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Stability and Durability of Intra- and Intersex Social Bonds of Captive Rhesus Macaques (*Macaca mulatta*)

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Abstract Many social species maintain differentiated relationships with their group members. These social bonds may reflect short-term interactions satisfying immediate needs. Alternatively, individuals of some species may entertain stable and valuable bonds that last much longer than opportunistic interactions would predict. This claim is supported by recent research that revealed clear fitness benefits for long-lasting social bonds. Here, we investigated the stability and equitability of social relationships in captive rhesus macaques, measured using their proximity and grooming patterns over a 3-yr period. We show that, in general, proximity patterns of the whole group were stable over 3 yr. More specifically, each individual's top two nonkin within and between sex relationships based on proximity were relatively stable and some of these relationships lasted the full 3 yr. Female grooming relationships within and between sex were also stable over 3 yr. Moreover, strong social bonds in females were not based on age similarity and were not sex specific, suggesting that a general underlying mechanism of social bonding in female rhesus macaques. In contrast, patterns of male grooming of other males and of females were relatively unstable and male social bonds were less equitable than those of females. The differences in stability of the relationships between the sexes may reflect the dispersal pattern of rhesus macaques, although we have limited data on non-natal males in our study. With these data we add to a growing body of literature describing the value and durability of relationships among primates and other species.

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Introduction

Individuals of many group-living animals show marked differentiation in how they interact with each other, entertaining both good and bad social relationships with group members. Good relationships in particular have been the subject of many studies and have been compared to human friendships (Massen *et al.* 2010; Seyfarth and Cheney 2012; Silk 2002a; Smuts 1985). Kummer (1978) suggested that animals cultivate good relationships because they provide adaptive benefits. For related individuals these adaptive benefits result from kin selection (Hamilton 1964). However, several recent studies (reviewed in Massen *et al.* 2010) show that good relationships between unrelated individuals can also be adaptive, and that the mechanism involved in the adaptive benefits of strong relationships among related individuals is not necessarily the promotion of an individual's genes through relatives (Hamilton 1964). For example, strong female–female (kin and nonkin) relationships increase survival rates in female chacma baboons (*Papio ursinus*: Silk *et al.* 2010a), increase vigilance against predators in crested macaques (*Macaca nigra*: Micheletta *et al.* 2012), and increase infant survival (yellow baboons, *P. cynocephalus*: Silk *et al.* 2003; chacma baboons: Silk *et al.* 2009; feral horses, *Equus caballus*: Cameron *et al.* 2009; bottlenose dolphins, *Tursiops aduncus*: Frére *et al.* 2010), strong male–male relationships enhance reproductive success in males (chimpanzees: Nishida and Hosaka 1996; bottlenose dolphins: Connor *et al.* 2001; Assamese macaques, *Macaca assamensis*: Schülke *et al.* 2010), and male–female relationships enhance reproductive success in males (rhesus macaques, *M. mulatta*: Kulik *et al.* 2011; Massen *et al.* 2012; yellow baboons: Smuts 1985) and may increase infant survival in olive baboons (*P. anubis*: Palombit *et al.* 1997) and chacma baboons (Huchard *et al.* 2013). As a consequence of these adaptive benefits, it is hypothesized that social animals not only form these good social relationships, but also maintain them in the long run and thus entertain long-lasting social bonds (Hinde 1981; Mitani 2009; Silk *et al.* 2006).

Several recent studies report stable relationship patterns, i.e., good relationships remain good and bad relationships remain bad over time, and long-term durability of specific bonds among primates, both in the wild, among female yellow baboons (Silk *et al.* 2006, 2012), female chacma baboons (Silk *et al.* 2010b, 2012), male chimpanzees (*Pan troglodytes*: Mitani 2009), and female chimpanzees (Langergraber *et al.* 2009; Lehmann and Boesch 2009), and in captivity, among both male and female chimpanzees (Koski *et al.* 2012). This phenomenon is not restricted to the primate order, and long-lasting bonds have also been reported among female African elephants (*Loxodonta africana*: Archie *et al.* 2006; Moss *et al.* 2010), and in male, female, and intersex relationships in bottlenose dolphins (Connor *et al.* 2000; Wiszniewski *et al.* 2010, 2012). Some of these studies also showed that long-lasting bonds are characterized by equitable grooming relations (Mitani 2009; Silk *et al.* 2006, 2010b). Moreover, the strength of these long-lasting bonds can be stronger for dyads of similar rank (Silk *et al.* 2006, 2010b, 2012), similar age (Schaffner *et al.* 2012; Silk *et al.* 2006), and for maternal relatives (Koski *et al.* 2012; Mitani 2009; Moss *et al.* 2010; Silk *et al.* 2006, 2010b, 2012; Wiszniewski *et al.* 2010). However, these long-lasting bonds are not necessary restricted to kin (Langergraber *et al.* 2009; Lehmann and Boesch 2009; Mitani 2009; Silk *et al.* 2006, 2010b; Wiszniewski *et al.* 2010, 2012). In contrast, there is some variation in primary grooming and proximity partnerships among females of some chacma baboon populations (Barrett and Henzi 2002), and clearly differentiated relationships are subject to cyclicity due to food abundance in these populations (Henzi *et al.* 2009). Consequently, the authors of these studies argue that more attention should be given to short-term local contingencies with regard to social bonds among primates.

Sex-biased dispersal patterns may also affect the formation of long-lasting bonds: the philopatric sex is predicted to maintain long-lasting bonds with same-sex group members (Pusey and Packer 1987; Sterck *et al.* 1997; van Schaik 1989). The formation of long-lasting bonds is predicted to be limited for the dispersing sex, e.g., male baboons (Alberts and Altmann 1995), female spider monkeys (*Ateles geofroyi*: Slater *et al.* 2009), male gray-cheeked mangabeys (*Lophocebus albigena*: Chancellor *et al.* 2011), female chimpanzees (Arnold and Whiten 2003; Pepper *et al.* 1999; *cf.* Langergraber *et al.* 2009) and may be found only when individuals disperse with or to join former group members, e.g., male vervets (Cheney and Seyfarth 1983), female gorillas (*Gorilla gorilla beringei*: Watts 1994), male long-tailed macaques (*Macaca fascicularis*: van Noordwijk and van Schaik 2001), and female Thomas langurs (*Presbythis thomasi*: Sterck *et al.* 2005). However, more data on different primate taxa and on different relationships, e.g., intersex as well as same-sex relationships and pre- or postdispersal from the natal group, are needed to understand the enduring features of primate social bonds in general.

We here investigate the stability of social bonds in a captive rhesus macaque group consisting of several matrilines and multiple natal males, but with only one non-natal male. With a marked mating season, rhesus macaques form an interesting test case to study the stability of social relationships among primates. Previous research has shown that captive rhesus macaques allocate more grooming to their own sex than to the other sex during the nonmating season, but that this pattern switches in the mating season, when both sexes allocate more grooming to the opposite sex than toward their own sex (Massen *et al.* 2012). This suggests that grooming might be influenced by short-term local contingencies in macaques. However, how this short-term variation in grooming patterns translates into long-term grooming patterns, and whether the relative distribution of grooming among same- and different-sexed individuals remains stable, remain to be investigated. Comparing relationships during multiple nonmating and mating seasons provides the possibility of studying whether these macaques only form short-lasting “business partnerships” concentrated around mating efforts (Barrett and Henzi 2002; Henzi and Barrett 2007), or whether they also maintain long-lasting stable bonds, as is proposed by other authors (Cheney *et al.* 1986; Hinde 1981; Massen *et al.* 2010; Seyfarth and Cheney 2012). Previous research has demonstrated longevity in immature rhesus macaque friendships (Weinstein and Capitanio 2012) and that both maternal and paternal relatedness are good predictors of affiliative relationships (Kapsalis and Berman 1996; Weinstein and Capitanio 2012; Widdig *et al.* 2001, 2006). Here we focus on nonkin relations. We hypothesize that unrelated rhesus macaques also form stable and enduring social relationships, both within their own sex and with members of the other sex. Therefore, we investigate whether nonkin intra- and intersex social relationships in rhesus macaques last longer than a mating season. We also predict that long-lasting bonds are characterized by grooming equitability, as contingent reciprocal grooming interactions between individuals seem to be important in the development and maintenance of primate social relationships (Silk *et al.* 2010b), and symmetry in affiliative interactions is one of the components of relationship quality in primates (Koski *et al.* 2012; McFarland and Majolo 2011). In addition, in accordance with some other species (Schaffner *et al.* 2012; Silk *et al.* 2006), we test whether these strong bonds are more frequent among individuals of similar age, owing to a possible preference for similarity (*cf.* de Waal and Luttrell 1988). In contrast, we predict that nonkin bonds will not be related to rank similarity, as rank position among rhesus macaques is strongly influenced by maternal relatedness (Seth 2000). Finally, we test whether bonds are stronger among philopatric females than among males, the dispersing sex (Pusey and Packer 1987; van Schaik 1989; Sterck *et al.* 1997).

Methods

Focal Group

The focal group was a captive group of rhesus macaques (Wodka group), housed at the Biomedical Primate Research Centre (BPRC), Rijswijk, the Netherlands. The group contained between 30 and 40 individuals. Changes in group composition were due to demographic processes; births, maturation, and deaths; and management reasons. Group composition was as follows: 1 adult non-natal male (alpha male since 2005), 2–6 adult natal males, 6–10 subadult natal males (2–5 yr of age and sexually active; Massen *et al.* 2012), 8–10 adult females in 5 matrilines, 3–6 subadult females (2–5 yr of age and sexually active; Massen *et al.* 2012) and 9–13 immatures (0–2 yr of age). We considered natal males as socially adult based on their body size (> adult female body size), testes, and muscular development and after the age of 5 yr (Malik *et al.* 1984; Manson and Perry 1993). We focused on adults and subadults because immatures often cling to their mothers, making it difficult to distinguish between immature and maternal relationships. We used only data for individuals that were present for ≥1 yr as adults and/or subadults during the study period. The position of alpha male was stable during the whole study period. Near the end of the study (November 2008), several subadult males started challenging the alpha male and were removed from the group for management reasons. In the wild such males would either replace the alpha male or disperse (Lindburg 1971). Consequently, colony management at our facility mimics natural dispersal patterns. See Electronic Supplementary Materials (ESM) for an overview of which individuals were present during which period.

All maternal genealogies were known, as all individuals were born in captivity, and these were entered as a coefficient of maternal relatedness (*r*) into analyses. We defined kin as maternal relatedness coefficient ≥ 0.125 (Chapais 2001; Kapsalis and Berman 1996; Silk 2002b). Each individual had a mean of 5.5 ± SD 3.0 maternal relatives in the group during the study. Unfortunately, we did not have paternity data for all our individuals and therefore did not include this factor in our analyses.

Housing Conditions

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

Ethical Note

Owing to its noninvasive, observational character, our study did not meet the definition of an animal experiment in Article 1 of the Dutch Experiments on Animals Act. Consequently, the ethics committees of Utrecht University and of the BPRC waived the need for approval, and thus this study complies with Dutch law.

Data Collection

We collected data between November 2006 and June 2009, encompassing three consecutive mating- and nonmating seasons. The subjects were locked in the outdoor enclosure during observations.

To assess proximity and grooming patterns, we took a mean of 3.85 (range 2–4) scan samples (Martin and Bateson 1993) each day, recording who was sitting in contact with whom and who was grooming whom for all group members. To ensure independence of the data, scans were ≥1 h apart and spread randomly over the course of the day. In total we collected 1138 scans on 296 separate days, spread over the data collection period. See ESM for the matrices containing numbers of scans in sitting in contact and grooming for the whole study period.

To examine the duration and stability of social relationships, we split our data into 4-mo periods, such that one period encompassed the whole mating season (November–February), while the two other periods in a year (March–June and July–October) encompassed the nonmating season. We omitted July–October 2008 from analysis as we had too few data (only 40 scans on only 10 separate days) for this period. Consequently, we analyzed seven 4-mo periods, including three mating seasons (see Table I for the dates of periods 1–7). Within these periods we had a mean of 38.9 ± SD 6.4 observation days, which corresponds to a mean of 155.7 ± SD 25.7 scan samples.

To evaluate the dominance hierarchy, we used both focal and *ad libitum* data of unprovoked submissive behavior (bare teeth display and make room; Altmann 1962). Although dominance hierarchies are quite stable in rhesus macaques (Seth 2000), the rank order may change over time owing to demographic processes such as births, maturation, and deaths, especially among males (Lindburg 1971) so we calculated the dominance hierarchy for each observation year (November 2006–June 2007, July 2007–June 2008, and November 2008–June 2009). We did not have enough data on submissive behaviour to calculate a dominance hierarchy for each separate 4-mo period.

To calculate dominance hierarchies, we arranged all submissive behaviors in matrices with actors in rows and recipients in columns. We used MatMan (version 1.1; 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 significantly linear hierarchies in all 3 yr: November 2006–June 2007: $h' = 0.303$, $N = 19$, $P = 0.027$, based on 93 interactions and with 67.3% unknown relationships; July 2007–June 2008: $h' = 0.294$, $N = 24$, $P = 0.001$, based on 263 interactions and 63.0% unknown relationships; November 2008–June 2009:

Table I Row-wise matrix correlations of proximity data for each of six observation periods with the subsequent period in a 3-yr study of a captive group of rhesus macaques and comparing the first and last period for **(a)** all individuals, **(b)** females only (FF), **(c)** males only (MM), **(d)** females with males (FM), and **(e)** males with females (MF), and partial row-wise matrix correlations for the same data controlling for maternal relatedness (*r*) and rank differences

a) All periods	Row-wise matrix correlation			Partial (*r*)		Partial (rank difference)	
	Kendall's τ	*N*	*P*	$K' \tau\ xy,z$	*P*	$K' \tau\ xy,z$	*P*
1 (*m*) vs. 2	0.57	19	**<0.001**	0.53	**<0.001**	0.57	**<0.001**
2 vs. 3	0.55	18	**<0.001**	0.48	**<0.001**	0.54	**<0.001**
3 vs. 4 (*m*)	0.54	24	**<0.001**	0.46	**<0.001**	0.53	**<0.001**
4 (*m*) vs. 5	0.53	24	**<0.001**	0.45	**<0.001**	0.52	**<0.001**
5 vs. 6 (*m*)	0.41	20	**<0.001**	0.33	**<0.001**	0.38	**<0.001**
6 (*m*) vs. 7	0.56	22	**<0.001**	0.52	**<0.001**	0.54	**<0.001**
Long term: 1 vs. 7	0.39	14	**<0.001**	0.32	**<0.001**	0.32	**<0.001**

b) FF periods[a]	Row-wise matrix correlation			Partial (relatedness *r*)		Partial (rank difference)	
	Kendall's τ	*N*	*P*	$K' \tau\ xy,z$	*P*	$K' \tau\ xy,z$	*P*
1 (*m*) vs. 2	0.47	10	**<0.001**	0.37	**<0.001**	0.49	**<0.001**
2 vs. 3	0.61	10	**<0.001**	0.53	**<0.001**	0.63	**<0.001**
3 vs. 4 (*m*)	0.68	13	**<0.001**	0.60	**<0.001**	0.67	**<0.001**
4 (*m*) vs. 5	0.48	13	**<0.001**	0.33	**<0.001**	0.45	**<0.001**
5 vs. 6 (*m*)	0.38	13	**<0.001**	0.22	**0.008**	0.31	**<0.001**
6 (*m*) vs. 7	0.60	13	**<0.001**	0.51	**<0.001**	0.57	**<0.001**
Long term: 1 vs. 7	0.44	9	**<0.001**	0.32	**0.003**	0.42	**<0.001**

c) MM periods	Row-wise matrix correlation			Partial (relatedness *r*)		Partial (rank difference)	
	Kendall's τ	*N*	*P*	$K' \tau\ xy,z$	*P*	$K' \tau\ xy,z$	*P*
1 (*m*) vs. 2	0.72	9	**<0.001**	0.70	**<0.001**	0.72	**<0.001**
2 vs. 3	0.77	8	**<0.001**	0.74	**<0.001**	0.77	**<0.001**
3 vs. 4 (*m*)	0.45	11	**<0.001**	0.37	**<0.001**	0.45	**<0.001**
4 (*m*) vs. 5	0.48	11	**<0.001**	0.41	**<0.001**	0.48	**<0.001**
5 vs. 6 (*m*)	0.40	7	**0.009**	0.39	**0.012**	0.40	**0.009**
6 (*m*) vs. 7	0.57	9	**<0.001**	0.56	**<0.001**	0.59	**<0.001**
Long term: 1 vs. 7	0.17	5	**0.415**	0.18	**0.310**	0.18	**0.304**

d) FM periods	Row-wise matrix correlation			Partial (relatedness *r*)		Partial (rank difference)	
	Kendall's τ	$N_{f,m}$	*P*	$K' \tau\ xy,z$	*P*	$K' \tau\ xy,z$	*P*
1 (*m)* vs. 2	0.6286	10,9	**<0.001**	0.5988	**<0.001**	0.6128	**<0.001**
2 vs. 3	0.5178	10,8	**<0.001**	0.4138	**<0.001**	0.4944	**<0.001**
3 vs. 4 (*m*)	0.5033	13,11	**<0.001**	0.4395	**<0.001**	0.4772	**<0.001**
4 (*m*) vs. 5	0.4990	13,11	**<0.001**	0.4466	**<0.001**	0.4802	**<0.001**
5 vs. 6 (*m*)	0.3917	13,7	**<0.001**	0.3359	**<0.001**	0.3759	**<0.001**
6 (*m*) vs. 7	0.5056	13,9	**<0.001**	0.4651	**<0.001**	0.4677	**<0.001**
Long term: 1 vs. 7	0.3492	9,5	**0.006**	0.3277	**0.008**	0.3365	**0.007**

Table I (continued)

e) MF periods	Row-wise matrix correlation			Partial (relatedness r)		Partial (rank difference)	
	Kendall's τ	$N_{m,f}$	P	$K'\ \tau\ xy,z$	P	$K'\ \tau\ xy,z$	P
1 (*m*) vs. 2	0.5198	9,10	**<0.001**	0.4852	**<0.001**	0.5085	**<0.001**
2 vs. 3	0.3758	8,10	**<0.001**	0.3007	**<0.001**	0.3248	**<0.001**
3 vs. 4 (*m*)	0.5381	11,13	**<0.001**	0.4482	**<0.001**	0.5191	**<0.001**
4 (*m*) vs. 5	0.6086	11,13	**<0.001**	0.5430	**<0.001**	0.5942	**<0.001**
5 vs. 6 (*m*)	0.4361	7,13	**<0.001**	0.3901	**<0.001**	0.4108	**<0.001**
6 (*m*) vs. 7	0.5645	9,13	**<0.001**	0.5207	**<0.001**	0.5460	**<0.001**
Long term: 1 vs. 7	0.3847	5,9	**<0.001**	0.3575	**0.002**	0.3718	**0.001**

All P-values reflect significance after Holm–Bonferroni corrections

[a] Periods: 1, November 2006–February 2007; 2, March 2007–June 2007; 3, July 2007–October 2007; 4, November 2007–February 2008; 5, March 2008–June 2008; 6, November 2008–February 2008; 7, March 2009–June 2009. Mating seasons are marked with (*m*)

$h' = 0.593$, $N = 22$, $P < 0.001$, based on 419 interactions and with 38.5% unknown relationships). Conclusions about dominance hierarchies should be drawn with great caution owing to the large proportion of unknown relationships (Klass and Cords 2011). The relative positions of matrilines remained the same, but changes occurred in relative rank position within matrilines and in the rank of maturing males. These changes were due mainly to changes in group composition (deaths, maturation of young males, and management interventions, see ESM).

Data Processing and Analyses

To test the stability of proximity and grooming patterns among all the subadult and adult individuals in the group, we examined whether the proximity or grooming data for one period correlated with those of the subsequent period. To test for long-term stability of relationships, we also tested whether the proximity or grooming data for period 1 (November 2006–February 2007) correlated with those for the last period (period 7, March–June 2009). To compare proximity and grooming data across periods, we calculated the relative amount of times an individual sat in contact with another individual or groomed another individual by dividing the number of scans we observed each behavior by the number of observation days within a period. Consequently, for each period we had data on the relative amount individuals were in proximity with each other or were grooming per day. We arranged these data in matrices with actors in rows and recipients in columns and calculated row-wise Kendall's τ correlations in Matman 1.1 (Hemelrijk 1990a; de Vries 1993; de Vries *et al.* 1993). We calculated P values on the basis of 10,000 permutations. We used only data on individuals present in both periods in these tests. This led to a total of seven tests, including the test comparing periods 1 and 7. To avoid committing type I errors when making multiple comparisons, we adjusted the criterion using the sequential Holm–Bonferroni technique (Holm 1979).

We also used partial row-wise correlations (Hemelrijk 1990b; de Vries 1993) to control for maternal kinship or rank differences. For each analysis we calculated rank differences using the dominance hierarchy of the corresponding period. For analyses that involved periods that included two dominance hierarchy periods, we calculated a mean rank for each individual between those two periods.

To assess the duration of the best social bonds, we assessed the top intrasex and intersex nonkin individuals in terms of contact sitting per individual per period. We attempted to identify the top two individuals in each case. However, in 43 of the 294 cases it was not possible to identify two top individuals when either of both ranks were shared. In these occasions we set a maximum of three top individuals. Where two or three individuals shared the first rank, we included only these individuals, and excluded individuals ranked second; where more than two individuals shared the second rank, we excluded all of these individuals. As such we identified only 1 top individual in 15 of the 294 cases and 3 top individuals in 28 of the 294 cases (see ESM for an example). We also assessed how many possible nonkin partners were available for each individual in each period.

We assessed the percentage of grooming directed toward kin and toward nonkin over the whole study period, and the percentage of all nonkin grooming that each individual directed toward their top partners and other nonkin individuals per period. We compared the mean number of individuals in, and the mean duration of, intersex and intrasex top relationships, as well as the mean percentages of nonkin grooming with intrasex and intersex top relationships using Wilcoxon signed ranks tests, and compared measures for males and females using Mann–Whitney U tests. Males and females did not differ significantly in the number of different intrasex individuals in their top relationships (Mann–Whitney $U = 73.5$, $N = 11$ males and 13 females, $P = 0.910$); number of different intersex individuals in their top relationships ($U = 52$, $P = 0.277$); percentage of total time of intrasex top-two relationships ($U = 66$, $P = 0.776$); percentage of total time of intersex top-two relationships ($U = 90$, $P = 0.303$); duration of intrasex relationships ($U = 63.5$, $P = 0.649$); duration of intersex relationships ($U = 67.5$, $P = 0.820$); % of nonkin grooming directed to intrasex top relationships ($U = 52.5$, $P = 0.277$); or % of nonkin grooming directed to intersex top relationships ($U = 82$, $P = 0.313$). Consequently, we report results for the sexes combined.

To assess grooming equitability, we focused on the total amount of grooming over the whole study period, as we had too few grooming data to calculate equitability per separate period reliably, particularly for dyads that did not groom one other very often. Consequently, we focused only on individuals that were present throughout the whole study period ($N = 14$). Following Silk and collegues (2006), we calculated grooming equitability as:

$$1-\mathrm{abs}\left[\mathrm{Gr}_{\mathrm{ab}}-\mathrm{Gr}_{\mathrm{ba}}\Big/\mathrm{Gr}_{\mathrm{ab}}+\mathrm{Gr}_{\mathrm{ba}}\right],$$

where 1 reflects a perfectly equal grooming relation, and 0 a completely skewed or one-way grooming relationship.

To compare grooming equitability in dyads with strong and less strong bonds, we calculated the upper quartile (UQ) of contact-sitting data with all nonkin per individual, and considered all dyads above that UQ as strong bonds, and all others as not. We then compared grooming equitability between kin, strong nonkin bonds, and all other nonkin relationships (other three quartiles: OQ). Sample sizes differ as 2 of the 14 individuals had no kin (comparisons with kin: 12; comparisons of nonkin: 14). As grooming equitability may be skewed if there are only few grooming interactions between a dyad, we also reran these analyses using only dyads that had at least 4 grooming interactions.

To assess whether strong bonds were related to rank similarity, we compared the mean rank differences between kin-relations, strong nonkin bonds, and all other nonkin relationships. Intrasubject comparisons between kin, UQ, and OQ were performed using Friedman's tests, and *post hoc* analyses were performed using Wilcoxon signed ranks tests. Significance of multiple comparisons was determined using Bonferroni corrections.

To assess whether strong bonds were related to age similarity, we compared the mean age differences between strong nonkin bonds and all other nonkin relationships. Intrasubject comparisons between UQ and OQ were performed using a Wilcoxon signed ranks test.

Finally, to assess whether grooming equitability was due to rank or age differences, we correlated rank differences and age differences with grooming equitability using row-wise Kendall's τ (Hemelrijk 1990a; de Vries 1993; de Vries *et al.* 1993). We entered grooming equalities for dyads that never groomed (19.8% of all dyads) as missing values and calculated *P* values based on 10,000 permutations.

All statistical tests were two-tailed and we set α to 0.05.

Results

Stability of Proximity Patterns Within the Whole Group

A mean of 92.8 ± SD 6.8% of dyads were observed to sit in contact at least once during each 4-mo period (female–female [FF] dyads: 94.8 ± SD 4.0%; male–male [MM] dyads: 94.8 ± SD 6.0%; female–male [FM] dyads: 91.3 ± DS 9.1%). The relative amount of contact sitting between each dyad in each period was significantly correlated with that of the subsequent period, and these proximity patterns were also stable over the "long" term, as contact-sitting during the first period also correlated significantly with that in the last period (Table Ia). Although maternal relatedness affected the original correlations, as indicated by a deviation of the τ statistic from the original correlation (Vervaecke *et al.* 2000), all correlations remained significant after controlling for maternal relatedness (Table Ia). In contrast, rank difference had no effect on the stability of contact-sitting data, as partialing out rank differences from the original matrix correlations did not change the τ statistics or the significance of correlations (Table Ia).

For both sexes we found that intrasex proximity patterns were stable across all periods, and for females it was also stable "long" term (Table Ib, Ic). In contrast, male proximity patterns were not stable "long" term, as male contact-sitting data for the first period did not correlate significantly with those for the last period (Table Ic). These correlations for both sexes remained significant after controlling for maternal relatedness and rank, although maternal relatedness did have a small effect (Table Ib, Ic).

FM and MF proximity patterns were stable across all periods and over the "long" term (Table Id, Ie). These correlations remained significant after controlling for maternal relatedness and rank, although maternal relatedness did have a small effect (Table Id, Ie).

Stability of Grooming Patterns Within the Whole Group

A mean of 20.7 ± SD 7.0% of all dyads were observed to groom directionally, i.e., A grooms B, at least once during each 4-mo period (FF dyads: 24.2 ± SD 10.3%; MM dyads: 23.0 ± SD 9.0%; FM dyads: 17.3 ± DS 4.7%; MF dyads: 19.3 ± 7.2%). Grooming patterns between all individuals were also stable across all periods and over the “long” term (Table IIa). These correlations remained significant after controlling for maternal relatedness and rank, although maternal relatedness did have a small effect (Table IIa).

FF grooming patterns were stable across all periods and over the “long” term (Table IIb). In contrast, MM grooming patterns were not stable across all periods, nor over the long term, as male grooming data for one period did not always correlate with data for the subsequent period, nor did the male grooming data from the first period correlate with those of the last period (Table IIc). Males also tended to groom less than females in general, although this difference was not significant (Mann–Whitney $U = 77.5$, $N = 31$, $P = 0.099$). After controlling for maternal relatedness and rank, originally significant correlations remained significant although maternal relatedness did have a small effect (Table IIb, IIc).

FM grooming patterns were stable across almost all periods and over the “long” term (Table IId). MF grooming patterns were not always significant, and therefore not stable, across all periods, nor over the “long” term (Table IIe). Originally significant correlations remained significant after controlling for maternal relatedness and rank, although maternal relatedness did have a small effect (Table IId, IIe).

Social Bonds: Top Intrasex Relationships

Although only 19.0% of all dyads were maternal kin dyads in this group, 59.0% of all grooming was directed at kin. Among nonkin, grooming patterns were strongly biased: individuals had a mean of 7.8 ± SD 1.6 available nonkin intrasex partners, but directed a mean of 54.8 ± SD 23.8% of nonkin grooming to only their top intrasex relationships. For intrasex dyads subjects had a mean of 4.5 ± SD 1.3 nonkin individuals occupying these top partner positions during the whole study period. These top relationships constituted a mean of 52.5 ± SD 17.1% of the time the two individuals could possibly be observed as partners, i.e., time when both individuals were in the group and old enough to contribute data. These top relationships lasted (continuously) a mean of 40.7 ± SD 16.3% of the time the two individuals could possibly be observed together, which corresponds to 10.4 mo if both individuals were present throughout the whole study period. Further, 12 of 144 top relations lasted the full 100% of the time the two individuals could possibly be observed together (Fig. 1), which corresponds to 32 mo if both individuals were present throughout the whole study (Fig. 2).

Social Bonds: Top Intrasex Relationships

While individuals had a mean of 8.6 ± SD 1.6 available nonkin intrasex partners, they directed a mean of 56.9 ± SD 28.0% of all nonkin grooming to only their top relationships. Subjects had a mean of 5.1 ± SD 1.2 different individuals occupying the top intersex partner positions during the whole study period. These intersex top relationships constituted a mean of 44.2 ± SD 8.2% of the time the two individuals could possibly be observed together and lasted (continuously) a mean of 31.5 ± SD 10.2% of the time the two individuals could possibly be observed together, which corresponds to 8.8 mo if both individuals were present throughout the whole study

Table II Row-wise matrix correlations of grooming data for each of six observation periods with the subsequent period in a 3-yr study of a captive group of rhesus macaques and comparing the first and last period for **(a)** all individuals, **(b)** females only (FF), **(c)** males only (MM), **(d)** female grooming of males (FM), and **(e)** male grooming of females (MF), and partial row-wise matrix correlations for the same data controlling for maternal relatedness (*r*) and rank differences

a) All periods	Row-wise matrix correlation			Partial (*r*)		Partial (rank difference)	
	Kendall's τ	*N*	*P*	*K′* τ *xy,z*	*P*	*K′* τ *xy,z*	*P*
1 (*m*) vs. 2	0.35	19	**<0.001**	0.32	**<0.001**	0.35	**<0.001**
2 vs. 3	0.44	18	**<0.001**	0.38	**<0.001**	0.43	**<0.001**
3 vs. 4 (*m*)	0.33	24	**<0.001**	0.26	**<0.001**	0.33	**<0.001**
4 (*m*) vs. 5	0.34	24	**<0.001**	0.25	**<0.001**	0.33	**<0.001**
5 vs. 6 (*m*)	0.28	20	**<0.001**	0.18	**0.001**	0.26	**<0.001**
6 (*m*) vs. 7	0.28	22	**<0.001**	0.21	**<0.001**	0.28	**<0.001**
Long term: 1 vs. 7	0.27	14	**<0.001**	0.24	**0.001**	0.27	**<0.001**

b) FF periods	Row-wise matrix correlation			Partial (relatedness *r*)		Partial (rank difference)	
	Kendall's τ	*N*	*P*	*K′* τ *xy,z*	*P*	*K′* τ *xy,z*	*P*
1 (*m*) vs. 2	0.40	10	**<0.001**	0.35	**0.001**	0.40	**<0.001**
2 vs. 3	0.43	10	**<0.001**	0.31	**0.003**	0.43	**<0.001**
3 vs. 4 (*m*)	0.38	13	**<0.001**	0.24	**0.004**	0.38	**<0.001**
4 (*m*) vs. 5	0.42	13	**<0.001**	0.25	**0.002**	0.41	**<0.001**
5 vs. 6 (*m*)	0.45	13	**<0.001**	0.24	**0.006**	0.41	**<0.001**
6 (*m*) vs. 7	0.34	13	**<0.001**	0.14	**0.065**	0.33	**<0.001**
Long term: 1 vs. 7	0.28	9	**0.012**	0.25	**0.022**	0.27	**0.013**

c) MM periods	Row-wise matrix correlation			Partial (relatedness *r*)		Partial (rank difference)	
	Kendall's τ	*N*	*P*	*K′* τ *xy,z*	*P*	*K′* τ *xy,z*	*P*
1 (*m*) vs. 2	0.29	9	0.017	0.28	0.019	0.29	0.015
2 vs. 3	0.44	8	**<0.001**	0.42	**<0.001**	0.44	**<0.001**
3 vs. 4 (*m*)	−0.03	11	0.684	−0.01	0.534	0.01	0.460
4 (*m*) vs. 5	0.24	11	0.014	0.18	0.042	0.24	0.012
5 vs. 6 (*m*)	0.23	7	0.165	0.23	0.104	0.29	0.040
6 (*m*) vs. 7	0.22	9	0.047	0.21	0.051	0.23	0.035
Long term: 1 vs. 7	0.20	5	0.301	0.41	0.019	0.19	0.224

d) FM periods	Row-wise matrix correlation			Partial (relatedness *r*)		Partial (rank difference)	
	Kendall's τ	$N_{f,m}$	*P*	*K′* τ *xy,z*	*P*	*K′* τ *xy,z*	*P*
1 (*m*) vs. 2	0.28	10,9	**0.007**	0.27	**0.007**	0.29	**0.006**
2 vs. 3	0.43	10,8	**<0.001**	0.36	**<0.001**	0.42	**<0.001**
3 vs. 4 (*m*)	0.34	13,11	**<0.001**	0.25	**0.003**	0.33	**<0.001**
4 (*m*) vs. 5	0.33	13,11	**<0.001**	0.25	**0.002**	0.32	**<0.001**
5 vs. 6 (*m*)	0.10	13,7	0.202	0.00	0.473	0.07	0.248
6 (*m*) vs. 7	0.29	13,9	**0.002**	0.22	**0.015**	0.28	**0.007**
Long term: 1 vs. 7	0.41	9,5	**0.007**	0.41	**0.006**	0.41	**0.005**

Table II (continued)

e) MF periods	Row-wise matrix correlation			Partial (relatedness *r*)		Partial (rank difference)	
	Kendall's τ	$N_{m,f}$	*P*	$K'\ \tau\ xy,z$	*P*	$K'\ \tau\ xy,z$	*P*
1 (*m*) vs. 2	0.44	9,10	**<0.001**	0.43	**<0.001**	0.44	**<0.001**
2 vs. 3	0.31	8,10	**0.004**	0.27	**0.007**	0.31	**0.003**
3 vs. 4 (*m*)	0.28	11,13	**0.002**	0.24	**0.005**	0.28	**<0.001**
4 (*m*) vs. 5	0.25	11,13	**0.005**	0.20	**0.019**	0.25	**0.006**
5 vs. 6 (*m*)	0.18	7,13	0.058	0.16	0.073	0.18	0.059
6 (*m*) vs. 7	0.17	9,13	0.050	0.15	0.058	0.17	0.038
Long term: 1 vs. 7	0.11	5,9	0.247	0.07	0.321	0.12	0.213

Bold *P*-values reflect significance after Holm–Bonferroni corrections. Periods are numbered: 1, November 2006–February 2007; 2, March 2007–June 2007; 3, July 2007–October 2007; 4, November 2007–February 2008; 5, March 2008–June 2008; 6, November 2008–February 2008; 7, March 2009–June 2009. Mating seasons are marked with (*m*)

period. Nine of 172 top intersex relations lasted the full 100% of the time the two individuals could possibly be observed together (Fig. 1), which corresponds to a 32-mo period if both individuals were present throughout the whole study period (Fig. 2).

Intersex and intrasex relationships did not differ significantly in the number of individuals occupying the top positions (Wilcoxon signed ranks test: $T^+ = 129$, $N = 24$, $P = 0.151$). However, there was a trend toward intrasex relationships lasting longer (percentage of time of the whole period these relationships constituted: $T^+ = 183$, $N = 24$, $P = 0.067$; percentage of the whole period these relationships lasted continuously: $T^+ = 211$, $N = 24$, $P = 0.081$) (Fig. 3). There was no significant difference in the percentage of nonkin grooming that was directed at either the top intrasex or the top intersex relationships ($T^+ = 153$, $N = 23$, $P = 0.648$).

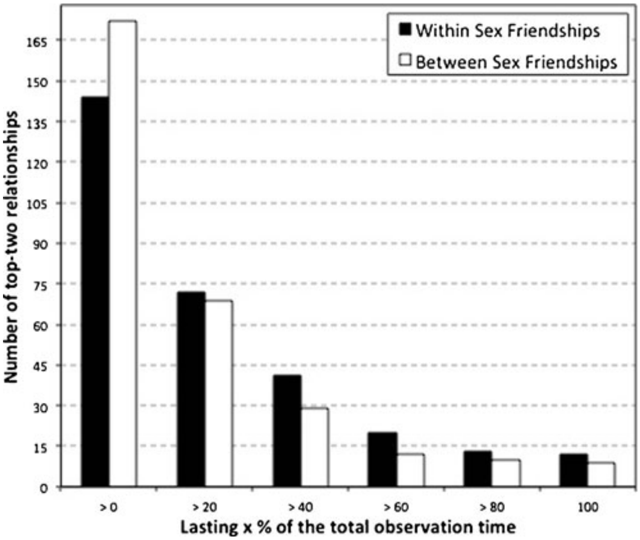

Fig. 1 Number of top relationships that lasted longer than 0, 20, 40, 60, and 80 % and those that lasted the whole period (100 %) these two individuals were seen together, for same- (black bars) and different-sex (white bars) friendships in a 3-yr study of a captive group of rhesus macaques.

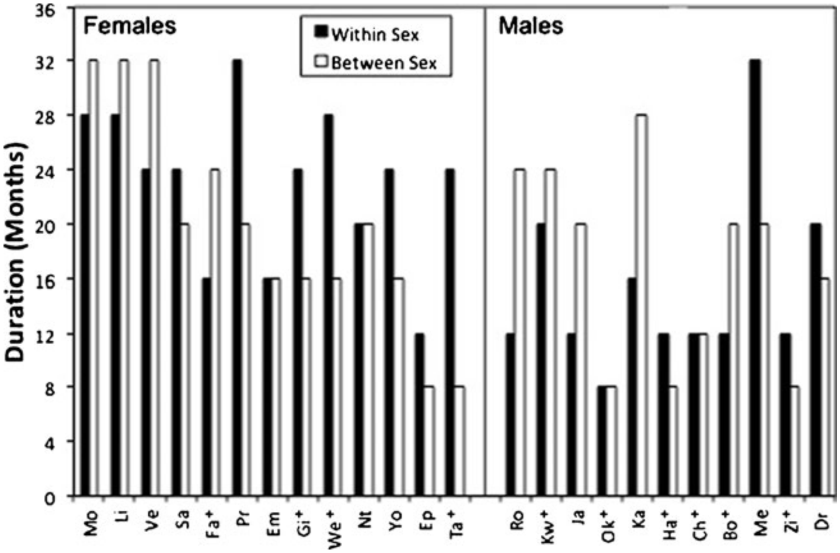

Fig. 2 Total duration of the longest lasting intrasex strong bond (gray bars) and intersex strong bond (black bar) per individual (females left, males right) in a 3-yr study of a captive group of rhesus macaques. *Indicates individuals that were not present in the group during the whole observation period (see ESM for an overview).

Rank Similarity, Age Similarity, and Grooming Equitability

There were significant differences in rank similarity among kin relationships, strong nonkin bonds (UQ), and all other nonkin relationships (OQ) (Friedman's: $\chi^2 = 19.5$, $N = 12$, $P < 0.001$). *Post hoc* analyses revealed that this effect was due to kin relations, which had significantly more similarity in rank than strong nonkin bonds (Wilcoxon signed ranks: $T^+ = 78$, $N = 12$, $P = 0.006$ after Bonferroni correction) and all other nonkin relationships ($T^+ = 78$, $N = 12$, $P = 0.006$ after Bonferroni correction), while there was no difference in rank similarity between strong nonkin bonds and all other nonkin bonds ($T^+ = 26$, $N = 14$, $P = 0.288$ after Bonferroni correction). Similarly, we found a significant correlation between rank similarity and overall contact-sitting (Kendall's $\tau_{rw} = 0.215$, $P = 0.008$), but this correlation became weaker and nonsignificant when we controlled for maternal relatedness using partial row-wise correlations (Kendall's $\tau_{rw} = 0.116$, $P = 0.068$).

There was no significant difference in age similarity among strong nonkin bonds and all other nonkin relations (Wilcoxon signed ranks: $T^+ = 50$, $N = 14$, $P = 0.875$). Likewise, there was no significant correlation between age similarity and overall contact-sitting (Kendall's $\tau_{rw} = 0.021$, $P = 0.420$).

There were significant differences in grooming equitability among kin relationships, strong nonkin bonds (UQ), and all other nonkin relationships (OQ) (Friedman's: $\chi^2 = 6.5$, $N = 12$, $P = 0.039$). *Post hoc* analyses revealed that there was no significant difference in grooming equitability between kin relationships and strong nonkin bonds (Wilcoxon signed ranks: $T^+ = 29$, $N = 12$, $P = 0.433$). However, both kin relations and strong nonkin bonds were significantly more equitable than all other nonkin relations (Kin vs. OQ: $T^+ = 71$, $N = 12$, $P = 0.036$ after Bonferroni correction; UQ vs. OQ: $T^+ = 91$, $N = 14$, $P = 0.048$ after Bonferroni correction; Fig. 4a). However, this pattern was no longer significant when we re-ran the analyses using only data for dyads that had at least four grooming interactions (Friedman's: $\chi^2 = 3.8$, $N = 11$, $P = 0.148$; Fig. 4b). In

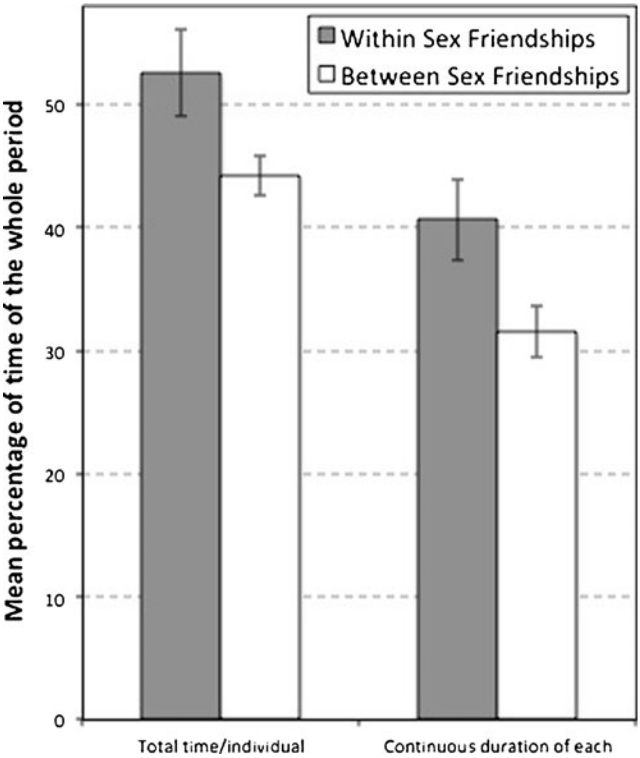

Fig. 3 Mean ± SEM percentage of time a top relationship with a particular individual constituted the whole period these two individuals were seen together (left), and the mean ± SEM percentage of time each top relationship lasted continuously within the whole period these two individuals were seen together (right), for same- (gray bars) and different-sex (white bars) friendships in a 3-yr study of a captive group of rhesus macaques.

addition, grooming equitability and overall contact-sitting data correlated significantly and positively (Kendall's $\tau_{rw} = 0.314$, $P < 0.001$), and this correlation remained significant when we controlled for maternal relatedness (Kendall's $\tau_{rw} = 0.267$, $P < 0.001$), again suggesting that the stronger the bond the more equitable the grooming relation. We found no significant difference in grooming equitability between intra- and intersex relationships (Wilcoxon signed ranks: $T^+ = 69$, $N = 14$, $P = 0.300$). However, within the same-sex relationships we found a significant difference in grooming equitability between the sexes (Mann–Whitney $U = 44$, $N = 5$ males and 9 females, $P = 0.002$); FF grooming relationships were more equitable than male–male grooming relationships.

Finally, we found no significant relationship between the equitability of grooming and rank similarity or age similarity in a dyad (rank similarity vs. grooming equitability; Kendall's $\tau_{rw} = -0.066$, $P = 0.186$; age similarity vs. grooming equitability: Kendall's $\tau_{rw} = -0.068$, $P = 0.176$).

Discussion

Our data show that, in general, proximity and grooming patterns among all group members were stable within and over a 3-yr period in a captive group of rhesus macaques.

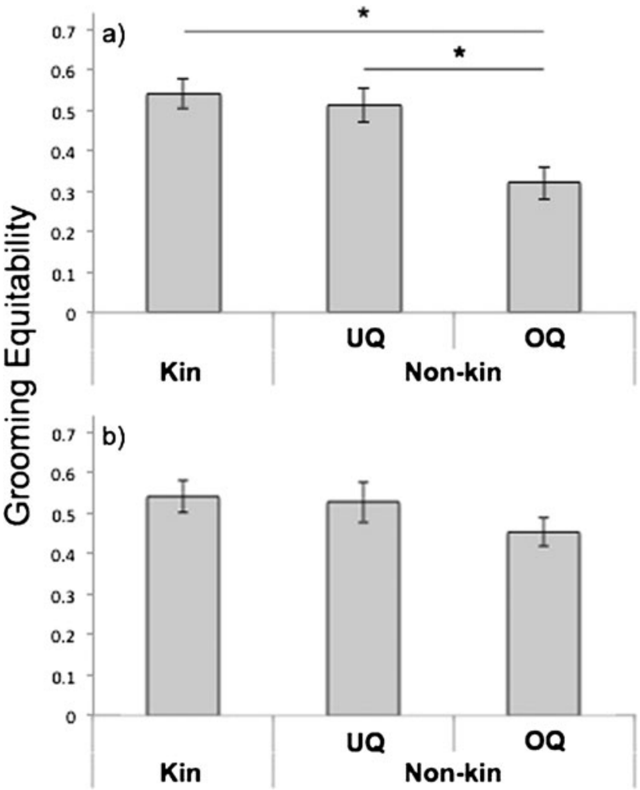

Fig. 4 Mean grooming equitability ± SEM of kin relations, nonkin strong bonds (UQ), and all other nonkin relations (OQ) in a 3-yr study of a captive group of rhesus macaques of **(a)** all dyads and **(b)** dyads that had at least four grooming interactions. *$P < 0.05$.

Female intra- and intersex proximity and grooming patterns were stable over a 3-yr period. In contrast, although male proximity patterns were also reasonably stable, male grooming patterns intra- and intersex were not stable over the 3-yr period. On an individual level our data show that both male and female rhesus macaques can maintain strong, stable, and durable bonds with both particular nonkin intrasex and nonkin intersex members of their group. These bonds seem characterized by a relatively high percentage of grooming and by grooming equitability similar to the values found for kin relationships. However, we found a strong sex difference in grooming equitability: male social bonds had much lower grooming equitability than those of females. Finally, strong nonkin bonds seemed to be unrelated to rank similarity, and were not determined by age similarity.

General Patterns

Analysis of the stability of proximity patterns over the whole group showed that most of these patterns were very stable within and over the 3-yr study period, suggesting that good relationships remain good and bad relationships remain bad. Only “long”-term male proximity patterns were not stable, as the proximity patterns of males during the first period did not correlate significantly with the proximity patterns of the last period. This may reflect the low number of males that was present at the start and end of our study ($N=$

5), or a true deviation from the general pattern. Interestingly, grooming patterns were stable at a group level and in females. Male and female rhesus macaques change their grooming allocation to the different sexes between the mating and nonmating season, allocating more grooming to the opposite sex during the mating season (Massen *et al.* 2012). The current data suggest that each individual's relative distribution of grooming over the group remains relatively stable despite this effect. In contrast, patterns of grooming among males and of male grooming of females were unstable. However, these unstable patterns were not restricted to transitions between nonmating seasons and mating seasons (see Table II) and may reflect an inherent general instability in male relationships.

Strong Relationships

In addition to general proximity and grooming patterns, we also focused on the strongest relationships of nonkin intersex and intrasex individuals. Initial studies of the stability and durability of social bonds focused only on the stability of social bonds among members of the philopatric sex (Mitani 2009; Moss *et al.* 2010; Silk *et al.* 2006, 2010b), as it is assumed that stable social bonds among individuals that remain in the natal group are particularly adaptive (Pusey and Packer 1987). There has also been a great deal of focus on kin relationships. Here, we show that nonmaternal kin rhesus macaques can also entertain stable social bonds among each other, of which some can last for at least 3 yr. One possible explanation for this is the influence of paternal kinship on affiliative interactions (Widdig *et al.* 2001, 2006).

The strong intra- and intersex bonds in nonkin rhesus macaques seem to be valuable, as they are characterized by high degrees of grooming (Cords and Aureli 2000). We also investigated whether these social bonds are characterized by grooming equitability. Reciprocal grooming data over a long period are more balanced than those for shorter periods (Gomes *et al.* 2009; Massen 2010; Schino *et al.* 2009), while grooming equitability may fluctuate over time, especially among individuals with strong social bonds, who are predicted to be tolerant of short-term unbalances (Deutsch 1975; Massen *et al.* 2010). We were not able to investigate such fluctuations, as we lumped our grooming data over the whole 3-yr period. However, we could differentiate between balanced and skewed grooming relations overall and examine how such effects influence the grooming equitability of strong social bonds. Our analyses indicated that, similar to the strong social bonds in female baboons and male chimpanzees (Mitani 2009; Silk *et al.* 2006, 2010b), strong social bonds in rhesus macaques seem to be characterized by grooming equitability, suggesting that such relationships are mutually valuable (Cords and Aureli 2000). However, our sample of grooming interactions among not so strong bonds is restricted and may have driven the results of comparisons of grooming equitability. When we did a more conservative analysis on grooming equitability involving only dyads with four or more grooming interactions, our finding was not significant. However, matrix analyses did show a relationship between relationship quality and grooming equitability. Consequently, the results concerning the relationship between relationship quality and grooming equitability remain inconclusive. Nevertheless, the grooming relations of nonkin individuals maintaining strong bonds seem to be as equitable as those of related rhesus macaques, indicating that stable, durable, and equitable relationships are at least not necessarily restricted to kin.

Differences in dominance rank may also affect relationship quality. However, we found no effect of rank similarity on grooming equitability, contrasting with findings for male chimpanzees (Mitani 2009) and female yellow baboons (Silk *et al.* 2006), but in accordance with findings for female chacma baboons (Silk *et al.* 2010b). This suggests that this pattern varies among primate taxa, possibly reflecting different social systems, and needs further comparative attention. Further, the strong social bonds among the rhesus macaques in our study seemed not to be related to rank similarity. However, this result should be treated with caution as our dominance hierarchies were based on a relatively low number of known relationships. Nevertheless, this pattern is similar to that reported for male chimpanzees (Mitani 2009), but contrasts with data for female baboons (Silk *et al.* 2006, 2010b) and another study of rhesus macaques (de Waal and Luttrell 1986). As rhesus macaque hierarchies are based partly on maternal relatedness and rank similarity is very high among kin, the lack of such an effect may be due to our focus on unrelated strong bonds. However, Silk and colleagues (2006, 2010b) also found this effect after correcting for maternal kinship in baboons, which have a similar dominance structure to rhesus macaques. Lastly, strong social bonds among rhesus macaques were not necessarily characterized by age similarity, nor did age similarity have an effect on grooming equitability. This is in contrast to female baboons (Silk *et al.* 2006) and male spider monkeys (Schaffner *et al.* 2012), but in accordance with male chimpanzees (Mitani 2009). Thus, what truly drives a strong, endurable and equitable bond may differ per species and between the sexes, and these differences need further examination.

Female Relationships

The philopatric sex may benefit more from maintaining stable relationships with nonkin group members. We found that the social bond of philopatric female rhesus macaques were stable across the 3 yr of our study, and that these females also entertain long-lasting bonds with specific individuals, similar to studies of female yellow baboons (Silk *et al.* 2006), female chacma baboons (Silk *et al.* 2010b), female elephants (Moss *et al.* 2010), and male chimpanzees (Mitani 2009). The adaptive benefits of these social bonds among the philopatric sex may differ between the sexes. Whereas chimpanzee males may benefit from their social bonds by increased mating access (Nishida and Hosaka 1996), for baboons it has been reported that the strong and stable bonds among philopatric females contribute to infant survival (Silk *et al.* 2003, 2009) and longevity (Silk *et al.* 2010a). Whether there are similar fitness effects for stable long-term bonds in female rhesus macaques remains to be investigated.

Male Relationships

In contrast to members of the philopatric sex, the bonds of members of the dispersing sex are predicted to be less stable (Pusey and Packer 1987), and have therefore received considerably less attention. More recently, however, studies of the stability of social bonds have also started to focus on social bonds among members of the dispersing sex. Interestingly, individuals of the dispersing sex also maintain stable and durable bonds in female chimpanzees (Langergraber *et al.* 2009; Lehmann and Boesch 2009; *cf.* Arnold and Whiten 2003) and both sexes in bottlenose dolphins (Wiszniewski *et al.* 2010, 2012). The results for male rhesus macaques in our group were rather inconclusive. The individual data suggest that males can entertain long-term stable relationships with each other. However, as our sample of males was relatively small, the stability on an individual level may be due to having few options. The overall proximity patterns of males were also stable, albeit not over the long term. In contrast, male grooming patterns were relatively unstable, and grooming was much more inequitable among males than among females. These results may reflect a general effect that male relationships are in general less stable, which concurs with the hypotheses about social bonds among the dispersing sex (Pusey and Packer 1987). Alternatively, males may entertain relatively stable bonds with regard to proximity, but these bonds are not characterized by grooming and males, in contrast to females, may use grooming in a more instrumental manner, securing short-term needs (Barrett and Henzi 2002; Henzi and Barrett 1999, 2007). However, our small sample of males may also cause these inconclusive results, as males groomed less in general. There were also more changes in group composition among males than among females (1.7 changes per change of period vs. 0.8 among females; see ESM), and such changes influence the stability of bonds. In addition, most of the males in our study were natal males, restricting our study to patterns of male bonding in the natal group. Whether natal bonds hold after dispersing, as bonds in some rhesus macaque male relatives do (Drickamer and Vessey 1973), and how stable male bonds are after dispersal remains to be investigated, preferably with a larger sample of both natal and immigrant males.

Intersex Relationships

As suggested for yellow baboons (Smuts 1985) and Japanese macaques (*Macaca fuscata*: Takahata 1982), we found that female–male social bonds are stable and durable in rhesus macaques. In contrast, the results for male–female social bonds are rather inconclusive, similar to male–male bonds. These bonds are relatively stable on an individual level and proximity patterns are stable on a group level, but grooming patterns are unstable at a group level. Again this may reflect a general tendency of male rhesus macaques being less able to maintain stable relationships, a difference between males and females in how they employ grooming, or our small sample of mostly natal males. Nevertheless, as males are known to reproduce in their natal group in both captivity and semiwild conditions (Dubuc *et al.* 2011; Massen *et al.* 2012), these social bonds may have adaptive benefits for both males and females. The adaptive benefits of these intersex social bonds can differ between the sexes, as male social behavior may increase reproductive success through more mating access (Kulik *et al.* 2011; Massen *et al.* 2012; Smuts 1985), males and females may increase reproductive success through reduced infant mortality as a result of male protection against predators and infanticidal or harassing males (Huchard *et al.* 2013; Palombit *et al.* 1997), and males may provide infants access to richer food patches (Huchard *et al.* 2013). It has been suggested that in contrast to intrasex bonds, intersex bonds are relatively short and last for only one mating season and the subsequent dependent period of the offspring's development, and end if the infant dies or the mother resumes sexual cycling (Seyfarth and Cheney 2012). Although the male–female bonds among the rhesus macaques in our study do tend to be shorter and less stable than those of same-sex bonds, on an individual level they are nonetheless stable and can last up to 3 yr, much longer than suggested based on the length of the mating season or the subsequent vulnerable period of the infant. This indicates that also male–female relationships can be stable.

Our correlational data do not allow us to make any inferences about the mechanism maintaining long-lasting bonds. There is an ongoing debate in the primate literature about whether primates actually recognize these bonds (Seyfarth and Cheney 2012), or whether long-lasting bonds are merely a byproduct of short-term social interactions satisfying immediate needs (Barrett and Henzi 2002; Henzi and Barrett 1999, 2007), and short-term benefits that, in contrast, can lead to cyclicity of social networks (Henzi *et al.* 2009). If primates recognize the extent of their social relationships, it remains unclear if they do so via cognition and calculation of past events (de Waal and Luttrell 1988), a summation of emotions or attitudes associated with past events (Schino *et al.* 2007; de Waal 2000), or a combination of both (Massen *et al.* 2010; Seyfarth and Cheney 2012). Future studies that dissociate temporally distant events and current commodity exchanged (Berghänel *et al.* 2011) may shed a better light on this debate and are much needed.

In conclusion, we showed that female rhesus macaques seem to maintain stable relationships with a subset of group members of the same and different sex. These strong bonds are comparable to human friendships in some aspects and similar to the stable bonds found among several other primate species and some other social mammals (Massen *et al.* 2010; Seyfarth and Cheney 2012; Silk 2002a; Smuts 1985). Moreover, such bonds are not restricted to kin, to dyads of similar age, or to a specific sex, suggesting that the underlying mechanism of female social bonding may be a general trait in rhesus macaques. In contrast, our data on male relationships are rather inconclusive. Although individual data show that male rhesus macaques can entertain long-lasting social bonds with other males or females, male grooming patterns are rather instable, and male–male grooming relations are relatively inequitable. Future research, with a larger sample of both natal and immigrant males, may establish whether this inconclusiveness is an artefact of our relatively meagre sample of males, or whether this discloses a true effect and reflects differences between the philopatric and the dispersing sex in the stability and durability of rhesus macaque social bonds.

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