Male Mating Tactics in Captive Rhesus Macaques (*Macaca mulatta*): The Influence of Dominance, Markets, and Relationship Quality

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Abstract Male mating success in a multimale–multifemale group can depend on several variables: body condition, dominance, coalitions, "friendship," or an exchange of services for mating access. Exchange patterns may also be determined by market effects or social relationships. We studied the mating tactics of males in a captive, multimale–multifemale group of rhesus macaques and the resulting patterns of mating and paternity to determine the influence of dominance rank, mating markets, and relationship quality on their mating tactics. Male rank was positively related to the total number of copulations and the number of mating partners, but did not explain male mating distribution completely. Moreover, male fertilization success was not related to male rank. Males did not exchange grooming for mating access on the same day and neither the supply nor the rank (as a proxy for quality) of receptive females affected the amount of male grooming, suggesting that market effects did not explain male mating access. However, there was a positive correlation between long-term grooming patterns of both males and females and mating access, indicating that social relationships were important for male mating access. Paternity data revealed that these social relationships were also important for male reproductive success. We conclude that both male rank and male–female "friendship" determined male mating access in these rhesus macaques, but that "friendship" was more important in determining paternity, emphasizing the

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importance of intersex social bonds in male mating success in multimale primate societies.

Keywords Biological market theory · Dominance · *Macaca mulatta* · Mating tactics · Paternity · Relationship quality

Introduction

Males competing for mating access to females will use mating tactics, i.e., distinct behavioral patterns leading to mating access, depending on their age, health, and body condition (Bercovitch 1997; Bercovitch and Nürnberg 1996) and on their competitors' characteristics (Andersson 1994). For example, strong or dominant males can gain mating access based on their fighting abilities or dominance rank, e.g., mountain goats (*Oreamnos americanuc*: Mainguy *et al.* 2008), meerkats (*Suricata suricata*: Spong *et al.* 2008), anthropoid primates (Cowlishaw and Dunbar 1991), whereas subordinate males may use other tactics, e.g., satellite males in fallow deer (*Dama dama*: Apollonia *et al.* 1992), "coursing" in mountain goats (Mainguy *et al.* 2008), coalitions in savanna baboons (*Papio cynocephalus*: Noë and Sluijter 1990), and special relationships in olive baboons (*Papio anubis*: Smuts 1985). However, male mating success depends not only on the behavior of other males, but also on female mating tactics (Trivers 1972). Females may prefer particular males (Andersson 1994) or mate with many males (Nikitopoulos *et al.* 2005; Richard 1992; Widdig *et al.* 2004), allowing mating access for multiple males that employ different tactics.

Males of many species form clear dominance hierarchies, e.g., primates (Smuts *et al.* 1987), elephants (Payne 2003), spotted hyenas (*Crucuta crocuta*: Drea and Frank 2003), and cooperatively breeding carnivores (Creel and Sands 2003). These hierarchies often play a major role in male mating opportunities, and many studies report a positive correlation between male dominance rank and mating activity, e.g., primates (Cowlishaw and Dunbar 1991), mountain goats (Mainguy *et al.* 2008), or fertilization success, e.g., macaques (Rodriguez-Llanes *et al.* 2009) and lions (*Panthera leo*: Packer *et al.* 1991). Dominant males ensure their mating access and success by possessive following of females and by disrupting consorts of females with other males (Berard *et al.* 1994). However, in some species, males are able to monopolize only 1 female at a time (Carpenter 1942). This combination of hierarchy and monopolization led Altmann (1962) to propose his Priority-of-Access model (PoA), in which male dominance rank and the number of simultaneously sexually receptive females determine the probability that a male will obtain mating access to a receptive female. The PoA model predicts that if there is only 1 receptive female, mating will be monopolized by the alpha male; if there are 2 receptive females, 1 will be monopolized by the alpha male and 1 by the beta male, etc. Some researchers found a mating pattern that supports this model (savanna baboons: Bulger 1993; olive baboons: Packer 1979), whereas in other studies subordinate males have more mating access to females than predicted: savanna baboons (Bercovitch 1986; Noë and Sluijter 1990), olive baboons (Smuts 1985), and rhesus macaques (*Macaca mulatta*: Dubuc *et al.* 2011). This suggests that subordinate males employ other tactics or that females have other preferences (Alberts *et al.* 2003). Especially in

primates, where multiple males can live in the same group with multiply mating females (Dixson 1997), there are ample opportunities for males to employ different mating tactics. Middle-ranking males may form coalitions against high-ranking males to gain access to females, e.g., revolutionary coalitions (Alberts *et al.* 2003; Noë and Sluijter 1990; van Schaik *et al.* 2004), or hide their matings and mate quickly (Berard *et al.* 1994). Alternatively, male affiliation with females may lead to mating opportunities, and developing bonds with females may be very important for individual males to attain mating opportunities (Alberts *et al.* 2003).

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

Biological market theory describes social behavior from an economic perspective. Social acts, such as grooming or mating access, are considered to be valuable commodities that 2 classes of individuals exchange within a biological market to the benefit of both parties (Noë and Hammerstein 1994; Noë *et al.* 1991). These commodities cannot be taken by force and the exchange is preceded by partner choice. The price of a commodity is influenced by supply and demand: when there is little supply and much demand, prices will be high and vice versa (Noë and Hammerstein 1994, 1995). In a primate mating market, males are the demanding class and females can supply mating access. Therefore, males will groom females in exchange for mating access and females will reciprocate by allowing mating access. Biological market theory further predicts that the value of a commodity predicts the price to be paid (Noë and Hammerstein 1994, 1995). For example, mating opportunities with high-ranking females have a greater value because high-ranking females produce more offspring with better survivorship chances compared to low-ranking females (long-tailed macaques: van Noordwijk and van Schaik 1999). High-ranking males may provide more genetic, i.e., direct, benefits to a female or be better able to force a female to mate than low-ranking males (Gumert 2007). In addition, a more dominant male may provide better protection, i.e., indirect benefits, for the female and her future offspring (Smuts 1985). Therefore, the prediction is that males will groom high-ranking females more than low-ranking females, and high-ranking males may groom less than low-ranking males to gain mating access (Gumert 2007). Recently, such market effects have been found in the mating context of long-tailed macaques (Gumert 2007).

Alternatively, males may employ longer-term tactics. Primates maintain differential relationships with group members, varying from good to bad. Individuals with a good relationship have frequent affiliative interactions, e.g., grooming and high proximity levels, often support each other in conflicts, are tolerant toward each other,

and show low degrees of stress when together (Silk 2002). Nonkin individuals with a good social relationship are often referred to as friends (Massen *et al.* 2010; Palombit *et al.* 1997; Smuts 1985). "Friendships" between males and females have been reported for baboons (olive baboons: Lemasson *et al.* 2008; Smuts 1985). A friendship's functional significance for males is probably related to mating access (Palombit 2003), while females obtain protection against infanticide (Palombit *et al.* 1997) or nonlethal harassment (Lemasson *et al.* 2008). Because both sexes benefit from such a relationship, both the male and female are expected to groom each other to maintain the social relationship. Although mating access is not exchanged directly for grooming within friendships, over the long-term a male's grooming behavior will relate to his access to mating partners.

We investigate male mating tactics, i.e., dominance, aggression, mate guarding, sneaky matings, and grooming, in a multimale–multifemale group of captive rhesus macaques (*Macaca mulatta*). Female rhesus macaques mate with multiple males within 1 cycle (Dixson 1998; Manson 1992) and are seasonal breeders. Both male and female rhesus macaques form a clear linear dominance hierarchy at group level (Sade 1972; Thierry 2000), creating ample possibilities for hierarchy-based mating tactics, female choice, and differences in the value of commodities in a possible mating market. Using an observational approach, we aim to determine whether rhesus macaque male mating tactics are influenced by dominance rank, whether mating access is exchanged for grooming, and whether this exchange is governed by short-term market effects or by long-term affiliative patterns ("friendships") between mating partners. In addition, we use paternity data for subsequent offspring to study the effect of male rank and male–female "friendships" on fertilization success.

If male mating tactics are governed by male dominance rank (H1), then we predict that high-ranking males will have more mating partners (H1P1) and mate more (H1P2). Further, we predict that the PoA model governs the distribution of male matings (H1P3). Finally, we predict that higher ranking males have better fertilization success (H1P4). If rhesus macaques exchange mating access for grooming (H2), we predict that the distribution among the sexes of male grooming differs between the mating and the nonmating season (H2P1). Moreover, we predict a clear relationship between grooming and mating access (H2P2), that males groom their mating partners more during the mating season compared to the nonmating season (H2P3), and that males groom the females they mate with in particular (H2P4). Further, if the exchange of grooming for mating access is governed by short-term market effects (H3) (Noë and Hammerstein 1994; Noë *et al.* 1991), then we predict exchanges within the day when both commodities (grooming and mating access) are available, i.e., when the females are receptive (H3P1). In addition, we predict that there will be competition among the demanding class, i.e., males, reflected in outbidding, i.e. trying to offer more (grooming) than your competitor (H3P2), and that the value of the commodity (mating access) will be influenced by supply and demand (H3P3) and by male and female rank (H3P4). However, if the exchange of grooming for mating access is governed by longer-term affiliative patterns between mating partners (H4), then we predict no short-term exchange (H4P1) but a positive relationship between male grooming and mating access/ fertilization success that is influenced by mutual proximity of the particular male and female (H4P2) and by female grooming as well (H4P3) because both mutual

proximity and *mutual* grooming are considered characteristics of a longer-term affiliative relationship or "friendship" (Massen *et al.* 2010).

Methods

Focal Group

We studied a captive group of rhesus macaques (Wodka group) housed at the Biomedical Primate Research Centre (BPRC), Rijswijk, The Netherlands, which contained 30–39 individuals. Changes in group composition were due to demographic processes, births, maturation and deaths, and management reasons. The group was composed of 1 adult nonnatal male, 2 or 3 adult natal males, 5 or 6 sexually active immature natal males (2–5 year of age), 7–9 adult females in 5 matrilines, 3 or 4 sexually active immature females (2–5 year of age), and 11–18 sexually inactive immatures (0–2 year of age). Males were categorized as adult when their body size surpassed adult female body size, and when their testes and muscles were fully developed (Malik *et al.* 1984; Manson and Perry 1993).

The composition of our focal group does not reflect that of wild rhesus macaques (Lindburg 1971; Malik *et al.* 1984), particularly because it included only 1 adult nonnatal male. However, both adult and sexually active but immature natal males experience high levels of copulatory success in the wild (Catchpole and van Wagenen 1975; Manson 1993; Manson and Perry 1993). Moreover, because immature males may lack the strength to compete directly with the alpha male, they are particularly interesting subjects in which to study alternative mating strategies.

The mating access of natal males may be affected by inbreeding avoidance, as natal males avoid mating with their matrilineal relatives (Manson and Perry 1993; Smith 1995). However, because the focal group consisted of 5 matrilines, there were at least 7 nonrelated females available for each natal male (range = 7–10). In comparison, there were 11 females available for the nonnatal alpha male (Table I).

Housing Conditions

The group was housed in an indoor enclosure, 72 m^2 and 2.85 m high, and an outdoor compound, 208 m^2 and 3.1 m high, connected by 2 tunnels. The indoor enclosure had sawdust bedding, the outdoor enclosure sand. Both enclosures had multiple elevated sitting locations and enrichment devices (Vernes and Louwerse 2010). The subjects were fed a diet of commercially available monkey chow, fruits, vegetables, and grains. Water was available ad libitum.

Data Collection

We collected data between November 2006 and February 2007 and between September 2007 and August 2008. Subjects were locked in the outdoor compound during observations.

Table I Age, rank, and potential number of nonkin female mating partners of all males aged ≥2 year in the study by mating season, their observed female mating partners, and the number of mating days (2006/2007) or matings (2007/2008) observed

2006/2007	Male	Age	Rank	Potential no. of nonkin mating partners	Mating partners	No. of mating days	Age of partner	Rank of partner
	Robbedoes	11	1	10	Mona	1	10	2
					Natasha	2	10	14
	Timon	5	4	9	Lisa	4	3	3
					Priegel	1	4	5
					Saravi	1	5	6
					Emoe	1	10	11
					Wenk	1	18	16
	Jam	3	8	7	Nala	1	6	7
					Epha	7	18	19
	Moer	4	10	9	Lisa	3	3	3
					Yota	3	2	17
	Bout	4	12	7	Lisa	1	3	3
					Priegel	2	4	5
	Kaas	5	15	7	Saravi	1	5	6
	Ham	2	18	7	Yota	2	2	17
					Epha	7	18	19
	Zier	3	21	9	–			

2007/2008	Male	Age	Rank	Potential no. of nonkin mating partners	Mating partners	No. of matings	Age of partner	Rank of partner
	Robbedoes	12	1	11	Mona	15	11	2
					Saravi	1	6	4
					Natasha	4	11	14
	Moer	5	5	10	Lisa	4	4	7
					Emoe	1	11	10
					Girl	6	2	13
	Jam	4	7	7	Natasha	16	11	14
					Wenk	4	19	17
					Epha	21	19	19
	Bout	5	9	8	Priegel	3	5	3
					Saravi	1	6	4
	Kaas	6	11	8	Priegel	1	5	3
	Ham	3	12	8	Girl	1	2	13
	Zier	4	15	10	–			
	Dremel	3	16	10	Yota	1	3	18

Scan Data We took 4 scans a day, 4 or 5 day/week, recording the individuals with which subjects were sitting and which individuals they groomed for all group members. Scans occurred randomly over the course of the day, yet were always ≥1 h apart to ensure independence of the data.

Focal Data We recorded 518 h of focal observations during the 2006/2007 mating season (November 2006–February 2007; 65 h), the 2007 pre-mating season (September 2007–October 2007; 100 h), the 2007/2008 mating season (November 2007–March 2008; 163 h), and the 2008 post-mating season (May 2008–August 2008; 190 h). Several observers conducted these observations (range of interobserver reliability between all other observers and J. J. M. Massen calculated via Cohen's κ, 0.93–0.96). We studied the group 4 or 5 day/week, between 09:00 h and 17:00 h and recorded 15-min focal samples for all sexually active individuals (2006/2007: 9 females and 8 males; 2007/2008: 11 females and 8 males) using The Observer 5.0 and XT (Noldus) according to a semirandom time schedule; i.e., the order of focal individuals was created randomly, yet repeated every day. However, every day we started focal observations with the next individual in the order ensuring that each individual was observed an equal amount of time during the different periods of a day, and that focal observations of each individual were independent.

We recorded behavior continuously (Martin and Bateson 1993) and employed an ethogram of rhesus macaque social behavior based on Altmann (1962) and supplemented by Angst (1974). We recorded agonistic behavior (bared teeth display and make room), sexual behavior (sexual mounts, copulations, and thrusts without, and with ejaculation, and refusals to mate), and grooming (direction, number of bouts, and grooming duration). We subdivided grooming behavior into sexual grooming (grooming that either directly preceded sexual activity or grooming in between bouts of sexual activity) and normal grooming (grooming that did not concur with any sexual activity between a male and female) (Gumert 2007). We also recorded alternative male mating tactics, i.e., forced copulations, sneaky matings (matings not witnessed by higher ranking males), mate-guarding, and disruption of ongoing mate-guarding or matings (Berard *et al.* 1994). However, we never witnessed any of these alternative male tactics and witnessed only 1 refusal to mate by a female. Therefore, we did not include these behaviors in further analyses. The lack of sneaky matings may be due to a lack of opportunity to hide in the outdoor compound.

In addition to the focal data we recorded all sexual behaviors ad libitum during the 2 mating seasons. Consequently, in our analyses all data on sexual behavior are a composite of focal and ad libitum data.

Dominance Hierarchy

Rhesus macaques are considered despotic, and have a distinct and clear dominance hierarchy (Thierry 2000). To calculate the dominance hierarchy, we used the unidirectional submissive behavior elements bare teeth and make room from ad libitum and focal observations and arranged these behaviors in a matrix with actors in rows and recipients in columns. We used MatMan (version 1.1; earlier version described in de

Vries *et al*. 1993) to calculate Landau's linearity indices (h') and to reorder matrices to best fit a linear hierarchy (de Vries 1995, 1998). We found a significantly linear hierarchy in both 2006/2007 ($h'=0.249$, $p<0.001$) and 2007/2008 ($h'=0.453$, $p<0.001$). The hierarchy of both years was comparable, with few (8=4.7%) changes in the relative position of individuals, mainly due to changes in group composition.

Young rhesus macaques inherit their rank position from their mothers (Manson 1993). However, in contrast to that of females, the dominance status of males changes during maturation based on a combination of aggressive and social skills (Berard 1999; Lindburg 1971). To test the PoA model we used the relative ranks of the males to create a male-only hierarchy.

Female Receptivity

We defined female receptivity, i.e., a female's willingness to mate (Beach 1976), using female mating behavior. We defined females as receptive on days they did mate and nonreceptive on days they did not mate. We never witnessed any forced copulations.

Paternity Data

To establish fertilization success of all males, we analyzed parentage of all infants born in 2007 and 2008 (see Table SI of the electronic supplementary material [ESM]) using previously published methods (Penedo *et al*. 2005; Roeder *et al*. 2009). We used 20 microsatellite markers located on 11 different chromosomes. We performed allele frequency analysis for 40 unrelated rhesus macaques using Cervus 3.0 (Kalinowski *et al*. 2007) and 20 loci. The mean number of alleles per locus was 18.62 with a mean expected heterozygosity of 0.88, a mean PIC index of 0.86, and a total exclusionary power for the first and second parent of 1.000 (see Table SII of the ESM).

Data Processing and Analyses

For each analysis, we first tested whether there were differences in the patterns of our data between the 2 mating seasons. When we found no significant differences, we present overall data and statistics. When differences were significant, we report the results separately by mating season.

To assess whether male mating tactics are governed by male dominance rank (H1), we correlated male rank with the number of female mating partners (H1P1) and with the number of mating days (2006/2007) and with the number of matings (2007/2008) (H1P2) using Spearman's rank correlation tests. To test the PoA model (H1P3) we calculated the expected and actual distribution of mating days for all males in both years and compared these with a χ^2 test. We expected the alpha male to mate on each day 1 female was observed mating, the beta male to mate on each day 2 females were observed mating, the gamma male to mate on each day 3 females were observed mating, and so on. Finally, we used a Spearman's rank correlation test to assess the effect of male rank on male fertilization success (H1P4).

To study exchange patterns of grooming and mating access (H2), we first tested whether the distribution of grooming among the sexes differed between the mating and the nonmating season (H2P1) using an ANOVA. Second, we arranged grooming

and sexual behavior in matrices with actors in rows and recipients in columns. We then tested exchange patterns (H2P2) in MatMan with row-wise matrix correlations (de Vries 1993), using Kendall's τ as a correlation statistic (Hemelrijk 1990a). Third, we used a Friedman tests to assess whether each particular male groomed its mating partner more during the mating season than during the pre- or the post-mating season (H2P3) and Wilcoxon signed rank tests as a *post hoc* test. Finally, we used Wilcoxon signed ranks test to compare male grooming toward mating partners and toward nonmating partners in the mating season (H2P4).

To test whether the exchange of grooming for mating was governed by short-term market effects (H3), we first tested whether males groomed their mating partners more and longer on the actual day of mating compared to other days within the mating season (H3P1 and alternatively H4P1) using Wilcoxon signed ranks tests. Second, we compared the number of grooming bouts and the duration of grooming females received from males they did not mate with a particular female between days they were receptive and days they were not receptive using Wilcoxon signed ranks tests, to assess whether there was any outbidding (H3P2). Third, to investigate whether there was an influence of supply and demand on male grooming of females (H3P3), we determined the number of grooming bouts and the duration of grooming of males toward their female mating partners depending on the number of mating females per day (1–6 females/day) and examined the correlation between these variables using a Spearman's rank correlation test. Finally, to assess the effect of male and female rank on a particular commodity (H3P4), we used partial row-wise correlations (de Vries 1993; Hemelrijk 1990b) of male grooming and mating access, with dominance rank as a third variable. The effect of this variable is reflected in its effect on the correlation statistic τ compared to the original correlation.

To assess whether exchange patterns are governed by longer-term affiliative patterns (H4), we tested the effect mutual proximity (H4P2) and grooming received from the females (H4P3) on the exchange patterns of male grooming and mating access, using partial row-wise correlations (de Vries 1993; Hemelrijk 1990b). Again, the effect of these variables is reflected in their effect on the correlation statistic τ compared to the original correlation. Finally, we also used paternity data to determine whether fatherhood was more likely if males were socially close to females (H4P2). To do so, we ranked all nonrelated males according to proximity data during the mating season for each female (1 = closest), and compared the rank of the sire pair-wise with the mean rank of all nonkin males. For females that gave birth in both years, we averaged the proximity ranks of the sires and all nonkin males of both mating seasons.

We used nonparametric tests because our data were not normally distributed. We set $\alpha = 0.05$. Tests were always 2-tailed. When we used Wilcoxon signed ranks tests, we show the sum of positive ranks and the exact *p*-values (Mundry and Fischer 1998).

Results

Dominance Rank (H1)

We found a significant positive correlation between male dominance rank and the number of mating partners per male (H1P1) (Spearman's rank correlations: 2006/

2007: $\rho=-0.868$, $n=8$, $p=0.005$; 2007/08: $\rho=-0.801$, $n=8$, $p=0.017$) (Fig. 1). In 2007/2008, we also found a significant positive correlation between male dominance rank and the number of matings per male (H1P2) ($\rho=-0.854$, $n=8$, $p=0.007$). However, there was no significant relationship between the number of days with mating activity and male rank in 2006/2007 ($\rho=-0.590$, $n=8$, $p=0.123$, Fig. 1). Moreover, the observed distribution of mating days of the males differed significantly from the PoA model (H1P3) ($\chi^2=82.16$, df = 5, $p<0.001$). This suggests that, although male dominance rank relates to mating access in 1 of 2 years, the PoA model does not explain the observed male mating pattern.

There was no significant relationship between male rank and the number of offspring sired in either year (H1P4) (2006/2007: $\rho=-0.245$, $n=8$, $p=0.558$; 2007/08: $\rho=-0.436$, $n=8$, $p=0.280$, Fig. 1). Moreover, the alpha male did not sire any offspring in either year, although he had sired offspring in previous years. This suggests that, in line with the mating access data, male rank, and the PoA model do not govern male fertilization success.

Grooming for Mating Access (H2)

The distribution of grooming during the mating season tended to differ from the distribution of grooming during the nonmating season (H2P1) (scan data: ANOVA; $n=9$ males and 10 females, $F=3.859$, df = 3, $p=0.058$, Fig. 2) because both males and females groomed individuals of their own sex more often during the nonmating season
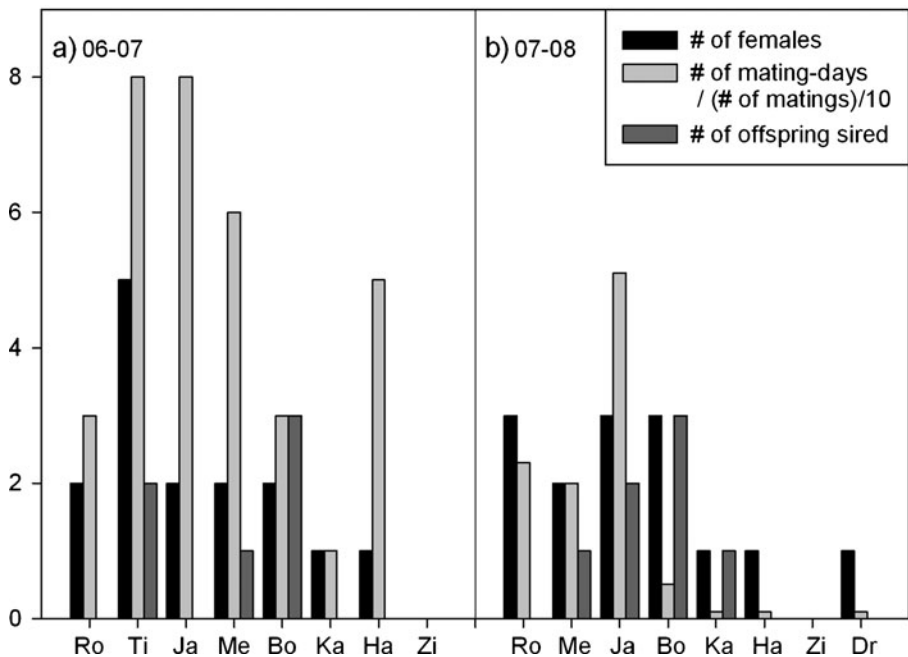
Fig. 1 Number of female mating partners, observed mating days/matings (#/10), and number of offspring sired by males in (a) the 2006–2007 mating season and (b) the 2007–2008 mating season. Males are listed in order of dominance hierarchy, with the alpha male on the left.
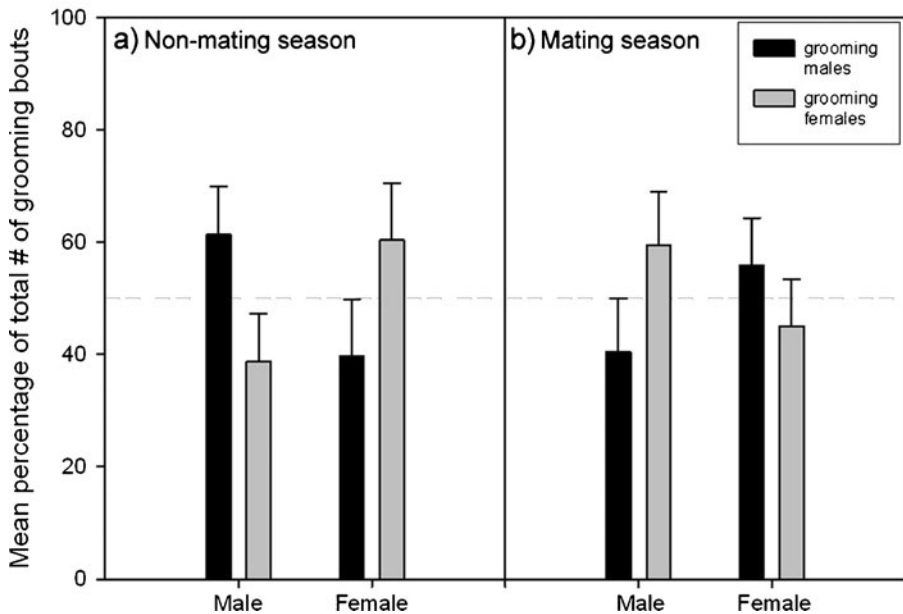
Fig. 2 Mean percentage + SEM of the total number of grooming bouts from males and females directed toward males and females, in (a) the nonmating season and (b) the mating season. Data for 2006–2007 and 2007–2008 are combined.

and groomed the opposite sex more often during the mating season. This allows for the possibility that males use grooming to gain access to a particular mating partner.

There was a significant positive correlation between male grooming (both number of grooming bouts and duration of grooming) and mating access (H2P2) (number of mating days in 2006/2007, and number of matings in 2007/2008) (Table II). Thus, the grooming given to a female in a mating season is related to male mating access to this female.

There was a nonsignificant trend suggesting that male grooming of female mating partners differed among pre-mating season, mating season, and post-mating season (H2P3) (Friedman tests: number of grooming bouts: $\chi^2=4.923$, $n=7$, df = 2, $p=0.085$; duration of grooming: $\chi^2=4.923$, $n=7$, df = 2, $p=0.085$). *Post hoc* analyses revealed that males groomed their female mating partners significantly more in the mating season than in the post-mating season (Wilcoxon signed ranks tests: $T^+=26$, $n=7$, $p=0.047$). Moreover, there was also a slight, yet nonsignificant, difference in the duration of grooming between the mating season and the post-mating season ($T^+=25$, $n=7$, $p=0.078$). There was no difference in the amount ($T^+=14$, $n=7$, $p=0.156$) or duration ($T^+=18$, $n=7$, $p=0.578$) of male grooming of female mating partners between the pre-mating season and the actual mating season. In addition, the number of grooming bouts ($T^+=23$, $n=7$, $p=0.125$) and the duration of grooming ($T^+=14$, $n=7$, $p=0.125$) of males toward their female mating partners did not differ significantly between the pre-mating season and the post-mating season. These results indicate that males groom their mating partners more often and longer during the period in which they can mate with them, but already have a similar grooming investment in these females before the mating season starts, although it drops after

Table II Row-wise matrix correlations of grooming bouts (Gr#) and grooming duration (Grdur) with the number of mating days (2006/2007) or number of matings (2007/2008) (sex#) of males and females; and (partial) row-wise matrix correlations of the effects of rank, proximity, and received grooming on these correlations

Mating season 2006/2007

Male

	K. τ_{rw}	P	Partialed out	K. $\tau_{rw; XY.Z}$	p	K. $\tau_{rw; XZ}$	K. $\tau_{rw; YZ}$
Gr# vs., sex#	0.24	0.019	Rank	0.24	0.017	0.06	−0.03
			Proximity	0.19	0.045	0.38	0.18
			Received gr.	0.21	0.032	0.21	0.19
Grdur vs. sex#	0.36	0.003	Rank	0.37	0.001	0.07	−0.03
			Proximity	0.02	0.439	0.23	0.24
			Received gr.	0.29	0.009	0.32	0.32

Female

	K. τ_{rw}	P	Partialed out	K. $\tau_{rw; XY.Z}$	p	K. $\tau_{rw; XZ}$	K. $\tau_{rw; YZ}$
Gr# vs. sex#	0.25	0.026	Rank	0.26	0.021	0.13	−0.09
			Proximity	0.18	0.078	0.35	0.25
			Received gr.	0.17	0.077	0.30	0.31
Grdurvs.sex#	0.42	0.002	Rank	0.44	0.000	0.15	−0.09
			Proximity	0.18	0.070	0.35	0.25
			Received gr.	0.30	0.012	0.38	0.44

Mating season 2007/2008

Male

	K. τ_{rw}	P	Partialed out	K. $\tau_{rw; XY.Z}$	p	K. $\tau_{rw; XZ}$	K. $\tau_{rw; YZ}$
Gr# vs. sex#	0.39	0.001	Rank	0.40	0.001	0.12	−0.01
			Proximity	0.28	0.005	0.46	0.35
			Received gr.	0.21	0.027	0.49	0.47
Grdur vs. sex#	0.44	0.001	Rank	0.44	0.001	0.06	−0.01
			Proximity	0.37	0.002	0.32	0.35
			Received gr.	0.38	0.000	0.26	0.42

Female

	K. τ_{rw}	P	Partialed out	K. $\tau_{rw; XY.Z}$	p	K. $\tau_{rw; XZ}$	K. $\tau_{rw; YZ}$
Gr# vs. sex#	0.49	0.001	Rank	0.48	0.001	−0.12	−0.22
			Proximity	0.43	0.001	0.28	0.42
			Received gr.	0.38	0.001	0.41	0.43
Grdur vs. sex#	0.48	0.001	Rank	0.46	0.001	−0.15	−0.22
			Proximity	0.47	0.001	0.13	0.42
			Received gr.	0.42	0.002	0.24	0.48

K. Kendall

the mating season. In contrast, males did not differ significantly in the number of grooming bouts (Friedman test: $\chi^2 = 0.783$, $n = 7$, df = 2, $p = 0.676$) or grooming duration ($\chi^2 = 1.652$, $n = 7$, df = 2, $p = 0.438$) in the pre-mating, mating, and post-mating season toward females with which they did not mate (Fig. 3).

Males groomed their mating partners significantly more often compared to females with which they did not mate (H2P4) (Wilcoxon signed rank tests: $T^+ = 27$, $n = 7$, $p =$
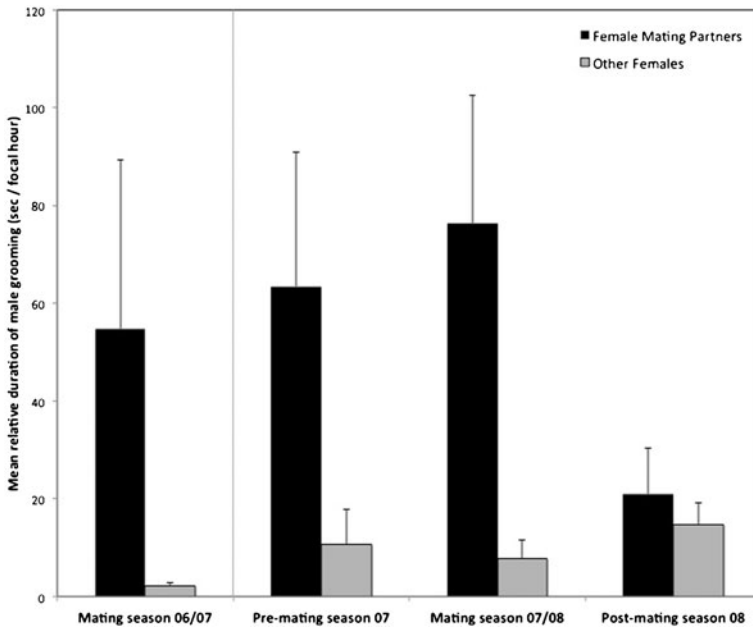
Fig. 3 Mean relative duration (seconds/focal hours) + SEM of male grooming directed toward the females they mated with during the mating season or toward the other females, in the 2006–2007 mating season, in the 2 month preceding the 2007–2008 mating season (Pre-mating season 2007), in the 2007–2008 mating season, and in the 5 month after the 2007–2008 mating season (Post-mating season 2008).

0.031) in the 2007/2008 mating season and also tended to groom them for longer ($T^+=24$, $n=7$, $p=0.109$). The 2006/2007 mating season showed a similar, but nonsignificant, pattern (number of grooming bouts: $T^+=22$, $n=7$, $p=0.219$; duration of grooming: $T^+=22$, $n=7$, $p=0.219$, Fig. 3). This seemingly specific allocation of grooming of males toward the females with which they mated, and during the relevant period, opens the possibility of a mating market.

Mating Market (H3)

In 2007/2008 there was no significant difference between mating days and nonmating days in the number of grooming bouts (H3P1/H4P1) (Wilcoxon signed rank tests: $T^+=26$, $n=10$, $p=0.313$), or the duration of grooming ($T^+=17$, $n=10$, $p=0.219$). Moreover, in 2006/2007, males groomed their mating partners more (Wilcoxon signed rank tests: $T^+=36$, $n=10$, $p=0.008$) and longer ($T^+=28$, $n=10$, $p=0.016$) on days they did not mate than on mating days, opposite to the prediction of a biological market for mating. In addition, we observed sexual grooming only twice.

In a biological mating market partner choice is based on competition among the whole demanding class, irrespective of the outcome of this competition (H3P2). However, females did not receive more (Wilcoxon signed rank tests; $T^+=44$, $n=11$, $p=0.365$) or longer ($T^+=46$, $n=11$, $p=0.278$) grooming from males they did not mate with on days they were receptive than on days they were not receptive. These results indicate that there is no direct interchange of grooming for mating access on

the actual day of mating and no outbidding of the demanding class and are not consistent with a biological mating market.

We found no relationship between the number of mating females available on a day and the number of male grooming bouts or the duration of male grooming (H3P3), both when we took all cases of no grooming into account (Spearman's rank correlations: number of grooming bouts: $\rho=-0.024$, $n=67$, $p=0.847$; duration of grooming: $\rho=-0.016$, $n=67$, $p=0.898$), and when we considered cases of no grooming as missing values (Spearman's rank correlations: number of grooming bouts: $\rho=0.008$, $n=8$, $p=0.986$; duration of grooming: $\rho=0.483$, $n=8$, $p=0.226$). Therefore, there are no indications that the supply of receptive females determines male grooming behavior. Again, this is not consistent with a biological mating market.

Finally, partial row-wise correlations of male grooming of females and mating access with dominance rank showed that rank does not play an important role in the interchange between grooming and mating (H3P4) because Kendall's τ did not change substantially when rank is partialed out (Table II) (Vervaecke et al. 2000). This indicates that high-ranking males do not groom less to obtain mating access vs. low-ranking males, and that no more grooming is required to obtain mating access to a high-ranking female vs. a low-ranking female.

"Friendship" (H4)

There was a significant correlation between female grooming (both number of grooming bouts and duration of grooming) and mating access (H4P3) (number of mating days in 2006/2007, and number of matings in 2007/2008) (Table II). Thus, both male and female grooming patterns of the opposite sex correlate with mating behavior. Female grooming of male mating partners did not differ significantly among pre-mating season, mating season, and post-mating season (Friedman tests: number of grooming bouts: $\chi^2=0.839$, $n=9$, df = 2, $p=0.657$; duration of grooming: $\chi^2=2.000$, $n=9$, df = 2, $p=0.368$). However, in contrast to the males that groomed their female mating partners more before and during the mating season (Fig. 3), there was a slight trend in which females seem to groom their male mating partners more during and after the mating season (see ESM).

Partial row-wise correlations showed that female grooming changed the Kendall's τ of the correlation between male grooming and mating access substantially (H4P3) (Table II), indicating a strong effect of this variable (Vervaecke et al. 2000) and suggesting that males that groom particular females more often are also groomed in return by those females. Proximity also had a strong effect on the original correlation (Table II), suggesting that the mutual grooming relationship of those male–female dyads is related to their mutual proximity (H4P2).

Finally, paternity data revealed that sires are generally in close proximity to their female mating partners (H4P2) because sires were almost always (with only 1 exception) among the 3 top male proximity partners of the female with which they sired offspring. Consequently, the mean proximity rank of the male that sired a female's offspring was significantly lower than the mean proximity rank to the same female of all possible nonkin males (Wilcoxon signed ranks test: $T^+=41$, $n=9$, $p=0.023$, Fig. 4). This suggests that social bonds between males and females enhance male reproductive success.
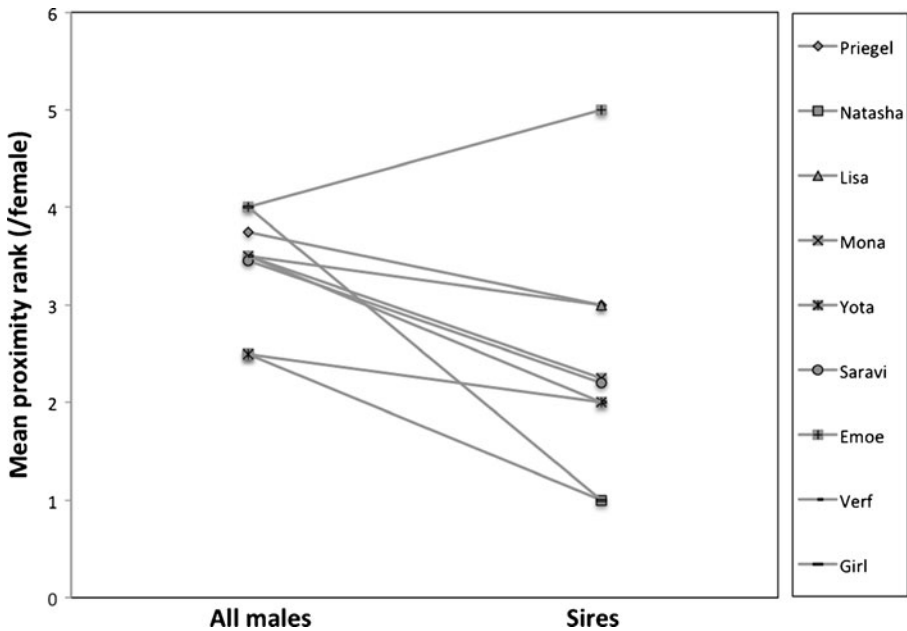
Fig. 4 Mean proximity rank to a given female of males that sired their offspring (sires) and of all possible nonkin males (all males).

Discussion

We found that the distribution of matings was best explained by male dominance rank and long-term affiliative patterns, but was not related to short-term friendly behavior, in contrast to predictions of biological market theory. Moreover, paternity was related to male–female social bonds, but not to male dominance rank.

The male dominance hierarchy was a good predictor of mating access (H1): high-ranking males mated with more females (H1P1) and more often (H1P2) than low-ranking ones. However, the observed distribution of mating partners did not match the distribution of mating partners predicted by the PoA model (H1P3), and we observed males as young as 3 year of age mating when only a few females were receptive. The alpha male did not sire any offspring during the study period, and sirehood was not related to male rank (H1P4). These findings are in line with a recent study that also found that the PoA model does not explain observed mating patterns or paternity in rhesus macaques (Dubuc *et al.* 2011).

Coalitions between middle-ranking males may explain deviations from the distributions of mating partners predicted by PoA (Noë and Sluijter 1990), especially in groups with large age differences between the alpha male and other males (Alberts *et al.* 2003), such as our focal group. However, we did not observe any male coalitions. This is in line with the findings of Chapais (1983), who reported that, although they may occur (Altmann 1962), coalitions are very rare in rhesus macaques (cf. Higham and Maestripieri 2010).

Females in our study were not habitually forced to mate by the males. This is in line with Manson (1992) and contrasts with female chimpanzees (Muller *et al.* 2007). Moreover, rhesus macaque females show marked multiple mating (Lindburg

1971), suggesting that female choice may play a role in male and female mating access and success.

In the nonmating season both sexes groomed their own sex more often than the opposite sex. In contrast, during the mating season both males and females groomed the opposite sex more often (H2P1), suggesting that grooming in the mating context may enhance access to mating partners (H2). Also, there was a clear relation between male grooming and mating access (H2P2). In addition, males groomed their mating partners more often and longer in the pre-mating and mating season than in the post-mating season (H2P3). Moreover, during the mating season males groomed females with which they mated more often and longer than the females with which they did not mate (H2P4). However, our analyses did not support the predictions of a mating market (H3) (Noë and Hammerstein 1994, 1995). First, females did not receive more grooming from the males with which they mated on the actual day of mating vs. other days (H3P1), suggesting there is no direct exchange of grooming for mating access (H4P1). In fact, sexual grooming almost never occurred. Second, females did not receive more grooming on these days from males with which they did not mate (H3P2). This suggests that neither males that mate with a female, nor males that do not gain mating access, use grooming to bid for mating access. Third, we did not find any effect of the number of receptive females available on a day on the amount of grooming received by those females (H3P3). Fourth, high-ranking males did not groom their female mating partners less often vs. low-ranking males, nor did high-ranking females receive more grooming for mating vs. low-ranking females (H3P4). Finally, female grooming data also suggest that there is no mating market. Although male grooming of females may serve as "payment for sex" (Gumert 2007), the grooming of male mating partners by females counters this interpretation because biological market theory predicts that the demanding class, i. e., males, grooms, whereas the suppliers, i.e., females, mainly provide mating access and are not expected to groom their mating partners more often than any other male.

Our results do support the hypothesis that male–female "friendships" lead to mating access (H4) (Smuts 1985). Matrix correlations revealed an interchange of grooming for mating access, but this interchange of grooming for mating access does not seem to take place within 1 day (H4P1). This is in accordance with data on grooming reciprocation in other primates (Schino and Aureli 2008), including Japanese macaques (*Macaca fuscata*: Schino *et al.* 2003), capuchins monkeys (*Cebus paella*: Schino *et al.* 2009), and chimpanzees (Gomes *et al.* 2009), and on the exchange of grooming for support in Japanese macaques (Schino *et al.* 2007) and Barbary macaques (*Macaca sylvanus*: Berghänel *et al.* 2011). Instead, the time frame of this exchange is found over a relatively long time-span of weeks or months. In addition, the interchange of grooming and mating was strongly influenced by proximity (H4P2) and reciprocal grooming (H4P3) in our study. Consequently, not only males but also females groom mating partners more often than nonmating partners. This suggests that a mutual good relationship between a male and female is important in securing mating opportunities (Hinde 1979; Silk 2002). Accordingly, in our group of captive rhesus macaques the relationship between grooming and mating access is explained mostly by affiliation during a particular mating season toward particular individuals, suggesting the formation of social relationships between these males and females. These social relationships also resulted in reproductive success

for the males. This is in accordance with a recent study on the positive effect of social bonds on mating success in Assamese macaques (*Macaca assamensis*: Schülke *et al.* 2010), similar to the male–female "friendships" in baboons (Palombit *et al.* 1997; Smuts 1985) and may be a result of female choice.

Whereas the savanna baboon male–female "friendships" described by Smuts (1985) preceded and possibly led to mating, those described in olive baboons (Palombit *et al.* 1997) succeeded mating association and males may provide protection for the female and her offspring. In our study the timeframe of a male–female "friendship" seemed to differ between males and females. Males seemed to invest more in their social bond with a female before and during the mating season, and their investment ceased after the mating season. In contrast, females did not seem to invest in male–female "friendships" before the mating season, but invested in this relationship during and after the mating season. This suggests that males invest in male–female "friendships" to ensure mating access, and females try to sustain these "friendships" to ensure male protection after the mating season for themselves and their offspring, as suggested for baboons (Lemasson *et al.* 2008; Palombit 2003; Palombit *et al.* 1997).

We conclude that male mating access is only partly explained by male dominance hierarchy in our group of captive rhesus macaques. Males also exchange grooming for mating access. However, this exchange is not over the short term or driven by a biological market. Instead, grooming of both males and females seems to be exchanged for mating access over a longer period. Instead of truly exchanging grooming for mating access, males and females create a positive relationship by grooming each other. Such a friendship allows them to mate and is a better predictor of paternity than male dominance rank.

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