jaromír Beneš, Ph.D. |
| 2010 – 2015 | Molecular analysis, Institute of Parasitology, Laboratory of Molecular Ecology and Evolution |

| | |
|---|---|
| 10/2008 – 2/2009 | Field work in Gibraltar: Behavioural observation of social behaviour of Barbary macaques – data collection |
| 11/2007 – 2/2008 | Field work in Gibraltar: Behavioural observation of social behaviour of Barbary macaques – data collection |
| 2000 – 2010 | Voluntary work in Ústí nad Labem, Jihlava and Plzeň Zoo |

### Pedagogical experience

| | |
|---|---|
| 2011 – 2015 | Seminars of zoology of vertebrates – field and laboratory courses for students of zoology |
| 2013 | Oral presentation for people interested in archaeogenetic in Netolice |
| 2010 | Oral presentation at 36. festival named Ekofilm |

### Conference contributions

| | |
|---|---|
| 2013 | Genetic conference of University of South Bohemia (Retreat) – oral presentation |
| 2012 | Genetic conference of University of South Bohemia (Retreat) – oral presentation |
| 2011 | Conference of Czech and Slovak Ethological Society – poster |
| 2011 | International conference focused on Behavioural ecology and socio-biology in Germany - Göttinger Freilandtage – poster |
| 2011 | Oral presentation on meetings of Czech and Slovak zoological gardens (UCSZOO) |
| 2010 | Oral presentation on meetings of Czech and Slovak zoological gardens (UCSZOO) |

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|---|---|
| 2009 | Oral presentation on conference of Czech and Slovak Ethological Society |
| 2009 | Oral presentation on meetings of Czech and Slovak zoological gardens (UCSZOO) |
| 2009 | Zoological conference of Czech Republic - poster |

## Funding awards

| | |
|---|---|
| 2008 | Czech and Slovak Ethological Society student award for Master thesis project |

## Other experience

| | |
|---|---|
| 2010 | Cooperation with Czech public radio on nature and wildlife related programs. Participation in their program focused on behaviour of orangutans in the Dvůr Králové Zoological garden |
| 2009, 2013 | Seasonal marine biologist and conservationist for tourist groups during Red Sea trips – oral presentations |

## Publications

**Roubová V**, Konečná M, Šmilauer P, Wallner B (2015). Whom to Groom and for What? Patterns of Grooming in Female Barbary Macaques (Macaca sylvanus). PLoS ONE 10(2): e0117298. doi:10.1371/journal.pone.0117298

Martinů J, **Roubová V**, Nováková M, Smith VS, Hypša V, Štefka J (2015). Characterisation of microsatellite loci in two species of lice, *Polyplax serrata* (Phthiraptera: Anoplura: Polyplacidae) and *Myrsidea nesomimi* (Phthiraptera: Amblycera: Menoponidae). Folia Parasitologica 62: 016

Beneš J, Pták M, Růžička P, Divišová M, Bumerl J, Hojerová H, Konrádová M, **Roubová V** (2016). The Archaeopark at Netolice: Reconstruction of an early medieval hillfort in South Bohemia. Circumstances of its establishment, impact, and perspectives, Fines Transire 25, 1–7

### Upcoming publications

Lhota S, Roubová V, Gregorová V, Konečná M. Not just payment for mating: patterns of grooming and sexual activity in Barbary macaques *(Macaca sylvanus)*.
Submitted to American Journal of Primatology

Roubová V, Lhota S, Wallner B, Konečná M. Time constraints rather than attraction to infants may explain the effect of maternal status on grooming among Barbary macaque *(Macaca sylvanus)* females.
Submitted to Primates

### Popular articles

| | |
|---|---|
| 2010 | Series of articles focused on Borneo natural heritage published on the Czech public radio station web site |
| 2009 | Series of articles about biodiversity of Red Sea in journal Potápění |

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