

RESEARCH ARTICLE

Sex Differences in Kin Bias at Maturation: Male Rhesus Macaques Prefer Paternal Kin Prior to Natal Dispersal

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Dispersal and mating patterns are known to affect the availability of both maternal and paternal kin within social groups, with important effects on the evolution of sociality. It is generally assumed that the philopatric sex forms stronger social bonds than the dispersing sex, possibly as a result of reduced kin availability for the dispersing sex after departure. However, few primate studies have directly compared whether sex differences in association patterns, particular with kin, are already present prior to dispersal when kin availability should be the same for both sexes. Here, we compared affiliative and aggressive interactions in a female philopatric species, the rhesus macaque (*Macaca mulatta*), to test whether sex differences in kin bias already occur around the age of maturation, when both sexes still live together with kin in their natal group. Our data confirmed that kin availability was the same for both sexes prior to male dispersal. Similar kin availability was partially reflected by comparable association patterns, as both females and males preferentially interacted with maternal kin. However, females had stronger affiliative bonds with maternal kin than males of the same age, indicating that kin associations not only depended upon kin availability, but were also sex-specific. Similarly, males were significantly more likely to affiliate with paternal kin than non-kin, as compared to females, suggesting that males discriminated paternal kin from non-kin earlier in life than females. Males might have a stronger need than females to affiliate with paternal kin due to a reduced integration in the matrilineal family prior to dispersal and the high availability of paternally related age-peers, with whom males could potentially migrate. Females, in contrast, form stronger affiliations with maternal kin, which may enhance their offspring's survival. More comparative studies are needed to understand the impact of different dispersal regimes on patterns of kin associations. *Am. J. Primatol.* 78:78–91, 2016. © 2016 Wiley Periodicals, Inc.

Key words: sex difference; social bonds; kin bias; dispersing sex; rhesus macaques; paternal kin

INTRODUCTION

Dispersal and mating patterns are known to affect kin availability within social groups, with important consequences for the evolution of sociality [e.g., Avise, 1994; Di Fiore, 2003, 2012; Chepko-Sade & Halpin, 1987; Chesser, 1991; Clutton-Brock & Lukas, 2012; Ross, 2001; Storz, 1999; Sugg et al., 1996; Widdig, 2013]. In particular, individuals of the philopatric sex have a higher chance to be closely related and to be available as long-term social partners in the group, and are therefore expected to form stronger social bonds [Di Fiore, 2003; Chepko-Sade & Halpin, 1987; Clutton-Brock, 2002; Clutton-Brock & Lukas, 2012; Sterck et al., 1997]. In primates, females often stay in their natal group throughout their lives together with their maternal kin, while males disperse around puberty to breed elsewhere [reviewed in e.g., Greenwood, 1980; Pusey & Packer, 1987; Lawson Handley & Perrin, 2007]. Dispersal patterns, therefore, have a direct effect on

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the availability of kin, in particular of maternal kin, within the social group, whereby philopatric females are predicted to have stronger social bonds [i.e., close, long-term affiliation with particular partners, cf. Silk et al., 2009] than dispersing males.

Similarly, mating patterns are expected to shape the availability of paternal kin [Altmann, 1979]. In multi-male groups, dominant males generally benefit from preferential access to fertile females for a restricted period of time, resulting in a yearly skewed distribution of male reproduction [reviewed in Di Fiore, 2003; Widdig, 2013]. Consequently, the availability of paternal kin is expected to be high in those species, in particular for the philopatric sex, as paternal relatives remain in the same social group throughout their lives. Therefore, philopatric females, for example, will spend their life together with both maternally and paternally related females, and a variable number of unrelated female social partners.

So far, genetic data have supported the hypothesis that philopatric females have a higher average degree of relatedness than dispersing males in their non-natal group e.g., savannah baboons, *Papio cynocephalus* [Altmann et al., 1996]; long-tailed macaques, *Macaca fascicularis* [De Ruiter & Geffen, 1998]; white sifakas, *Propithecus verreauxi verreauxi* [Lawler et al., 2003]. Moreover, there is strong evidence that maternal relatedness predicts association patterns in philopatric females [Bernstein, 1991; Berman & Kapsalis, 1999; Chapais, 2001; Gouzoules, 1984; Gouzoules & Gouzoules, 1987; Kapsalis & Berman, 1996; Silk, 2002; Walters, 1987; Walters & Seyfarth, 1987]. The very existence of life-long bonds between mothers and daughters *per se* causes an increased level of proximity among other maternal kin [Chapais, 2001]. As a result, adult philopatric females appear to have strong social bonds e.g., rhesus macaques, *Macaca mulatta* [Kapsalis & Berman, 1996]; vervet monkeys, *Cercopithecus aethiops* [Seyfarth, 1980]; capuchin monkeys, *Cebus capucinus* [Perry, 1996]; savannah baboons [Seyfarth, 1976; Silk et al., 1999]. Furthermore, in some species, philopatric females prefer to associate with paternal kin over non-kin e.g., rhesus macaques [Widdig et al., 2001]; savannah baboons [Silk et al., 2006]; mandrills, *Mandrillus sphinx* [Charpentier et al., 2007]. Notably, in some species philopatric females have stronger social bonds with other group members than the bonds males exhibit prior to male dispersal e.g., blue monkeys, *Cercopithecus mitis stuhlmanni* [Cords et al., 2010]; long-tailed macaques [Van Noordwijk et al., 1993]; patas monkeys, *Erythrocebus patas* [Rowell & Chism, 1986].

Likewise, males show similar strong association patterns in male philopatric species e.g., red colobus, *Colobus badius* [Struhsaker & Leland, 1976]; spider monkeys, *Ateles geoffroyi* [Slater et al., 2009]; miquis, *Brachyteles arachnoides hypoxanthus*

[Strier et al., 2002]; chimpanzees, *Pan troglodytes* [Arnold & Whiten, 2003; Gilby & Wrangham, 2008; Goodall, 1986; Lonsdorf et al., 2014b; Nishida, 1979; Watts, 2000a, ; Wrangham et al., 1992; but see Lehmann & Boesch, 2008, 2009]. Moreover, philopatric males were found to be more closely related on average than dispersing females e.g., spider monkeys [Di Fiore et al., 2009]; wolly monkeys, *Lagothrix poeppigii* [Di Fiore & Fleischer, 2005]; chimpanzees [Inoue et al., 2008], although this has not been consistently reported [e.g., Di Fiore et al., 2009; Lukas et al., 2005; Vigilant et al., 2001]. Finally, males staying in their natal group may form stronger affiliative and cooperative bonds with their maternal kin [Langergraber et al., 2007; Mitani, 2009; but see Strier et al., 2002].

Therefore, philopatric individuals appear to be more closely related and form stronger social bonds, especially with maternal kin and partially with paternal kin. However, much less is known about the sociality and association patterns of the dispersing sex, for whom kin availability differs between life history stages. In many primate species, for example, dispersing males change groups several times during their lives [Greenwood, 1980]. When leaving their natal group, males leave all maternally related females behind. In general, males may disperse together with familiar (i.e., males they grew up with in their natal group) kin or non-kin, if the age difference between males is sufficiently small to allow parallel dispersal [e.g., Albers & Widdig, 2013; Boelkins & Wilson, 1972; Cheney & Seyfarth, 1983; Jack & Fedigan, 2004; Meikle & Vessey, 1981; Pusey & Packer, 1987; reviewed in Lawson Handley & Perrin, 2007]. Alternatively, males may join new groups that contain some relatives, either familiar or unfamiliar (i.e., males or females who grew up in different natal groups). However, due to the lack of genetic data after dispersal, information on kin availability is still limited in most free-ranging populations. Nonetheless, recent genetic studies have confirmed the predicted decline of kin availability for male primates after dispersal [Albers & Widdig, 2013; Chancellor et al., 2011]. Hence, kin availability is fundamentally reduced for males after natal migration and probably further diluted with any secondary dispersal. Unless males produce a large number of offspring in their new group(s) of residence, they are likely to have a rather limited number of related partners to interact with as compared to philopatric females. It can therefore be expected that dispersing males rely more on unrelated social partners, where social bonds can potentially increase their reproductive success [Schülke et al., 2010]. However, there is evidence that the dispersing sex also forms strong social bonds after dispersal, both with non-kin [Langergraber et al., 2009; Lehmann & Boesch, 2008, 2009] and with kin [male rhesus macaques Meikle & Vessey,

1981]. Moreover, in species with a high male reproductive skew and short breeding tenure, kin can remain available for males even after dispersal, as paternal (but not maternal) half-siblings tend to be of similar age [Altmann, 1979] and thus may disperse together.

To better understand sex differences in sociality after dispersal, it might be relevant to investigate at which life history stage sex differences in associations, especially kin associations, emerge. In particular, patterns of kin associations might be linked to differences in kin availability that sexes experience during their life histories. Therefore, a suitable time period to investigate this question is prior to dispersal when both sexes are about to reach sexual maturation and prepare for different life history stages, where we expect the availability of maternal and paternal kin to be similar between sexes. So far, however, very few studies have directly compared patterns of kin interactions in both sexes prior to dispersal [Charpentier et al., 2007; Cords et al., 2010] and only one of these studies has included information on paternal kinship [Charpentier et al., 2007].

The main aim of this study was to compare patterns of associations in both sexes around the age of maturation in order to investigate whether sex differences in overall kin bias emerge already prior to male dispersal. Before sexual maturation, the philopatric and the dispersing sex both presumably learn to recognize their maternal and paternal kin [Widdig, 2007] and could thus potentially gain additional fitness benefits by supporting and cooperating with kin [Chapais, 2001]. If patterns of kin association predominantly depend on kin availability, and kin availability is similar for both sexes, males and females should have similar patterns of kin association prior to male dispersal (Hypothesis 1). The fact that kin availability dramatically decreases for the dispersing sex after migration may explain why the dispersing sex is generally reported to form weaker social bonds after maturation. Alternatively, patterns of association, in particular kin association, might be sex-specific and hence already differ prior to dispersal. In this case, prior to male dispersal females should already exhibit stronger social bonds than males, particularly with kin (Hypothesis 2), as they should invest more in their social bonds given that they remain in the group. To our knowledge, no study has specifically addressed this question, although this may be crucial to understand sex differences in sociality after dispersal.

Here, we observed social interactions of male and female rhesus macaques between the third and fourth year of their life (i.e., the period when females start breeding and males prepare for departure from their natal group) and combined them with pedigree data derived from genetic paternity analyses. Rhesus macaques live in multi-male, multi-female groups

with female philopatry [Gouzoules & Gouzoules, 1987] and male dispersal [Lindburg, 1969]. Males leave their natal group around the time of puberty [Colvin, 1986; Lindburg, 1969]. Adult females form the strongest associations with their close maternal kin, but also prefer to affiliate with their paternal kin rather than with unrelated individuals [Widdig et al., 2001, 2002]. Due to male reproductive skew in male rhesus [Dubuc et al., 2011; Widdig et al., 2004], kin availability is suggested to be high with regard to paternal relatedness, whereby paternal siblings are likely to be of similar age [Altmann, 1979].

METHODS

Study Species, Population and Subjects

Rhesus macaques are distributed across Asia and occupy habitats varying from semi-desert, temperate forest to tropical woodland and swamp [Seth & Seth, 1986]. Group size varies between 10 and 125 individuals, but up to 240 individuals have been observed close to human populations [Seth & Seth, 1986; Southwick et al., 1996]. Rhesus macaques breed on a seasonal basis [Drickamer, 1974] with males and females mating with multiple partners [Lindburg, 1971].

The study was conducted on the rhesus macaque population of Cayo Santiago, a 15.2 ha island off Puerto Rico (USA). All monkeys inhabiting the island were direct descendants of the 409 founder animals captured in different locations in India in 1938 [Rawlins & Kessler, 1986]. Although no individual has been added to the population except via natural births, pedigree analyses revealed only rare cases of inbreeding after 75 years of isolation [Widdig et al. in revision]. Census data including the date of birth and death, the sex of all study subjects, the period of group membership and the number of maternal kin have been continuously recorded by the Caribbean Primate Research Center (CPRC) since 1956. During the study period, the mating season on Cayo Santiago occurred from approximately March to August and was followed by a 6-month birth season from September to February, but both mating and birth season are progressively shifting forward due to climate changes [Hoffman et al., 2008]. The inter-birth interval of females in this population is approximately one year and females predominantly give birth to a single offspring [Rawlins & Kessler, 1986]. Infants can therefore be assigned to non-overlapping birth cohorts even though infants from the same cohort may differ in age by up to 6 months. Data from captivity report that in rhesus macaques females reach sexual maturation between 2.5 and 3.5 years of age [Zehr et al., 2005] and males between 3 and 3.5 years of age [Dixson & Nevison, 1997]. In our study population, the youngest reported mother was

2.9 years old [Bercovitch & Berard, 1993] and the youngest sire was 3.8 years old [Bercovitch et al., 2003], however, substantial inter-individual variation in sexual maturation can be expected [Bercovitch & Goy, 1990]. Male dispersal occurs most frequently during the mating season [Drickamer & Vessey, 1973; Lindburg, 1971], with males leaving their natal group between an age of 3–5.5 years (median age = 4.5 years) [Berard, 1990].

We followed 28 focal subjects (13 males, 15 females) of troop R, which represent all surviving individuals of the 2005 cohort. Focal subjects were close to completing their third year of life when we started the observations for this study, with males being 2.81 ± 0.07 (mean \pm SD) and females 2.84 ± 0.06 years of age on the first day of observation. Behavioral data collected for this study covered a full year (September 7th 2007–August 24th 2008) and thus the time around sexual maturation of focal subjects. Female subjects started to mate during the mating season while male subjects prepared for the departure from the natal group [Widdig, unpublished data]. During the study period, the study group consisted of a total of 325 members (270.27 ± 12.26 , mean \pm SD), including all immigrants and emigrants. Hence, for each focal subject we considered all group members (i.e., 297 non-focal animals plus the remaining 27 focal subjects) as potential social partners.

This study was conducted in compliance with the respective animal care regulations; it also followed all legal requirements as well as principles of the American Society of Primatologists for the ethical treatment of nonhuman primates (see Acknowledgements).

Behavioral Data

We collected behavioral data using 20 min. *focal samples* [Altmann, 1974]. For each focal subject we recorded a maximum of one focal sample per day. We balanced sample collection over the entire day (7 a.m.–5 p.m.) and across subjects. The total observation time was 689.33 hours, resulting in 24.62 ± 0.17 (mean \pm SD) hours per focal subject. We continuously recorded grooming as an important form of affiliative bonds as well as physical and non-physical aggression between the focal subjects and a given social partner. As physical aggression we considered push, hit, grab, bite and attack, as non-physical aggression we reported stare, head-bobbing, vocal/open mouth threat, lunge, charge and chase, as used in Widdig et al. [2002]. For each interaction involving the focal subject, we also recorded whether or not the mother of the focal subject was within two meters of the focal. In addition, every 4 min we collected data on focal activity and spatial proximity to other group members by recording all neighbors within a two meter range of the focal subject

[Altmann, 1974]. To construct dominance hierarchies (see details below), we further collected *ad libitum* data on displacement, aggression or submission between group members [Altmann, 1974]. We were able to individually recognize all group members including the focal subjects using tattoos and natural markings.

Data for this study were collected by DL after two months of training and reaching a mean interobserver reliability of 97% when conducting 101 simultaneous focal samples with a trainer [Kaufman & Rosenthal, 2009]. Data were collected using Psion Workabout™ handheld and processed with Observer software (version 5.0). The observer was blind to paternity across the entire study period.

Parentage Analysis

For parentage assignment we used the long-term genetic database of this population implemented in 1992 [for details see supplement and Widdig et al. in revision]. In brief, either hair, blood, tissue or fecal samples were systematically collected for nearly the entire population. We were able to sample and genotype all 28 focal subjects plus 291 of the 297 (97.98%) animals belonging to the group during our study.

Maternity derived from long-term field observations was genetically tested (when samples were available) and subsequently used in the paternity analyses. Paternity was determined using a combination of exclusion and likelihood analyses by considering all potential sires present on the island around conception of the respective infant. To increase the power of our kinship data, we also assigned maternal and paternal grandparents (for details on parentage analysis see supplement).

Determining Kin Relationships

We used a pedigree-based approach including available data of parentage assignments and demographic data, to establish kin relationship for all dyads including (i) a focal subject and a group member or (ii) two focal subjects (8694 unique dyads in total).

Our analysis included a total of 7837 focal-partner dyads which we were able to classify either into (i) maternal kin, (ii) paternal kin, or (iii) non-kin. As maternal kin we included dyads that were related only over the maternal line, i.e., that shared the same mother and/or maternal grandmother. We excluded 28 focal-mother dyads from this analysis as mother-offspring bonds represent the strongest social bonds within rhesus groups [Schülke et al., 2013]. Paternal kin comprised dyads that were related only over the paternal line, i.e., that shared the same father and/or paternal grandfather. Dyads related over both the maternal and paternal line were excluded from this analysis, in order to study them in more detail

elsewhere [cf. Albers & Widdig, 2013]. As non-kin we considered all dyads which were not related either matrilineally or patrilineally for at least two generations, i.e., that did not share a common individual among their parents or grandparents (for details on pedigree completeness, the proportion of dyads per kin category and degree of relatedness in our study group see supplement).

Establishing Dominance Hierarchies

Adult male dominance hierarchy was calculated using the Elo method [Elo, 1978; Neumann et al., 2011] applying an R function written by LK. The score allows estimating the competitive abilities of individuals by looking at interactions sequentially over time, with the outcome of these interactions continuously updating the scores [Neumann et al., 2011].

Using the I&SI method [De Vries, 1998], the adult female dominance hierarchy was also based on the outcomes of dyadic agonistic interactions. Once established in 1997 [as used in Widdig et al., 2001], the hierarchy was continuously updated using agonistic data from our long-term observations [Widdig, unpublished data]. The female hierarchy was highly stable over time, with offspring of a given female ranking directly below their mother inversely to their birth order [Datta, 1988]. We observed only two exceptions to this rule in our study group [Widdig, unpublished data].

In our study, focal subjects might not have yet reached full maturation, so their rank (and that of all non-adults of the group) was assigned according to the rank of their mothers, which was calculated on a daily basis to control for rank changes due to births and deaths. For each day, we standardized the ranks of males and females separately (including non-adults) to a range from 0–1 (lowest to highest ranking) to make both hierarchies comparable.

Data Analysis and Statistical Tests

To investigate a potential sex difference in kin bias prior to male dispersal we tested the influence of focal sex and kin category on the probability of different behaviors (e.g., grooming) between focal subjects and group members using a Generalized Linear Mixed Model (GLMM) [Baayen, 2008]. To calculate probabilities the dataset used in our analyses was derived through several steps. First, we determined all possible interaction partners per focal per day, which represented all group members present on a given day. Second, we calculated how often a focal interacted with each possible partner per day. Due to the large number of possible interaction partners, however, the probability to interact with a given partner on a given day is expected to be small. Indeed, focal subjects only

interacted with a small proportion of all possible partners per day, and consequently data distribution was highly skewed towards zero. It was therefore not possible to treat the observed count data as a Poisson distribution. Hence, we transformed the response into a binary variable (i.e., focal and partner interacted or not), which made it possible to calculate a model with binomial error distribution. For this purpose, we transformed the counts by setting all values greater than zero to one. While this step represents a data reduction, we consider it the optimal statistical approach for our data set for the following reasons. First, the number of data points in which the considered behavior occurred more than once a day constituted only a minor part of the full data set (grooming = 0.06%, proximity = 0.33%, aggression = 0.02%), and hence, the reduction affected only a small proportion of the data. Second, a zero inflated count model (Poisson or binomial) is currently not an alternative because, to our knowledge, no implementation of such models can account for the occurrence of excess zeros as a function of the predictors. Overall, using a binomial model constitutes a conservative approach.

As maternal presence influenced the probability of their offsprings' interaction [Langos et al., 2013], we distinguished social interactions in which the focal mother was within two meters of the focal-partner dyad or not. In the model we included focal sex and kin categories as fixed effects. Since we consider sex differences in kin bias as our main predictors in this study, we included focal sex and kin category as a two-way interaction into the model to test for the sex difference over all three kin categories (global test). To facilitate interpretation of these results, we further compared each combination of kin categories between the sexes (pair-wise comparisons). In this way, we were able to compare males versus females over two kin categories only: a) maternal kin versus paternal kin, b) maternal kin versus non-kin, and c) paternal kin versus non-kin (see Tables I to III). To determine the P-value for these pair-wise comparisons, we re-leveled the factors (i.e., we assigned another reference level to kin and sex category) and ran the model again [Cohen & Cohen, 1983]. As control factors we included the age and rank of the focal subject and focal partner, respectively, as well as the sex of the focal partner as previous studies showed that these factors significantly influence social relationships [e.g., Charpentier et al., 2007; Cords et al., 2010; Van Noordwijk et al., 1993]. Additionally, we controlled for the age differences between focal subjects and focal partners, as age proximity is known to promote social bonds in rhesus macaques [e.g., Widdig et al., 2001]. We finally controlled for the mother's presence during interactions involving a focal subject, as the mother's presence can influence affiliation between adult males and immatures [Langos et al., 2013]. To

account for the varying numbers of scans in which the mother was present or absent, we included this number (calculated as a per day ratio) as an offset variable in the model. Finally, we included the identity of both focal subject and focal partner as well as the date of the interaction as random effects into the model. Due to limitations in computational capacity we did not incorporate random slopes (which would require approximately 200 calculation days on this dataset), although this would have revealed more reliable *P*-values [Barr et al., 2013].

The data analyzed were likely to show temporal autocorrelation (*ac*), i.e., residuals of data points recorded closer in time could be more similar to one another than data points recorded further apart in time. This might lead to the violation of the assumption of independent residuals and thus devaluing the reliability of the model. Thus, we included two terms, one for the focal subject (*ac* 1) and one for the interacting group member (*ac* 2) to explicitly account for temporal autocorrelation in the model (for details on the calculation of the *ac* see supplement).

Before running the model, we *z* transformed all covariates (including the *ac* terms) to a mean of zero and a standard deviation of one. The model was run in R [version 2.15.0, R Development Core Team, 2012] using the function “lmer” from the R package “lme4” [version 0.999375-42, Bates et al., 2011]. The GLMM was fitted with binomial error structure and logit link function. Using a likelihood ratio test (LRT) [Dobson, 2002] (R function “anova”), we determined the statistical significance of the full model by comparing its fit with that of the null model (comprising only the random effects, the *ac* terms and the offset term) [Forstmeier & Schielzeth, 2011].

We performed two further GLMMs using the same approach as above, but included the probability of spatial proximity and aggression, respectively, as response variables. To check for the assumptions of the model, we calculated variance inflation factors [Quinn & Keough, 2002], which indicated that collinearity was not an issue for all our models.

RESULTS

Kin Availability

In our data set, kin availability was similar for both sexes prior to dispersal (maternal kin availability, excluding mothers, for females: 10.87 ± 5.96 , for males: 11.38 ± 8.52 ; paternal kin availability for females: 15.60 ± 7.76 , for males: 14.23 ± 6.76 ; non-kin availability for females: 267.93 ± 15.54 ; for males: 264.84 ± 18.32 ; mean \pm SD). We furthermore investigated mean kin availability for both sexes by calculating confidence intervals (CI) using bootstrapping. The results revealed a clear overlap in the 95% confidence intervals for males and females in each kin category

suggesting no significant difference in mean kin availability (maternal kin availability for females: 8.13–13.74, for males: 7.46–16.08; paternal kin availability for females: 11.73–19.14, for males: 10.46–17.31; non-kin availability for females: 259.87–275.41, for males: 254.85–274.31; CI 2.5–97.5%).

Grooming

The set of predictors used had a clear influence on the probability of grooming observed between focal subjects and their social partners (LRT comparing the full model with the null model: $\chi^2 = 1937.4$, *df* = 12, *P* < 0.001; see Table I for final results of model). We found a significant interaction between focal sex and kin categories on the probability of grooming, indicating a sex difference in the overall kin bias (LRT for interaction: $\chi^2 = 11.29$, *df* = 2, *P* = 0.003; see Fig. 1a). Although maternal kin were the preferred grooming partners for both males and females, the sexes differed in their grooming patterns with regard to the other kin categories. Specifically, our pair-wise comparisons revealed that the preference for maternal kin over paternal kin and non-kin, respectively, was more pronounced in female than in male focals (Table I, Fig. 1a). Furthermore, compared to females, male focals showed a preference for grooming paternal kin over non-kin (Table I, Fig. 1b).

Spatial Proximity

The set of predictors used also significantly affected the probability of spatial proximity between focal subjects and their social partners (LRT comparing the full model with the null model: $\chi^2 = 10474.00$, *df* = 12, *P* < 0.001; see Table II for final results of model). We found a significant interaction between focal sex and kin categories on the probability of spatial proximity (LRT for interaction: $\chi^2 = 37.67$, *df* = 2, *P* < 0.001; see Fig. 2a) suggesting that the sexes differ in their overall kin bias in proximity too. Focal subjects were predominantly found in spatial proximity of maternal kin, but differed in their proximity patterns with regard to the other kin categories. Similar to grooming, our pair-wise comparisons revealed that the preference for maternal kin over paternal kin was more pronounced in female than in male focals, however, the sexes did not differ in their preference for maternal kin over non-kin (Table II, Fig. 2a). As for grooming, male focals had a higher probability to share spatial proximity with paternal kin than with non-kin in comparison to females (Table II, Fig. 2b).

Aggression

Finally, the results of our third model also indicated that the set of predictors had a clear

TABLE I. Final Results of the GLMM for Grooming

Predictor variable	Estimate	SE	<i>z</i>	<i>P</i>
Intercept	-5.90	0.17		
Control variables				
Focal age	0.02	0.04	0.52	0.602
Focal rank	0.04	0.09	0.48	0.634
Partner sex (♀ = 0; ♂ = 1)	0.34	0.17	2.02	0.043
Partner age	0.59	0.13	4.70	<0.001
Partner rank	0.02	0.08	0.27	0.788
Age difference	-0.53	0.12	-4.39	<0.001
Mother's presence (yes = 1; no = 0)	0.37	0.10	3.60	<0.001
Ac for focal	0.32	0.02	14.48	<0.001
Ac for partner	0.12	0.01	8.25	<0.001
Predictors included in interaction				
Focal sex (♀ = 0; ♂ = 1)	-0.70	0.22	b	b
Kin line (maternal vs. non-kin) ^a	-4.23	0.12	b	b
Kin line (maternal vs. paternal kin) ^a	-4.22	0.32	b	b
Two-way interaction ^c				
Sex*kin (maternal vs. paternal kin)^d	1.31	0.44	3.01	0.003
Sex*kin (maternal kin vs. non-kin)^e	0.43	0.20	2.17	0.030
Sex*kin (paternal kin vs. non-kin)^f	-0.88	0.42	-2.08	0.038

Control variables are not interpreted. Significant interactions are marked in bold.

^aReference level is maternal kin.

^bValues are not shown because there is no meaningful interpretation as they are part of the interaction.

^cThe global testing (LRT sex*kin) revealed $\chi^2 = 11.29$, $df = 2$, $P = 0.003$.

^dReference levels are males and paternal kin.

^eReference levels are males and non-kin.

^fReference levels are males and non-kin.

influence on the probability of aggression observed between focal subjects and their social partners (LRT comparing the full model with the null model: $\chi^2 = 403.27$, $df = 12$, $P < 0.001$; see Table III for final results of model). As in the previous models we found a significant interaction between focal sex and kin categories and thus a sex difference in the overall kin bias for the probability of aggression (LRT for interaction: $\chi^2 = 9.25$, $df = 2$, $P = 0.009$; see Fig. 3). Focal subjects predominantly exchanged aggression with maternal kin, but differed in their pattern of aggression with regards to the other kin categories. Notably, the pair-wise comparisons showed that the bias of aggressively interacting with maternal rather than paternal kin was more pronounced in females, while males interacted aggressively with paternal kin almost as frequently as with maternal kin (Fig. 3). We detected no sex differences in the probability of aggression with maternal kin versus non-kin. Finally, compared to females, male focals had a higher probability to exchange aggression with paternal kin than with non-kin (Table III, Fig. 3).

DISCUSSION

The results of our study suggest that patterns of kin associations in male and female rhesus macaques partially depend on the availability of kin (hypothesis 1), but also reveal sex-specific characteristics (hypothesis 2). Around the age of maturation, female

and male rhesus macaques preferred maternal kin as social partners but also showed sex differences in kin bias before male dispersal despite kin availability being the same for both sexes. In particular, female rhesus macaques formed stronger affiliative bonds with their maternal kin than males did. Moreover, our study provided the first evidence that the dispersing sex also biases its affiliation towards paternal kin. In particular, focal males had a significantly higher probability to share spatial proximity, exchange grooming but also aggression with paternal kin than non-kin when compared with focal females of the same age. Although the probability of aggression was generally lower than the probability of grooming and proximity, both sexes exchanged most aggression with maternal kin; however, males also frequently competed with paternal kin.

In our study, individuals of both sexes formed the strongest social bonds with maternal kin already around maturation, which is in line with previous research on adults and juveniles [philopatric females e.g., Charpentier et al., 2007; Silk et al., 2006; Widdig et al., 2001; philopatric males e.g., Langergraber et al., 2007; Mitani, 2009]. These results are also consistent with a study on blue monkeys prior to male dispersal. Comparing association patterns directly in both sexes, this study found that both sexes interacted more with maternal kin than with non-maternally related partners [Cords et al., 2010].

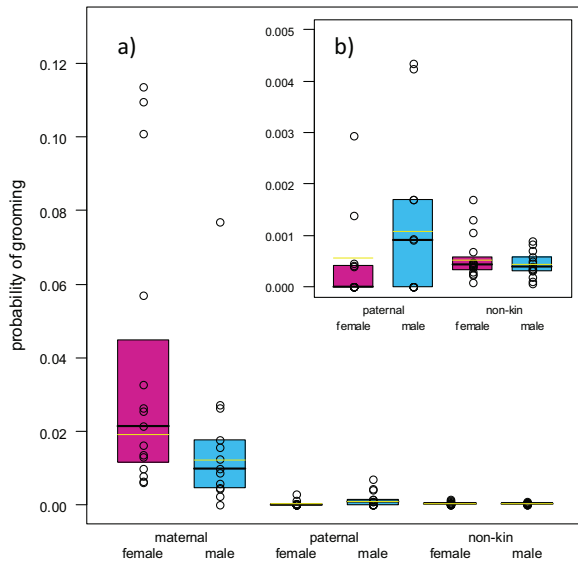


Fig. 1. Influence of the interaction between focal sex and kin categories on the probability of grooming. (a) Global comparison of the probability of grooming maternal kin, paternal kin and non-kin by female (purple) and male subjects (blue), respectively, (b) Detail showing only comparison between paternal kin and non-kin. For Figures 1–3, boxes represent the first to third quartile of observed values, black lines show the median, and yellow lines show the values fitted by the model. Each circle represents a data point per focal subject.

However, females around sexual maturation had even stronger social bonds than males, suggesting that females might be selected for investing more heavily in bonding within their maternal family than males [Cords et al., 2010].

Moreover, both females and males were most aggressive towards maternal kin. The few studies accounting for both affiliative and aggressive interactions have actually found that maternal relatives exchange both affiliation and aggression most frequently [Bernstein & Ehardt, 1986; Widdig et al., 2002, 2006; but see Silk et al., 1981, 2004]. Indeed, kin are often the closest associates, but likewise the closest competitors within the group [Alexander, 1974; Chapais, 1995; Smith, 2014; West et al., 2002]. These findings support the need to include not only affiliative, but also aggressive interactions when assessing the quality and strength of social bonding [Fraser et al., 2008].

The fact that maternal kin bias is more pronounced than paternal kin bias is neither new nor surprising for primates living in bisexual groups [Widdig, 2013]. Mothers, not fathers, continuously associate with their offspring even after weaning, so that juveniles easily become familiar with other maternal kin. Hence, mother-offspring bonds play a crucial role in kin associations across primate species, even among philopatric males who also form their closest bonds with maternal kin [e.g., Langergraber et al., 2007]. Accordingly, individuals can be reliably identified as maternal kin by means of

familiarity through long-lasting association [Widdig, 2013]. In contrast, familiarity is less likely to be used to identify paternal kinship; hence other recognition mechanisms, probably less precise, are likely to account for paternal kin recognition [reviewed in Widdig, 2007, 2013].

That said, males still had a significantly higher probability than females of the same age to socially interact with paternal kin as compared to non-kin. The probability to interact was generally small in our study group, which was caused by the large number of potential, and small number of actual, interaction partners. However, males, in contrast to females, used their chances to interact with paternal kin at least twice as often as their chances to interact with non-kin, therefore we think that the sex differences in kin bias is biologically relevant. While past studies on paternal kin discrimination focused on the philopatric sex [Langergraber et al., 2007; Perry et al., 2008; Smith et al., 2003; Silk et al., 2006; Widdig et al., 2001], the current study provides the first evidence that the dispersing sex also biases its affiliation towards paternal kin rather than non-kin. Just before leaving their natal group, males preferred to share spatial proximity and exchange grooming with their paternal kin rather than non-kin, in contrast to philopatric females who prepare for breeding in their natal group while being embedded in their maternal kin network. However, males also have a significantly higher probability than females to aggressively compete with their paternal kin as compared to non-kin. When male reproductive skew is high and breeding tenure is short, paternally related peers are more likely to be of the same age than maternally related peers. Hence, paternally related peers can be expected to be highly competitive as they require the same limited resources at the same time [Widdig, 2013]. The reasons why males exhibited an increased competitiveness towards paternal kin in comparison to female focals remain to be addressed in further studies.

Based on our findings and the fact that female rhesus macaques show paternal kin bias in adulthood [Widdig et al., 2001, 2002] one might conclude that males behaviorally discriminate paternal kin from non-kin earlier in life than females do. However, the fact that we did not detect paternal kin bias in females in this study does not necessarily imply that females are unable to recognize paternal kin at this age [cf. Charpentier et al., 2007; Mateo, 2002]. Earlier studies demonstrating paternal kin bias in adult female rhesus macaques investigated subjects being 5.99 ± 1.94 year old (mean \pm SD) at the beginning of the study [Widdig, unpublished data]. In contrast, female subjects in this study were on average younger (2.84 ± 0.06 years) at the start of the study. This difference suggests potential changes in behavioral preferences for paternal kin during

TABLE II. Final Results of the GLMM for Spatial Proximity

Predictor variable	Estimate	SE	Z	p
Intercept	-4.99	0.10		
Control variables				
Focal age	-0.12	0.02	-6.56	<0.001
Focal rank	0.17	0.06	2.71	0.007
Partner sex (♀ = 0; ♂ = 1)	0.05	0.07	0.67	0.502
Partner age	-0.16	0.05	-3.24	0.001
Partner rank	0.11	0.03	3.27	0.001
Age difference	-0.11	0.05	-2.18	0.029
Mother's presence(yes = 1; no = 0)	0.85	0.03	25.83	<0.001
Ac for focal	0.34	0.01	33.56	<0.001
Ac for partner	0.03	0.01	3.00	0.003
Predictors included in interaction				
Focal sex (♀ = 0; ♂ = 1)	-0.28	0.14	b	b
Kin line (maternal vs. non-kin) ^a	-3.31	0.04	b	b
Kin line (maternal vs. paternal kin) ^a	-3.35	0.10	b	b
Two-way interaction ^c				
Sex*kin (maternal vs. paternal kin)^d	0.77	0.13	5.76	<0.001
Sex*kin (maternal kin vs. non-kin) ^e	0.00	0.07	-0.04	0.966
Sex*kin (paternal kin vs. non-kin)^f	-0.77	0.13	-6.07	<0.001

Control variables are not interpreted. Significant interactions are marked in bold.

^aReference level is maternal kin.

^bValues are not shown because there is no meaningful interpretation as they are part of the interaction.

^cThe global testing (LRT sex*kin) revealed $\chi^2 = 37.67$, $df = 2$, $P < 0.001$.

^dReference levels are males and paternal kin.

^eReference levels are males and non-kin.

^fReference levels are males and non-kin.

female ontogeny. Ontogenetic variations in social preferences have been reported in cercopithecines, with preferences for social partners changing depending on their life history stage [Cords et al., 2010]. When philopatric females reach sexual maturation, they enjoy full social integration in their matrilineal family and probably still benefit from an intact maternal family, with little need to interact with paternal kin [Silk et al., 2006]. However, when females get older their maternal family is less likely to be complete, as mothers and older sisters might have died. Accordingly, paternal age-peers may become relevant for females only at later life history stages. In line with this suggestion, female baboons formed significantly stronger bonds with their paternal sisters when fewer close maternal kin were available [Silk et al., 2006]. In particular, paternal half-sisters formed the strongest bonds when both mothers were unavailable, and the weakest bonds when both mothers were present [Silk et al., 2006]. When females have both maternal and paternal kin available, it seems likely that females receive larger fitness benefits by interacting with maternal, rather than paternal kin.

In contrast to females, males shared spatial proximity and exchanged grooming with paternal kin with a significantly higher probability than with non-kin. Male rhesus macaques seem to be less integrated into their matrilineal family than females already during their first year of life, as evident by a

lower probability of grooming and shared spatial proximity [Kulik et al. in revision]. Similarly, a 4-year study showed that young male Japanese macaques (*Macaca fuscata*) interacted with their mothers less than young females did [Nakamichi, 1989]. This looser integration into the matrilineal family could reflect the need of immature males to establish early social bonds outside of the matrilineal family, with immature males affiliating more with adult males [Langos et al., 2013] or with paternal kin (this study) than immature females. As paternal siblings are likely to be in close age proximity [Altmann, 1979; Altmann et al. 1996; Widdig et al., 2002], male bonding with paternal half-siblings might be especially relevant during natal dispersal, when males are likely to leave together with age-peers that potentially include paternal brothers. However, this question needs to be explored in detail by future studies.

So far, only few studies have investigated the effect of kinship on natal dispersal. An early study looking only at maternal kinship suggested that male rhesus macaques frequently transferred into the same non-natal groups as their older maternal brothers [Meikle & Vessey, 1981]. Those males spent more time close to their maternal brothers and formed alliances more frequently with them than with non-brothers [Meikle & Vessey, 1981]. A study of long-tailed macaques, inferring relatedness from blood protein markers, reported that natal migrants

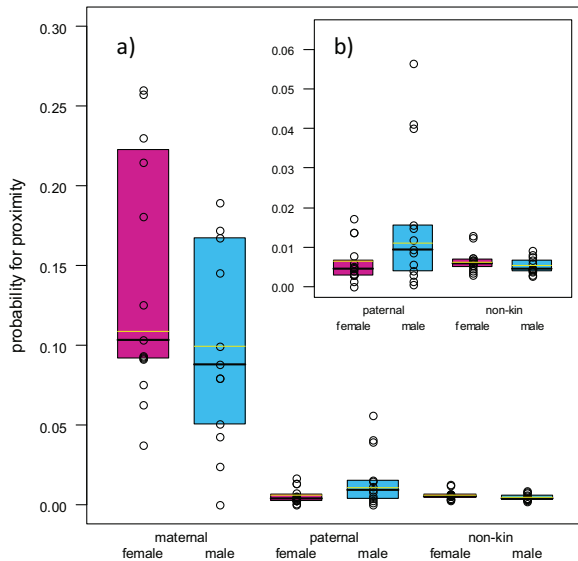


Fig. 2. Influence of the interaction between focal sex and kin categories on the probability of spatial proximity. (a) Global comparison of the probability of sharing spatial proximity with maternal kin, paternal kin and non-kin by female (purple) and male subjects (blue), respectively, (b) Detail showing only comparison between paternal kin and non-kin.

leaving the same group were sometimes, but not always, closely related [De Ruiter & Geffen, 1998]. Estimating relatedness using microsatellites, data on Gray-cheeked mangabeys (*Lophocebus albigena*) revealed that male opportunities of kin-biased dispersal were rare, and related males shared groups no more often than expected by chance [Chancellor et al., 2011]. Using pedigree data, a recent study on the Cayo Santiago rhesus macaques supported the hypothesis that natal migrants indeed have a reduced availability of kin, with 80.7% of all familiar dyads being unrelated [Albers & Widdig, 2013]. However, this study also suggested that kinship influenced spatial proximity between recent natal immigrants and familiar males (i.e., males who were born in the same group as the immigrant and also dispersed into the same group). In particular, immigrants were closer in spatial proximity to more closely than distantly related familiar males. Moreover, natal migrants were significantly closer to familiar males being maternally or paternally related, as compared to familiar non-kin [Albers & Widdig, 2013].

At this stage, it is not yet possible to discern why sex differences in patterns of kin association already emerge prior to dispersal even when kin availability is the same for both sexes. One reason might be that individuals choose social partners on the basis of their current and future utility, so that members of the philopatric sex develop a larger intra-sexual social integration already prior to the departure of the dispersing sex [Cords et al., 2010]. In line with this, there is evidence that rhesus mothers are

more aggressive towards sons than daughters, resulting in a lower social connectivity of sons within the family from the first year of their life [Kulik et al. in revision]. A second explanation, not necessarily exclusive, is that sex differences in the development of social behavior or motor skills are not only due to social influences, but might also be biologically rooted, as suggested in humans and chimpanzees [Lonsdorf et al., 2014a, b].

Taken together, our data suggest that males and females around the age of maturation already show a sex difference in kin bias, with females bonding more than males with maternal kin, although maternal kin are the strongest bonding partners for both males and females. Moreover, male rhesus macaques behaviorally discriminated paternal kin from non-kin around the time of sexual maturation, while females of the same age showed no such behavioral differentiation. Future studies should assess maternal and paternal kin availability for both sexes prior to and after dispersal in order to investigate the link between kin availability and kin associations. Furthermore, possible ontogenetic changes in kin bias of both sexes should be addressed by long-term studies. Finally, comparative studies would help to understand the impact of different dispersal regimes on kin association.

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TABLE III. Final Results of the GLMM For Aggressions

Predictor variable	Estimate	SE	<i>z</i>	<i>P</i>
Intercept	-6.92	0.13		
Control variables				
Focal age	-0.18	0.04	-5.02	<0.001
Focal rank	-0.04	0.04	-0.89	0.374
Partner sex (♀ = 0; ♂ = 1)	0.53	0.08	6.59	<0.001
Partner age	0.65	0.07	9.19	<0.001
Partner rank	0.06	0.04	1.58	0.114
Age difference	-0.71	0.06	-11.82	<0.001
Mother's presence (yes = 1; no = 0)	-0.89	0.13	-7.10	<0.001
Ac for focal	0.17	0.02	7.57	<0.001
Ac for partner	0.05	0.02	2.35	0.019
Predictors included in interaction				
Focal sex (♀ = 0; ♂ = 1)	-0.41	0.20	b	b
Kin line (maternal vs. non-kin) ^a	-1.53	0.13	b	b
Kin line (maternal vs. paternal kin) ^a	-1.57	0.23	b	b
Two-way interaction ^c				
Sex*kin (maternal vs. paternal kin)^d	0.89	0.31	2.84	0.005
Sex*kin (maternal kin vs. non-kin) ^e	0.17	0.20	0.83	0.407
Sex*kin (paternal kin vs. non-kin)^f	-0.72	0.26	-2.77	0.006

Control variables are not interpreted. Significant interactions are marked in bold.

^aReference level is maternal kin.

^bValues are not shown because there is no meaningful interpretation as they are part of the interaction.

^cThe global testing (LRT sex*kin) revealed $\chi^2 = 9.25$, $df = 2$, $P = 0.009$.

^dReference levels are males and paternal kin.

^eReference levels are males and non-kin.

^fReference levels are males and non-kin.

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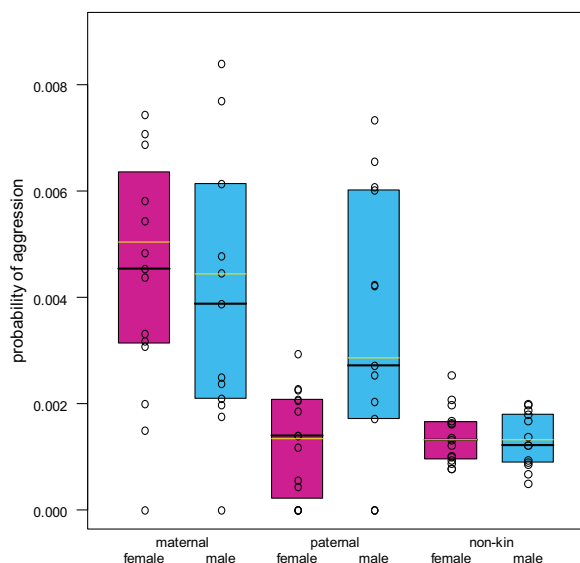


Fig. 3. Influence of the interaction between focal sex and kin categories on the probability of aggression. Global comparison of the probability of aggression exchanged with maternal kin, paternal kin and non-kin by female (purple) and male subjects (blue), respectively.

Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico (protocol number 4060105). The sample transfer was approved as required (Cites Export permission #05US101361/9, #06US112079/9, #07US133766/9, #08US163309/9, #09US200870/9, #09US230435/9, #11US28371A/9, Cites Import permission #E-1426/05, #E-1082/06, #E-1207/07, #E-1215/08, #E01146/09, #E-00049/10, #E-00836/11). The population of Cayo Santiago was supported by the grant number 8 P40 OD012217-25 from the National Center for Research Resources (NCR), 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 NCR or ORIP. This project is part of a long-term study on the mechanisms of paternal kin discrimination conducted within the Jr. Research Group of Primate Kin Selection, an Emmy-Noether Group funded by the German Research Foundation (DFG) (grant numbers WI 1808/1-1, 1-2, 2-1, 3-1 awarded to AW). 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 as well as the KKGS Stiftung, Elsa-Neumann Stiftung and the University of Leipzig for graduate funding awarded to DL and LK.

REFERENCES

- Albers M, Widdig A. 2013. The influence of kinship on familiar natal migrant rhesus macaques (*Macaca mulatta*). *International Journal of Primatology* 34:99–114.
- Alexander RD. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383.
- Altmann J. 1974. Observational study of behavior sampling methods. *Behaviour* 49:227–267.
- Altmann J. 1979. Age cohorts as paternal sibships. *Behavioral Ecology and Sociobiology* 6:161–164.
- Altmann J, Alberts SC, Haines SA, et al. 1996. Behavior predicts genetic structure in a wild primate group. *Proceedings of the National Academy of Sciences* 93:5797–5801.
- Arnold K, Whiten A. 2003. Grooming interactions among the chimpanzees of the Budongo forest, Uganda: Tests of five explanatory models. *Behaviour* 140:519–552.
- Awise JC. 1994. Molecular markers, natural history and evolution. New York: Chapman and Hall.
- Baayen H. 2008. Analyzing linguistic data: A practical introduction to statistics using R. 1st ed. Cambridge: Cambridge University Press.
- Barr DJ, Levy R, Scheepers C, Tily HJ. 2013. Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language* 68:255–278.
- Bates D, Maechler M, Bolker B. 2011. lme4: linear mixed-effects models using S4 classes. Available from: <http://CRAN.R-project.org/package=lme4>
- Berard JD. 1990. Life history patterns of male rhesus macaques on Cayo Santiago. Unpublished Ph.D. thesis. University of Oregon.
- Bercovitch FB, Berard JD. 1993. Life history costs and consequences of rapid reproductive maturation in female rhesus macaques. *Behavioral Ecology and Sociobiology* 32:103–109.
- Bercovitch FB, Goy RW. 1990. The socioendocrinology of reproductive development and reproductive success in macaques. In: Ziegler TE, Bercovitch FB, editors. *Socioendocrinology of primate reproduction*. New York: Wiley-Liss. p 59–93.
- Bercovitch FB, Widdig A, Trefilov A, et al. 2003. A longitudinal study of age-specific reproductive output and body condition among male rhesus macaques, *Macaca mulatta*. *Naturwissenschaften* 90:309–312.
- Berman CM, Kapsalis E. 1999. Development of kin bias among rhesus monkeys: maternal transmission or individual learning? *Animal Behaviour* 58:883–894.
- Bernstein IS. 1991. The correlation between kinship and behaviour in non-human primates. In: Hepper PG, editor. *Kin recognition*. Cambridge: Cambridge University Press. p 6–29.
- Bernstein IS, Ehardt CL. 1986. Selective interference in rhesus monkey (*Macaca mulatta*) intragroup agonistic episodes by age-sex class. *Journal of Comparative Psychology* 100:380–384.
- Boelkins RC, Wilson AP. 1972. Intergroup social dynamics of the Cayo Santiago rhesus (*Macaca mulatta*) with special reference to changes in group membership by males. *Primates* 13:125–140.
- Chancellor RL, Satkoski J, George D, et al. 2011. Do dispersing monkeys follow kin? Evidence from gray-cheeked mangabeys (*Lophocebus albigena*). *International Journal of Primatology* 32:474–490.
- Chapais B. 1995. Alliances as a means of competition in primates: evolutionary, developmental, and cognitive aspects. *Yearbook of Physical Anthropology* 38:115–136.
- Chapais B. 2001. Primate nepotism: what is the explanatory value of kin selection? *International Journal of Primatology* 22:203–229.
- Charpentier MJE, Peignot P, Hossaert-Mckey M, Wickings EJ. 2007. Kin discrimination in juvenile mandrills, *Mandrillus sphinx*. *Animal Behaviour* 73:37–45.
- Cheney DL, Seyfarth RM. 1983. Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *The American Naturalist* 122:392–412.
- Chepko-Sade BD, Halpin ZT. 1987. Mammalian dispersal patterns: the effects of social structure on population genetics. Chicago: University of Chicago Press.
- Chesser RK. 1991. Influence of gene flow and breeding tactics on gene diversity within populations. *Genetics* 129:573–583.
- Clutton-Brock TH. 2002. Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72.
- Clutton-Brock TH, Lukas D. 2012. The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology* 21:472–492.
- Cohen J, Cohen P. 1983. *Applied multiple regression/correlation analysis for the behavioral sciences*. New Jersey: Lawrence Erlbaum Associates, Inc.
- Colvin JD. 1986. Proximate causes of male emigration at puberty in rhesus macaques. In: Rawlins RG, Kessler MJ, editors. *The Cayo Santiago Macaques. History, behavior and biology*. Albany: State University of New York Press. p 131–157.
- Cords M, Sheehan MJ, Ekernas LS. 2010. Sex and age differences in juvenile social priorities in female philopatric, nondespotic blue monkeys. *American Journal of Primatology* 72:193–205.
- Datta SB. 1988. The acquisition of dominance among free-ranging rhesus monkey siblings. *Animal Behaviour* 36:754–772.
- De Vries H. 1998. Finding a dominance order most consistent with a linear hierarchy: A new procedure and review. *Animal Behaviour* 55:827–843.
- Dixon AF, Nevison CM. 1997. The socioendocrinology of adolescent development in male rhesus monkeys (*Macaca mulatta*). *Hormones and Behavior* 31:126–135.
- Dobson AJ. 2002. *An introduction to generalized linear models*. 2nd ed. Boca Raton: Chapman & Hall/CRC.
- Drickamer LC. 1974. A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. *Folia Primatologica* 21:61–80.
- Drickamer LC, Vessey SH. 1973. Group changing in free-ranging male rhesus monkeys. *Primates* 14:359–368.
- Di Fiore A. 2003. Molecular genetic approaches to the study of primate behavior, social organization, and reproduction. *American Journal of Physical Anthropology* 122:62–99.
- Di Fiore A. 2012. Genetic consequences of primate social organization. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB, editors. *The Evolution of Primate Societies*. Chicago, Illinois: University of Chicago Press. p 269–292.
- Di Fiore A, Fleischer RC. 2005. Social behavior, reproductive strategies, and population genetic structure of *Lagothrix poeppigii*. *International Journal of Primatology* 26:1137–1173.
- Di Fiore A, Link A, Schmitt CA, Spehar SN. 2009. Dispersal patterns in sympatric woolly and spider monkeys: Integrating molecular and observational data. *Behaviour* 146:437–470.
- Elo AE. 1978. *The rating of chess players, past and present*. New York: Arco.
- Forstmeier W, Schielzeth H. 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology* 65:47–55.
- Fraser ON, Schino G, Aureli F. 2008. Components of relationship quality in chimpanzees. *Ethology* 114:834–843.
- Gilby I, Wrangham R. 2008. Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology* 62:1831–1842.

- Goodall J. 1986. The chimpanzees of Gombe. Patterns of behavior. Cambridge, MA: Belknap Press of Harvard University.
- Gouzoules S. 1984. Primate mating systems, kin associations, and cooperative behavior: evidence for kin recognition? *Yearbook of Physical Anthropology* 27:99–134.
- Gouzoules S, Gouzoules H. 1987. Kinship. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago, IL: University of Chicago Press. p 299–305.
- Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- Hoffman C, Ruiz-Lambides A, Davila E, et al. 2008. Sex differences in survival costs of reproduction in a promiscuous primate. *Behavioral Ecology and Sociobiology* 62: 1711–1718.
- Inoue E, Inoue-Murayama M, Vigilant L, Takenaka O, Nishida T. 2008. Relatedness in wild chimpanzees: influence of paternity, male philopatry, and demographic factors. *American Journal of Physical Anthropology* 137:256–262.
- Jack KM, Fedigan L. 2004. Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: Patterns and causes of natal emigration. *Animal Behaviour* 67:761–769.
- Kapsalis E, Berman CM. 1996. Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) I. Criteria for kinship. *Behaviour* 133:1209–1234.
- Kaufman AB, Rosenthal R. 2009. Can you believe my eyes? The importance of interobserver reliability statistics in observations of animal behaviour. *Animal Behaviour* 78:1487–1491.
- Kulik L, Langos D, Widdig A. in revision. Mothers make a difference: Mothers inhibit social bonding towards sons.
- Langergraber KE, Mitani JC, Vigilant L. 2009. Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology* 71:1–12.
- Langergraber K, Mitani J, Vigilant L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences* 104:7786–7790.
- Langos D, Kulik L, Mundry R, Widdig A. 2013. The impact of paternity on male-infant association in a primate with low paternity certainty. *Molecular Ecology* 22:3638–3651.
- Lawler R, Richard A, Riley M. 2003. Genetic population structure of the white sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar (1992–2001). *Molecular Ecology* 12:2307–2317.
- Lawson Handley LJ, Perrin N. 2007. Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology* 16:1559–1578.
- Lehmann J, Boesch C. 2008. Sexual differences in chimpanzee sociality. *International Journal of Primatology* 29:65–81.
- Lehmann J, Boesch C. 2009. Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour* 77:377–387.
- Lindburg DG. 1969. Rhesus monkeys: mating season mobility of adult males. *Science* 166:1176–1178.
- Lindburg DG. 1971. The rhesus monkeys in North India: an ecological and behavioral study. In: Rosenblum LA, editor. *Primate behavior*. New York: Academic Press. p 1–106.
- Lonsdorf EV, Anderson KE, Stanton MA, et al. 2014a Boys will be boys: sex differences in wild infant chimpanzee social interactions. *Animal Behaviour* 88:79–83.
- Lonsdorf EV, Markham AC, Heintz MR, et al. 2014b Sex differences in wild chimpanzee behavior emerge during infancy. *PLoS ONE* 9: e99099.
- Lukas D, Reynold V, Boesch C, Vigilant L. 2005. To what extent does living in a group mean living with kin? *Molecular Ecology* 14:2181–2196.
- Mateo JM. 2002. Kin-recognition abilities and nepotism as a function of sociality. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269:721–727.
- Meikle DB, Vessey SH. 1981. Nepotism among rhesus monkey brothers. *Nature* 294:160–161.
- Mitani JC. 2009. Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour* 77:633–640.
- Nakamichi M. 1989. Sex differences in social development during the first 4 years in a free-ranging group of Japanese monkeys, *Macaca fuscata*. *Animal Behaviour* 38:737–748.
- Neumann C, Dubosq J, Dubuc C, et al. 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour* 82:911–921.
- Nishida T. 1979. The social structure of chimpanzees at the Mahale Mountains. In: *The great apes*. Menlo Park, CA: Benjamin Cummings. p 73–121.
- Perry S. 1996. Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology* 40:167–182.
- Perry S, Manson JH, Muniz L, Gros-Louis J, Vigilant L. 2008. Kin-biased social behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. *Animal Behaviour* 76:187–199.
- Pusey AE, Packer C. 1987. Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 250–266.
- Quinn GP, Keough MJ. 2002. *Experimental design and data analysis for biologists*. 1st ed. Cambridge, UK: Cambridge University Press.
- Rawlins RG, Kessler MJ, editors. 1986. *The Cayo Santiago macaques. History, behavior and biology*. Albany: State University of New York Press.
- R Development Core Team. 2012. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ross KG. 2001. Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. *Molecular Ecology* 10:265–284.
- Rowell TE, Chism J. 1986. The ontogeny of sex differences in the behavior of patas monkeys. *International Journal of Primatology* 7:83–107.
- De Ruiter JR, Geffen E. 1998. Relatedness of matriline, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). *Proceedings of the Royal Society B: Biological Sciences* 265:79–87.
- Schülke O, Bhagavatula J, Vigilant L, Ostner J. 2010. Social bonds enhance reproductive success in male macaques. *Current Biology* 20:2207–2210.
- Schülke O, Wenzel S, Ostner J. 2013. Paternal relatedness predicts the strength of social bonds among female rhesus macaques. *PLoS ONE* 8: e59789.
- Seth PK, Seth S. 1986. Ecology and behavior of rhesus monkeys in India. In: Else JG, Lee PC, editors. *Primate Ecology and conservation*. Vol. 2. Cambridge: Cambridge University Press. p 192–305.
- Seyfarth RM. 1976. Social relationships among adult female baboons. *Animal Behaviour* 24:917–938.
- Seyfarth RM. 1980. The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour* 28:798–813.
- Silk JB. 2002. Kin selection in primate groups. *International Journal of Primatology* 23:849–875.
- Silk JB, Alberts SC, Altmann J. 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour* 67:573–582.
- Silk JB, Altmann J, Alberts SC. 2006. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology* 61:183–195.
- Silk JB, Beehner JC, Bergman TJ, et al. 2009. The benefits of social capital: close social bonds among female baboons

- enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences* 276:3099–3104.
- Silk JB, Samuels A, Rodman PS. 1981. The Influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). *Behaviour* 78:111–137.
- Silk JB, Seyfarth RM, Cheney DL. 1999. The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. *Behaviour* 136:679–703.
- Slater KY, Schaffner CM, Aureli F. 2009. Sex differences in the social behavior of wild spider monkeys (*Ateles geoffroyi yucatanensis*). *American Journal of Primatology* 71:21–29.
- Smith JE. 2014. Hamilton's legacy: Kinship, cooperation and social tolerance in mammalian groups. *Animal Behaviour* 92:291–304.
- Smith KL, Alberts SC, Altmann J. 2003. Wild female baboons bias their social behaviour towards paternal half-sisters. *Proceedings of the Royal Society B* 270:503–510.
- Southwick CH, Yongzu Z, Haisheng J, Zhenhe L, Wenyuan Q. 1996. Population ecology of rhesus macaques in tropical and temperate habitats in China. In: Fa JE, Lindburg DG, editors. *Evolution and ecology of macaque societies*. Cambridge: Cambridge University Press. p 95–105.
- Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology* 41:291–309.
- Storz JF. 1999. Genetic consequences of mammalian social structure. *Journal of Mammalogy* 80:553–569.
- Strier KB, Dib LT, Figueira JE. 2002. Social dynamics of male muriquis (*Brachyteles arachnoides hypoxanthus*). *Behaviour* 139:315–342.
- Struhsaker TT, Leland L. 1976. *Socioecology of five sympatric monkey species in the Kibale Forest, Uganda*. New York: Academic Press.
- Sugg DW, Chesser RK, Dobson FS, Hoogland JL. 1996. Population genetics meets behavioral ecology. *Trends in Ecology & Evolution* 11:338–342.
- Van Noordwijk MA, Hemelrijk CK, Herremans LAM, Sterck EHM. 1993. 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. p 77–85.
- Vigilant L, Hofreiter M, Siedel H, Boesch C. 2001. Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences* 98:12890–12895.
- Walters JR. 1987. Kin recognition in non-human primates. In: Fletcher DJC, Michener CD, editors. *Kin recognition in animals*. Chichester: John Wiley and Sons. p 359–393.
- Walters JR, Seyfarth RM. 1987. Conflict and cooperation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 306–317.
- Watts D. 2000a Grooming Between Male Chimpanzees at Ngogo, Kibale National Park. II. Influence of Male Rank and Possible Competition for Partners. *International Journal of Primatology* 21:211–238.
- Watts DP. 2000b Grooming Between Male Chimpanzees at Ngogo, Kibale National Park. I. Partner Number and Diversity and Grooming Reciprocity. *International Journal of Primatology* 21:189–210.
- West SA, Pen I, Griffin AS. 2002. Cooperation and competition between relatives. *Science* 296:72–75.
- Widdig A. 2007. Paternal kin discrimination: the evidence and likely mechanisms. *Biological Reviews* 82:319–334.
- Widdig A. 2013. The impact of male reproductive skew on kin structure and sociality in multi-male groups. *Evolutionary Anthropology* 22:239–250.
- Widdig A, Kulik L, Muniz L, et al. in revision. Multi-generational pedigree data reveal a low incidence of present-day inbreeding in a long-lived primate population isolated for 75 years.
- Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB. 2001. Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proceedings of the National Academy of Sciences* 98:13769–13773.
- Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB. 2002. Affiliation and aggression among adult female rhesus macaques: A genetic analysis of paternal cohorts. *Behaviour* 139:371–391.
- Widdig A, Streich WJ, Nürnberg P, et al. 2006. Paternal kin bias in the agonistic interventions of adult female rhesus macaques (*Macaca mulatta*). *Behavioral Ecology and Sociobiology* 61:205–214.
- Wrangham RW, Clark AP, Isabirye-Bosuta. 1992. Female social relationships and social organisation of Kibale Forest chimpanzees. In: *Topics in primatology*. Tokyo: Tokyo University Press. p 81–98.
- Zehr JL, Meter PEV, Wallen K. 2005. 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* 72:1087–1094.

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