Published in final edited form as:
Int J Primatol. 2015 April 1; 36(2): 353–376. doi:10.1007/s10764-015-9826-4.

Sex Differences in the Development of Social Relationships in Rhesus Macaques (*Macaca mulatta*)

Lars Kulik,
Junior Research Group of Primate Kin Selection, Department of Primatology, Max-Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany. Institute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, 04103 Leipzig, Germany

Federica Amici,
Institute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, 04103 Leipzig, Germany. Department of Comparative and Developmental Psychology, Max-Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

Doreen Langos, and
Junior Research Group of Primate Kin Selection, Department of Primatology, Max-Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany. Institute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, 04103 Leipzig, Germany

Anja Widdig
Junior Research Group of Primate Kin Selection, Department of Primatology, Max-Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany. Institute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, 04103 Leipzig, Germany

Lars Kulik: lars_kulik@eva.mpg.de

Abstract

Several studies have documented the importance of social bonding for the enhancement of individual fitness. However, little is known about how social relationships develop through ontogeny, and whether their development follows the same trajectory in males and females. Here we analyzed affiliative interactions (proximity, social grooming, play) combined with demographic and genetic data in semi-free-ranging rhesus macaques (*Macaca mulatta*) on Cayo Santiago over their first 4 yr of life (from birth to sexual maturation) to understand how these interactions change through development in both sexes. Generalized linear mixed models revealed that social behaviors mostly followed different developmental trajectories in males and females and were highly dependent on the social context. In particular, sex differences in social behavior varied through development depending on the partner's sex and age. Females engaged in more social interactions than males, especially with other females, and were more involved in grooming around the time of maturation. In contrast, males interacted more with males and age peers, especially around maturation. Sex differences in social behavior varied through development, but

---

Correspondence to: Lars Kulik, `lars_kulik@eva.mpg.de`.

Electronic supplementary material The online version of this article (doi:10.1007/s10764-015-9826-4) contains supplementary material, which is available to authorized users.

also depended on rank, partner's rank, and kin line, although not consistently. High-ranking individuals, especially older females, were generally preferred as social partners. Moreover, both male and female individuals interacted mostly with maternal kin, although males also preferred paternal kin over nonkin. Importantly, most developmental changes in sociality happened when individuals were *ca*. 2 yr old, suggesting that this might be a milestone in the development of sociality in rhesus macaques. The only notable exception to this pattern was play, which was more pronounced in males from the beginning of their lives. We propose that play might serve as a trigger of sex differences in social behavior, with sex differences emerging early in development and increasing through time as males and females gradually grow into their adult social roles.

Keywords

Development; Ontogeny; Rhesus macaques; Sociality; Social bonding; Social relationships

Introduction

Several studies have shown that primates form strong and enduring social bonds with their conspecifics (Lehmann and Boesch 2009; Silk *et al.* 2012). Although strong social relationships are typically observed between genetically related individuals (Chapais 2001; Silk 2002a), long-term cooperative relationships are also common between unrelated individuals (Seyfarth and Cheney 2012; Silk 2002b). The existence of strong social relationships among nonkin has long been considered an evolutionary puzzle (Cheney 2011; Clutton-Brock 2009; Seyfarth and Cheney 2012). However, recent evidence has shown that the quality of social relationships plays a crucial role in enhancing primates' fitness even when social relationships involve nonkin. The quality of female baboons' social relationships, for example, positively affected their ability to cope with stressful events (Crockford *et al.* 2008; Engh *et al.* 2006a, 2006b; Wittig *et al.* 2008) and increased offspring survival (Silk *et al.* 2003, 2009) and longevity (Silk *et al.* 2010). Similarly, enduring social relationships enhanced reproductive success in male macaques (Schülke *et al.* 2010).

Given these premises, it is not surprising that group-living primates are characterized by a complex network of social relationships. However, few studies so far have explored how social relationships develop through ontogeny, and especially whether sex differences exist in the development of these relationships. There is evidence that some aspects of sociality change through development in a similar way for both sexes. For example, both male and female Japanese macaques (*Macaca fuscata*) showed a decrease in the variety of social behaviors exchanged with their mothers after the first year of life and mostly groomed each other as they grew older (Nakamichi 1989). Similarly, in chimpanzees (*Pan troglodytes*) the percentage of time dedicated to social grooming of other group members increased with age for both male and female juveniles (Lonsdorf *et al.* 2014), whereas in patas monkeys (*Erythrocebus patas*) the time spent playing decreased with age in both sexes (Rowell and Chism 1986).

There is also evidence that patterns of social relationships differ between adult males and females. In female philopatric species adult females have very strong social bonds, e.g., rhesus macaques (Kapsalis and Berman 1996), capuchins (*Cebus capucinus*: Perry 1996), vervets (*Cercopithecus aethiops*: Seyfarth 1980), savannah baboons (*Papio cynocephalus*: Seyfarth 1976; Silk *et al.* 1999). In male philopatric species, in contrast, adult males form the strongest social bonds, e.g., red colobus (*Colobus badius*: Struhsaker and Leland 1976), spider monkeys (*Ateles geoffroyi*: Slater *et al.* 2009), muriquis, *Brachyteles arachnoids*: Strier *et al.* 2002; chimpanzees: Gilby and Wrangham 2008; Nishida 1979; Watts 2000a, b; *cf*. Lehmann and Boesch 2008, 2009).

In several primate species sex differences in bonding strength appear before adulthood (Cords *et al.* 2010; Nakamichi 1989; Nikolei and Borries 1997; Pereira 1988; van Noordwijk *et al.* 1993; see Fedigan 1982), whereby the dispersing sex appears to form looser social relationships from the first years of life onward (Andres *et al.* 2013; Frère *et al.* 2010; Kulik unpub. data; Stumpf *et al.* 2009). Moreover, sex differences in play are widespread in juveniles, with males playing generally more than females (Meredith 2013). The fact that sex differences are rather consistent across species and partially emerge early on during infancy (Glick *et al.* 1986; Lonsdorf *et al.* 2014; Milton 2002; Nakamichi 1989; *cf*. Eaton *et al.* 1986) might suggest that they are not flexible, but preponderantly genetically encoded, or that environmental effects act prenatally or very early in life (Cords *et al.* 2010; Lonsdorf *et al.* 2014; Roney and Maestripieri 2005). For example, young male spider monkeys developed species-typical social patterns despite any male model being present in the isolated population studied, which suggests intrinsic sex differences in social behavior (Milton 2002; for a similar conclusion, see Eaton *et al.* 1986; Roney and Maestriperi 2003).

There is also evidence that important sex differences in social behavior emerge later in infancy (Japanese macaques: Eaton *et al.* 1986; Nakamichi 1989; patas monkeys: Rowell and Chism 1986; blue monkeys (*Cercopithecus mitis stuhlmanni*): Cords *et al.* 2010; chimpanzees: Lonsdorf *et al.* 2014). Through ontogeny, for example male monkeys decreased the time spent with their mothers more than females did (Japanese macaques: Eaton *et al.* 1986; Nakamichi 1989; patas monkeys: Rowell and Chism 1986), but increased the time spent with male age peers (Nakamichi 1989). Moreover, through ontogeny females increased the time spent grooming and decreased the time spent playing more than males did (Eaton *et al.* 1986; Nakamichi 1989), and male chimpanzees reached a peak in social play earlier than females (Lonsdorf *et al.* 2014). Further, males began to show increased distances from their mothers at the end of their infancy and thereafter maintained farther distances than females (Lonsdorf *et al.* 2014). In blue and patas monkeys, females were found in spatial proximity of other group members more often than males, especially when older (Cords *et al.* 2010; Rowell and Chism 1986). Through ontogeny blue monkey females also associated with infants more than males did, whereas males preferentially associated with other juvenile males (Cords *et al.* 2010). Depending on their sex and age, therefore, young individuals flexibly use a variety of behavioral strategies to interact with their partners, possibly to best fit the sex-specific social roles that are typical of their adult lives (Eaton *et al.* 1986; Nakamichi 1989).

Although previous studies provide valuable information on the development of social relationships in both sexes, they also have important limits. For example, statistical constraints did not allow exact determination of when sex differences in social behavior appear during ontogeny. Moreover, social behavior in nonhuman primates varies depending on the partners' sex, kinship, rank, and age, which needs to be taken into account to understand how social preferences develop during ontogeny and how sex-specific differences arise depending on the social context (Cords *et al.* 2010) Adult philopatric females, for example, preferentially interact with other females (Kapsalis and Berman 1996; Perry 1996; Seyfarth 1976, 1980; Silk *et al.* 1999). Moreover, philopatric females bias their bonds toward maternal kin (Chapais 2001; Silk 2002a, 2009) and in some species also toward paternal kin as compared to nonkin (Charpentier *et al.* 2007; Widdig *et al.* 2001, 2002), in particular, when maternal kin are not available (Silk *et al.* 2006). Primates also compete to interact with high-ranking individuals (Schino 2001; Seyfarth 1977; Tiddi *et al.* 2012), and preferentially interact with age peers if partners of different ages are present in the group (Nakamichi 1989; Suomi 2005; Widdig *et al.* 2001). All of this evidence suggests that, depending on the composition of their social group, primates actively select their interaction partners (Berman *et al*., 1997; Lonsdorf *et al.* 2014; Silk *et al.* 2006; Suomi 2005). Although sociality plays such an important role in primate social systems, no study has so far analyzed how sex differences in social behavior change from birth to maturation while taking partners' sex, age, rank, and kinship into account.

We conducted our study on rhesus macaques, which live in multimale, multifemale groups, with females being philopatric (Gouzoules and Gouzoules 1987) whereas males disperse at puberty (Colvin 1983; Lindburg 1969). Breeding is seasonal (Drickamer 1974), and both males and females mate with several partners (Lindburg 1971). Given the complexity of their social life, rhesus macaques are therefore an ideal model to study how sex differences in social behavior emerge during ontogeny.

The aim of this study was therefore to investigate sex differences during the development of social relationships. We extended previous studies by analyzing affiliative behavior observed between birth and sexual maturation, i.e., covering the entire developmental phase, in relation to several important predictors and using powerful multivariate statistical tools. Long-term behavioral data allowed us to investigate whether sex differences are present since birth or whether they develop through time as a function of the social context and experience acquired. In particular, we observed affiliative behavior (proximity, grooming, and play) and analyzed whether affiliation patterns follow different developmental trajectories in males and females. Based on the literature reviewed in the preceding text, we hypothesized most social behaviors to gradually differ between sexes through development (H1), with philopatric females being more socially integrated than males especially around maturation. In particular, we predicted females to increase the frequency of (H1a) grooming and (H1b) spatial proximity through development, more than males, and (H1c) males to play more than females, especially in the first years of life. We also hypothesized that the development of sex differences in social behavior to strongly depend on the social context (H2). In particular, we predicted focal subjects to preferentially interact with partners having (H2a) the same sex, (H2b) a similar age and (H2c) being maternally related, across all behaviors observed. Finally, we predicted high-ranking focal subjects and partners to be more involved in social interactions than low-ranking conspecifics (H2d).

Materials and Methods

Study Population and Subjects

We conducted our study on the rhesus macaque population of Cayo Santiago, a 15.2-ha island offshore Puerto Rico. All monkeys on the island are direct descendants of the 409 founder animals captured in India at various locations in 1938 (Rawlins and Kessler 1986). Although no individual has been added to the population except through natural births, pedigree data show no evidence of inbreeding over time (Widdig unpub. data). The population is managed by the Caribbean Primate Research Center (CPRC) and is partly provisioned; however, *ca.* 50 % of feeding time is spent on natural vegetation (Marriott *et al.* 1989). Demographic data including the date of birth, date of death and sex of focal subjects, as well as group membership and the number of maternal kin have been continuously recorded by CPRC census takers since 1956. Male dispersal was noted by census takers and subsequent group membership was checked for ≥2 mo after dispersal: if the dispersing male remained in the same new group during that time, the first day he was seen in the new group was defined as the date of immigration. The interbirth interval for females in this population is *ca.* 1 yr, with females mostly giving birth to a single offspring (Rawlins and Kessler 1986). Infants can be easily assigned to nonoverlapping birth cohorts, although infants from the same cohort can differ up to 6 mo in age. Data from captivity report that in rhesus macaques females reach sexual maturation between 2.5 and 3.5 yr of age (Zehr *et al.* 2005) and males between 3 and 3.5 yr of age (Dixson and Nevison 1997). In our study population, the youngest reported mother was 2.9 yr old (Bercovitch and Berard 1993) and the youngest sire was 3.8 yr old (Bercovitch *et al.* 2003), although substantial interindividual variation in sexual maturation is expected (Bercovitch and Goy 1990). Males were leaving their natal group between 3 and 5.5 yr of age (median age = 4.5 yr) (Berard 1990).

During the study period (from October 2004 to August 2008), our study troop (group R) consisted of 78.53 ± 5.77 (mean ± SD) adult females and 47.87 ± 7.11 (mean ± SD) adult males across study years. Starting immediately after birth, we followed all 55 focal subjects (26 females and 29 males) born in the birth cohort 2005 (hereafter focal subjects). A total of 28 focal subjects (15 females, 13 males) survived until they reached maturation and the study was completed, while 13 died during the study period for unknown reasons and 16 subjects were removed by the CPRC owing to colony management. Over the entire study period group R consisted of a total of 522 potential social partners for our focal subjects (hereafter focal partners). All group members, including focal subjects, were recognized on an individual basis using natural markings and tattoos.

Behavioral Data

Using focal animal sampling (Altmann 1974), we collected a total of 3543 observational hours over the entire study period, resulting in 64.42 ± 37.33 h (mean ± SD; range 8.3–95.3 h) per focal subject. We recorded no more than one 20 min sample per day and focal subject, with focal observations being evenly distributed over the day and balanced weekly among subjects. During each sample we continuously recorded affiliative interactions between the focal and all other group members. In this study, we particularly analyzed data on grooming and play. In addition, we recorded spatial proximity, i.e., neighbors of the focal subject within a 2.0 m range, based on point time samples taken every 4 min (including the start) during focal samples. For each interaction involving the focal subject we also recorded whether or not the mother of the focal subject was present within a 2.0 m range of the focal subject. Finally, we collected *ad libitum* data (Altmann 1974) on displacement, aggression, or submission among adult males and females to construct dominance hierarchies (see later). A. Widdig, D. Langos, and two field assistants collected the data. Interobserver reliability tests ranged between 90 and 97 %, with subsequent assistants conducting simultaneous focal samples with A. Widdig or D. Langos, respectively (Kaufman and Rosenthal 2009). We used Psion Workabout™ handhelds and processed the collected data with Observer software (version 5.0). All observers were blind to paternity across the entire study period.

Parentage Assignment and Determination of Kinship

For parental assignment we used the long-term genetic database of this population, which was first implemented in 1992 and continuously extended since (Kulik *et al.* 2012; Nürnberg *et al.* 1998; Widdig *et al.* 2001, 2006). Nearly the entire present population has been systematically sampled by collecting hair, blood, tissue, or fecal samples for DNA extraction. For our study we were able to sample all 55 focal subjects plus 445 of all 522 (95.79 %) individuals belonging to our study group during this study.

We derived maternity from long-term field observations and it was genetically tested whenever a sample was available. For all 55 focal subjects we were able to genetically confirm the behaviorally assigned mother. We determined paternity by using a combination of exclusion and likelihood analyses, considering as potential sires all mature males present on the island around conception for a given infant. We also assigned maternal and paternal grandparents to increase the power of our kinship data. Based on these parentage assignments we used pedigree information up to the grandparental generation to establish kin relationship for all dyads (classified either as maternal kin, paternal kin, or nonkin). For more details on how parentage assignment and determination of kinship were implemented, please see the Electronic Supplementary Material (ESM).

Establishing Dominance Hierarchies

We calculated the male dominance hierarchy using the Elo method (Elo 1978; Neumann *et al.* 2011) and an R function written by L. Kulik. In this way, we estimated individuals' competitive abilities by considering agonistic interactions sequentially over time, whereby the outcome of these interactions continuously updated the scores used to estimate competitive abilities (Neumann *et al.* 2011). The results we obtained from the Elo method correlated highly (Spearman's rank correlation: $N = 65$ individuals, $\rho = 0.64$, $P < 0.001$) with other commonly used ranking methods such as I&SI, which minimizes the number of inconsistencies (I) within a dominance matrix and subsequently the strength of inconsistencies (SI) (de Vries 1998; Neumann *et al.* 2011). The adult female hierarchy was also based on the outcome of dyadic agonistic interactions collected in 1997 and calculated using the I&SI method (de Vries 1998; as used in Widdig *et al.* 2001). Given that the dominance relationships among sexually mature females were largely stable over time (as confirmed via *ad libitum* sampling over our entire study period), we assigned focal subjects an individual rank according to the rank of their mother, with offspring of the same female ranking directly below their mother and inverse to birth order (Chapais 1992; Datta 1988; Pereira 1995). We calculated the individual rank on a daily basis to control for minor rank changes due to births and deaths. We standardized the ranks of males and females (including focal subjects) separately per day to a range from 0 to 1 (lowest to highest ranking).

Data Analyses

To analyze what affects the ontogeny of sociality in immature rhesus macaques we used generalized linear mixed models (GLMMs; Baayen 2008). For each of three different behaviors, i.e., grooming, play, and proximity, we calculated a model with an identical set of predictors (see below). Data preparation included several steps. For each behavior we first determined the frequency of events for each day and dyad involving a focal subject and any of the individuals present in our study group based on the demographic records. We further differentiated between interactions with mothers being within or outside of a 2.0 m range from the focal subject. As most of the derived frequency values were 0, we transformed these values into a binary variable by setting all values >0 to 1. We then calculated the frequency of all these daily values over 3 mo periods (determined based on the focal subject’s age), leading to a total of 301,694 data points, i.e., including one data point per quarter for each potential focal-partner dyad per mother-presence condition.

To model the probability of grooming (or other behaviors, respectively), we used the number of days with grooming vs. the number of days without grooming (or play, or shared spatial proximity) for each 3 mo period as the binomial response variable. To analyze whether focal subject’s sociality toward group members varied through ontogeny, we included subject age (averaged over the 3 mo period) in our model. Moreover, for each subject we included squared age (as the relation between subject age and grooming was expected to be nonlinear), sex, rank, and number of maternal kin (up to the grandparent generation, 10.72 ± 6.55; mean ± SD). For social partners we included partner’s rank, age difference between focal subject and partner (as age peers preferentially associate with each other: see Widdig *et al.* 2001), and kin relation between focal subject and partner, i.e., maternal kin, paternal kin, nonkin. As a control variable we included the mother’s presence, as mothers can influence the behavior of focal subjects, e.g., by exerting control over social partners (Langos *et al.* 2013). We also included sex ratio and group size (averaged over the 3 mo period) as control variables, as they have been shown to also affect focal subjects’ social behavior (Berman *et al.* 1997). Finally, we included the identity of both focal subject and partner as random effects into the model. We did not control for proximity in grooming and play because although both behaviors necessitate close proximity, close proximity does not automatically lead to grooming or play and each behavior thus provides different information about social relations than proximity *per se*.

We expected several interactions between these main effects to be significant, as the study explored sociality over a long time frame, from birth to maturation of focal subjects. Specifically, we included six three-way interactions, each of them including the focal subject’s age/age squared (to explore ontogenetic changes in sociality) and the focal subject’s sex (as sociality might vary between the philopatric and dispersing sex). As a third variable in the three-way interactions, we included 1) partner's rank, 2) subject's rank, 3) partner's sex, 4) age difference between subject and partner, or 5) kin relation between subject and partner, as each of these variables might affect sociality in primates (Range and Noë 2002; Seyfarth 1976, 1977); subject's rank (Schino 2001; Seyfarth 1977); partner's sex (Perry 1996; Seyfarth, 1976; Silk *et al.* 2006); age difference (Widdig *et al.* 2001); kin relation (Chapais 2001; Silk 2002a, 2009; Smith, 2014); and 6) mother's presence, which was included as a control and not interpreted (*cf.* Mundry 2014). To achieve a valid model we also included all two-way interactions covered by these interactions.

Our dataset was likely to show temporal autocorrelation (ac, i.e., residuals of data points recorded closer to one another in time could be more similar to one another than data points recorded further apart). This might lead to the violation of the assumption of independent residuals and thus devalue the reliability of the model. Therefore, we included two ac terms, one for the focal subject and one for the partner, to account clearly for temporal ac in the data (for more details, please see ESM). We fitted the models in R (version 2.15.0, R Development Core Team 2012) using the function lmer from the R package lme4 (Bates *et al.* 2011). The models revealed the probabilities of grooming, play, or spatial proximity, respectively, as we modeled the proportions of days with grooming (or other behaviors, respectively) out of the total of all possible days. The GLMM was fitted with binomial error structure and logit link function. For each model, we determined the statistical significance of the full model by comparing its fit with that of the null model (comprising only the random effects and the autocorrelation terms) by using a likelihood ratio test (LRT; Dobson 2002) available as R function anova, package stats. We also tested all terms in the models for their statistical significance by running additional LRTs, comparing the fit of the full model with that of a reduced model lacking the particular term of interest but comprising all the other terms. If an interaction did not reveal significance, we removed it from the model to reliably interpret the lower terms included. Such removal was done only if the full-null model comparison revealed significance (Barr *et al.* 2013; Schielzeth and Forstmeier 2009).

To check that the model assumptions were satisfied, we calculated variance inflation factors (VIFs; Quinn and Keough 2002) by running models without the random effects. The results revealed that collinearity was not an issue (largest VIF = 1.78). We determined VIFs using the function vif of the R package car (Fox and Weisberg 2011). We considered P-values ≤ 0.05 significant. Although the incorporation of random slopes into the model and a model stability estimation would reveal more reliable P-values (Barr *et al.* 2013), we had to forgo this because of computational power leading to the unfeasible calculation time of *ca.* 400 days. Likewise we had to drop analyses on the initiation and reciprocity in maintaining social relations, which would have required the incorporation of computation-intensive four-way-interactions.

Results

Overall, we were able to extract a total of 11,256 grooming (0.59 ± 1.55; mean ± SD per focal subject and day) and 5540 play events (0.52 ± 1.81; mean ± SD per focal subject and day) between the focal subjects and their partners over the study period. In addition, we observed on average 1.43 ± 1.13; mean ± SD focal partners within 2 m proximity to a focal subject in 62,367 recorded point time samples.

Null vs. full model comparisons revealed that the set of predictor variables used had a clear influence on the respective behavioral responses for each of our three models (LRT for proximity: $\chi^2 = 75{,}790.0$, d.f. = 50, $P < 0.001$; grooming: $\chi^2 = 9284.6$, d.f. = 50, $P < 0.001$; play: $\chi^2 = 8981.1$, d.f. = 50, $P < 0.001$). The full results of each model are reported in ESM (Tables SI, SII and SIII).

Our analyses revealed several significant three-way interactions of focal subject's age; focal subject's sex; and one social context variable, i.e., partner's sex, age difference, focal subject's rank, partner's rank, or kin line, indicating that social behaviors largely followed different developmental trajectories depending on the subject's sex and the social context. In the following we present the detailed results depending on the social context variable.

Effect of the Partner's Sex

We found a significant three-way interaction of focal subject's age, focal subject's sex, and partner's sex for all behaviors (for proximity: LRT: $\chi^2 = 434.16$, d.f. = 2, $P < 0.001$; grooming: LRT: $\chi^2 = 27.236$, d.f. = 2, $P < 0.001$; play: LRT: $\chi^2 = 32.189$, d.f. = 2, $P < 0.001$). Both sexes had a higher probability of proximity, grooming, and play with female partners, although male subjects switched their preference to male partners at around 2 yr of age. While the probability of shared proximity generally declined over time (Fig. 1), it increased for grooming (especially in females; Fig. S1) and play (Fig. S2). We found that only for play had male focal subjects higher probabilities than females from a very early age, preferentially playing with other males (and with females only in the very first months of their lives).

Effect of Age Difference Between the Focal Subject and the Partner

Sex differences in social behavior during development depended on the age difference between focal subject and social partner for all three behaviors (three-way interaction focal subject's age × focal subject's sex × age difference, for proximity: LRT: $\chi^2 = 48.634$, d.f. = 2, $P < 0.001$; grooming: LRT: $\chi^2 = 10.672$, d.f. = 2, $P = 0.005$; play: LRT: $\chi^2 = 60.39$, d.f. = 2, $P < 0.001$). In general, female focal subjects were closer to social partners (Fig. S3) and were involved in more grooming events (Fig. 2) than male focal subjects. Both sexes interacted more with age-peers than with other animals. This preference increased for grooming over time, with a peak around 2 yr, although grooming between female focal subjects and nonpeers generally increased. For proximity (Fig. S3), the preference of both sexes for age peers was high at an early age and decreased over time. In contrast, the probability of play with peers was already higher for male subjects than for females at the very beginning of their lives, and until they were older (Fig. S4).

Effect of the Focal Subject's Rank

The focal subject's rank had a different effect depending on the social behavior. Generally, the older the focal subjects were, the more high-ranking focal subjects were involved in social interactions. For grooming and play, this effect was much more pronounced in females (three-way interaction focal subject's age × focal subject's sex × focal subject's rank, for grooming: LRT: $\chi^2 = 6.492$, d.f. = 2, $P = 0.039$; play: LRT: $\chi^2 = 11.352$, d.f. = 2, $P = 0.003$). Grooming increased in the first 2 yr for male and female focal subjects independently of their rank (but generally more for females), and later decreased, except for high-ranking female focal subjects (Fig. 3). In males the probability of play decreased over time slightly more for high-ranking focal subjects (Fig. 4).

In females, the probability of play remained constant for low-ranking focal subjects and decreased over time for high-ranking focal subjects (after reaching a peak around 2 yr), so that around maturation low-ranking focal subjects played more than high-ranking ones (Fig. 4). In both sexes, high-ranking focal subjects had a higher probability of spatial proximity (two-way interaction focal subject's age × focal subject's rank: LRT: $\chi^2 = 124.08$, d.f. = 2, $P < 0.001$), with low-ranking focal subjects having a lower probability of sharing proximity as they got older (Fig. S5).

Effect of the Partner's Rank

The partner's rank had a different effect depending on the social behavior. Both male and female focal subjects were closer to high-ranking partners throughout ontogeny, but this tendency decreased over time, especially for male focal subjects (three-way interaction focal subject's age × focal subject's sex × partner's rank: LRT: $\chi^2 = 7.309$, d.f. = 2, $P = 0.026$; Fig. 5). As both sexes got older, the probability of play with low-ranking partners decreased, while the probability of play with high-ranking partners increased (two-way interaction focal subject's age × partner's rank: LRT: $\chi^2 = 14.349$, d.f. = 2, $P = 0.001$; Fig. S6). Finally, the probability of grooming with low or high-ranking partners was balanced across focal subject's sex and focal subject's age.

Effect of Kin Line

The kin line had a different effect depending on the social behavior. In general, there were higher probabilities for all behaviors to happen with maternal kin, with a peak of interactions around 2 yr of age. In the first year, both sexes had a similar probability of being in proximity to maternal kin, but then the probability decreased, especially for male focal subjects (three-way interaction focal subject's age × focal subject's sex × kin line: LRT: $\chi^2 = 13.515$, d.f. = 4, $P = 0.009$; Fig. 6). Spatial proximity with paternal kin and nonkin was generally low in both sexes and across the four years (Fig. 6). Similarly, focal subjects of both sexes had a higher probability of grooming and play with maternal kin (two-way interaction focal subject's age × kin line, for grooming: LRT: $\chi^2 = 24.455$, d.f. = 4, $P < 0.001$; play: LRT: $\chi^2 = 29.894$, d.f. = 4, $P < 0.001$), while the probability of grooming and play was very low for interactions with paternal kin and nonkin (Figs. S7 and S8). Considering only maternal kin, the probability of grooming decreased through ontogeny, especially for males (two-way interaction focal subject's sex × focal subject's age LRT: $\chi^2 = 27.852$, d.f. = 2, $P < 0.001$; Fig. 7). Independently of age, female focal subjects had a higher probability than male focal subjects of exchanging grooming with maternal kin, while males preferred paternal kin over nonkin as grooming partner more than females did (two-way interaction focal subject's sex × kin line: LRT: $\chi^2 = 9.077$, d.f. = 2, $P = 0.011$; Fig. S9). Male focal subjects had a higher probability of play with maternal and paternal kin as compared to female focal subjects independently of age, while both sexes showed roughly the same probability of play with nonkin (two-way interaction focal subject's sex × kin line: LRT: $\chi^2 = 33.016$, d.f. = 2, $P < 0.001$; Fig. 8).

Discussion

In rhesus macaques, social behaviors largely followed different developmental trajectories in males and females (supporting H1). Females had a higher probability of proximity (H1b) and grooming than males, especially around maturation (H1a), whereas play was already more pronounced in males than in females at the very beginning of their lives (H1c). The development of these sex differences was not homogeneous, but strongly depended on the social context (supporting H2), with social interactions preferentially involving partners having the same sex (H2a), a similar age (H2b), being maternally related (H2c), and high-ranking (H2d). Notably, most developmental changes in social behavior took place when individuals were *ca.* 2 yr old, suggesting that this might be a milestone in the development of sociality in this species.

Sex differences in social behavior varied through development depending on the partners' sex: female focal subjects generally had a higher probability of being in proximity to and, at later ages, of grooming female partners (H2a). This probability was generally higher for female than for male focal subjects, increasing around maturation for females' grooming (H1a), but not for proximity (partially rejecting H1b). These findings confirm that philopatric females have stronger social bonds than dispersing males, and that this is so already prior to sexual maturation (blue monkeys: Cords *et al.* 2010; Japanese macaques: Nakamichi 1989; patas monkeys: Rowell and Chism 1986; long-tailed macaques: van Noordwijk *et al.* 1993). Interestingly, females seems to become more independent through ontogeny, as the probability of shared proximity was decreased through time, but at the same time to become strongly integrated in the group, as the probability of grooming increased around sexual maturation.

Social behavior varied through development depending on the focal subject's sex and partner's age. Both sexes preferred to be closer to age peers than to nonpeers over time (H2b), but males more drastically reduced spatial proximity to nonpeers as compared to females, especially around sexual maturation (H1b). Age proximity is clearly an important factor for promoting social bonds (Janus 1989; Widdig *et al.* 2001), and in earlier studies male infant macaques were found to form closer social bonds with their age peers (Berman 1982; Nakamichi 1989; Suomi 2005), which have a higher chance of sharing the same father (Altmann 1979). Given that males *ca.* 2 yr of age also start preferentially being in proximity to and grooming other males (H2a), interactions with male age peers around sexual maturation might be a male strategy to increase their chances to disperse with paternal kin (Albers and Widdig 2013; Widdig *et al.* 2004). Reduced integration in the maternal family, together with a high attraction for male age peers and other factors, might favor male dispersal around sexual maturity (Nakamichi 1989). Female focal subjects, in contrast, preferred to groom age peers especially at *ca.* 2 yr of age, but then increased the probability of grooming with nonpeers around maturation, suggesting that age peers might not be as important for females at this age (partially rejecting H2b). Finally, both male and female focal subjects preferred to play with age peers (H2b), as they possibly match best in terms of body size and social skills (Fagen 1981; Fairbanks 1993; Maestriperi and Ross 2004).

Through ontogeny, the probability of being in spatial proximity remained constant for high-ranking individuals in both sexes, while it generally decreased for low-ranking individuals (H2d). These results confirm that high-ranking individuals are the preferred partners in social interactions (Chapais 1983; de Waal and Luttrell 1986; Fairbanks 1980; Mehlman and Chapais 1988; Oki and Maeda 1973; Pereira 1988; Seyfarth 1976, 1977; Silk *et al.* 1981; Tiddi *et al.* 2012), especially when they approach sexual maturation and might more effectively provide agonistic support and other rank-related benefits (Seyfarth 1977; Tiddi *et al.* 2012). Similarly, female focal subjects had a higher probability of grooming than males, especially as they got older (H1a), but only high-ranking female focal subjects continuously increased the probability of grooming throughout development (H2d). In contrast, low-ranking females and males played slightly more than high-ranking individuals around sexual maturation (partially rejecting H2d). Given that social play promotes social integration in infants (Bekoff and Byers 1998; Fagen 1981; Koyama 1985; Meaney *et al.* 1985), it is possible that low-ranking individuals, having limited access to others as compared to high-ranking individuals, might rely more on play to explore possibilities of social bonding with others (Baldwin and Baldwin 1974; Fairbanks 1993; Maestriperi and Ross 2004; Nakamichi 1989; *cf.* French 1981).

Individuals generally preferred to be in spatial proximity to high-ranking partners, but were not preferentially involved in grooming with them. It is plausible that the ability to discriminate among partners becomes more selective through ontogeny, as primates acquire the social skills that allow them to interact with group members in the complex ways adults do (Bergman *et al.* 2003; Cheney and Seyfarth 1986, 1999; Gunst *et al.* 2010; Lonsdorf and Ross 2012; Ross and Jones 1999; Suomi 2005; Tomonaga *et al.* 2004). Very young infants might not have the ability to differentiate between low-and high-ranking partners, and may acquired it only as they get older, playing less with low-ranking partners. At the very beginning of the infants' live, the higher probability of proximity to high-ranking partners might be a simple by-product of spatial proximity to their adult mothers, who likely prefer to interact with high-ranking partners (Chapais 1983; de Waal and Luttrell 1986; Fairbanks 1980; Mehlman and Chapais 1988; Oki and Maeda 1973; Pereira 1988; Seyfarth 1976; Silk *et al.* 1981). Alternatively, it might be that very young infants can already discriminate partners, but they are too young to impose their partner preferences toward other group members. In both cases, individuals would become more selective only when getting older. Future studies should address whether specific cognitive changes correspond to the increased preference for high-ranking partners.

The kin line also affected the probability of grooming and play through development, but in a similar way for both sexes. Individuals interacted mostly with maternal kin, i.e., being in proximity, playing and grooming with maternal kin more than with paternal kin and nonkin (H2c). However, proximity and grooming with maternal kin decreased for both sexes (especially for males) over time, as the number of unrelated partners in their social networks likely increased. These results are not surprising, as mothers (but not fathers) continuously associate with their offspring even after weaning. Accordingly, individuals become more familiar with maternal kin and tend to interact more with maternal than with paternal kin (Widdig 2007, 2013). However, male individuals were also more affiliative to paternal kin than nonkin, confirming that some species recognize paternal kin (Charpentier *et al.* 2007) from an early age. Females, in contrast, did not preferentially interact with paternal kin as compared to nonkin, and also had a higher probability than males to be closer to maternal kin. This is in line with the idea that male infants are less integrated than female infants in their matrilineal family (Eaton *et al.* 1986; Kulik unpub. data; Nakamichi 1989) and therefore have to search for alternative social partners outside of their maternal family.

Our results suggest that major developmental changes in social behavior might happen in rhesus macaques at *ca.* 2 yr of age. Although sex differences in play behavior appeared in the first year of life, it was only around 2 yr of age, for example, that individuals showed a peak in grooming. After 2 yr of age, males preferred to be closer to males and groom with them, while females no longer preferred to groom age peers. These are crucial changes that might allow individuals to best prepare for their social role depending on their sex (Koyama 1985; Nakamichi 1989; Roney and Maestripieri 2003, 2005; Suomi, 2005). These results therefore suggest that around 2 yr of age individuals might experience a social “revolution,” in which sex differences in social behavior become stronger and individuals start behaving more similar to adults. Around this time, rhesus macaques might have possibly acquired the cognitive and emotional skills and experiences that are required to interact with group members in the complex ways adults do (*cf.* Cheney and Seyfarth 1986, 1999; Gunst *et al.* 2010; Ross and Jones 1999; see Lonsdorf and Ross 2012; Tomonaga *et al.* 2004). Indeed, other studies on rhesus macaques (Suomi 2005) and other macaque species with a similar life history (Eaton *et al.* 1986; Gunst *et al.* 2013; Nakamichi 1989; Suomi 2005) have reported important changes in social interactions around this age, suggesting that this might be a key milestone in the development of sociality in macaques. It is tempting to consider this life stage as a “prepubertal phase,” in which important hormonal changes start taking place (Stephens and Wallen 2013). We suggest that in this phase macaques, like human adolescents (Beltz and Berenbaum 2013; Blakemore *et al.* 2009; Liben *et al.* 2002; Negriff and Susman 2011), might be finally able to produce the behavioral patterns typical of adulthood, but do so with higher intensity. Future studies should address the possible benefits of such an increase in the intensity of social interactions, and whether these changes are also accompanied by other important changes in cognitive and emotional skills, as shown in humans (Beltz and Berenbaum 2013).

Although most behavioral patterns drastically changed shortly before 2 yr of age, play constituted an important exception. Play did indeed differ between sexes from the very beginning, being more pronounced in males throughout ontogeny, especially in the first years of life (H1c); as in Koyama 1985; Lonsdorf *et al.* 2014; Nakamichi 1989. This is also in line with other studies showing that males play more than females do (rhesus macaques: Brown and Dixson 2000; Japanese macaques: Eaton *et al.* 1986; blue monkeys: Förster and Cords 2005; olive baboons, *Papio anubis*: Owens 1975; chimpanzees: Lonsdorf *et al.* 2014; gorillas, *Gorilla* gorilla: Brown, 1988; reviewed in Fagen 1993; Roney and Maestripieri 2003). This very early emergence of sexual differences in social play suggests that play might have an important role as a trigger of future sex differences in social behavior. During play, individuals learn to respond appropriately to others' behavior and practice subsequent adult skills (Burghardt 2005; Kuczaj and Horback 2013). By playing differently, individuals of both sexes learn different responses, incur different experiences, and possibly also develop different ways of interacting with others. Future studies should further explore this hypothesis and the potential role of play as a trigger of sex differences in social behavior. Moreover, future studies could more carefully differentiate how different forms of play, e.g., with more or less physical contact, develop in both sexes depending on the social context.

In conclusion, our study showed important changes in the development of macaques' social behavior, which were mostly different in females and males and highly dependent on the social context. Although the first sex differences in social behavior appeared in the first year of life, especially in terms of play, sex differences steadily increased throughout infancy. This suggests that the first years of development represent the first social arena to practice sex-specific social roles, with males and females further differentiating their behavior and gradually growing into their social roles. In the future it will be necessary to explore how the development of social bonding is related to changes in individuals' fitness, and the extent to which the psychological and emotional changes occurring in nonhuman primates during the prepubertal phase are comparable to those that occur in humans. Given the importance of the social context for the emergence of sex differences in social behavior, future studies will also benefit from taking social context into account in their analyses.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

We are most grateful to the CPRC for their permission and support of this study. In particular, we thank the staff of the Cayo Santiago Field Station, especially Edgar Davila, Julio Resto, Giselle Caraballo Cruz, and Angelina Ruiz, for their cooperation throughout the observational study and the collection of the DNA samples. We are also grateful to Joyce Moewius and Akie Yanagie for their enthusiasm during data collection and to Klaus Leipholz and Margaret Chiavetta for their cooperation during sampling collection. Fred Bercovitch, Matt Kessler, John Berard, Michael Krawczak, Peter Nürnberg, and Jörg Schmidtke are acknowledged for their effort to start the genetic data base of the Cayo Santiago population, mainly funded by National Science Foundation, National Institutes of Health, and the German Research Foundation (DFG). We are especially grateful to Andrea Trefilov, Elisabeth Kirst, Peter Nürnberg, Petra Otremba, Marion Nagy, Laura Muniz, and Stefanie Bley for their input and collaboration in improving and extending the genetic database, and to Linda Vigilant for laboratory access. We also thank Michael Krawczak, Bernd Hundrieser, and Olaf Junge for access and improvement of the FINDSIRE, a management program of genetic data. Hagen Stenzel kindly wrote a number of macros for data analysis. We are grateful to Roger Mundry for statistical advice, Brigitte Schloegl for helpful discussion and comments, and Joanna Setchell and two unfortunately anonymous reviewers who have provided very helpful comments on an earlier version of this manuscript. The population of Cayo Santiago was supported by grant number 8P40 OD012217-25 from the National Center for Research Resources (NCRR), the Office of Research Infrastructure Programs (ORIP) of the National Institutes of Health and the Medical Sciences Campus of the University of Puerto Rico. The content of this publication is solely the responsibility of the authors and does not necessarily represent the official views of NCRR or ORIP. This project was conducted within the Jr. Research Group of Primate Kin Selection, an Emmy-Noether Group funded by the German Research Foundation (DFG) (grant numbers WI 1801/1-1, 1-2, 2-1, 3-1 awarded to A. Widdig). In addition, funding was received through a Ph.D. grant of the University of Leipzig (awarded to L. Kulik and D. Langos) as well as from the KKGS Stiftung, Elsa-Neumann Stiftung, and DAAD (awarded to D. Langos). We thank the Max-Planck Institute for Evolutionary Anthropology, Leipzig, for their logistic support and for hosting the Jr. Research Group of Primate Kin Selection.

References

Albers M, Widdig A. The influence of kinship on familiar natal migrant rhesus macaques (*Macaca mulatta*). International Journal of Primatology. 2013; 34:99–114. [PubMed: 24850977]

Altmann J. Observational study of behavior sampling methods. Behaviour. 1974; 49:227–267. [PubMed: 4597405]

Altmann J. Age cohorts as paternal sibships. Behavioral Ecology and Sociobiology. 1979; 6:161–164.

Andres D, Clutton-Brock TH, Kruuk LEB, Pemberton JM, Stopher KV, Ruckstuhl KE. Sex differences in the consequences of maternal loss in a long-lived mammal, the red deer (*Cervus elaphus*). Behavioral Ecology and Sociobiology. 2013; 67:1249–1258.

Baayen, H. Analyzing linguistic data: A practical introduction to statistics using R. 1. Cambridge, U.K: Cambridge University Press; 2008.

Baldwin JD, Baldwin JJ. The dynamics of interpersonal spacing in man and monkeys. American Journal of Orthopsychiatry. 1974; 44:790–806. [PubMed: 4611232]

Barr DJ, Levy R, Scheepers C, Tily HJ. Random effects structure for confirmatory hypothesis testing: Keep it maximal. Journal of Memory and Language. 2013; 68:255–278.

Bates, D.; Maechler, M.; Bolker, B. lme4: Linear mixed-effects models using S4 classes. 2011.

Bekoff, M.; Byers, JA. Animal play: Evolutionary, comparative and ecological perspectives. Cambridge, U.K: Cambridge University Press; 1998.

Beltz AM, Berenbaum SA. Cognitive effects of variations in pubertal timing: Is puberty a period of brain organization for human sex-typed cognition? Hormones and Behavior. 2013; 63:823–828. [PubMed: 23603479]

Berard, JD. PhD thesis. University of Oregon; 1990. Life history patterns of male rhesus macaques on Cayo Santiago.

Bercovitch FB, Berard JD. Life history costs and consequences of rapid reproductive maturation in female rhesus macaques. Behavioral Ecology and Sociobiology. 1993; 32:103–109.

Bercovitch, FB.; Goy, RW. The socioendocrinology of reproductive development and reproductive success in macaques. In: Ziegler, TE.; Bercovitch, FB., editors. Socioendocrinology of primate reproduction. New York: Wiley Liss; 1990. p. 59-93.

Bercovitch FB, Widdig A, Trefilov A, Kessler MJ, Berard JD, Schmidtke J, Nurnberg P, Krawczak M. A longitudinal study of age-specific reproductive output and body condition among male rhesus macaques, *Macaca mulatta*. Naturwissenschaften. 2003; 90:309–312. [PubMed: 12883773]

Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM. Hierarchical classification by rank and kinship in baboons. Science. 2003; 302:1234–1236. [PubMed: 14615544]

Berman CM. The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys I. Social networks and differentiation. Animal Behaviour. 1982; 30:149–162.

Berman CM, Rasmussen KLR, Suomi SJ. Group size, infant development and social networks in free-ranging rhesus monkeys. Animal Behaviour. 1997; 53:405–421.

Blakemore, JEO.; Berenbaum, SE.; Liben, LS. Gender development. New York: Psychology Press/ Taylor & Francis; 2009.

Brown GR, Dixson AF. The development of behavioural sex differences in infant rhesus macaques (*Macaca mulatta*). Primates. 2000; 41:63–77.

Brown SG. Play behaviour in lowland gorillas: Age differences, sex differences, and possible functions. Primates. 1988; 29:219–228.

Burghardt, GM. The genesis of animal play: Testing the limits. Cambridge, MA: The MIT Press; 2005.

Chapais, B. Dominance, relatedness and the structure of female relationships in rhesus monkeys. In: Hinde, RA., editor. Primate social relationship: An integrated approach. Oxford: Blackwell; 1983. p. 208-219.

Chapais, B. The role of alliances in social inheritance of rank among female primates. In: Harcourt, AH.; de Waal, FBM., editors. Coalitions and alliances in humans and other animals. Oxford: Oxford University Press; 1992. p. 29-59.

Chapais B. Primate nepotism: What is the explanatory value of kin selection? International Journal of Primatology. 2001; 22:203–229.

Charpentier MJE, Peignot P, Hossaert-Mckey M, Wickings EJ. Kin discrimination in juvenile mandrills, *Mandrillus sphinx*. Animal Behaviour. 2007; 73:37–45.

Cheney DL. Extent and limits of cooperation in animals. Proceedings of the National Academy of Sciences of the USA. 2011; 108:10902–10909. [PubMed: 21690405]

Cheney DL, Seyfarth RM. The recognition of social alliances by vervet monkeys. Animal Behaviour. 1986; 34:1722–1731.

Cheney DL, Seyfarth RM. Recognition of other individuals' social relationships by female baboons. Animal Behaviour. 1999; 58:67–75. [PubMed: 10413542]

Clutton-Brock T. Cooperation between non-kin in animal societies. Nature. 2009; 462:51–57. [PubMed: 19890322]

Colvin, J. Familiarity, rank, and the structure of rhesus male peers networks. In: Hinde, RA., editor. Primate social relationships: An integrated approach. Oxford: Blackwell; 1983. p. 190-200.

Cords M, Sheehan MJ, Ekernas LS. Sex and age differences in juvenile social priorities in female philopatric, nondespotic blue monkeys. American Journal of Primatology. 2010; 72:193–205. [PubMed: 19953556]

Crockford C, Wittig RM, Whitten PL, Seyfarth RM, Cheney DL. Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). Hormones and Behavior. 2008; 53:254–265. [PubMed: 18076884]

Datta SB. The acquisition of dominance among free-ranging rhesus monkey siblings. Animal Behaviour. 1988; 36:754–772.

De Vries H. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Animal Behaviour. 1998; 55:827–843. [PubMed: 9632471]

De Waal FBM, Luttrell LM. The similarity principle underlying social bonding among female rhesus monkeys. Folia Primatologica. 1986; 46:215–234.

Dixson AF, Nevison CM. The socioendocrinology of adolescent development in male rhesus monkeys (*Macaca mulatta*). Hormones and Behavior. 1997; 31:126–135. [PubMed: 9154433]

Dobson, AJ. Texts in Statistical Science. 2. Boca Raton, FL: Chapman & Hall/CRC; 2002. An introduction to generalized linear models.

Drickamer LC. A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. Folia Primatologica. 1974; 21:61–80.

Eaton GG, Johnson DF, Glick BB, Worlein JM. Japanese macaques (*Macaca fuscata*) social development: Sex differences in Juvenile behavior. Primates. 1986; 27:141–150.

Elo, AE. The rating of chess players, past and present. New York: Arco; 1978.

Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL. Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). Proceedings of the Royal Society of London B: Biological Sciences. 2006a; 273:707–712.

Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL. Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. Animal Behaviour. 2006b; 71:1227–1237.

Fagen, R. Animal play behavior. New York: Oxford University Press; 1981.

Fagen, R. Juvenile primates: Life history, development and behavior. New York: Oxford University Press; 1993. Primate juveniles and primate play; p. 182-196.

Fairbanks LA. Relationships among adult females in captive vervet monkeys: Testing a model of rank-related attractiveness. Animal Behaviour. 1980; 28:853–859.

Fairbanks, LA. Juvenile primates: Life history, development, and behavior. New York: Oxford University Press; 1993. Juvenile vervet monkeys: Establishing relationships and practicing skills for the future; p. 211-227.

Fedigan, LM. Primate paradigms: Sex roles and social bonds. Chicago: University of Chicago Press; 1982.

Förster S, Cords M. Socialization of infant blue monkeys (*Cercopithecus mitis stuhlmanni*): Allomaternal interactions and sex differences. Behaviour. 2005; 142:869–896.

Fox, J.; Weisberg, S. An {R} companion to applied regression. 2. Thousand Oaks, CA: SAGE; 2011.

French JA. Individual differences in play in *Macaca fuscata*: The role of maternal status and proximity. International Journal of Primatology. 1981; 2:237–246.

Frère CH, Krützen M, Mann J, Watson-Capps JJ, Tsai YJ, Patterson EM, Connor R, Bejder L, Sherwin WB. Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. Animal Behaviour. 2010; 80:481–486.

Gilby I, Wrangham R. Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. Behavioral Ecology and Sociobiology. 2008; 62:1831–1842.

Glick BB, Eaton GG, Johnson DF, Worlein JM. Social behavior of infant and mother Japanese macaques (*Macaca fuscata*): Effects of kinship, partner sex, and infant sex. International Journal of Primatology. 1986; 7:139–155.

Gouzoules, S.; Gouzoules, H. Kinship. In: Smuts, BB.; Cheney, DL.; Seyfarth, RM.; Wrangham, RW.; Struhsaker, TT., editors. Primate societies. Chicago: University of Chicago Press; 1987. p. 299-305.

Gunst N, Boinski S, Fragaszy DM. Development of skilled detection and extraction of embedded prey by wild brown capuchin monkeys (*Cebus apella apella*). Journal of Comparative Psychology. 2010; 124:194–204. [PubMed: 20476819]

Gunst N, Leca JB, Vasey PL. Development of sexual and socio-sexual behaviours in free-ranging juvenile male Japanese macaques, *Macaca fuscata*. Behaviour. 2013; 150:1225–1254.

Janus M. Reciprocity in play, grooming, and proximity in sibling and nonsibling young rhesus monkeys. International Journal of Primatology. 1989; 10:243–261.

Kapsalis E, Berman CM. Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) I. Criteria for kinship. Behaviour. 1996; 133:1209–1234.

Kaufman AB, Rosenthal R. Can you believe my eyes? The importance of interobserver reliability statistics in observations of animal behaviour. Animal Behaviour. 2009; 78:1487–1491.

Koyama N. Playmate relationships among individuals of the Japanese monkey troop in Arashiyama. Primates. 1985; 26:390–406.

Kuczaj, SA.; Horback, KM. Play and emotion. In: Watanabe, S.; Kuczaj, SA., editors. Emotions of animals and humans: Comparative perspectives. Tokyo: Springer; 2013. p. 283

Kulik L, Muniz L, Mundry R, Widdig A. Patterns of interventions and the effect of coalitions and sociality on male fitness. Molecular Ecology. 2012; 21:699–714. [PubMed: 21880090]

Langos D, Kulik L, Mundry R, Widdig A. The impact of paternity on male–infant association in a primate with low paternity certainty. Molecular Ecology. 2013; 22:3638–3651. [PubMed: 23682587]

Lehmann J, Boesch C. Sexual differences in chimpanzee sociality. International Journal of Primatology. 2008; 29:65–81. [PubMed: 19816541]

Lehmann J, Boesch C. Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees, *Pan troglodytes*. Animal Behaviour. 2009; 77:377–387.

Liben LS, Susman EJ, Finkelstein JW, Chinchilli VM, Kunselman S, Schwab S, Dubas JS, Demers LM, Lookingbill G, D'Arcangelo MR, Krogh MR, Kulin HE. The effects of sex steroids on spatial performance: A review and an experimental clinical investigation. Developmental Psychology. 2002; 38:236–253. [PubMed: 11881759]

Lindburg DG. Rhesus monkeys: mating season mobility of adult males. Science. 1969; 166:1176–1178. [PubMed: 17775579]

Lindburg, DG. The rhesus monkeys in North India: An ecological and behavioral study. In: Rosenblum, LA., editor. Primate behavior. New York: Academic Press; 1971. p. 1-106.

Lonsdorf EV, Markham AC, Heintz MR, Anderson KE, Ciuk DJ, Goodall J, Murray CM. Sex differences in wild chimpanzee behavior emerge during infancy. PLoS ONE. 2014; 9:e99099. [PubMed: 24911160]

Lonsdorf, EV.; Ross, SR. Socialization and Development of Behavior. In: Mitani, JC.; Call, J.; Kappeler, PM.; Palombit, RA.; Silk, JB., editors. The evolution of primate societies. Chicago: University of Chicago Press; 2012. p. 245-268.

Maestripieri D, Ross SR. Sex differences in play among western lowland gorilla (*Gorilla gorilla gorilla*) infants: Implications for adult behavior and social structure. American Journal of Physical Anthropology. 2004; 123:52–61. [PubMed: 14669236]

Marriott BM, Roemer J, Sultana C. An overview of the food intake patterns of the Cayo Santiago rhesus monkeys (*Macaca mulatta*): Report of a pilot study. Puerto Rico Health Sciences Journal. 1989; 8:87–94. [PubMed: 2780973]

Meaney MJ, Stewart J, Beatty WW. Sex differences in social play: The socialization of sex roles. Advances in the Study of Behavior. 1985; 15:1–58.

Mehlman PT, Chapais B. Differential effects of kinship, dominance, and the mating season on female allogrooming in a captive group of *Macaca fuscata*. Primates. 1988; 29:195–217.

Meredith, SL. Identifying proximate and ultimate causation in the development of primate sex-typed social behavior. In: Clancy, KBH.; Hinde, K.; Rutherford, JN., editors. Building babies. New York: Springer Science+Business Media; 2013. p. 411-433.Developments in Primatology: Progress and Prospects

Milton, K. Juvenile primates: Life history, development and behavior. Chicago: University of Chicago Press; 2002. Diet and social organization of a free-ranging spider monkey population: The development of species-typical behavior in the absence of adults; p. 173-181.

Mundry, R. Statistical issues and assumptions of phylogenetic generalized least squares. In: Garamszegi, LZ., editor. Modern phylogenetic comparative methods and their application in evolutionary biology. Berlin and Heidelberg: Springer Science+Business Media; 2014. p. 131-153.

Nakamichi M. Sex differences in social development during the first 4 years in a free-ranging group of Japanese monkeys, *Macaca fuscata*. Animal Behaviour. 1989; 38:737–748.

Negriff S, Susman EJ. Pubertal timing, depression, and externalizing problems: A framework, review, and examination of gender differences. Journal of Research on Adolescence. 2011; 21:717–746.

Neumann C, Duboscq J, Dubuc C, Ginting A, Irwan AM, Agil M, Widdig A, Engelhardt A. Assessing dominance hierarchies: Validation and advantages of progressive evaluation with Elo-rating. Animal Behaviour. 2011; 82:911–921.

Nikolei J, Borries C. Sex differential behavior of immature hanuman langurs (*Presbytis entellus*) in Ramnagar, South Nepal. International Journal of Primatology. 1997; 18:415–437.

Nishida, T. The great apes. Menlo Park, CA: Benjamin Cummings; 1979. The social structure of chimpanzees at the Mahale Mountains; p. 73-121.

Nürnberg P, Sauermann U, Kayser M, Lanfer C, Manz E, Widdig A, Berard JD, Bercovitch FB, Kessler M, Schmidtke J, Krawczak M. Paternity assessment in rhesus macaques (*Macaca mulatta*): Multilocus DNA fingerprinting and PCR marker typing. American Journal of Primatology. 1998; 44:1–18. [PubMed: 9444319]

Oki, J.; Maeda, Y. Grooming as a regulator of behavior in Japanese macaques. In: Carpenter, CR., editor. Behavioral regulators of behaviour in primates. Lewisburg, PA: Bucknell University Press; 1973. p. 149

Owens NW. Social play behaviour in free-living baboons, *Papio anubis*. Animal Behaviour. 1975; 23:387–408.

Pereira ME. Effects of age and sex on intra-group spacing behaviour in juvenile savannah baboons, *Papio cynocephalus cynocephalus*. Animal Behaviour. 1988; 36:184–204.

Pereira ME. Development and social dominance among group-living primates. American Journal of Primatology. 1995; 37:143–175.

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

Quinn, GP.; Keough, MJ. Experimental design and data analysis for biologists. 1. Cambridge, U.K: Cambridge University Press; 2002.

Range F, Noë R. Familiarity and dominance relations among female sooty Mangabeys in the Taï National Park. American Journal of Primatology. 2002; 56:137–153. [PubMed: 11857651]

Rawlins, RG.; Kessler, MJ., editors. History, behavior and biology. Albany: State University of New York Press; 1986. The Cayo Santiago macaques.

Roney, JR.; Maestriperi, D. Primate Psychology. Cambridge, MA: Harvard University Press; 2003. Social development and affiliation; p. 171-204.

Roney, JR.; Maestripieri, D. Social development and affiliation. In: Maestripieri, D., editor. Primate psychology. Cambridge, MA: Harvard University Press; 2005.

Ross, C.; Jones, KE. Comparative primate socioecology. Cambridge, U.K: Cambridge University Press; 1999. Socioecology and the evolution of primate reproductive rates; p. 73-110.

Rowell TE, Chism J. The ontogeny of sex differences in the behavior of patas monkeys. International Journal of Primatology. 1986; 7:83–107.

Schielzeth H, Forstmeier W. Conclusions beyond support: Overconfident estimates in mixed models. Behavioral Ecology. 2009; 20:416–420. [PubMed: 19461866]

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

Schülke O, Bhagavatula J, Vigilant L, Ostner J. Social bonds enhance reproductive success in male macaques. Current Biology. 2010; 20:2207–2210. [PubMed: 21093261]

Seyfarth RM. Social relationships among adult female baboons. Animal Behaviour. 1976; 24:917–938.

Seyfarth RM. A model of social grooming among adult female monkeys. Journal of Theoretical Biology. 1977; 65:671–698. [PubMed: 406485]

Seyfarth RM. The distribution of grooming and related behaviours among adult female vervet monkeys. Animal Behaviour. 1980; 28:798–813.

Seyfarth RM, Cheney DL. The evolutionary origins of friendship. Annual Review of Psychology. 2012; 63:153–177.

Silk JB. Kin selection in primate groups. International Journal of Primatology. 2002a; 23:849–875.

Silk JB. Using the ‘F’-word in primatology. Behaviour. 2002b; 139:421–446.

Silk JB. Nepotistic cooperation in non-human primate groups. Philosophical Transactions of the Royal Society of London B: Biological Sciences. 2009; 364:3243.

Silk JB, Alberts SC, Altmann J. Social bonds of female baboons enhance infant survival. Science. 2003; 302:1231–1234. [PubMed: 14615543]

Silk JB, Alberts SC, Altmann J, Cheney DL, Seyfarth RM. Stability of partner choice among female baboons. Animal Behaviour. 2012; 83:1511–1518. [PubMed: 23885128]

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

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proceedings of the Royal Society of London B: Biological Sciences. 2009; 276:3099–3104.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. Strong and consistent social bonds enhance the longevity of female baboons. Current Biology. 2010; 20:1359–1361. [PubMed: 20598541]

Silk JB, Samuels A, Rodman PS. The Influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). Behaviour. 1981; 78:111–137.

Silk JB, Seyfarth RM, Cheney DL. The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. Behaviour. 1999; 136:679–703.

Slater KY, Schaffner CM, Aureli F. Sex differences in the social behavior of wild spider monkeys (*Ateles geoffroyi yucatanensis*). American Journal of Primatology. 2009; 71:21–29. [PubMed: 18942094]

Smith JE. Hamilton’s legacy: Kinship, cooperation and social tolerance in mammalian groups. Animal Behaviour. 2014; 92:291–304.

Stephens SBZ, Wallen K. Environmental and social influences on neuroendocrine puberty and behavior in macaques and other nonhuman primates. Hormones and Behavior. 2013; 64:226–239. [PubMed: 23998667]

Strier KB, Dib LT, Figueira JE. Social dynamics of male muriquis (*Brachyteles arachnoides hypoxanthus*). Behaviour. 2002; 139:315–342.

Struhsaker, TT.; Leland, L. Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. New York: Academic Press; 1976.

Stumpf RM, Emery Thompson M, Muller MN, Wrangham RW. The context of female dispersal in Kanyawara chimpanzees. Behaviour. 2009; 146:629–656.

Suomi SJ. Mother-infant attachment, peer relationships, and the development of social networks in rhesus monkeys. Human Development. 2005; 48:67–79.

Tiddi B, Aureli F, Schino G. Grooming up the hierarchy: The exchange of grooming and rank-related benefits in a New World primate. PLoS ONE. 2012; 7:e36641. [PubMed: 22590582]

Tomonaga M, Tanaka M, Matsuzawa T, Myowa-Yamakoshi M, Kosugi D, Mizuno Y, Okamoto S, Yamaguchi MK, Bard KA. Development of social cognition in infant chimpanzees (*Pan troglodytes*): Face recognition, smiling, gaze, and the lack of triadic interactions. Japanese Psychological Research. 2004; 46:227–235.

Van Noordwijk, MA.; Hemelrijk, CK.; Herremans, LAM.; Sterck, EHM. Spatial position and behavioral sex differences in juvenile long-tailed macaques. In: Pereira, ME.; Fairbanks, LA., editors. Juvenile primates: Life history, development and behavior. Chicago: University of Chicago Press; 1993. p. 77-85.

Watts D. Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. International Journal of Primatology. 2000a; 21:211–238.

Watts DP. Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. International Journal of Primatology. 2000b; 21:189–210.

Widdig A. Paternal kin discrimination: The evidence and likely mechanisms. Biological Reviews. 2007; 82:319–334. [PubMed: 17437563]

Widdig A. The impact of male reproductive skew on kin structure and sociality in multi-male groups. Evolutionary Anthropology. 2013; 22:239–250. [PubMed: 24166924]

Widdig A, Bercovitch FB, Streich WJ, Sauermann U, Nürnberg P, Krawczak M. A longitudinal analysis of reproductive skew in male rhesus macaques. Proceedings of the Royal Society of London B: Biological Sciences. 2004; 271:819–826.

Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB. Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. Proceedings of the National Academy of Sciences of the USA. 2001; 98:13769–13773. [PubMed: 11698652]

Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB. Affiliation and aggression among adult female rhesus macaques: A genetic analysis of paternal cohorts. Behaviour. 2002; 139:371–391.

Widdig A, Streich WJ, Nürnberg P, Croucher PJP, Bercovitch FB, Krawczak M. Paternal kin bias in the agonistic interventions of adult female rhesus macaques (*Macaca mulatta*). Behavioral Ecology and Sociobiology. 2006; 61:205–214.

Wittig RM, Crockford C, Lehmann J, Whitten PL, Seyfarth RM, Cheney DL. Focused grooming networks and stress alleviation in wild female baboons. Hormones and Behavior. 2008; 54:170–177. [PubMed: 18396288]

Zehr JL, Meter PEV, Wallen K. Factors regulating the timing of puberty onset in female rhesus monkeys (*Macaca mulatta*): Role of prenatal androgens, social rank, and adolescent body weight. Biology of Reproduction. 2005; 72:1087–1094. [PubMed: 15625235]

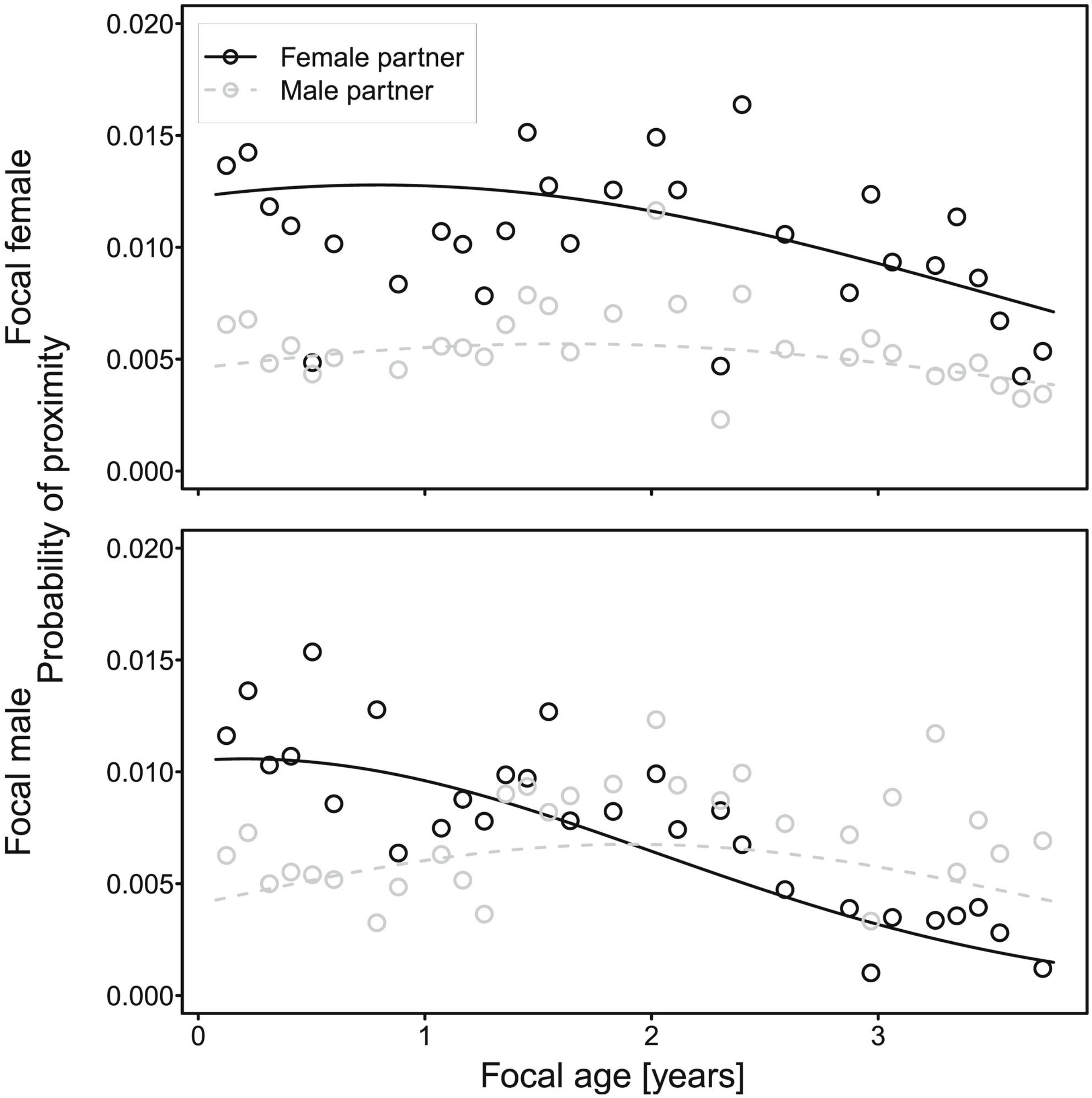

Fig. 1.

The development of sex differences in proximity, depending on the partner’s sex, in rhesus macaques from 2004 to 2008 on Cayo Santiago, Puerto Rico. The lines represent the calculated model and the points the binned and averaged observed values.

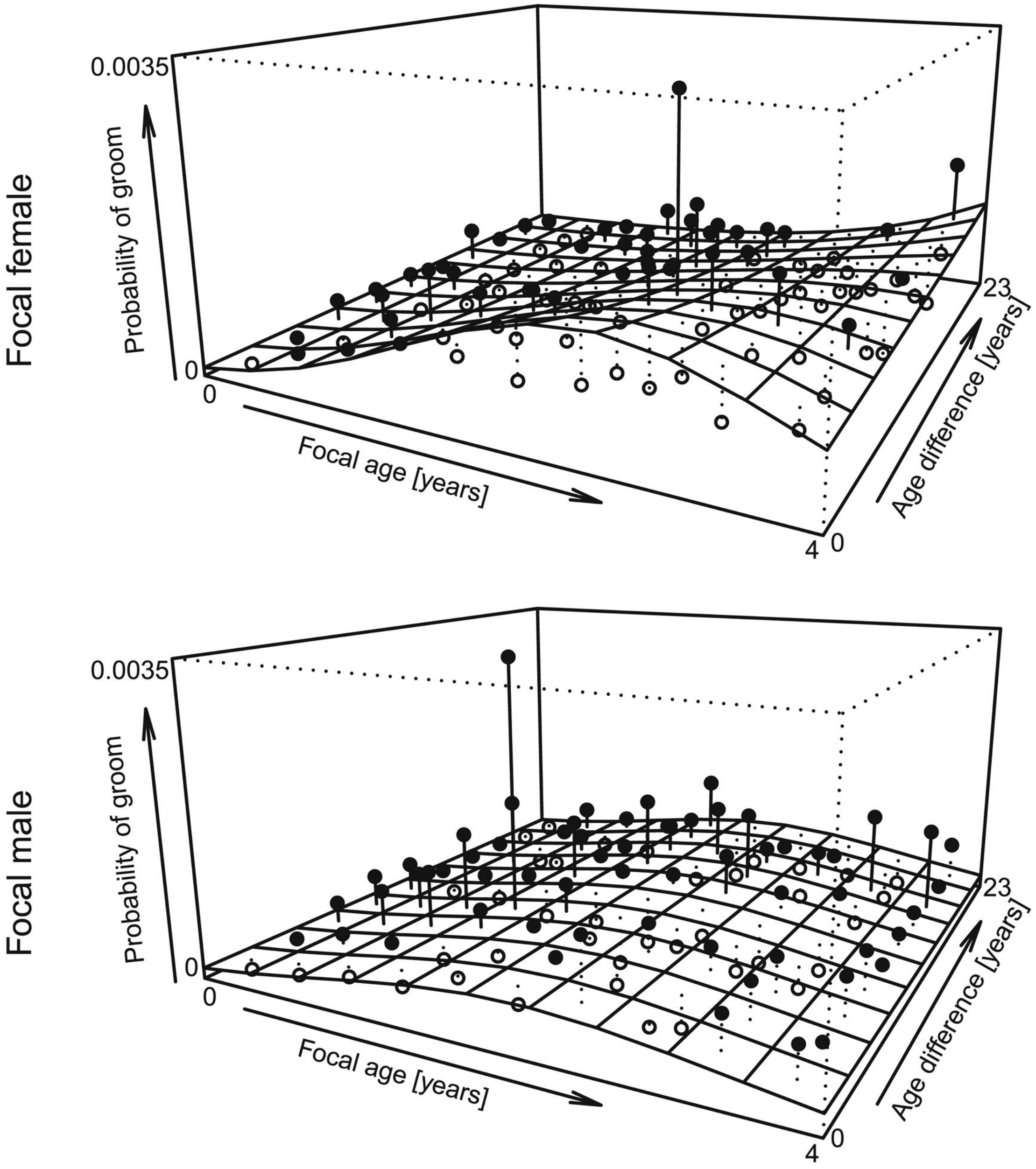

Fig. 2.

The development of sex differences in grooming, depending on the age difference between focal subject and partner, in rhesus macaques from 2004 to 2008 on Cayo Santiago, Puerto Rico. The points represent the mean response for each cell (white points have a mean below and black points have a mean above the plane representing the model).

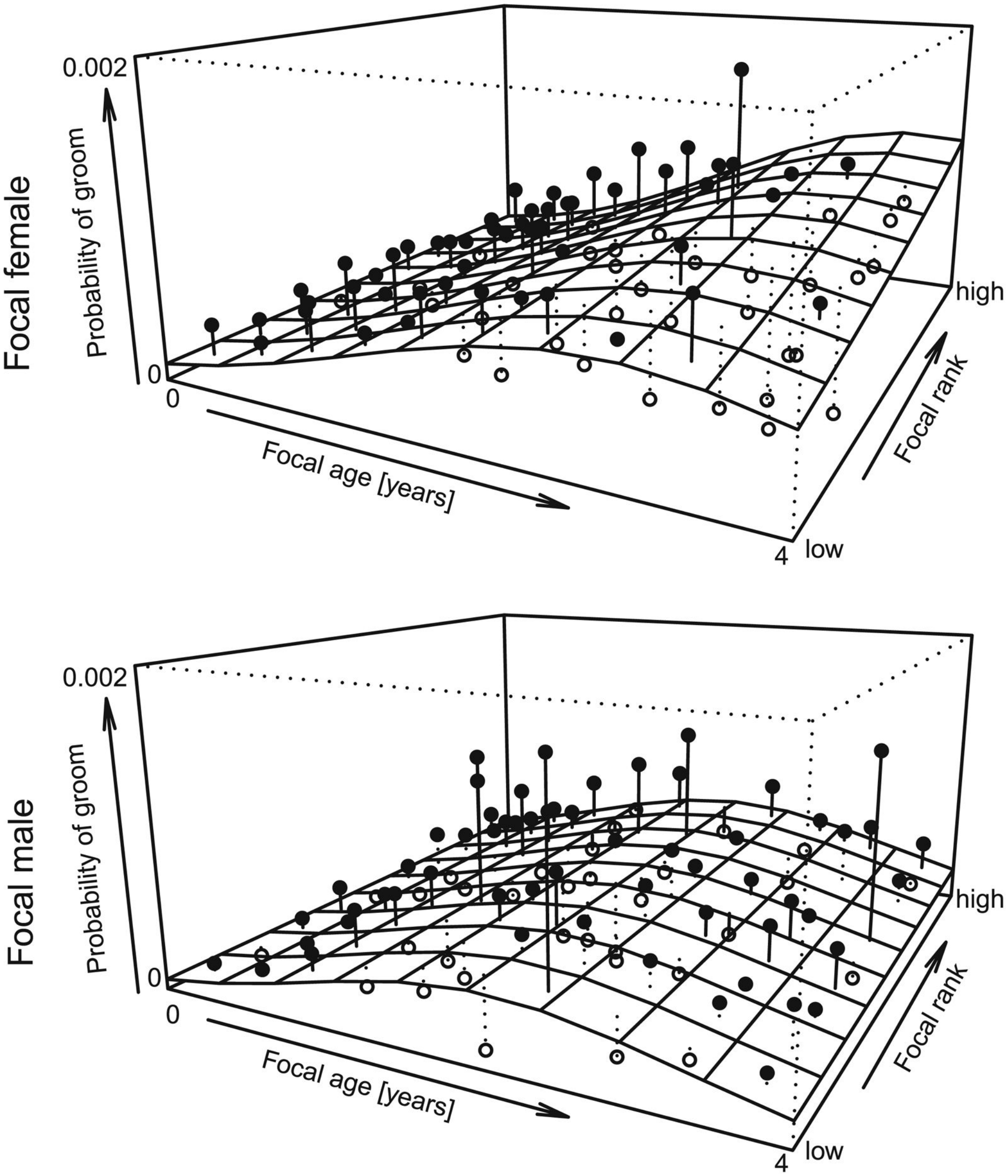

Fig. 3.

The development of sex differences in grooming, depending on the focal subject's rank, in rhesus macaques from 2004 to 2008 on Cayo Santiago, Puerto Rico. The points represent the mean response for each cell (white points have a mean below and black points have a mean above the plane representing the model).

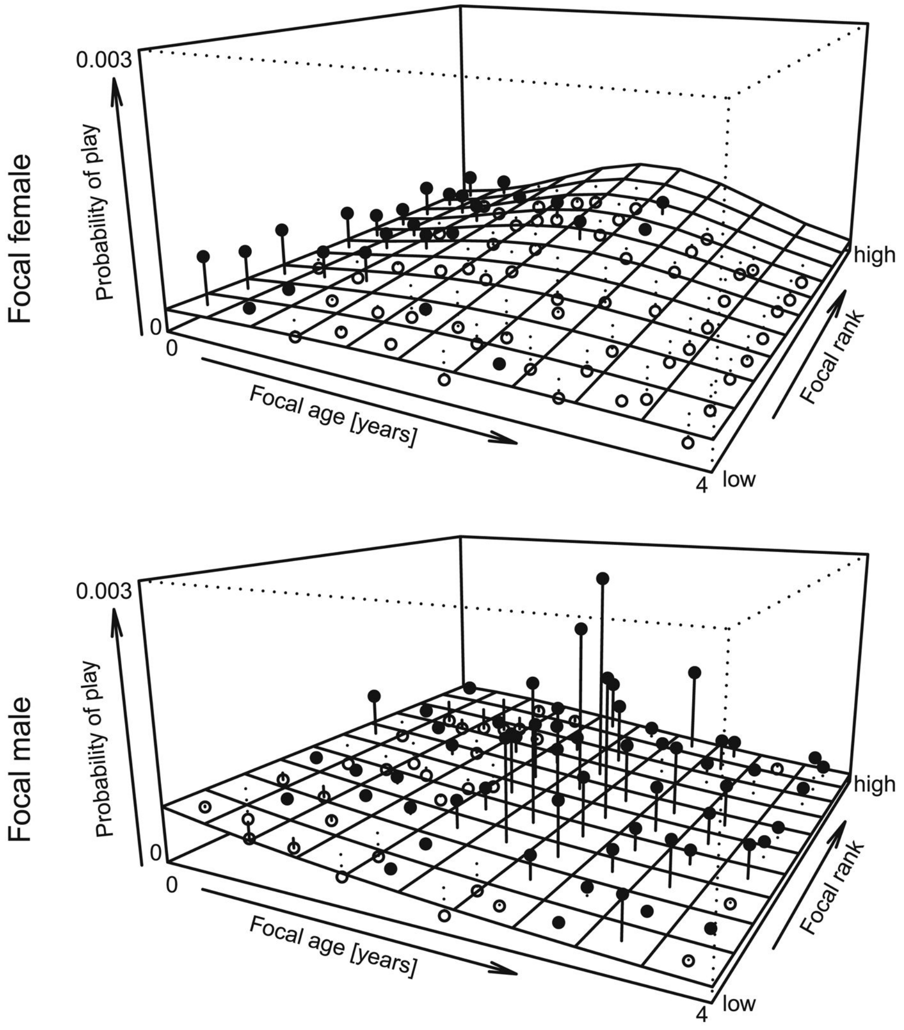

Fig. 4.

The development of sex differences in play, depending on the focal subject's rank, in rhesus macaques from 2004 to 2008 on Cayo Santiago, Puerto Rico. The points represent the mean response for each cell (white points have a mean below and black points have a mean above the plane representing the model).

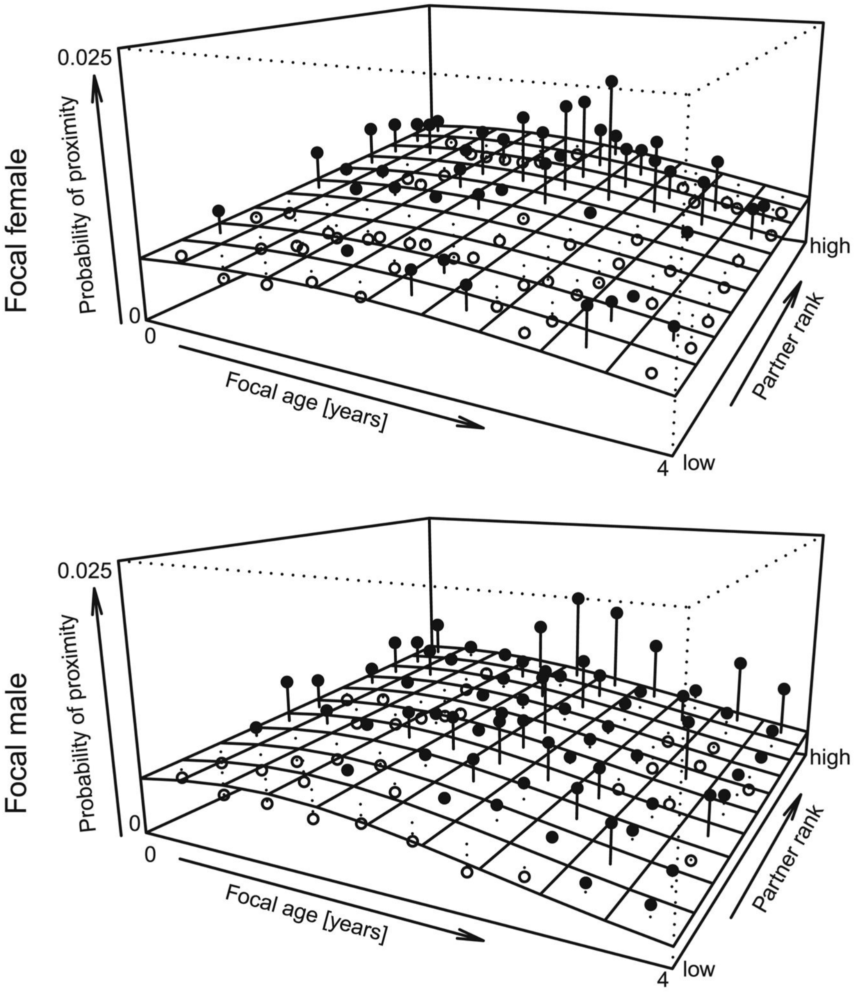

Fig. 5.

The development of sex differences in proximity, depending on the partner's rank, in rhesus macaques from 2004 to 2008 on Cayo Santiago, Puerto Rico. The points represent the mean response for each cell (white points have a mean below and black points have a mean above the plane representing the model).

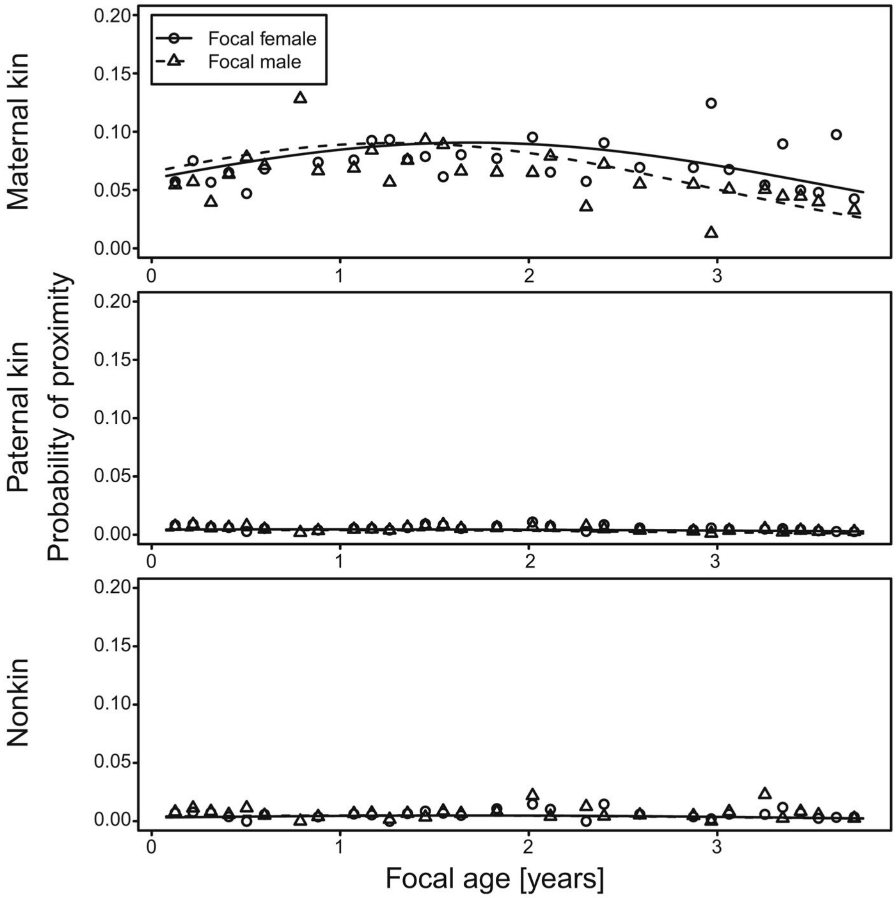

Fig. 6.

The development of sex differences in proximity, depending on kin line, in rhesus macaques from 2004 to 2008 on Cayo Santiago, Puerto Rico. The lines represent the calculated model and the symbols the binned and averaged observed values.

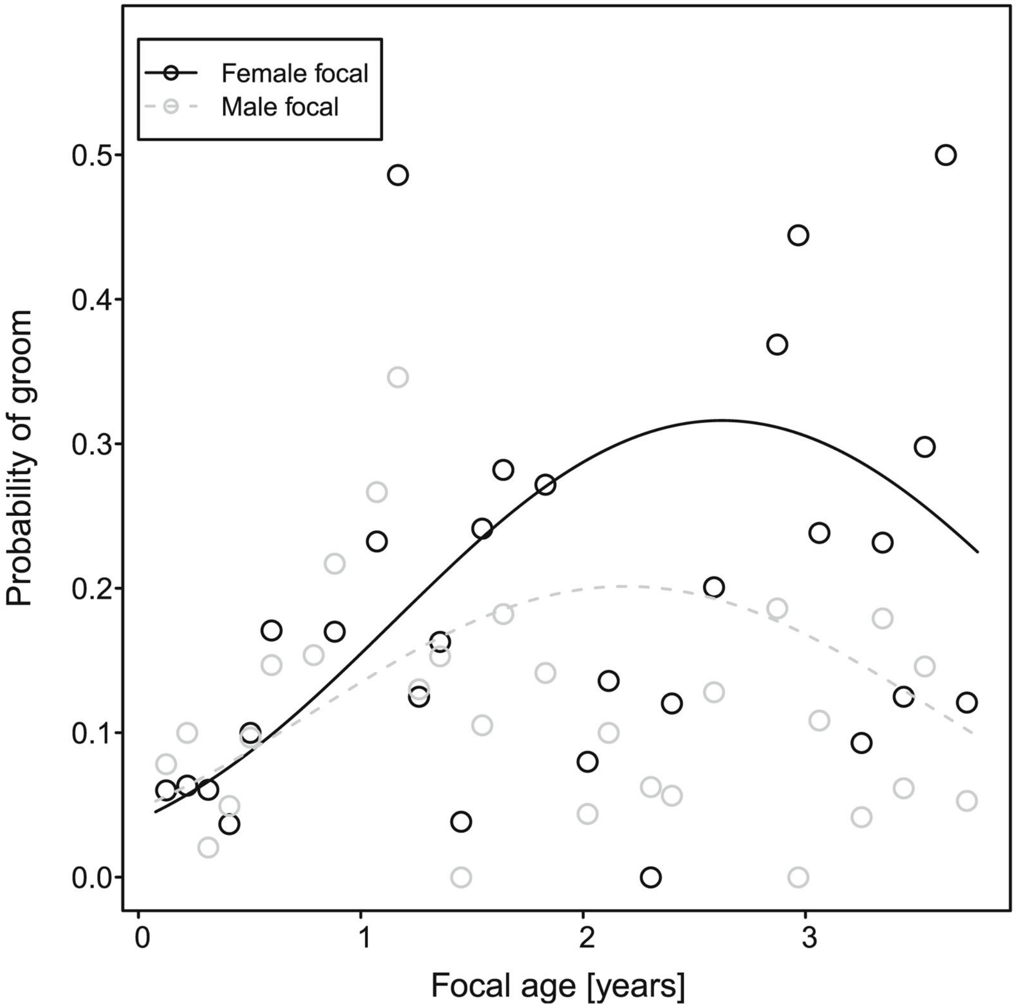

Fig. 7.

The development of grooming (only maternal kin are shown), depending on kin line, in rhesus macaques from 2004 to 2008 on Cayo Santiago, Puerto Rico. The lines represent the calculated model and the points the binned and averaged observed values.

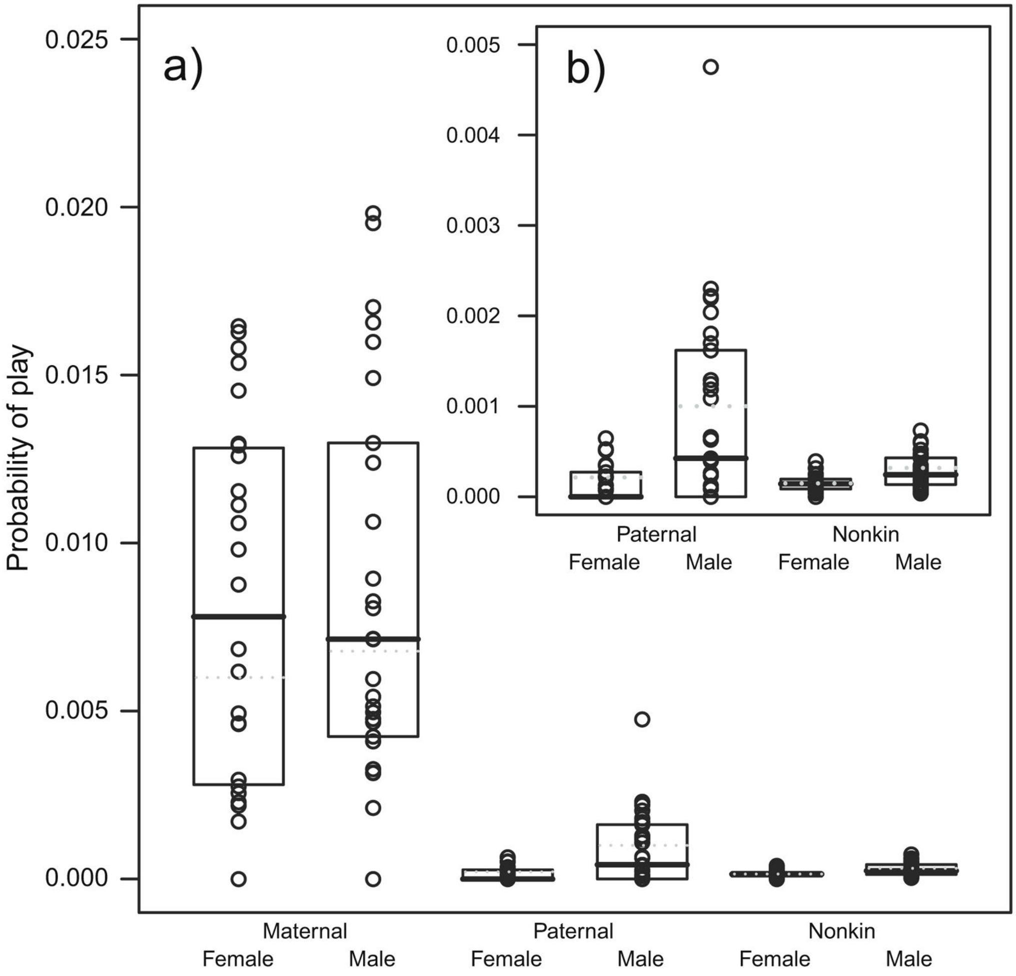

Fig. 8.

The probability of play, depending on the focal subject's sex and on kin category, in rhesus macaques from 2004 to 2008 on Cayo Santiago, Puerto Rico. Boxes represent the first to third quartile of observed values, solid lines show the median, dashed lines show the values fitted by the model, and each circle represents a data point for a focal subject. (**a**) Comparison over all three kin categories. (**b**) Detail showing only comparison between paternal kin and nonkin.