UNIVERSITY OF SOUTH BOHEMIA

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GROOMING IN FEMALE BARBARY MACAQUES:
ROLE OF DOMINANCE, KINSHIP AND RELATIONSHIP QUALITY.

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Master thesis

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Annotation:

This study investigates the influence of dominance, kinship and relationship quality on grooming distribution in female Barbary macaques. Data were collected in free-ranging group of Barbary macaques during two four-month periods. The results demonstrate that all tested factors are important for females choice of grooming partners in given group. Moreover, the relative importance of each variable was evaluated. This approach enables to establish which factor plays the most important role in grooming distribution among female Barbary macaques. The relationship quality had the strongest effect on distribution of grooming interactions among females. In other words females groomed more often and for longer time social partners with whom they have better relationship.

Financial support:

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1.1. Why do primates groom?

Primates (especially *Catharrine* species) spend a relatively large part of their time carefully inspecting and cleaning the fur of other individuals, a behaviour named allogrooming (grooming, hereafter) *(Schino, 2006)*. Grooming is one of the most common forms of affiliative behaviour among primates. Moreover, the fact that grooming may occupy up to 20% of the daily time budget and is conserved despite the other demands (e.g. increased foraging requirements), suggests that it has a great biological significance for the animals involved *(Henzi and Barrett, 1999)*. Thus it is not surprising that grooming has been recognized as a fundamental of primate sociality since the early days of primatology *(Kummer, 1968; Dunbar, 1991)*.

Some of the first hypotheses about the function of grooming claimed that the original function of grooming was keeping the fur in good hygienic condition by removing paracites, old skin, or dust *(Goosen, 1987)*. Currently, it is generally assumed that the main function of grooming is a direct exchange of grooming for other benefits. It seems that grooming can serve as a "commodity" that is interchange for other "services" on a biological market. It could be changed for coalitionary support from others *(Henzi and Barrett, 1999)*, tolerance *(de Waal, 1997)*, infant handling *(Henzi and Barrett, 2002)*, or for reciprocal grooming *(Schino and Aureli, 2008)*.

Based on these findings, we can suppose that primates tend to choose the best partners and that their choices influence grooming distribution inside the group. This raises a question: Who is the best partner? Despite the numerous publications focused on grooming, little is known about how primates choose their grooming partners. Schino et al. (2007) reported that kinship, rank of recipient, and rank distance had a significant influence on grooming in primates. In other words, kins and dominant individuals were preferred as grooming partners. Differences in social grooming can also reflect differences in relationship quality between partners, which is supported by Hohmann and Fruth (2000) for bonobo females. Distribution of grooming can be also widely influenced by the dominance style in a given species *(Slater, 2002)* where despotic social groups have a different grooming distribution than species living in tolerant social groups.

There is no doubt that grooming is one of the most important social activities in primates. It is influenced by the wide range of factors and thus the answers to the questions as

to why primates groom or who they chose as a grooming partner would be rather complex.

The aim of this study is to find out what factors can possibly influence partner choice and distribution of grooming among female Barbary macaques.

1.2: Hygienic function of grooming.

There are many hypotheses about the main function of grooming among primates. Hygienic function – keeping the fur in good hygienic conditions by removing paracites, old skin, or debris – have been offered as one of the explanations of grooming behaviour. Moreover, some authors emphasize that this is the very original function of grooming *(Goosen, 1987; Dunbar, 1991)*.

Hygienic function hypothesis predicts that sites on the body that are difficult to access received more grooming than sites easy to reach. Despite this prediction Barton (1985) claimed that within accessible and inaccessible sites, grooming was not differently distributed over the body surface, despite any special social or communicatory significance that particular sites may have. However, he admitted that analytic and methodological differences are the probable explanation for discrepancies between these results and those obtained in other studies. Perez and Vea (1999) analysed distribution of the behaviour over the body surface in the individuals of two captive groups of white-crowned mangabeys (*Cercocebus torquatus lunulatus*). Contrary to the findings of Barton (1985), their results obtained show that in both groups inaccessible sites received more grooming than predicted by their actual surface area and those easy to reach received less grooming than expected. This complementarity between the distribution of autogrooming and allogrooming (grooming hereafter) is consistent with the hygienic functional hypothesis of grooming *(Perez and Vea, 1999)*. The same result can be found in a study by Reichard and Sommer (1994) who tested the distribution of grooming over the body surface in gibbons (*Hylobates lar*). The fact that injured individuals are groomed more intensively than before their injuries *(Perez and Vea, 2000)* would also support the hygienic function hypothesis. A potentially confusing factor that influences distribution of grooming over the body is hierarchical rank because lower-ranking individuals tend to avoid a frontal eye contact (regarded as a threat) with higher-ranked individuals *(Boccia et al., 1982; Franz, 1999)*. This can disrupt the hygienic function hypothesis of grooming based on site preferences because low-ranking individuals preferentially groomed dorsal and caudal regions of the body.

Nevertheless, Perez and Vea (1999) admit that the strong distributional selectivity of grooming and the inter-individual variability in preferred grooming sites suggest that the hygienic function hypothesis cannot fully account for all the aspects of the body distribution of such behaviour. Thus, in support of the multifunctional nature of grooming, they conclude that there must be more than cleaning involved in non-human primate grooming. Similarly, Zamma (2002) concluded that grooming in Japanese macaques (*Macaca fuscata*) is needed not only for the removal of ectoparazites but also for maintaining of social bonds with others.

1.3: Biological market theory.

The giving of grooming is assumed to be costly, reducing the amount of time available for other activities, such as foraging and vigilance *(Dunbar, 1991)*. Therefore, such behaviour has to be profitable for individuals involved to evolve. Biological market models are designed to predict the manner in which animals trade valuable "commodities" depending on their status within the market place, and the supply and demand of the commodities in question *(Barrett and Henzi, 2002)*.

An animal offering its services is presumably selected to choose a partner offering the largest return benefits. The biological market theory *(Noe and Hammerstein, 1995),* which emphasized bargaining and outbidding among multiple partners, constituted a natural development of reciprocal altruism theory. Primates groups represent biological markets in which individuals trade grooming in a reciprocal manner for the direct benefits that grooming itself offers *(Silk, 2002a)* or exchange it for tolerance by more powerful animals *(Henzi and Barrett, 1999),* food sharing with others *(de Wall, 1997)*, support during agonistic interactions – when an individual intervenes in an aggressive conflict to support one party against the other *(Hemelrijk, 1994; Koyama, 2006)*, and access to infants *(Henzi, and Barrett, 2002)*. Individuals may form reciprocal grooming relationships solely for the benefits that grooming itself offers – e.g. parasite removal, release of β-endorphines, or reduction of tension *(Shutt, 2007; Zamma, 2002)*. Silk (2002a) found that females groomed preferentially those individuals that groomed them most, which means that we can find more or less stable dyads within the particular groups. De Waal (1997) showed that prior grooming facilitated sharing of a limited food supply in captive chimpanzees (*Pan troglodytes*). Hohmann and Fruth (2000) found similar tendencies of food sharing in free living bonobos. Though most authors assume that the main function of grooming is to ensure coalitionary support from others, either by the direct exchange of grooming for coalitionary support *(Schino, 2006)* or by using

grooming as a means of strengthening social bonds *(Dunbar, 1991; Henzi and Barrett, 1999; Schino and Aureli, 2008)*. It is supported by both naturalistic and experimental evidence *(Hemelrijk, 1994; Koyama, 2006)*. In this case, the benefits of grooming (paracite removal, endorphin production) are traded for the benefit of support during competitive interactions. For instance, female vervets were more likely to come to help an animal that had recently groomed them than one who had not *(Seyfarth and Cheney, 1984)*. Moreover, it has been shown that interchange of grooming and agonistic support is significant even when potentially confounding factor of kinship is taken into account *(Schino, 2006)*. The results of Hohmann and Fruth's (2000) study suggest that previous grooming interactions also limit aggressive interactions in bonobos.

Henzi and Barrett (1999) suggest that when grooming represents an interchange currency, it is used to increase the level of tolerance between dominant and subordinate individuals, resulting in reduced levels of aggression in chacma baboons (*Papio ursinus*). Henzi and Barrett (2002) determined that grooming also tended to promote an exchange with infant handling. This would support an idea that grooming may be payment for infant handling. Grooming-infant handling interchanges tended to be unidirectional as mothers usually did not reciprocate grooming for infant handling. Lower-ranked females groomed higher-ranked mothers and their infants longer than vice versa *(Gumert, 2007)*. Gumert (2007) also noted that grooming interactions were longer when infants were scarce in the surrounding social environment than when they were abundant, indicating a possible supply-and-demand effect. It follows that scarcity will increase the price of the demanded commodity and overabundance will decrease the price. It is possible that social animals may exchange valuable acts to gain access to social partners or commodities to which they have limited access and demand to obtain *(Noë and Hammerstein, 1995)*. The result supports the biological market prediction that scarcity of available partners increases their value, while abundance of partners decreases it.

In conclusion, primates frequently exchange behaviours that can be classified as services for other commodities. An animal offering its services is presumably selected to choose the partner offering the largest return benefits. Grooming seems to promote immediate reciprocation of other social acts e.g., grooming, tolerance, coalition support, and access to infants *(Mehlman and Chapais, 1988; Hemelrijk, 1994; Koyama et al., 2006; Schino et al., 2007)*.

1.4: Stress reduction.

Grooming is usually associated with reduction of stress levels and release of β-endorphins *(Keverne et al, 1989)* in non-human primates. A number of studies have documented the stress-reducing effects of being groomed *(Schino et al., 1988; Aureli et al., 1999; Shutt, 2007; Aureli and Yates, 2010)* via direct observation or physiological values.

Commonly, the underlying hypothesis is that being groomed is relaxing and grooming can therefore be traded for other services *(Shutt, 2007)*. Evidence for the relaxing effects of grooming comes from a range of non-human primate species, using either different or comparable measures of stress reduction. Aureli et al. (1999) as well as Aureli and Yates (2010) have supported this view by showing a reduction in heart rate in individuals receiving grooming. This physiological evidence is further supported by Aureli (1997) in a study using behavioural indicators of stress and anxiety such as self-directed behaviours (self-scratching, self-grooming). Long-tail macaques *(Macaca fascicularis)* were found to display less self-directed behaviour soon after they were groomed *(Schino et al., 1988)*. Whereas the short-term benefits for the groomee have often been investigated, little is known about the effects for the groomer. Aureli and Yates (2010) have provided an evidence for short-term stress reduction in the groomer in crested black macaques (*Macaca nigra*). The reduction of stress and the increase of tolerance provide evidence that grooming others is beneficial. Thus, this study supports the tension-reduction function of grooming and suggests that this functional explanation is applicable to the groomer as well as the groomee *(Aureli and Yates, 2010)*. These short-term effects, together with the longer-term effects of large and/or strong grooming networks confirm that grooming others, as well as receiving grooming, has a great importance for social dynamics.

In conclusion, physiological and behavioural data often confirm that animals exhibit stress reduction during the grooming session. Recent findings provide new evidence that grooming is profitable not only for the groomee but also for the groomer, which can be tied with lower possibility to be attacked by the individuals who are groomed. Thus, under certain conditions, delivering benefits to others seems to be gratifying to non-human primates *(de Waal et al. 2008; Aureli and Yates, 2010)* but on the other hand there are a few studies that found no correlation between grooming and stress reduction.

1.5: Factors influencing partner's choice.

Several factors have been identified as potentially influencing partner's choice such as age, sex, dominant status of the particular individual, and kinship or relationship between the groomer and the groomee. All of these factors may influence distribution of grooming interactions in primates. In the following part I focus on the review of the current literature mainly concerned with dominant status, kinship and relationship quality, as these are the factors directly tested in this study. As mentioned above, it is presumed that primates carefully choose their grooming partners because grooming is time and energy consuming activity. Their choice thus depends on benefits that can be inferred from interaction with a given partner.

1.5.1: Dominance

Dominance hierarchy usually has an important effect on social interactions. Many researchers have found that the distribution of grooming is mainly influenced by dominance rank, especially in all *cercopithecoid* primates *(Seyfarth 1977; Mehlman and Chapais, 1988; Kato, 1999; Shino, 2006; Gumert, 2007)*. Seifahrt (1977) hypothesized that grooming may be exchanged with different benefits and that these benefits may be rank related.

Socially living animals usually develop a hierarchical order – a system that, for instance, enables individuals to recognize potentially stronger counterparts and avoid unwanted injuries. Therefore dominance status is an important factor for socially living animals and influences the choice of their social partners. This can be illustrated on grooming partner choice in primates, who often direct their grooming up the dominance hierarchy *(Nakamichi and Shazawa, 2003; Schino, 2006)*. In other words, lower-ranking females direct more grooming toward higher-ranking females than is reciprocated *(Seyfarth, 1977)*. They may have more to gain by socially trading with these high-ranking females, such as tolerance or agonistic support *(Gumert, 2007)*. Exchanging grooming for agonistic support was described in studies by Schino (2006) or Seyfarth and Cheney (1984). In contrast, high ranking females do not need to groom as much to access commodities from lower-ranking partners, because dominant females can exert their social power to obtain access to wanted resources. Such positive relationship between dominance and grooming have been reported in long-tailed macaques (*Macaca fascicularis*) *(Gumert and Ho, 2008)* as well as in stump-tailed macaques (*Macaca arctoides*) *(Estrada et al., 1977)*. However, this pattern is not universal in

all non-human primates and the effect of dominance hierarchy can be strongly influenced by the dominance style of a given species. The effect of dominance style on a grooming distribution is described in a detailed comparative study of the genus *Macaca (Thierry, 2000)*. The species-specific dominance style affects how an individual chooses partners for proximity or affiliation and whether the distribution of choices is skewed in favour of higher-ranking or related individuals *(Thierry, 2000)*. Inter-specific differences in a power asymmetry thus determine who may interact with whom. Grooming is strictly directed up the hierarchy in despotic species (such as Japanese or rhesus macaques), however, dominance is not determining grooming distribution in egalitarian species (such as Tonkean or crested macaques). Japanese macaque females, for example, directed more of their grooming to higher-ranking females *(Schino, 2006)* but on the other hand, dominance had no effect on the form or distribution of social grooming among adult females in Tonkean macaques (*Macaca tonkeana*) *(Thierry, 1990)*.

Some of the New World monkeys direct their grooming down the hierarchy. For instance, dominant breeding females in common marmosets (*Callithrix jacchus*) groomed subordinate individuals more than vice versa *(Lazaro-Perea et al., 2004)*. Subordinates cooperate with dominant individuals by providing alloparental care and cooperation in territorial defence and anti-predator vigilance, and therefore they are valuable social partners for dominant animals *(Schaffner and Caine, 2000)*. Lazaro-Perea et al. (2004) suggest that, in cooperatively breeding systems, dominant females may use grooming as an incentive for helper females to stay in the group. Also capuchin monkeys (*Cebus apella)* groom down the hierarchy. Observations of captive female brown capuchin monkeys in five groups revealed that grooming is primarily the occupation of dominant females *(Parr et al., 1997)*. When categorized according to rank class, high-ranking females performed significantly more grooming than they received. The authors explained these findings with the help of the similarity principle *(de Waal & Luttrell 1986; de Waal 1991)*. According to this hypothesis, individuals of similar genetic and social background, age, hierarchical position and social class are mutually attractive and thus groom as well as affiliate, socialize and support one another and consequently may achieve similar rank.

Classical models of grooming predict that subordinate primates will direct grooming towards dominants to receive coalitionary support or different benefits *(Seifarth, 1977)*. However, the situation is more complex, because grooming distribution is also influenced by the dominance style of a given species, the necessity to maintain subordinate individuals in the natal group or inter-individual relatedness.

1.5.2: Kinship

Kin selection may influence social interactions in a way that acts to increase an individual's inclusive fitness. Thus in grooming interactions, individuals should preferentially choose their close kin *(Silk, 2002a, 2002c)*. Indeed, a previous meta-analysis has shown that primates groom preferentially their maternal kin *(Schino, 2001)*. Coalitions between kin play, in fact, a decisive role in the ability of individuals to acquire and defend food sources from other group members *(Aureli et al.,* 1997).

In the 1950s, female kinship was first described as a key factor for understanding the social behaviour of Japanese macaques (*Macaca fuscata*) *(Kawamura, 1958)*. Intuitively, one expects that relationship establishment will be easier in dyads with overlapping interests and hence among relatives. Not only will relatives be more familiar with each other, but they also incur greater costs from harming each other and more benefits from helping each other, through inclusive fitness effects *(van Schaik and Aureli, 2000)*. Among the cercopithecines, in which kinship is an important variable in social dynamics, affiliative interactions are more frequent among kin than non-kin *(Aureli et al., 1997; Thierry, 1990)*. Many studies have demonstrated that females of most Old world monkeys remain in their natal group throughout their lives and associate preferentially with their relatives *(Aureli et al., 1997; Silk, 2002a)*. They form so called matrilinear structure, the core of the group, in which individuals preferentially interact with each other *(van Schaik and Aureli, 2000)*. These individuals frequently strengthen their social bonds by grooming to maintain good relationships with each other. A meta-analysis of 36 studies carried out on 14 different species showed that grooming is preferentially directed to related individuals *(Schino, 2006)*. Despite this quite strong evidence, there are a number of works that didn't support this finding. As previously mentioned (1.5.1) the species specific dominance style has a wide influence on social partners' preferences. A weaker kin bias in affiliative behaviours, for example grooming, has been found in less despotic species, such as stump-tailed and Tonkean macaques *(Thierry et al., 1990)*. Schino and Aureli (2008) admit that grooming reciprocation as observed in their study was not simply due to the influence of maternal kinship. Similar results were published by Hohmann et al. (1999) who found that differences in social grooming in bonobos appeared to be related to patterns of spatial association rather than to kinship. Rowell et al. (1991) found no evidence that grooming was preferentially directed at kin in a wild group of blue monkeys (*Cercopithecus mitis stuhlmanni*).

In conclusion, kinship represent one of the factors significantly affecting the grooming

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partner choice. Many species prefer to interact with close relatives however others exhibit weaker or no kin bias during affiliative interactions such as grooming. In addition, many studies have reported a consistent pattern of lower levels of affiliation toward non-kin in more despotic species than in more tolerant species *(Aureli, et al., 1997)*, which supports an indispensable influence of dominance style on social behaviour in particular species.

1.5.3: Relationship quality

Relationship quality has only recently received more attention as a factor potentially influencing grooming preferences. The number of studies directly testing this factor is low in comparison to those testing dominance or kinship, although it is widely assumed that differences in social grooming reflect differences in affiliative relations *(Hohmann and Fruth, 2000)*. Relationship quality does not affect only grooming preferences but also reconciliation tendencies among individuals (in *Call et al., 1999; Aureli et al., 2002)*.

Intensive close social relationships among primates exist, and they are roughly analogous to human friendships *(Silk, 2002b)*. It is presumed that individuals have differentiated relationships with their social partners and that these relationships (also referred to as friendships) do exist outside of particular interactions. In this respect, relationship quality resembles a concept of dominance hierarchy that also expands beyond displacement interactions *(Bernstein, 1981)*. Social grooming is an unambiguous, easily measurable behaviour and therefore is frequently used to index the level of affiliation (relationship quality) between pairs of individuals *(Seyfarth and Cheney, 1984; Henzi and Barrett, 1999)*. Not only grooming but also spatial associations are generally used for relationship quality assessment, the more grooming or/and the more time spend together the better the relationship. Analyses of data from a community of bonobos revealed a positive correlation between grooming and close spatial associations *(Hohmann et al., 1999)*. Cords (2002) found that the time spent grooming the favourite partner (measured by time in proximity) was at least 10 times greater than the time spent grooming the least favourite partner, and these figures exclude females who were not partners at all. Silk et al. (2006) 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 female savannah baboons. Social relationships, particularly social bonds that extend beyond dominance relationships, are generally a more profitable long-term investment for females than for males *(Silk, 2002b)*. This can be influenced mainly by female philopatry in particular species. The

fact that grooming is asymmetrical, involving a groomer and a recipient (groomee), further complicates comparisons of dyads. A period of grooming may have a different meaning if the active role is assumed mostly by one individual rather than being more equitably assumed by both *(Cords, 1997b)*. The relationship quality is also used in studies that are focused on reconciliation between individuals after agonistic interactions *(Cords, 1997a; Aureli et al., 2002; Preuschoft, 2002)*. There is considerable evidence suggesting that the occurrence of reconciliation varies with factors related to the quality of the social relationship between opponents. Results of several studies *(Aureli, 1997; Das et al. 1998; Palagi et al., 2008)* supported the prediction that good relationship quality increases the tendency to reconcile, although others did not find any relationship between reconciliation and relationship quality *(Matheson, 1999;* Cooper et al., 2005*)*.

The variation in quality of social relationships leads to a great flexibility in the frequency and quality of interaction with various group members and with the same individual over time *(Aureli and Schaffner, 2002)*. In primates that live in larger groups, it is particularly obvious that individuals do not interact similarly with all group members, even when these belong to the same age, sex, or kinship class *(Cords, 1997)*. We can observe very different patterns of affiliative interactions such as grooming or spatial distributions among individuals. There is no uniform conclusion about standard methods for relationship assessment yet.

1.5.4: Conclusion

Only few studies have tested the effects of at least two factors on grooming distribution with the same data set (Stump-tail macaques – *Butovskaya and Kozintsev, 1996;* Rhesus macaques - *Matheson and Bernstein, 2000;* a meta-analysis for 14 different species *Schino, 2001)*. These two factors are usually kinship and dominance hierarchy. Therefore, it is a problematic issue to assess the importance of all three factors contributing to partner choice for grooming interaction within one particular species or in species comparison. However, it is widely assumed that all three factors reviewed in this thesis influence grooming distribution but it is also assumed that the importance of each of these factors is species-specific.

Revision of previously published studies revealed that there are no publications (as far as I know) testing all of these three factors (dominance, kinship, and relationship quality) on the same data set. So, this is very first study that tests the effect of all three factors on distribution of grooming using one data set.

1.6: Genus *Macaca.*

The macaques are the most geographically widespread and behaviourally diverse primate genus *(Thierry et al., 2000a)* that occupies the widest variety of habitats from tropical to temperate regions including grassland, mangrove swamps, deciduous or coniferous forests, tropical rainforests, rocky cliffs, semi-deserts, or areas of human settlement *(Thierry, 2007)*.

Macaques are medium-sized primates (adult body weights range from 3-17 kg) of the family *Cercopithecidae* (Old World Monkeys), with currently recognized 21 species *(Groves, 2001)* inhabiting a broad geographical range from west Morocco (Barbary macaques, *M. sylvanus*) to Japan (Japanese macaques, *M. fuscata*). With the exception of *M. sylvanus*, living in the North Africa, all species inhabit Asia. There is also Barbary macaque's population living in Gibraltar – the only one European wild non-human primates. Macaques have a promiscuous mating system and live in multimale/multifemale troops *(Thierry, 2007)*. The sex ratio among adult macaques in the group is biased in favour of females *(Thierry, 2000)* who are typically able to breed annually. Females stay in their natal group and form matrilinear sub-groups with their relatives. Individuals inside these sub-groups usually cooperate together and preferentially support each other. Conversely, male macaques may change groups several times in their lives and so are rarely related to other males in their resident group *(Slater, 2002; Thierry, 2007)*. Macaques are considered to be opportunistic frugivores and are generally semi-terrestrial, although the degree of frugivory and arboreality is quite variable according to species *(Rowe, 1996)*. Beside fruit, the diet includes leaves, buds, seeds, and insects *(Thierry, 2000)*. The evolutionary diversification of this genus began around 5 Mya ago *(Abegg and Thierry, 2002)*. Macaques are considered a monophyletic group, on the basis of morphology and genetics *(Morales and Melnick, 1998)* and several species groups have been distinguished *(Morales and Melnick, 1998; Thierry, 2000; Thierry et al., 2000a)*. Barbary macaques (*M. sylvanus*), based on morphological and molecular data, are considered as phylogenetically basal macaque species *(Thierry et al., 2000a)*.

Social system of the genus *Macaca* is one of the most diversified primate genera at all. Diversity of the genus comes not only from geographical and ecological differences but also from the social variation among particular species.

1.6.1: Dominance style

Despite the fact that all macaque species share basic features of social system, they display inter-species variation, which is unique among primates. Species differ more or less in patterns of aggression, affiliation, reconciliation, dominance, nepotism, socialization, and temperament *(Thierry, 1985; Thierry, 1990; Thierry et al., 2000a)*.

There has been a tendency to explain the observed differences in social behaviour and organization by the differences in ecology *(Isbell and Young, 2002)*. However, Thierry et al. (2000a) suggested that inter-species variation in social organization is more closely linked to phylogeny than to environment. Based on this inter-species variation Thierry (2000) proposed a 4-grade scale of social organization ranging from highly despotic societies in grade 1, through the less despotic species in grade 2 to the most tolerant societies in grade 3 and 4 (Figure 1). Through this scale we can notice remarkable differences in several behaviours as e.g. a tendency to retaliate to attacks by the subordinates. Despotic species such as Japanese or rhesus macaques (grade 1) are met with a low probability of retaliation. In contrast, subordinates of tolerant species as Tonkean or crested macaques (grade 4) have a higher tendency to retaliate and are more likely to exhibit affiliative rather than submissive behaviour following the encounter *(Thierry et al., 2000a)*. It follows that interactions of individuals in grade 1 tend to be more asymmetrical than those for tolerant species in grade 4. Retaliation tendencies are closely tied with an intensity of aggression. When the intensity of aggression is low and severe injuries are quite rare then subordinate individuals are much more involved in retaliation and also intensity of reconciliation is higher *(Aureli et al., 1997)*. Tolerant species are characterized by the development of special behaviours e.g. silent bared-teeth display that may reduce social tension and facilitate social contact *(Thierry, 2000)*. Silent bared-teeth display signals the sender's peaceful intentions and serves to initiate affiliative interactions such as reconciliation in species from the fourth grade *(Thierry et al., 1994)*. In the third and second grades, the silent bared-teeth display is mainly a submissive gesture as it is in the first grade. Species in the first grade exhibit the steepest dominance gradient and social life is governed by rigid hierarchies. Power asymmetry determines who may interact with whom and affects how an individual chooses partners for proximity, affiliation, or play and whether the distribution of choices is skewed in favour of higher ranking individuals *(Thierry, 2000)*. For instance, in despotic macaque species, grooming is mainly directed up the hierarchy *(Nakamichi and Shazawa, 2003)*. Conversely, in egalitarian macaque species, dominance rank tends to have a little influence on the distribution of grooming. Thierry et al. (1990) concluded

that social systems that are characterized by mild dominance relations allow individuals the freedom to interact in the way and with whom they wish.

The influence of kinship on competition and proximity among partners is important in all four grades. The degree to which females prefer relatives, however, in affiliative contact, social grooming, and support in conflicts is less pronounced in the third and fourth grade than in the first one *(Butovskaya and Kozintsev, 1996)*. The social relationships of despotic species such as rhesus or Japanese macaques are marked by strong kinship networks *(Kawamura, 1958)* and females have a high preference for relatives. Conversely, for females from tolerant species kin bias is less pronounced, coalitions involving non-relatives are more common and also close ties exist even between non-relatives *(Thierry, 2000)*. Males, on the other hand, do not depend on their kin to the same extent as females because they break their social ties when emigrating from their natal troop across all dominant styles.

In general, species from the third and fourth grade display higher rates of affiliative contacts in comparison to the species from the first and second grade *(Thierry, 2000)*. It is predicted that neither kinship nor dominance rank has a strong influence on the partner choice and thus distribution of grooming in the third and fourth grade *(Nakamichi and Shazawa, 2003)* as affiliative interactions are not restricted by kinship or social hierarchy as it is in the other two grades.

Figure 1: The distribution of Thierry's (2000) social organization grades are mapped onto the phylogenetic tree provided by Morales and Melnick (1998). The trait is significantly associated with phylogeny. The most despotic species are in grade 1, the most tolerant species are in grade 4. Taken from Thierry (2000).
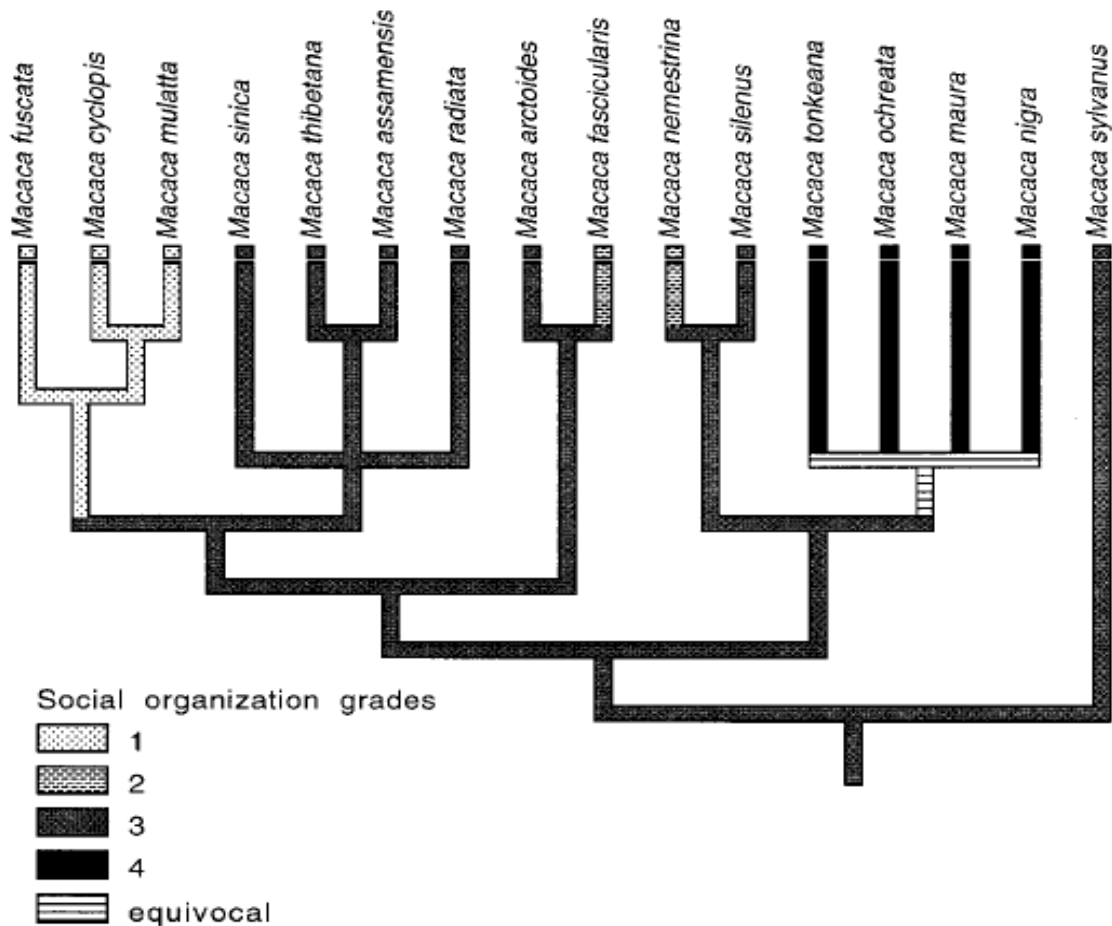
1.7: Barbary macaque.

In this chapter I will briefly summarize species specific characteristics of Barbary macaques (*Macaca sylvanus*) such a grouping patterns or ecological and social characteristics.

1.7.1: Biology of Barbary macaque

The adaptive radiation of macaques occurred mainly in Southeast Asia. The only species still present in northern Africa, *M. sylvanus*, is considered to be primitive, relic population *(Thierry et al., 2000a)*. Extant natural populations of *M. sylvanus* are disjunctively distributed in the Atlas and Rif Mountain ranges in Morocco and Algeria and the population currently inhabiting Gibraltar – apparently not native *(Fooden, 2007)*.

Barbary macaques, like other macaques, form multimale/multifemale groups with matrilinear hierarchies. Groups are usually characterized by a more or less balanced adult sex ratio *(Ménard, 2002)*. Group size ranges from 13 to 88 individuals in the wild *(Ménard, 2002)* and up to 200 individuals in food-enhanced settings. Modal size is around 40 individuals. Most natal male migrations occur around puberty (3 – 5 years), but usually only one third of all males leave the natal group *(Kuester and Paul, 1999)*. Females stay in the natal group throughout their life. Females reach sexual maturity between the third and fourth year of their life. Males reach sexual maturity later – between the third and fifth year *(Paul and Kuester, 1985)*. Barbary macaques are seasonal breeders and the mating season usually starts in November *(Rowe, 1996)* and lasts for the next few months. They breed once per year and usually have one infant. Habitats of Barbary macaques are characterized by seasonal variations in resource availability and thus the species is considered as granivorous and folivorous. A folivorous phase occurs in winter and in early spring (leaves – up to 90% of the monthly diet), granivorous phase occurs in fall (herbaceous seeds and/or acorns – up to 86% of monthly diet), and an insectivorous phase is observed in spring (caterpillars – up to 83% of feeding time) *(Ménard, 2002)*. In less favourable conditions, macaques rely on food of relatively lower quality such as lichens, small roots, immature acorns, mushrooms, or sap from striped cedar *(Ménard, 2002)*.

Barbary macaques are diurnal, arboreal and terrestrial primates *(Rowe, 1996),* who usually sleep in a small groups when males and females are separated and females tend to form groups with their offspring *(Rowe, 1996)* on sleeping sites. The Barbary macaques are under high pressure due to human expansion. The present population is estimated to have declined at a rate exceeding 50% over the last 3 generations (24 years) *(Butynski et al., 2008)*. This species is endangered mainly because of habitat loss due to growing impact of overgrazing by mixed flocks *(Ciani et al., 2005)*. In 2000, this species was qualified as Vulnerable by IUCN. Now its rapid decline caused that this species is qualified as an Endangered species (IUCN, 2010).

In summary, Barbary macaques are social, diurnal, and arboreal as well as terrestrial primates living in multimale/multifemale groups with matrilinear hierarchies and female philopatry. They appeared mainly either granivorous or folivorous depending on the habitat and season *(Ménard, 2004)*. This species is qualified as endangered.

1.7.2: Evaluation of dominance style

The degree of despotism of Barbary macaques is frequently discussed, but the existing evidence suggests that their societies are characterized by a less despotic dominance style than those of Japanese and long-tailed macaques *(Aureli et al., 1997)*. Therefore Barbary macaques (*Macaca sylvanus*) were incorporated to the grade 3 together with stump-tail *(M. arctoides),* Assamese *(M. assamensis),* bonnet *(M. radiata),* long-tailed *(M. silenus),* toque *(M. sinica),* and Tibetan macaques *(M. thibetana) (Thierry and Aureli, 2006).*

Aureli et al. (1997) suggested that Barbary macaques resemble more tolerant species as far as the lack of kinship effects on reconciliation is concerned but resemble more despotic species as far as kin bias in affiliation (such a grooming or playing) is concerned. However, the proportion of support during the aggressive interactions provided by non-kin is especially high relative to other despotic macaque species *(Aureli et al., 1997)*. Further evidence for the less despotic style of Barbary macaques is provided by comparisons of the occurrence of facial expressions such as silent bared-teeth display. In Barbary macaques this expression can lead to affiliative behaviour, suggesting that Barbary macaques may occupy an intermediate position – second or third grade – among macaque species *(Preuschoft, 1992)*. Several aspects of the agonistic behaviour of Barbary macaques can also be interpreted as an indication of a less despotic dominance style and therefore they should be placed in the third grade *(Aureli et al., 1997)*. Similarly, the affiliative alloparental behaviour toward infants and relaxed attitude of Barbary macaque mothers toward other individuals which interact with their infants promote incorporation of Barbary macaques among the relatively tolerant species *(Paul, 1999)*. In addition, data on allogrooming, bites, and symmetrical contests suggest that Barbary macaques are less despotic than rhesus macaques but less tolerant than stump-tail macaques *(Aureli et al., 1997)*.

Barbary macaques are characterized as a relatively tolerant species and they were placed to the third grade. It is, however, not possible to draw definitive conclusions because more comparative data are needed *(Aureli et al., 1997)*.

1.7.3: Gibraltar groups

Barbary macaques in Gibraltar are the only free living non-human primates in Europe. However, they were originally introduced from Algeria and Morocco *(Modolo et al., 2005)*. Gibraltar sample was found to include Algerian and Moroccan haplotypes separated by at least 16 mutational steps, revealing a dual origin of the founding females *(Modolo, 2005)*. It is generally held that the present Gibraltar population descended from a dozen individuals imported during World War II. From before the turn of the 20th century until the mid-1990s there were two main groups of macaques on Gibraltar *(Fuentes et al., 2007)*. Later, when the population had increased, these two groups fissioned into six groups (Royal Anglian Way, Apes' Den, Prince Phillip's Arch, Middle Hill, Faringdon's Battery and Spur Battery) with group sizes ranging approximately between 25 and 70 animals. Today the number of Barbary macaques on the Rock of Gibraltar is slightly more than 200 individuals. The monkeys are managed by the Gibraltar Ornithological and Natural History Society (GONHS). The GONHS feed monkeys on a regular daily basis with vegetables, fruit and grain to reduce macaque incursions into Gibraltar city. The animals receive a supply of fresh water. In addition, monkeys also forage for natural food such as leaves, roots, seeds, flowers, and invertebrates (76% provisioned, 24% non-provisioned in *Fuentes et al., 2007*). Additional feeding by tourists and local inhabitants with sweets, crisps, or pasta is common and unfortunately causes that some of these animals become obese and unhealthy. The monkeys are caught to check their health status and measure their body size and weight. Finally, the animals are given a tattoo number and a micro chip, which makes their later identification easier. The population on Gibraltar is continually increasing, which in turn puts the pressure on their already limited habitat (900 hectares). Population control (culling) is therefore an essential part of effective management of the Gibraltar colony within the Upper Rock Nature Reserve. Moreover, culling of males that are more likely to disperse might slow down genetic homogenization among neighbouring groups in Gibraltar *(Modolo et al., 2008)*. Many previous studies and their results were criticised because of the fact that observed population is thought to be under inbreeding depression (decreased fitness of a population due to the mating of few animals which are closely genetically related to each other). However, there is evidence that primates generally avoid incest *(Kuester and Paul, 1997; von Segesser et al., 1999; Paul, 2006; Thierry, 2007)* and Barbary macaques are no exception *(Paul and Kuester, 1985; Modolo et al., 2008)*.

2.0: Research aims and hypothesis

The aim of this study was to evaluate the effect of three factors on the distribution of grooming among Barbary macaque females. Kinship, dominance hierarchy and relationship quality were tested as possible predictors. These factors were significant predictors of grooming in some previous primate studies, but their relative importance differs between species. Especially in macaques the importance of these factors has been related to differences in dominance style of the given species.

Based on the biological market theory, dominant individuals are more attractive grooming partners because trading with higher-ranked animals can bring more benefits. Individuals usually tend to prefer close relatives because kin can increase an individual's inclusive fitness. Moreover, individuals with a good relationship usually groom each other more. Thus I could predict that dominant females, relatives and individuals with a good relationship are preferred grooming partners before others. However, the importance of these factors differs depending on dominance style of the given species, where the social interactions of individuals of the most despotic species are mainly influenced by dominance hierarchy and kinship. Unlike in the despotic species, individuals of the most tolerant species tend to prefer mainly those individuals who have a good relationship with.

Based on the tolerant dominance style of Barbary macaque I predict that distribution, frequency, and time that an individual spend grooming other partners is relatively independent from dominance hierarchy or kinship. Moreover, the influence of the relationship quality on grooming distribution would be crucial in rather tolerant species as Barbary macaques.

3.0: Methods

3.1: Research subjects.

This study focused on 17 Barbary macaque females who were living in the Apes' Den troop in the Upper Rock Natural Reserve, Gibraltar. This group is free ranging, daily provisioned, and visited by tourists and the general public. In the first season, the troop consisted of 17 females, 6 adult males, and 15 animals under three years. These same

individuals, three new immigrant males (2 sub adult and 1 young adult male), and 7 new born monkeys were present during the second season. All observed females were over three years old (from 3 to 28 years), with only three females categorized as sub-adults in the first season (age data from local pedigree, GONHS). These females were individually recognized and well-habituated to the presence of human observers. Behavioural observation were made by two observers (Martina Konečná and Veronika Roubová) who were trained in data collection and the use of behavioural ethograms before the study began.

3.2: Study site.

The study was carried out on the Apes' Den troop of free-ranging Barbary macaques in the Upper Rock Nature Reserve, Gibraltar (N 36°08′, W 5°21′). The climate of study site is typically Mediterranean, with hot, very dry summers and cool, wet winters. The Upper Rock is covered mainly in a dense Mediterranean scrub known as maquis. The maquis in Gibraltar is composed mainly of tall bushes such as Wild Olive, Mediterranean Buckthorn, Lentisc, Osyris and Terebinth, with smaller bushes such as Shrubby Scorpion Vetch, Spiny Broom, Teline, Wild Jasmine and Shrubby and Felty Germander *(Perez and Bensusan, 2005)*.

3.3: Behavioral data collection.

Behavioural observations were conducted between November 2007 and February 2008 and between October 2008 and February 2009. All observations took place from 8:00 to 18:00. The observational time was divided into five two-hour-periods (8-10 AM, 10-12 AM, 12-2 PM, 2-4 PM, 4-6 PM) where observation of every single individual was equally distributed in given season. For each individual, data were equally distributed throughout observational time and during the entire study. Animals were observed using **focal continuous sampling** simultaneously with **focal instantaneous sampling** *(Altmann, 1974)* on the same animal at 2 min intervals. One observational session – focal period of one individual lasted 30 min. All occurrences of short-duration behaviours in given individual were recorded by the focal continuous sampling technique, together with the partner identity in case of social interactions. Focal instantaneous sampling was used to record long duration behavioural states, including grooming, contact or proximity of social partners, and substrate that animal used. Behaviours were recorded according to an ethogram that was prepared by combining

already existing behavioural ethogram for hanuman langurs *(Konečná, 2005)* with several specific behavioural traits for macaques *(Thierry et al., 2000b; Wiper and Semplet, 2007)*. This ethogram covers a broad range of everyday activities. For the purpose of this study, I used mainly information about grooming – time, frequency and identity of grooming partners, then also agonistic interactions such as number of displacements in dyads, and affiliative interactions such as number of approaches in dyads (for full list of behaviours used in this study see the Appendix I). There was a mean of 29,5 hours of behavioural data per individual for a total of 497 hours for all observed females. The number of individual focal sessions for each female ranged from 23 to 32 hours (30 to 32 in the first season and from 23 to 29 in the second season).

3.4: Grooming and Grooming Indices.

Grooming was characterized by five measures. I recorded frequency of grooming received and given for each individual and time of grooming received and given for each individual during observation session for all adult females. Three grooming indices were also calculated. These indices helped to describe grooming interactions among females and also to assess the stability of the interactions between seasons.

1. Shannon – Wiener Diversity Index (Shannon Diversity Index, H') measures the diversity of a female's grooming partners. The H' was calculated using the formula from Magurran (1988): $H' = -\sum_{i=1}^{S}(p_i \ln p_i)$, with p_i being the proportion of total grooming with individual i, s the number of grooming partners, and ln the natural logarithm. A low H' indicated that the female concentrated the majority of her grooming among a few partners. On the other hand, a high value indicated that the female distributed grooming more evenly among partners.

2. Hinde Index for Grooming Partners (HIGP) is measuring the proportion of partners whom a subject groomed relative to those who groomed the subject (derived from *Hinde and Atkinson, 1970 cited in Crockford et al., 2008*): $\text{HIGP} = \frac{P_A}{(P_A + P_B)}$, with P_A being partners that the subject groomed and P_B being partners that the subject was groomed by. A high HIGP indicated that the female groomed more partners than she was groomed by. A low index indicated that she was groomed by more partners than she groomed.

3. Hinde Index for Grooming Time (HIGT) is measuring whether the female received more grooming or gave more grooming: $\mathrm{HIGT} = \dfrac{T_A}{(T_A + T_B)}$, with T_A being time that the female groomed others and T_B being time that the subject was groomed by others. A high index indicated that the female spent more time grooming others than being groomed by them. A low index indicated that the female received more grooming time than she gave others.

4. Sociality is expressed as the time an individual spent with others divided by the total time a given individual was observed (based on data from a focal continuous sampling).

3.5: The relationship quality.

There have been several measurements of relationship quality used in previous studies. Relationship quality or friendship has been measured through grooming interactions *(Castles et al., 1996)*, coalitionary support *(Berman et al., 2004)*, approach interactions *(Cooper et al., 2005)*, mutual contact *(Call et al., 1999),* or mutual contact and proximity *(Cords, 1997b)*. Some authors computed relationship quality using a combination of two or more previously mentioned measurements *(Cords, 2002; Koski et al., 2007; Majolo et al., 2010).* Comparison of these different methods has never been published, that is why I computed relationship quality using more than one way and then compared the results.

The relationship quality between individuals A and B was computes as an amount of time individual A spends in **contact** with individual B divided by the amount of time individual A spends in contact with all other females (data from a focal instantaneous sampling). I also computed the relationship quality as an amount of time two individuals spend together in **contact and proximity** (in the same manner as described above only for contact) as previous studies used proximity as a relationship quality approximation. Moreover, relationship quality was computed using **approach** interactions where the number of approaches of individual A to individual B is divided by the total number of approaches of individual A to all individuals.

I also assess relationship quality by the **grooming interactions** between two particular individuals. It was computed as a proportion of total time of grooming interactions within given dyad and total grooming time individual spent grooming all partners (data from a focal instantaneous sampling). However, I could not use this way of computing relationship quality because I wanted to use the relationship quality to explain the distribution of grooming. So relationship quality measured by grooming does not represent a suitable

variable because it is dependent on grooming per se, but was computed to enable comparison with other relationship quality measurements. Another possible measurement of relationship quality is based on **coalitionary support** among individuals, but the very low frequency of these interactions did not enable us to employ this measurement. Relationship quality characteristics were computed for each season separately.

3.6: Dominance hierarchy.

Displacement interactions between pairs of individuals were used to assess dominance rank. Sociometric matrices were assembled using the displacement interactions to compute the dominance hierarchy. Hierarchy was computed for each season separately in a specialized program for performing frequency matrices – **MatMan 1.1.4** (Noldus 2003). MatMan 1.1.4 is a program for performing a variety of ethological analyses of frequency (interaction) matrices and transition matrices. These analyses include a directional consistency index, linear hierarchy indices for dominance matrices as well as reorganization of a dominance matrix such that the subjects are in linear rank order (*de Vries et al., 1993)*. Within each season, subjects were ranked in ascending order with the most dominant assigned a score of 1. Linearity of dominance hierarchy within each season was computed via linearity index h', which is based on Landau's index *(h)* but corrected for unknown relationships and the proportion of interactions in the less common direction *(Singh et al. 2003)*. Linearity index h' ranges form 0 to 1 where the absolute linearity gets the score of 1. Directional consistency index *(DC)* assesses if relationship is more unidirectional or more bidirectional. DC ranges from 0 to 1, where the closer to 1 the more unidirectional.

3.7: Kinship data.

3.7.1: Sampling

I received a **pedigree** from management of The Upper Rock Nature Reserve concerning kinship among females of the study group. Only maternal kinship data were available, and the kinship among some females remained unresolved. Hair samples were collected to ensure and to clarify the kinship relationships based on pedigree among adult females (samples were provided by GONHS). I observed 17 females but hair samples were obtained only from 14 of them (kinship of the remaining three females was derived from the

pedigree). Hair samples were stored in room temperature for approximately six months prior to **laboratory analysis**.

3.7.2: DNA extraction, PCR amplification and fragment analysis

A portion of hair containing the follicle was placed root-end down in 100 µl of 5% Chelex and firstly heated for 2 hours at 56ºC. Then the sample was heated at 95-100ºC for 10 min. After these steps samples were centrifuged at maximum speed (at Centrifuge 5415 R) for 5 min. Supernatant was placed into a new 1.5 ml microfuge tube and stored at -20 ºC.

I used 11 microsatellite loci designed for humans and rhesus macaques (D1S548, D3S1768, D5S1457, D6S311, D6S501, D7S503, D7S2204, D8S1106, D10S1432, D11S925, D14S255). These microsatellite loci were already used in several studies *(Coote and Bruford, 1996; Morin et al., 1998; von Segesser et al., 1999; Bradley et al., 2000; Lathuillière et al., 2001; Oka and Takenaka, 2001; Buchan et al., 2003; Charpentier et al., 2003; Andrade et al., 2004; Chambers et al., 2004; Kümmerli and Martin, 2005; Brauch et al., 2008; Charpentier et al., 2008; Liu et al. 2008; Modolo et al., 2008;).* All but two (D5S1457, D10S1432) were successfully amplified in our study. Most of the microsatellite sequences consisted of tetranucleotide repeats, but 3 markers (D7S503, D11S925, D14S255) contained dinucleotide repeats. Always one primer of each pair was labeled with the fluorescent dye, FAM, NED, PET, or VIC.

I amplified microsatellite loci in four multiplex sets (set A: D7S503, D14S255; set B: D3S1768, D6S501, D7S2204, D8S1106; set C: D1S548, D6S311, D11S925; set D: D5S1457, D10S1432) using the QIAGEN Multiplex PCR kit. **PCR reactions** were performed in a total volume of 10 µl consisting of 5 µl Qiagen Multiplex PCR kit, 2 pmol of each primer and template DNA (volume of supernatant was 1 µl). Amplification was run on XP Cycler (Bioer Technology) using the same PCR profile for all combination of primers. The PCR profile contained a 15 min initial denaturation at 95ºC, followed by 35 cycles (94ºC for 30s, 58ºC for 90s, 72ºC for 90s), and a final 10 min extension at 72ºC. 0.1 µl of PCR products was mixed with 12 µl deionized formamide and 0.3 µl GeneScan Internal Lane Size Standard-GeneScan-500 [TAMRA] (Applied Biosystems). **Fragment analysis** was carried out on an ABI 3130 Genetic Analyser (Applied Biosystem) and electrophoretograms were analysed manually in **GeneMapper v.3.7** (Applied Biosystem).

3.7.3: Data analysis

ML-Relate, a computer program, was used for maximum likelihood estimation of relatedness and relationship *(Kalinowski et al., 2006)*. This program is useful for discriminating among four pedigree relationships: unrelated (U), half-siblings (HS), full-siblings (FS), and parent-offspring (PO). Results were then used for assessment of maternal relatedness (Appendix II). In the following analysis, related individuals were labeled as those individuals that were members of the same matrilinear group *(as in Thierry et al., 1990, Call et al. 1996)* where degree of relatedness is r ≥ 0,125 (relatedness inside matrilinear groups was as follow: mother-daughter and full-sisters: r=0,5; half-sisters and grandmother-granddaughter: r=0,25, aunt-niece: r=0,125). Non-related individuals were all others out of the particular matrilinear group.

3.8: Data analysis.

I used non-parametric – Spearman correlation to test which variables can possibly influence grooming distribution. The same correlation was used to compare grooming distribution between seasons and to found relationship between different measurements of relationship quality. I tested if dyads of related and unrelated individuals differ in the relationship quality. I used One-Way Anova to found whether females with kin differ from females without kin in amount of grooming given or received. One-Way Anova was also used to describe whether females with infant (baby under 1 year of age) differ from females without infant in amount of grooming given or received. All the above analyses were computed in **Statistica ver. 9** (Statsoft). These basic statistic's results were used mainly as exploratory tests. It should be emphasized that the results of the correlation analyses with grooming frequency and grooming time data are statistically unacceptable due to pseudo-replications. In other words the basic unit of these analyses is grooming frequency or duration and the data are not independent because several data points belong to specific dyad of individuals. Moreover the number of grooming interaction is not comparable among group members; some individuals grooming each other more often (or longer) then others. Two different statistical approaches were employed to deal with the problem of pseudoreplications.

First, I used analyses in program **Matrix Tester 2.1**. developed by Hemelrijk (1990) The tests can be applied to all sorts of social behaviours. Permutation procedures for association between matrices (such as Mantel Z, R and K test, and Kr statistic) are used as a

statistical test for detecting reciprocity and/or interchange. These tests require the two correlated matrices to be of the same size. The most relevant test concerning data used in this study is the Kr test, because it measures observed behaviour per animal and its interactions with all of potential partners. The partial Kr test is a row-wise, distribution-free matrix permutation correlation technique based on the Kendall correlation test that uses data in all cells of a social interaction matrix, i.e., from all pairs of animals in a matrix, while avoiding problems of their interdependence. The Mantel Z test is less appropriate, because its results are more influenced by those individuals that groom extremely often (Hemelrijk, personal communication). The existence of only a few extreme values may strongly bias the results of the Mantel Z test. That is the reason why I preferred Kr test before Mantel Z in interpretation of the results. The remaining tests are used as supplementary tests. Matrix Tester 2.1 computes one-tailed probability value of a correlation in the right half of distribution (Pr). In test for interchange, only this right-sided one-tailed probability value is of interest, since left-sided P-value (Pl) indicates a negative correlation. The probability levels are based on 500 permutations as recommended by Hemelrijk (1990). The matrices contained data for all 17 females (17 rows and 17 columns) which made matrices with 289 cells. Correlations between pairs of matrices were computed for following pairs of variables: dominance and frequency of grooming given; dominance and time of grooming given; relationship quality and frequency of grooming given; relationship quality and time of grooming given; kinship and frequency of grooming given; kinship and time of grooming given. All of these correlations were made for each season separately.

Linear mixed effect models (LMM) were used to test the effect of proposed factors on grooming distribution. Grooming was represented by two measurements: frequency of grooming (the sum of grooming acts when A grooms B divided by the total time of observation of the two individuals) and time of grooming (the sum of grooming time when A groom B divided by the total time of observation of the two individuals) separately for each season. The grooming data were log transformed to increase the homogeneity of their distributions. The identity of a groomer and groomee were used as crossed random factors in the models. All the LMM analyses were run in **R 2.11.1** (R Development Core Team, 2010).

The two models (one for grooming frequency and one for grooming time) tested effects of 3 categorial and 1 continuous variables, including following:

categorial variables:

Kinship – this variable represented the maternal kin relationship between groomer and groomee, with two states: kin, and non-kin.

Dominance – this variable represented the rank position of the groomer relatively to groomee, with three states: dominant, same, submissive.

Season – this variable had two states: season one and season two corresponding with the first season 2007-2008 and with the second season 2008-2009 of the study.

continuous variables:

Relationship quality – this variable was measured by time spent in contact between the given pair of individuals relatively to time spent with other group members.

The Markov chain Monte Carlo simulation method was used to estimate the distribution of model parameters, using the highest posterior density (HPD) intervals (with 95% coverage) to characterize the parameter estimates *(Gelman et al. 1995)*.

4.0: Results

4.1: Dominance hierarchy.

Social dominance hierarchy was assessed on the basis of dyadic displacement interactions. The displacement interactions were entered into two sociometric matrices; one for each season. The resulting dominance hierarchies were significantly linear and the direction of interactions was highly consistent with the resulting rank order. No rank changes were identified during the given season, but several changes in rank order were found between the seasons. All dominance characteristics were computed in MatMan (Table 1).

Table 1: Dominance hierarchy characteristics for two seasons.

dominance characteristics	season 2007-2008	season 2008-2009
N of displacement interactions	495	395
linearity index h' (P)	0.78 (<0.001)	0.63 (<0.001)
directional consistency index	0.97	0.99
% (number) of unknown relationships	15,44%(21)	25,74% (35)
% (number) of one‑way relationships	79,41%(108)	73,53% (100)

4.2: Maternal kinship.

I identified these 8 matrilinear sub-groups: 1. Athene, Makeup, Emily (EMI), Livia (LIV), Princess (PRI), Sandy (SAN); 2. Blondini (BLO), Punta (PUN), Ruth (RUT); 3. Artemis (ARE), Sophie (SOP); 4. April, Tris (TRI); Other females has no relative female in the study group: 5. Artist (ART); 6. Lea (LEA); 7. Posh (POS); 8. Mercedes (MER); The kinship of Athene, Makeup and April was derived from the given pedigree (Table 2).

Table 2: Matrix of relationships from program ML-Relate.
This report shows the relationship between each pair of individuals that has the highest likelihood among the four following relationships: U = Unrelated, HS = Half Siblings, FS = Full Siblings, PO = Parent / Offspring

name	ART	RUT	PUN	BLO	MER	SOP	LEA	ARE	PRI	LIV	POS	TRI	EMI	SAN
ART	-													
RUT	U	-												
PUN	U	FS	-											
BLO	U	FS	FS	-										
MER	U	U	U	U	-									
SOP	U	U	HS	HS	U	-								
LEA	U	U	U	U	U	U	-							
ARE	U	U	U	U	HS	FS	U	-						
PRI	U	U	U	U	U	U	U	U	-					
LIV	U	U	U	U	U	U	U	U	HS	-				
POS	U	U	U	U	U	U	U	U	U	U	-			
TRI	U	HS	U	HS	U	U	U	U	U	U	U	-		
EMI	U	U	U	U	U	U	U	U	FS	FS	U	U	-	
SAN	U	U	U	U	U	U	U	U	HS	HS	U	U	FS	-

The fact whether an individual has or has not **maternal kin** (coded as 1 = has kin, 0 = has not kin) has not significant effect neither on time of received or given grooming nor on frequency of received or given grooming for both seasons (One-way Anova: for season 2007/2008: Df = 1, F = 0,31, p = 0,58; Df = 1, F = 0,02, p = 0,91; Df = 1, F = 0,28, p = 0,61; Df = 1, F = 1,4, p = 0,25; for season 2008/2009: Df = 1, F = 0,45, p = 0,51; Df = 1, F = 0,01, p = 0,92; Df = 1, F = 0,80, p = 0,39; Df = 1, F = 1,34, p = 0,27). Logarithmic transformation (log) was used for all data but categorical factor (kin).

4.3: Comparison of relationship quality measurements.

Previous literature used several different measures of **relationship quality** based on different behavioural characteristics and spacial proximity measures. I correlated 4 measures of relationship quality from our dataset to evaluate how comparable they are (Table 3, 4). Our results suggest that the 4 relationship quality measures are comparable and may be used interchangeably to some degree. For the next analyses, I chose the relationship quality computed by the time spent in body contact because it has the lower correlation coefficient with the relationship quality computed through the grooming compared to measurement based on approach.

Table 3: Correlations between different measurements of relationship quality for the first season 2007-2008. Marked correlations are significant at $p < 0,05$.

relationship quality	cont	cont+px	Grooming	approach
cont	1,00			
cont+px	**0,93**	1,00		
grooming	**0,56**	**0,60**	1,00	
approach	**0,64**	**0,66**	**0,65**	1,00

cont = contact, px = proximity

Table 4: Correlations between different measurements of relationship quality for the second season 2008-2009. Marked correlations are significant at $p < 0,05$.

relationship quality	cont	cont+px	Grooming	approach
cont	1,00			
cont+px	**0,65**	1,00		
grooming	**0,44**	**0,33**	1,00	
approach	**0,61**	**0,62**	**0,47**	1,00

cont = contact, px = proximity

Relationship quality was significantly different between dyads composed of **maternal kins** and dyads composed of **non-kins** (Mann-Whitney U-test: $N_{kin}= 34$, $N_{non}= 116$, $U = 845$, $p < 0,05$).

4.4. Correlations between grooming descriptors and other individual characteristics.

I used **Spearman correlation** to describe which variables can possibly influence grooming distribution and to describe basic relationships among collected data. Each season was tested

separately (Table 5; 6). I also correlated results between seasons to describe stability of recorded behaviors (Table 7; 8).

Dominance positively correlated with time of grooming given (results significant only in first season) and negatively with time of grooming received, which means that dominant females groomed others for shorter time and were groomed for longer time then subordinate females. No significant correlations between dominance and grooming frequency were found in either season. **Sociability** positively correlated with time of grooming received in the first season. Thus females who were more sociable were groomed longer then less sociable females. However **Sociability** had no influence on grooming distribution in the second season. **Number of maternal kins** positively correlated with time of grooming received, which means that female who had more related individuals were groomer for longer time in the second season but the results were not significant in first season (measured as a time) (Table 5).

Table 5: Correlations for dominance and sociability with time of grooming and frequency of grooming for both seasons. Marked correlations are significant at p < 0,05.

Grooming	Season 2007-2008			Season 2008-2009		
	dominance	Sociability	N of mat. kins	dominance	sociability	N of mat. kins
time given	**0,51**	-0,46	-0,19	0,35	0,11	-0,06
time received	**-0,52**	**0,51**	0,05	**-0,51**	0,29	**0,64**
frequency received	0,43	-0,24	-0,19	0,10	0,44	0,34
frequency given	-0,06	0,39	-0,17	0,42	0,36	0,20

N of mat. kins = number of maternal kins

Hinde index for partners positively correlated with dominance in both seasons, thus dominant females groomed fewer partners than they were groomed by contrary to subordinate females. Hinde index for partners was negatively correlated with sociability (results significant only in the first season), which means that more sociable females were groomed by more partners than they groomed. Hinde index for partners negatively correlated with number of kins in both seasons, which means that the less maternal kins female had the more partners she groomed than she was groomed by (Table 6).

Hinde index for time positively correlated with dominance in both seasons, which means that dominant females spent less time by grooming other partners relatively to grooming time they received from others. Hinde index for time negatively correlated with sociability (results significant only in the first season), thus more sociable females spent more time by grooming other partners relatively to grooming time they received from others. Hinde index for time negatively correlated with number of maternal kins (results significant only in the second season), which means that the more maternal kins the female had the less time she spent with grooming others, in comparison with grooming time she was groomed by others (Table 6).

Shannon index for frequency of grooming given and **Shannon index for frequency of grooming received** did not correlate with dominance, sociability, or number of kins in the first season, which means that the diversity of a female's grooming partners was not influenced by dominance, sociability, or number of kins. The same results were found for the second season with one exception – **Shannon index for frequency of grooming received** negatively correlated with dominance, which means that dominant individuals were groomed more evenly by fewer partners then subordinate individuals in the second season (Table 6).

Table 6: Correlations for Hinde index for partners, Hinde index for time, Shannon index for frequency of grooming given, and Shannon index for frequency of grooming received with dominance, sociability, and number of maternal kins for both seasons. Marked correlations are significant at p < 0,05.

	Season 2007-2008			Season 2008-2009		
	dominance	sociability	N of mat. kins	dominance	sociability	N of mat. kins
Hinde index for partners	**0,83**	**-0,60**	**-0,50**	**0,84**	-0,29	**-0,68**
Hinde index for time	**0,59**	**-0,59**	-0,16	**0,62**	-0,24	**-0,59**
Shannon index freq. giv.	-0,37	0,20	0,03	-0,17	0,00	-0,21
Shannon index freq. rec.	0,00	0,40	-0,34	**-0,55**	-0,12	0,01

N of mat. kins = number of maternal kins, Shannon index freq. giv. = Shannon index for frequency of grooming given, Shannon index freq. rec. = Shannon index for frequency of grooming received

Stability of grooming behaviours between seasons was also tested using several measures of grooming (Table 7). Only frequency of grooming given was significantly correlated and thus stable between seasons. The remaining three grooming characteristics also showed tendency for positive correlations however they did not reached statistical significance.

Table 7: Correlations of grooming behaviours between season 2007-2008 (1) and 2008-2009 (2). Marked correlations are significant at p < 0,05.

season 1x2	frequency given 2	frequency received 2	time given 2	time received 2
frequency given 1	**0,52**	0,12	**0,61**	**0,56**
frequency received 1	-0,12	0,42	-0,06	0,22
time given 1	0,35	0,10	0,45	**0,53**
time received 1	0,09	0,14	0,30	0,32

I also correlated indices computed separately for each season to test **stability of grooming descriptors between seasons**. Only Hinde index for partners and also Shannon index for frequency of grooming received correlated between seasons (Table 8).

Table 8: Correlations between indices describing grooming distribution across the seasons. Marked correlations are significant at p < 0,05

Seasons 1x2	Hinde index partners 2	Hinde inndex time 2	sociability 2	Shannon index frequency given 2	Shannon index frequency received 2
Hinde index partners 1	**0,88**	**0,63**	**-0,61**	0,28	**-0,69**
Hinde index time 1	**0,68**	0,41	-0,41	0,07	**-0,58**
sociability 1	-0,20	-0,06	0,35	-0,31	-0,07
Shannon index frequency given 1	-0,37	0,03	0,02	-0,07	-0,31
Shannon index frequency received 1	**-0,91**	**-0,54**	**0,55**	-0,29	**0,83**

4.5: Results of matrices correlations.

These matrices contained data for all 17 females (17 rows and 17 columns). The most relevant test regarding interpretation of the results is the Kr test, because it measures observed behaviour per animal and its interactions with all of potential partners (Hemelrijk, 2010 - personal communication). The probability levels are based on 500 permutations. Marked correlations are significant at p < 0,05. Data from each season were tested separately.

Correlation between dominance and frequency of grooming given

Positive correlation between these two matrices was significant for all used tests in both seasons. Higher-ranking females were groomed more often then lower-ranking females in both seasons.

Season 2007-2008

1. Tau Kr test: Kr = 304, Tau Kr = 0,269;

one-tailed probability value: right-sided **Pr= 0,0020**, left-sided Pl= 1,0000

2. Mantel Z test: Mantel Z = 4265;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

3. R test: R test = 5602419,25;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 304 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 406 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 710 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Season 2008-2009

1. Tau Kr test: Kr = 304, Tau Kr = 0,269;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

2. Mantel Z test: Mantel Z = 4265;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

3. R test: R test = 5602419,25;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 304 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 406 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 710 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Correlation between dominance and time of grooming given

Positive correlation between these two matrices was significant for all used tests in both seasons. High-raning females are groomed longer than lower-ranked females in both seasons.

Season 2007-2008

1. Tau Kr test: Kr = 311 , Tau Kr = 0,271;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

2. Mantel Z test: Mantel Z = 11343;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

3. R test: R test = 5636599;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 311 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 425 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 736 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Season 2008-2009

1. Tau Kr test: Kr = 337, Tau Kr = 0,335;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

2. Mantel Z test: Mantel Z = 6801;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

3. R test: R test = 5603254,25;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 337 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 401 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 738 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Correlation between relationship quality and frequency of grooming given

Positive correlation between these two matrices was significant for all used tests in both seasons. Females groomed more often those females with whom they had better relationship quality in both seasons.

Season 2007-2008

1. Tau Kr test: Kr = 655, Tau Kr = 0,505;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

2. Mantel Z test: Mantel Z = 43126;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

3. R test: R test = 5826366;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 655 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 728 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 1383 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Season 2008-2009

1. Tau Kr test: Kr = 525, Tau Kr = 0,451;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

2. Mantel Z test: Mantel Z = 33672;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

3. R test: R test = 5689727,5;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 525 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 580 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 1105 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Correlation between relationship quality and time of grooming given

Positive correlation between these two matrices was significant for all used tests for both seasons. Females groomed longer such social partners, which were characterized by better relationship quality in both seasons.

Season 2007-2008

1. Tau Kr test: Kr = 714, Tau Kr = 0,527;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

2. Mantel Z test: Mantel Z = 114028;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

3. R test: R test = 5876787,5:

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 714 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 658 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 1372 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Season 2008-2009

1. Tau Kr test: Kr = 432, Tau Kr = 0,377;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

2. Mantel Z test: Mantel Z = 77854;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

3. R test: R test = 5622463,25;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 432 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 509 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 941 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Correlation between kinship and frequency of grooming given

Positive correlation between these two matrices was significant for all used tests, with exception of Mantel Z test in second season. Females groomed more often females who are their maternal kin.

Season 2007-2008

1. Tau Kr test: Kr = 274, Tau Kr = 0,416;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

2. Mantel Z test: Mantel Z = 416;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

3. R test: R test = 5433608;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 274 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 324 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 598 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Season 2008-2009

1. Tau Kr test: Kr = 176, Tau Kr = 0,280;

one-tailed probability value: right-sided **Pr= 0,0040,** left-sided Pl= 0,9980

2. Mantel Z test: Mantel Z = 153;

one-tailed probability value: right-sided Pr= 0,1537, left-sided Pl= 0,8563

3. R test: R test = 5342148;

one-tailed probability value: right-sided **Pr= 0,0040,** left-sided Pl= 0,9980

4. K test:

K values and one-tailed probability value:

Rows: Kr = 176 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 232 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 408 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Correlation between kinship and time of grooming given

Positive correlation between these two matrices was significant for all used tests in both seasons. Females groomed longer those females who are their maternal kin.

Season 2007-2008

1. Tau Kr test: Kr = 255, Tau Kr = 0,336;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

2. Mantel Z test: Mantel Z = 950;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

3. R test: R test = 5402668;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 225 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Columns: Kc = 322 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 547 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

Season 2008-2009

1. Tau Kr test: Kr = 135, Tau Kr = 0,218;

one-tailed probability value: right-sided **Pr= 0,0120,** left-sided Pl= 0,9900

2. Mantel Z test: Mantel Z = 542;

one-tailed probability value: right-sided **Pr= 0,0299,** left-sided Pl= 0,9721

3. R test: R test = 5309916;

one-tailed probability value: right-sided **Pr= 0,0020,** left-sided Pl= 1,0000

4. K test:

K values and one-tailed probability value:

Rows: Kr = 135 - right-sided **Pr= 0,0080** left-sided Pl= 0,9940

Columns: Kc = 228 - right-sided **Pr= 0,0020** left-sided Pl= 1,0000

Sum: K = 363 - right-sided **Pr= 0,0020** left-sided PI= 1,0000

4.6: Results of LMM.

The first LMM tested the effect of kinship, dominance, relationship quality and season on grooming frequency. The second model tested effect of the same variables on duration of grooming interactions. The results of the two models yielded similar, although not identical results. Kinship, dominance and relationship quality had significant effect (the estimated

parameters are deduced non-zero, based on HDP intervals coverage) on grooming distribution, in both models. The effect of season was not significant in either of the two models. The dyads tied by maternal kinship have significantly higher frequency of grooming as well as longer grooming time. The subordinate individuals groomed dominant ones more often and for longer time then vice versa. Finally, dyads with higher (better) relationship quality have higher grooming frequency as well as longer grooming time. The estimated effect size shows that relationship quality represents the most important factor to explain the grooming distribution in both models. The results also suggest that kinship explains more variability in grooming frequency then social hierarchy, but the later explains more variability in grooming time then kinship.

Table 9: The results of grooming frequency model.

Fixed effects			
	estimate	lower HPD	upper HPD
kinship non	-0,72	-1,09	-0,35
Hierarchy sub	0,37	0,1	0,74
relationship	2,96	2,31	3,61
season 2	-0,21	-0,43	0,02

Highest posterior density (HPD) interval summary for grooming frequency model (Table 9): The HPD intervals characterize the effect of factors included in the model with 95% reliability.

Kinship: The model predicts that in the absence of maternal kinship between the grooming partners the grooming frequency is 66% to 33% lower when compared to grooming frequency among maternal kin dyads.

Hierarchy: The model predicts that when groomer is subordinate to groomee the frequency of grooming is 10 to 108% higher when compared to the state when groomer is dominant to groomee.

Relationship quality: The model predicts that a rise of 0.1 of the relationship quality value will lead to increase in grooming frequency from 26 up to 44% compared to original value.

Table 10: The results of grooming time model.

Fixed effects			
	estimate	lower HPD	upper HPD
kinship non	-0,83	-1,27	-0,15
Hierarchy sub	1,36	0,99	1,79
relationship	3,31	2,37	4,42
season 2	-0,17	-0,53	0,23

Highest posterior density (HPD) interval summary for grooming time model (Table 10):

The HPD intervals characterize the effect of factors included in the model with 95% reliability.

Kinship: The model predicts that in the absence of maternal kinship between the grooming partners the grooming time is from 6% to 23% shorter when compared to the time of grooming among maternal kin dyads.

Hierarchy: The model predicts that when groomer is subordinate to groomee the time of grooming is from 171 to 499% longer when compared to the state when groomer is dominant to groomee.

Relationship quality: The model predicts that a rise of 0.1 of the relationship quality value will lead to increase in grooming time from 27 to 56% compared to original value.

Previous analysis has shown that relationship quality and kinship were related. Thus I also tested whether the contribution of the relationship quality had significantly improved the models. I first computed models without the relationship quality (both for grooming frequency and grooming time) and then models where relationship quality was added. The models with relationship quality had lower AIC in both cases.

5.0: Discussion

The main aim of this study was to investigate which variables influence grooming distribution among Barbary macaque females. The effect of dominance hierarchy, kinship, and relationship quality was tested. The results suggest that all these variables were important for individual's choice of grooming partners. Moreover, the effects of all factors were analysed using LMM and thus relative strength and importance of each factor to other factors was compared.

5.1: Stability of grooming behaviours between seasons.

Stability of grooming behaviour and distribution among individuals between the two seasons was evaluated. Only Hinde index for grooming partners (proportion of partners whom a subject groomed relative to those who groomed the subject), Shannon index for grooming partners (diversity of a female's grooming partners based on frequency of received grooming), and frequency of grooming given were stable between seasons. I did not find any significant results for correlations of other six descriptors (see tab. 4 and 5).

The changes in grooming behaviour could be explained by immigration of three new males who immigrated to Apes'den group between the first and the second season. Immigration of new males could increase social instability inside the group and can be source of psychological stress as confirmed by Beehner et al., (2005) or Engh et al. (2006) for baboons. Newly arrived males could not only increase the level of stress but also change the grooming distribution. Such changes in social interactions under the unstable social conditions were reported in baboons *(Crockford et al., 2007)*, where females experienced lower stress hormone levels in months when the social situation was stable and when they concentrated their grooming among a smaller number of partners than when their grooming was more evenly distributed among many partners. In our study, only grooming interactions between females were analysed, however females also participated in grooming interactions with males. Thus the arrival of new males could directly affect the grooming behaviour of females, who might distribute their grooming interactions between more individuals (including males) in the second season. Total time of grooming interactions in given individual is restricted by the time necessary for other activities. Therefore females need to change the distribution of their grooming interactions with increasing number of individuals or changed social environment. They may change frequency, time and identity of their grooming partners.

5.2. Comparison of different measurements of relationship quality.

Different patterns of affiliative interactions such as grooming, coalitionary support, approach interaction, and body contact or proximity can be observed among group members. These social interactions have been used for assessment of relationship quality either separately or together in previous studies *(Castles et al., 1996; Call et al., 1999; Cords, 2002; Weawer, de Waal, 2002; Majolo et al., 2010)*. There is no uniform conclusion about standard

method for relationship quality assessment yet. Our data set enables us to compute several measurements of relationship quality based on: grooming interactions, approaches, and spatial distribution measured as a contact or contact plus proximity between two individuals. I obviously could not use relationship quality computed through the grooming interactions to test the effect of this factor on grooming distribution. However, our comparison showed that all these measurements of relationship quality correlated one with another and therefore results of studies using different way of measuring relationship quality are comparable to some degree. Our findings can be also supported by recent study of Majolo et al. (2010). Their results suggest that social relationship can be measured using different behaviours.

5.3. The effect of dominance, kinship and relationship quality on grooming distribution.

First I would like to discuss the results of the analyses where each factor was analysed separately.

I found strong evidence that dominance relationships influence female's preference for grooming partners. Female Barbary macaques directed their grooming up the hierarchy. This conclusion is based on results of correlations of matrices. Low-ranking females initiated grooming more often as well as groomed their partners longer than high-ranking females in both seasons. These results showed that dominant individuals were preferred as grooming partners. The same pattern was also found for other *cercopithecoid* primates in many other studies (for review see *Schino, 2006; Chacma baboon – Barret et al., 1999; Japanese macaque - Nakamichi and Shazawa, 2003; Lion-tailed macague – Singh et al., 2006; Crab-eating macagues - Gumert, 2007; Gumert and Ho, 2008).* The tendency to prefer dominant grooming partner is usually explained by the social market theory when low ranking females have more to gain from high ranking individuals than vice versa *(Slater, 2002)*. The low ranking females may exchange grooming for agonistic support from dominant individuals *(Schino, 2006)*, their tolerance *(Henzi and Barrett, 1999)*, or for access to wanted or scarce resources *(Gumert and Ho, 2008)*. Although I did not tested direct exchange of grooming for coalitionary support or tolerance, our results support classical model of grooming distribution *(Seyfarth, 1977)* when subordinate individuals direct grooming towards dominant ones.

I found that maternal kins represent preferred partners for grooming interactions. Females groomed more often and for longer time their maternal kins than non-relative females. Also female who had more maternal kins tend to received longer grooming session from others (see tab. 2). The affiliative interactions are much more frequent among kin than

among non-kin in the cercopithecines primates *(Barbary macaque - Aureli et al., 1997; Thierry, 1990; Silk, 2002a; Chacma baboon – Smith et al., 2003; Schino, 2006)*. Many studies have demonstrated that females of most Old world monkeys prefer their relatives *(van Schaik and Aureli, 2000; Schino, 2006)* which is beneficial for their reproductive success as predicted by inclusive fitness theory *(Hamilton, 1964a,b)*. Related individuals share genes due to common descent and therefore any protective or helpful behaviour towards the relatives is beneficial for actors too.

The distribution of grooming was strongly influenced by relationship quality. This was supported by the correlations among matrices in both seasons. Females preferred those females with whom they had a better relationship quality. It is particularly obvious that primates living in larger groups do not interact similarly with all group-mates *(Aureli and Schaffner, 2002)*, even when these belong to the same age, sex, or kinship class *(Cords, 1997b)*. They distribute particular behavioural interactions, such as grooming, differently across group members *(Cooper et al., 2005; Castles et al., 1996)* depending on the identity of the partner and his characteristics including their mutual relationship quality. Many previous studies found that the time individual spent grooming the most favourite partner was greater than the time individual spent grooming the least favourite one *(*for review see *Henzi and Barrett, 1999; Bonobo - Hohmann and Fruth, 2000; Blue monkey – Cords, 2002)*. Silk et al. (2006) 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. Individuals with good relationship quality are relatively tolerant of one another in feeding and social contexts, provide protection against predators either through alarm-calling or active defence, and may support one another in contests with other groups over feeding areas or territorial boundaries *(Cords, 1997b)*. Thus individuals may prefer those with whom they have good relationship simply because of the higher probability that their acts will be reciprocated.

5.4: Comparison of the relative effects of the factors.

The pattern of results acquired using LMM was very similar with results of other statistical analyses. I found that dominance, kinship, and relationship quality are important factors for grooming partner choice. The model also provided the comparison of all these observed variables and enables to assess what variable is the most important one. I found that the biggest effect on grooming distribution had the relationship quality. The relationship

quality was the strongest factor in both models (grooming frequency model, grooming time model). These results are in agreement with predictions based on more tolerant dominance style of Barbary macaques. According to Thierry (2000), dominance and kinship should not play such important role in species with more tolerant dominance style. And thus I predicted that relationship quality may represent the most important factor in grooming distribution in Barbary macaque females.

A general high level of social tolerance may decreased the need of low-ranking females to achieve tolerant relationships via grooming-tolerance exchanges with high-ranking females *(Henzi & Barrett, 1999)* and therefore their choice of grooming partners could depend more on relationship quality. The higher level of social tolerance also decrease the importance of kinship *(Thierry, 2000)*, because females engage less often in serious agonistic interaction where kin based coalitionary support is necessary. The second most powerful variable influencing grooming partner choice was the kinship in the grooming frequency model and dominance in the grooming time model. The third most powerful variables influencing grooming partner choice was the dominance in the grooming frequency model and kinship in the grooming time model. This fact could mean that kinship and dominance are variables with quite similar strength in Barbary macaques. However, it could be hypothesized that individuals employ different strategies to bond with maternal kin partners or with dominant individuals. Results of these two models may suggest that maternal kinship influence more the frequency of grooming meanwhile dominance relationship effect more the time of grooming.

5.5: Comparison of macaque species.

Macaque species differs in patterns of social interactions depending on their dominance style. Dominance gradient is the steepest and importance of hierarchy in social interactions is the most pronounced in species from the first grade e.g. Rhesus macaques *(Thierry, 2000)*. On the other hand, species belong to the third or fourth grade are supposed to be less biased toward the dominant individuals as found in e.g. Sulawesi macaques (*Thierry et al., 2000a*). In these species, status differences do not restrict contacts between group members and have little effect on grooming distribution *(Thierry et al., 1990)*. Our results show that hierarchy is important factor for partner choice despite the fact that Barbary macaques belong to the third grade. Similarly in lion-tailed macaques (grade 3), Singh et al. (2006) found that grooming given negatively correlated with dominance ranks indicating that

high ranking females gave less grooming. On the other hand, females of Tonkean macaques (grade 4) showed no correlation among grooming distribution and dominance rank (Thierry et al., 1994). Although it was predicted that grooming distribution in Barbary macaques is relatively independent on dominance hierarchy, dominance had a significant effect on grooming distribution. This result may be a consequence of human provisioning *(Hill, 1999)* in the group under study, including clumped food provisioning by local management and tourist provisioning. Provisioning thus represent a situation when dominant females can possibly exert their social power to obtain wanted resources. This could be the reason why low-ranking females tend to prefer dominant individuals as a grooming partner.

Thierry (2000) found very similar pattern of grooming distribution depending on the kinship. For instance, Japanese macaques (grade 1) are known for their strong kinship networks. Females have a high preference for relatives and strict rules of inheritance determine the acquisition of dominance rank within matrilines *(Kawamura, 1958)* grooming is also given more to family members *(Mehlman and Chapais, 1988)*. The degree to which females prefer relatives in affiliative contact, social grooming and support in conflicts is less pronounced in the third grade than in the first two grades *(Thierry, 2000)*. Despite the prediction that grooming distribution in Barbary macaques is relatively independent on kinship due to their more tolerant dominance style, it had significant effect on grooming distribution. Preference of related individuals can be also caused by the fact that females tend to form groups composed of their close relatives, who then support each other during agonistic interactions. The need to form such a group could be multiply because of the pressure caused by additional provisioning. This was supported by Hill (1999) in his study focused on comparison of provisioned and non-provisioned group of Japanese macaques. Females could tend to form matrilinear "supportive" groups more often in provisioned group than under conditions without additional feeding. Also Aureli et al. (1997) found that Barbary macaques are kin biased in affiliative interactions. Similarly, Butovskaya and Kozintsev (1996) found that grooming between maternal relatives of Stump-tailed macaque (grade 3) was significantly more frequent than between those individuals belonging to different matrilines. These results may suggest that kinship is an important factor even for macaques belonging to the more tolerant species. It has been already suggested that the categorisation of macaques species according to dominance style should be rather perceived as continuous scale then 4 strict categories. Previous studies have usually find support for the characterisation of the two extreme grades (1 and 4), but the two other grades are sometimes hard to distinguish and characterised *(Thierry, 1990)*. The main advantage of the LMM

approach was that it enables to compare the relative strength of every factor and the results showed that relationship quality is the strongest factor which is also predicted by the dominance style of Barbary macaques *(Thierry, 2000)*.

The preference for social partners with good relationship was also found in other macaque species of grade 3 *(Stump-tailed macaque – Call et al., 1999; Assam macaque – Cooper et al., 2005)*

Only a small number of previous studies included analysis of more then one factor and its effects on grooming behavior. The current results emphasized the importance of evaluation of more factors in one study. Such approach can lead to different conclusions in given species.

5.6: Summary

The main aim of this thesis was to evaluate the influence of dominance, kinship and relationship quality on distribution of grooming among Barbary macaque females. Data were collected observing 17 females living in one group of free-ranging Barbary macaques. The effects of dominance, kinship and relationship quality were evaluated. The results suggest that choice of grooming partner is definitely not random. Dominance, kinship, and relationship quality are important for grooming distribution among social partners in female Barbary macaques. The results suggest that the most important factor for the grooming distribution is relationship quality, which is explained by rather tolerant dominance style of Barbary macaques, when dominance and kinship are not so important (although not negligible) factors.

These results have also important implications for further research of factors effecting grooming distribution in groups of non human primates.

6.0: Acknowledgements

7.0: References

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Appendix I: Ethogram of Barbary macaque *(Macaca sylvanus)*

List of behaviours analysed in this study:

Behaviours recorded using focal continuous sampling:

approach – an animal comes into proximity of the other or others, stays in proximity for at least 5 sec. and the approach is not motivated by other obvious reason as food.

displacement – one animal in any way (threat, attack or target approach) drives away another from some kind of source (place, shadow, food, partner). Than stay on place and may or may not use the source.

groom – an animal grooms hair of the other, it watches the groomed place on the other's body, using its fingers or mouth, it may or not pick up some particles.

reciprocate groom – an animal, which was groomed, continue the grooming session by grooming it's partner.

Behaviours recorded using instantaneous sampling:

contact – two or more animals are touching with any part of the body including the first third of the tail. It's not any other defined behaviour as embrace, groom, etc.

proximity – two or more animals are in the distance where comfortable touch by hand is possible (it means, that hanging of the body is not necessary).

groom – an animal grooms hair of the other, it watches the groomed place on the other's body, using its fingers or mouth, it may or not pick up some particles.

Complete list of behaviours recorded during the study:

Behaviours recorded using focal continuous sampling (45 behaviours):

approach – an animal comes into proximity of the other or others intent on them.

approach food – an animal comes into proximity of the other or others obviously because of the presence of food source.

avoid – one individual while walking changes the direction of its locomotion because of presence of another individual in the original direction.

bite – one animal bite the other, included in antagonistic interactions, during serious wrestles or aggression.

bridging – two males simultaneously lifted up one infant. These two males usually accompany this behaviour by teeth chattering.

carry away food – an animal carry away food which may interest the others preferably to some safety place.

carry infant – adult male or female carry infant usually on its back.

chase – an animal chase the other within distance of several meters.

copulation – an animal mounts the other with sexual intention, activity is quite long and complete, not only indicative (as mount behaviour).

counter attack – an insulted animal immediately attack the attacking animal in any contact way of aggression.

departure – an animal goes out of proximity of the other, not as a reaction to the others behaviour.

displacement – one animal in any way (threat, attack or target approach) drives away another from some kind of source (place, shadow, food, partner). Than stay on place and use the source.

drink – an animal drink any kind of liquid.

eat – an animal consume natural kind of food (leaves, seeds, flowers etc.), including chewing and food manipulation.

ejaculation – an emission of semen, occurring during genital self-stimulation or mounting.

explore – an animal explore place where any food could be obtained, searching the substrate, looking under stones or other material.

follow – one animal moves to gain proximity or to keep visual contact after another which is moving away.

genital inspection sniff/look/touch – olfactory/visual/manual examination of another individual's genital area.

groom – an animal grooms hair of the other, it watches the groomed place on the other's body, using its fingers or mouth, it may or not pick up some particles.

groom-self – grooming the fur of some part of its own body, an animal is watching the groomed place, it may or not pick up some particles.

grunt – short mostly repeated grunting call.

hand attack – one animal moves its hand/hands toward another in an aggressive manner, clear physical contact : slaps or grasping hair.

hand threat – one animal moves its hand/hands toward another in an aggressive manner, no contact is made.

hold – male grasps female tights, act is sexually motivated, the grasped animal may present, no dorso-ventral contact is made.

hold bottom – one individual grasps other's bottom, act do not have to be sexually motivated, the grasped animal may present, no dorso-ventral contact is made.

invite groom – one animal invites grooming from another, different concrete actions occur, mainly presentation of the body or it's portions.

jump display – an animal runs and leaps, typically with long leaps, on a branches or on the ground, creating some noise if possible.

jump on car/bus – an animal jumps on a car or on a bus.

locomotion – any kind of locomotion, which is not defined as part of another behaviour, including walking/running for a distance longer than 5 metres or resulting in changing the substrate (tree-ground, wall-tree etc.).

lipsmack – the lips are pursed and the lower jaw is moved up and down rapidly and rhythmically. The jaw may be thrust upward. The mouth may be slightly open with the tongue moving back and forth.

mount – one animal comes into ventro-dorsal position similar to copulatory position, but without sexual intention.

play – non-serious behaviour without any obvious aim, including locomotory play, play with object or social play.

present – body is stressed, hindquarters are elevated toward the partner, the upper parts of the body is crouched. May or not connected with other gestures. Not only in sexual context.

provisioning – provisioning by people, sometimes accompanied by stress, not all animals are necessary included.

reciprocate groom – an animal, which was groomed, continue the grooming session by grooming it's partner.

scratch – scratching of the body surface, no serious attention to the scratched part.

search food – an animal is exploring the substrate with his hands, searching for parts of food and eats it afterward.

slap ground – an animal slaps one or both hands on the surface, often accompanied with other gestures (vocalisation, grimace).

take food – an animal intentionally takes food from a proximity of another individual.

take infant – an animal takes infant form another and carry it away.

teeth chattering – an open-mouth gesture with lips and cheeks contracted, mandible opening and closing rapidly, and teeth contacting teeth.

terminate groom – an animal grooming or groomed ends the grooming interaction.

tree shake – an animal shakes with tree to demonstrate its power.

wrestle – serious aggressive interaction including strong hand attacks, when the animals hold each other tight and try to bite the other, often with vocalisation.

yawn – clearly distinguishable activity, an animal open clearly the mouth in automatic manner.

Behaviours recorded using instantaneous sampling (13 behaviours):

contact – two or more animals are touching with any part of the body including the first third of the tail. It's not any other defined behaviour as embrace, groom, etc.

co-provisioning – proximity maintain during provisioning of both individuals simultaneously. Both animals are provisioning.

co-eat – proximity maintain during eating of both individuals simultaneously. Both animals are eating.

drink – an animal drink any kind of liquid.

eat – an animal consume natural kind of food (leaves, seeds, flowers etc.), including chewing and food manipulation.

groom-self – grooming the fur of some part of its own body. an animal is watching the groomed place. It may or not pick up some particles.

locomotion – any kind of locomotion, which is not defined as part of another behaviour, including walking/running for a distance longer than 5 metres or resulting in changing the substrate (tree-ground, wall-tree etc.).

look – an animal is looking around the area (turning his head), no fixed view.

provisioning – provisioning by people, sometimes accompanied by stress, not all animals are necessary included.

proximity – two or more animals are in the distance where comfortable touch by hand is possible (it means, that hanging of the body is not necessary).

rest – an animal is sitting or laying, eyes are closed, head may be or not sideways.

sunbath – an animal is in relaxed position on sunny place, directly presenting it's body to the sunlight.

watch – an animal for longer period (5 and more sec.) fixed his view on concrete object (for example other animal) or direction.

substrate:

bus – bus usually with tourists

car – any car except the bus

ground – any flat or slightly elevated place

rock – solid rocky place

shrub – plants with multiple stems and lower height, lower than 1 meter

tree – woody plant on a single main stem or trunk, higher than 1 meter

wall – any men-made structure, higher than 1 meter