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The Influence of Kinship on Familiar Natal Migrant Rhesus Macaques (*Macaca mulatta*)

Monika Albers and

Junior Research Group of Primate Kin Selection, Department of Primatology, Max-Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

Institute of Biology, Humboldt University, 10115 Berlin, Germany

Anja Widdig

Junior Research Group of Primate Kin Selection, Department of Primatology, Max-Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

Behavioural Ecology Group, Institute of Biology, University of Leipzig, 04103 Leipzig, Germany

Abstract

In most primate species, females remain in the natal group with kin while males disperse away from kin around the time of puberty. Philopatric females bias their social behavior toward familiar maternal and paternal kin in several species, but little is known about kin bias in the dispersing sex. Male dispersal is likely to be costly because males encounter an increased risk of predation and death, which might be reduced by dispersing together with kin and/or familiar males (individuals that were born and grew up in same natal group) or into a group containing kin and/or familiar males. Here we studied the influence of kinship on familiar natal migrant rhesus macaques (*Macaca mulatta*) on Cayo Santiago, Puerto Rico, by combining demographic, behavioral, and genetic data. Our data suggest that kinship influences spatial proximity between recent natal immigrants and males familiar to them. Immigrants were significantly nearer to more closely related familiar males than to more distantly related individuals. Within a familiar subgroup, natal migrants were significantly closer to maternal kin, followed by paternal kin, then non-kin, and finally to males related via both the maternal and paternal line. Spatial proximity between natal immigrants and familiar males did not decrease over time in the new group, suggesting that there is no decline in associations between these individuals within the first months of immigration. Overall, our results might indicate that kinship is important for the dispersing sex, at least during natal dispersal when kin are still available.

Keywords

Familiarity; Kinship; Male rhesus macaques; Natal dispersal; Spatial proximity

Introduction

Dispersal is commonly observed across the animal kingdom. For group-living mammals, sex-biased dispersal is the norm, with male dispersal and female philopatry (Greenwood 1980). In the majority of primate species, male dispersal occurs (Cheney and Seyfarth 1983; Harcourt 1978; Packer 1979), although females or both sexes disperse in some species (Kappeler 2006). Dispersal is either natal, wherein individuals leave their birth group and disperse to a new group, or secondary, i.e., all subsequent dispersal (Greenwood 1980; Mitchell 1994; Pusey and Packer 1987).

By dispersing, animals avoid potential costs of inbreeding (Clutton-Brock 1989; Greenwood 1980; Itani 1972; Moore 1993), which leads to increased homozygosity of individuals within a group or population and ultimately decreases the fitness of individuals (Packer 1979). Further, animals that have dispersed could benefit by outbreeding, i.e., breeding between distantly related or unrelated individuals (Alberts and Altmann 1995; Pusey and Wolf 1996). Dispersal can also lead to an increase in male dominance ranks and/or improve access to mates or other limited resources (Cheney and Seyfarth 1983). However, it is also associated with potential costs such as increased mortality rates due to predation and lost reproductive opportunities because of time spent alone, as found for instance in yellow baboons (*Papio cynocephalus*: Alberts and Altmann 1995). Natal dispersal resulted in a relative loss of social status in long-tailed macaques (*Macaca fascicularis*: van Noordwijk and van Schaik 2001) and increased exposure to aggression and injury from unfamiliar conspecifics in vervet monkeys (*Chlorocebus pygerythrus*: Cheney and Seyfarth 1983).

When males leave their natal group they often migrate with coresident males (parallel dispersal) or join groups containing males that previously dispersed from the same natal group (Jack and Fedigan 2004). Natal migrants that share a period of long and intimate association while growing up in the same natal group should therefore be more familiar with one another than individuals that grow up in different groups. Indeed, empirical evidence suggests that the cost/benefit ratio of dispersing is optimized by dispersing with familiar males or into groups containing familiar individuals (Boelkins and Wilson 1972; Cheney and Seyfarth 1983; Colvin 1983; Meikle and Vessey 1981; van Noordwijk and van Schaik 1985). As age proximity has been shown to influence social relationships among female primates (Silk *et al.* 2006; Widdig *et al.* 2001), predispersal males of a similar age that grow up in the same natal group may also be more familiar with each other than individuals of different ages.

Kin selection theory predicts that given equal costs and benefits, related individuals are more likely to cooperate with each other than unrelated individuals (Hamilton 1964). In addition, cooperation is expected to be more likely among closely related than among distantly related individuals. There is extensive evidence for maternal kin bias in primates, best illustrated for cercopithecines (Gouzoules 1984; Gouzoules and Gouzoules 1987; Silk 2001). In contrast, only few studies have examined paternal kin bias, even though a high frequency of paternal siblings due to male reproductive skew has been shown for many primate species (reviewed in Widdig 2007). Studies of rhesus macaques (*Macaca mulatta*: Widdig *et al.* 2001) and baboons (Silk *et al.* 2006; Smith *et al.* 2003) showed that adult

females bias affiliative behavior toward paternal half-sisters in comparison to unrelated females. Moreover, juvenile mandrills (*Mandrillus sphinx*) associated more with paternal relatives than with non-kin (Charpentier *et al.* 2007). As predicted by the socioecological model (Isbell and Young 2002; Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980), strong empirical evidence suggests that philopatric females of many primate species predominately form strong bonds with their kin, whereas for the dispersing sex less pronounced social bonds with kin are predicted, simply because kin should be less available for them (reviewed in Chapais 2001; Silk 2002). To date, kin bonds have rarely been investigated for dispersing males, probably because of the lack of the genetic data required. Nevertheless, according to kin selection theory, males could benefit from preferential treatment of kin. Indeed, kin bias has been demonstrated in male–infant dyads in baboons (Buchan *et al.* 2003).

If males emigrate together from their natal group, dispersing males should preferentially affiliate and cooperate with kin in comparison to unrelated individuals. Kinship has already been shown to influence male dispersal, but studies are limited and few present the relevant genetic data to assess kinship. An early study reported a potential influence of maternal kinship on patterns of dispersal in rhesus macaques, as males frequently transfer into the same non-natal groups as their older maternal brothers (Meikle and Vessey 1981). Inferring relatedness from blood protein markers, a study of long-tailed macaques found that groups of natal migrants from the same natal group were sometimes closely related, but could also be less related (de Ruiter and Geffen 1998). A recent study including microsatellite data on gray-cheeked mangabeys (*Lophocebus albigena*), a species with male dispersal, revealed that opportunities for kin-biased dispersal (both maternal and paternal) were scarce and related males shared groups no more often than expected by chance (Chancellor *et al.* 2011).

Here we aim to illuminate whether kinship influences patterns of spatial proximity of males that have recently left their natal group. Rhesus macaques are well suited to study this question as they live in multimale–multifemale groups characterized by female philopatry and male dispersal (Melnick and Pearl 1987). Additionally, females have been shown to form stronger bonds with maternal and paternal kin than with unrelated individuals, with the strongest bonds among maternal kin (Widdig *et al.* 2001, 2002). Moreover, the availability of kin within the natal group is likely to be high, particularly for paternal kin, because male reproductive skew has been identified in several studies (Dubuc *et al.* 2011; Widdig *et al.* 2004) and leads to paternal siblings of a similar age (Altmann 1979). Most male rhesus macaques leave their natal group between 3 and 5.5 yr of age (median age=4.5 yr; Berard 1990) either with males of a similar age or alone (Widdig *unpubl. data*). By combining demographic, genetic, and behavioral data we investigate spatial proximity between males transferring from their natal group (hereafter natal migrants) and males that were familiar to them. Familiar males were born and grew up in the same group and dispersed to the same new group as a given natal migrant. We included three predictor variables: 1) degree of relatedness, 2) kin category, and 3) time since immigration and tested the following predictions. First, we expect spatial distance to familiar males in their new group to decrease with increasing degree of relatedness. Second, if natal migrants bias their behavior toward kin, as reported for philopatric female rhesus macaques, then kin category should predict the

spatial distribution of natal migrants and males with which they are familiar to. Among familiar males we expect natal migrants to be in closer spatial proximity to maternal kin, followed by paternal kin and maternal/paternal kin, and ultimately non-kin. Finally, we predict a decrease in spatial proximity between natal migrants and familiar males over time, as we expect individuals to interact with other animals in their new group as they become more integrated.

Methods

Study Site and Population

We studied the provisioned, free-ranging rhesus macaque population of Cayo Santiago, a 16-ha island situated 1 km off the south east coast of Puerto Rico (18°09 N, 65°44 W). The colony was established in 1938 when *ca.* 400 monkeys were transferred from various locations in India to the island (Rawlins and Kessler 1986). Ever since, individuals have been added to the population only via natural births; however, genetic analyses from pedigree data revealed no evidence of inbreeding over a 20-yr study period (Muniz and Widdig *unpubl. data*). The breeding season on Cayo Santiago occurs from *ca.* March to August and is followed by a 6-mo birth season from *ca.* September to February, but a shift over time due to changes in climate was recently reported (Hoffman *et al.* 2008). Male dispersal occurs mostly during the mating season (Drickamer and Vessey 1973). We restricted our study to natal dispersal, though males can change groups several times. Male rhesus macaques mostly enter the dominance hierarchy in their new group at the bottom and increase in rank according to their tenure (Drickamer and Vessey 1973).

In 2009, when we conducted the behavioral observations for this study, there were six naturally formed social groups present on Cayo Santiago. During the 6-mo study period (March–August) the mean population size was $959.2 \pm \text{SD } 7.7$ individuals. We considered dispersing males that had not yet entered a new group as extra-group individuals. The island consists of two parts connected via an isthmus, and the home ranges of some groups overlap to a variable extent. Previous studies have shown that macaques on Cayo Santiago are able to distinguish outgroup from ingroup members (Mahajan *et al.* 2011).

Focal Subjects

We collected behavioral data on 15 focal males and males that were familiar to them. Focal males were natal migrants born in birth seasons 2004 or 2005 that dispersed during the mating season of 2009. Initially, we planned to include natal migrants solely from group R, but owing to limited events of natal dispersal in 2009 we added focal animals from other groups. Focal males were therefore either 1) natal to group R and immigrated to another group ($N=10$) or 2) natal to any other group and immigrated into group R ($N=5$). Natal migrants from group R immigrated into all five possible social groups; we therefore collected data in all groups on Cayo Santiago.

Familiar males were males born from birth seasons 2001 to 2005 in the same natal group as a given focal male and that dispersed to the same new group as the focal male during or before 2009. We restricted our analysis to familiar males in the focal male's new group

(ignoring unfamiliar subjects) because of the restricted availability of genetic data fulfilling our definition of kinship. We limited familiar males to the age cohorts 2004 and 2005, because familiarity arises particularly between subjects of a similar age (Widdig *et al.* 2001) and social interactions between these individuals are more likely. In addition, individuals of a similar age have an increased probability of being paternally related (Altmann 1979; Widdig *et al.* 2004). Because almost no males from the 2006 birth season migrated during the study period, we did not include this cohort in the familiar male category. Our study comprised a total of 45 males that were either focal males, familiar males, or both.

Behavioral Observations

D. Langos gathered behavioral data from March 20 to April 2, 2009 and M. Albers collected data from April 4 to August 20, 2009. M. Albers began data collection after achieving a mean of 80 % in interobserver reliability (including distance judgment and subject identification) with D. Langos. We accumulated a total of 194 h of focal sampling data with a mean of $776 \pm \text{SD } 29.0$ min per focal individual (range: 720–820 min) and balanced observation times between all focal individuals independent of whether they dispersed earlier or later in the season. We distinguished animals using a unique identification code (tattoos and ear notches) as well as individual characteristics, e.g., coloring and scars, and were able to identify all focal and familiar macaques individually before we began data collection.

The observation schedule was dependent on the boat schedule of the Caribbean Primate Research Center (CPRC); we started data collection at 07:00 and followed focal subjects until 14:30 (Monday, Wednesday, Friday), until 17:00 (Tuesday, Thursday) or until 13:30 (weekends, holidays). We scheduled observations to achieve an equal distribution per individual in the morning (mean of $354.4 \pm \text{SD } 19.6$ min) and in the early afternoon (mean of $346.9 \pm \text{SD } 16.9$ min). Owing to the late introduction of boats returning from the island at 17:00 h and hence the limited availability of late afternoon sessions, total observation times for these sessions (mean of $74.7 \pm \text{SD } 11.9$ min) were lower than those of morning and early afternoon sessions. However, we also tried to balance observations across focal individuals in the late afternoon.

Focal samples lasted 8–40 min. The majority of samples had a duration of 20 min (52.1 %) or 40 min (29.2 %). Originally we aimed to collect 20-min samples, but focal subjects were sometimes hard to find at the edge of the group, so we extended the sample duration to 40 min. Because young migrant focal subjects were occasionally lost during a sample, we decided to keep samples that had a minimum duration of eight minutes. We collected only one focal sample in one observation session per day. We interrupted a focal sample if the subject was out of sight. If we could not find the focal individual within 20 min, we stopped the sample and tried to complete it in the same session on the same day. If this was not possible, we completed the sample on a different day, but in the same session.

Using instantaneous sampling (Altmann 1974), we collected proximity data every 4 min during a focal sample (hereafter point time samples), which included the spatial proximity data of all macaques within a 2 m radius of the focal animal (Altmann 1974). For spatial proximity, we used four different distance categories (see “Statistical analysis”).

We used a Psion Workabout portable handheld computer and transferred data from the handheld computer into Microsoft Excel using Noldus Observer Mobile 5.0. At the time of data collection, neither observer had information on paternity.

Demographic Data

The CPRC demographic database includes dates of birth and death, birth group, maternal relatedness, dispersal events and group allocation, and the team of CPRC census takers monitors the population daily. When an individual disperses to a new group, census takers note its new group and check this assignment of group membership regularly for at least the following two month. If group membership remains constant, they define the first day the individual is seen in the new group as the date of immigration (A. Ruiz *pers. comm.*).

We defined a date of immigration for each focal and familiar male based on either our behavioral observations or on CPRC records if their date was earlier than the date we recorded. If we used our behavioral observations, we used the first focal sample recorded in the new group for focal individuals and the first occurrence of a familiar male in a focal sample for familiar males.

Genetic Analysis

Most of the genetic data were available from previous studies (Widdig *et al.* 2001, 2002, 2004) and are part of the genetic database of the Cayo Santiago population, which was started in 1992. Almost the entire population was systematically sampled for individuals 1) born between 1992 and 2000 or 2) born before 1992 if they survived until systematic sampling began in 1992. The CPRC samples newborns that have survived their first year for blood and tissue in the next annual trapping season (January–March), and has a well-established procedure for sampling individuals, which has been approved by the Institutional Animal Care & Use Committee (IACUC). After 2000, we began more extensive sampling of the study group R.

The database that we analyzed comprised 2290 individuals typed at 14.62 ± 2.44 (mean $\pm$ SD) loci out of a panel of 21 short tandem repeat (STR) markers (Dubuc *et al.* 2011; Kulik *et al.* 2012 and references therein). The mean number of alleles per locus was 7.38 ± 2.87 , the mean observed heterozygosity across loci was 0.75 ± 0.08 , the mean expected heterozygosity was 0.74 ± 0.07 , and the mean polymorphic information content was 0.69 ± 0.80 (all calculations performed with CERVUS 3.0) (Kalinowski *et al.* 2007). There was no evidence of a null allele occurring at these loci and only one locus deviated from the Hardy–Weinberg equilibrium either due to chance, mutation, or typing errors.

For the purpose of this study, we aimed to conduct genetic paternity analyses for all focal individuals and familiar males ($N_{\text{total}}=45$). If we lacked genetic data for a given male, after obtaining IACUC approval (protocol no. 4060105) we collected either blood or fecal samples; in the latter we followed an established protocol (Nsubuga *et al.* 2004).

We sampled behavioral mothers determined from long-term observations by CPRC census takers and confirmed maternity using genotypic data for 44 of the 45 focal and familiar males (97.78 %), and used the confirmed genetic mothers for all subsequent analyses.

Because we could not confirm behavioral mothers as genetic mothers in only 1.79 % of all individuals typed in the database, we felt confident to additionally accept four (of all 55) behavioral grandmothers lacking a DNA sample to determine kinship.

We considered all sampled males older than 1250 days (based on earliest age at reproduction; Bercovitch *et al.* 2003) and present on the island at least 200 days before the actual birth of a given infant (mean days $\pm$ SD gestation length: 166.5 $\pm$ 7.4; Silk *et al.* 1993) as potential sires for that infant to account for extra-group paternity (Widdig *et al.* 2004). For our 45 focal and familiar male subjects, we had 13–21 common loci typed for each mother–father–offspring trio. We determined paternity for all 45 males in our study using a combination of exclusion and likelihood analyses as follows: In 44 cases, we excluded all sampled potential sires for at least two loci, with the exception of the assigned sire, which matched the offspring–mother pair at all loci. For the remaining case, there was only one male on the island that had only one single mismatching locus out of 20 loci compared for the mother–father–offspring trio. We are nevertheless convinced that the assigned sire is the actual father of this infant, because 1) we included >98 % of potential sires from the entire population and all potential sires resident to group R in the analysis, greatly decreasing the chances of misassignment due to unsampled sires, and 2) all other sampled potential sires were excluded at four or more loci. The data suggest a mutation in the offspring's genotype. The paternity for this case was supported at the 95 % confidence level by the maximum likelihood method calculated by CERVUS 3.0 (Kalinowski *et al.* 2007).

To increase the power of our kinship data, we aimed to assign maternal and paternal grandfathers to our 45 males. We had DNA samples for all mothers (38 unique females, as some focal males shared the same mother). We were able to determine a total of 33 maternal grandfathers (94.29 %) because we could exclude all candidate sires on at least two loci, with the exception of the assigned sire. This corresponds to 84.44 % of known maternal grandparents for all focal males. Likewise, based on our 45 males, we detected 30 unique sires in our sample and were able to determine a total of 29 paternal grandfathers (96.67 %), excluding all candidate sires with at least two mismatches except for the candidate sire. This corresponds to 95.55 % of known paternal grandparents for all focal males.

Determining Kinship

Based on the 15 focal natal migrants transferring to a particular group containing a given number of familiar males we detected a total of 127 familiar dyads, i.e., dyads including a natal migrant and a familiar male. However, some dyads were listed twice, e.g., as focal male A and familiar male B and as focal male B and familiar male A. To calculate relatedness we included each dyad only once, resulting in a subset of 114 unique dyads. For each focal and familiar male dyad we 1) calculated relatedness coefficients and 2) determined kin categories.

We used a pedigree-based approach using the aforementioned parentage assignments to establish kin categories. Full genetic information up to the grandparent generation was available for 87 of 114 dyads (76.32 %). Twenty-seven of all 114 familiar dyads (23.68 %) had gaps in their genealogies, with a pedigree comprising 12 IDs per dyad up to the grandparent generation. Twenty-four dyads had one missing ID, three dyads had two

missing IDs, but missing individuals consisted solely of grandfathers as we solved all paternities. When the parentage assignment of an individual in a given dyad was incomplete, we used an exclusion rule to ensure that the dyad was indeed unrelated. Using CPRC census records, we first identified all reproductive males on the island at the time of conception of a given individual and then reduced the number by all males excluded as sires based on genotypic data. This provided us with a list of potential sires that could not be omitted due to a lack of samples or power. We then compared the identities of the potential sires not excluded for a given subject A with the identities of the assigned sire and grandfathers of a second subject B. If we found no overlap, we considered this dyad unrelated. If we found an overlap, we used an R script written by Roger Mundry and Lars Kulik to calculate the probabilities of the different possible degrees of relatedness between the individuals.

We calculated the coefficient of relatedness (r) for each dyad (Wright 1922). Kin categories contained 1) maternally, 2) paternally, 3) maternally and paternally related, or 4) unrelated dyads. Kin dyads were related through the maternal and/or paternal line via a common grandparent, or closer. Maternally and paternally related dyads were related via the maternal line from the perspective of individual A and via the paternal line from the perspective of individual B. We defined a given dyad as unrelated if individuals were not related for a minimum of two generations, i.e., they did not share a common individual among their parents or grandparents.

Statistical Analysis

The initial data set contained 791 data points from point time sampling, resulting in a total of 8513 data points considering all familiar males as potential proximity partners of focal subjects.

To determine patterns of spatial proximity among natal migrants and males that were familiar to them we used a generalized linear mixed model (GLMM; Baayen 2008) with Poisson error structure and log-link function. Because kin category and degree of relatedness are highly related, e.g., r is always 0 among non-kin, including both predictors in the same model would lead to collinearity; hence we ran two models. We used coefficient of relatedness and days since immigration as fixed effects in the first GLMM. Before running the model, we standardized both predictor variables, i.e., coefficient of relatedness and days since immigration, to a mean of 0 and a standard deviation of 1. The response variable was spatial proximity between focal individuals and familiar male partners. Spatial proximity contained four distance categories, which we each assigned a numerical value (Table I). As the frequencies of distance categories decreased from very common (distance category 3) to increasingly rare (distance categories 2–0), we reversed the numerical categories of the response variable (only in the GLMMs), so that the residuals of the data fitted a Poisson distribution. As random effects, we included focal individual ID, ID of familiar male partners, ID of the focal individual's new group, and ID of the particular observation of a focal (nested in focal individual ID).

Initially we explicitly accounted for temporal autocorrelation, as residuals for data points recorded closer to one another in time could be more similar to one another than data points recorded further apart in time (Burnham and Anderson 2003), violating an essential

assumption of the model. For this we obtained an autocorrelation term by first running the model as described in the preceding text and deriving residuals from it. We then, separately for each data point, took the mean of the residuals of all data points, after weighting them by their time lag to the particular data point under consideration and included the resulting variable as a further fixed effect (autocorrelation term) into the model. The weight function had the shape of a Gaussian distribution with a mean of 0 (maximum weight at time lag of 0) and a standard deviation chosen such that the likelihood of the model with the autocorrelation term included was maximized. However, the autocorrelation term appeared to be negative, obviously an artifact due to the response being heavily dominated by the largest distance class, hence we excluded this term from the model. We found no evidence for overdispersion ($\chi^2=6458.81$, $df=8510$, $P=1$, dispersion parameter=0.759). To determine whether the fixed effects as a whole influenced the response variable, we first compared the fit of the full model (including all fixed and random effects) with that of the null model (including only the random effects) using a likelihood ratio test (Dobson 2002).

In the second GLMM we used the same approach as in the first model, except we replaced degree of relatedness with kin category (maternal, paternal, maternal/paternal, non-kin). The fixed effects in this model were therefore kin category and time since immigration. We dummy-coded kin categories to include them. Again, we compared the fit of the full model with that of the null model using a likelihood ratio test to determine whether fixed effects as a whole influenced the response variable. Here too we detected no evidence for overdispersion ($\chi^2=5937.15$, $df=8508$, $P=1$, dispersion parameter=0.698). To determine the P -value for the difference between the dummy-coded kin categories we re-leveled the factor, i.e., assigned another reference kin category, and ran the model again. We originally included autocorrelation as described in the preceding text, but excluded it for the same reasons as before.

We calculated all tests using R, version 2.15 (R Development Core Team 2012) and fitted mixed models using the function “lmer” of the lme4 package (version 0.999375-42). For all statistical tests, we set the level of significance at $P = 0.05$.

Results

Kin Availability for Natal Immigrants

Of all 114 unique focal–familiar male dyads, five were paternally related, six were maternally related, eleven were maternally and paternally related, but the remaining 92 dyads (80.7 %) were unrelated. Related dyads can be further subdivided into one pair of paternal cousins (0.9 %), two pairs of maternal cousins (1.8 %), and ten pairs of maternal/paternal cousins (8.8 %; r -value for cousins ≈ 0.0625), one maternally related (0.9 %) and one maternally/paternally related uncle–nephew dyad (0.9 %; r -value for uncle–nephew dyads ≈ 0.125), four pairs of paternal (3.5 %) and three pairs of maternal half-siblings (2.6 %; r -value for half-siblings ≈ 0.25). The number of familiar individuals and familiar kin available to a focal individual depended on which group focal subjects dispersed to. The models, however, controlled for kinship availability.

Coefficient of Relatedness

Overall, the results revealed that the set of predictor variables used in the first model had a significant effect on the spatial proximity between natal migrants and familiar males (likelihood ratio test comparing the fit of full and reduced model: $\chi^2=12.338$, $df=2$, $P=0.002$). In more detail, the coefficient of relatedness was a significant predictor of spatial proximity (GLMM, estimate $\pm$ SE=0.26 $\pm$ 0.08, $z=3.31$, $P=0.001$) even though the effect was rather small, suggesting a positive influence of the coefficient of relatedness on spatial proximity. This indicates that focal individuals were on average closer to more closely related familiar kin than to more distantly related or unrelated familiar individuals (Fig. 1).

Kin Categories

Again, the set of predictor variables used in the second model had a clear effect on the spatial proximity between natal migrants and familiar males (likelihood ratio test comparing the fit of full and null model: $\chi^2=56.041$, $df=4$, $P<0.001$). More specifically, kin category significantly influenced the average spatial proximity (likelihood ratio test comparing full and reduced model excluding kin categories: $\chi^2=54.290$, $df=3$, $P<0.001$). Maternal kin were significantly closer than paternal kin (GLMM: estimate $\pm$ SE=-1.10 $\pm$ 0.45, $z=-2.42$, $P=0.015$), non-kin (estimate $\pm$ SE=-2.22 $\pm$ 0.44, $z=-5.08$, $P<0.001$), and maternal/paternal kin (estimate $\pm$ SE=-5.04 $\pm$ 1.06, $z=4.74$, $P<0.001$; Fig. 2). Further, maternal/paternal kin were significantly more distant than paternal kin (estimate $\pm$ SE=3.91 $\pm$ 1.01, $z=3.86$, $P<0.001$) and non-kin (estimate $\pm$ SE=2.80 $\pm$ 0.98, $z=2.86$, $P=0.004$), and finally nonkin were significantly more distant than paternal kin (estimate $\pm$ SE=1.11 $\pm$ 0.33, $z=3.37$, $P=0.001$; Fig. 2).

Time since Immigration

The results of both models indicated that time since immigration had no effect on spatial proximity (first GLMM: estimate $\pm$ SE=-0.09 $\pm$ 0.06, $z=-1.33$, $P=0.185$, second GLMM: estimate $\pm$ SE=-0.09 $\pm$ 0.06, $z=-1.35$, $P=0.177$). Hence, in contrast to our prediction, spatial proximity between natal migrants and familiar males did not decrease with the amount of time natal migrants spent in their new group.

Discussion

This is the first study that uses extensive pedigree data to investigate the influence of kinship on natal migrants. We examined three predictors of spatial proximity that we now discuss in detail.

Coefficient of Relatedness

Our results indicate that the degree of relatedness had a positive significant effect on spatial proximity between natal migrants and familiar males in the new group. Previous studies have shown that adult female macaques spend more time near close kin than more distant kin and non-kin in their natal group (Kapsalis and Berman 1996; Widdig *et al.* 2002). For young dispersing males, having close relatives nearby may help to reduce the costs of dispersal. However, males that leave their natal group will have less kin available than before dispersal, as suggested by theoretical work (Isbell and Young 2002; Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980) and shown by empirical data on male gray-

cheeked mangabeys (Chancellor *et al.* 2011). Our model controlled for kin availability but revealed that the influence of the coefficient of relatedness on spatial proximity was significant, but rather low. A possible explanation for this is that the relatedness coefficient predictor contains all kin categories. As each kin category has a different influence of spatial proximity, this impacts our results for the coefficient of relatedness.

Kin Categories

Our results support the importance of maternal kinship in cercopithecine life, as demonstrated in multiple studies of females (reviewed in Chapais 2001; Silk 2002). Natal migrants were significantly closer to their maternal kin than to any other kin category, suggesting that maternal kin are still the most important social partners within the familiar subgroup. As maternal relatedness plays such a pivotal role in social relationships in the birth group (Kapsalis 2004), it can also be expected to influence social patterns after natal dispersal to a new group, at least initially. Indeed, male rhesus macaques immigrating to new groups spent more time close to their maternal brothers than to other males and formed alliances more frequently than non-brothers (Meikle and Vessey 1981).

Natal migrants were significantly closer to maternal than to paternal kin. Previous studies of various primate species also demonstrate a much stronger maternal than paternal kin bias (Charpentier *et al.* 2007; Silk *et al.* 2006; Widdig *et al.* 2001, 2002), although kin selection theory predicts a similar kin bias in maternal and paternal kin because they share the same proportion of genes. However, most primate groups have a matrilineal structure with dominance ranks inherited from the mother and more pronounced maternal than paternal care. Maternal kin are therefore much more likely to be familiar with one another, which may explain why maternal kin bias is higher than paternal kin bias. Alternatively, our result could simply be due to increased familiarity among maternal kin and not reflect kin bias toward maternal over paternal kin.

Based on previous studies indicating that paternal kinship had a positive impact on patterns of affiliation in adult female rhesus macaques (Widdig *et al.* 2001), we expected males to prefer paternal kin to unrelated familiar males. Our data indeed suggest closer spatial proximity between paternally related than between unrelated individuals. Paternal kin discrimination, i.e., differentiation between paternally related and unrelated individuals, has been demonstrated for philopatric females of various species in different social contexts (Charpentier *et al.* 2007; Silk *et al.* 2006; Widdig *et al.* 2001, 2002, 2006). In contrast, some studies have not found discrimination among paternal kin, e.g., philopatric female white-faced capuchins (*Cebus capucinus*: Perry *et al.* 2008) and philopatric male chimpanzees (Pan troglodytes: Langergraber *et al.* 2007). Recent analyses of kin associations of male rhesus macaques before natal dispersal suggest that males form similar bonds as philopatric females, but predispersal males were significantly more likely to affiliate with paternal kin than non-kin in comparison to females of the same age (Widdig and Kulik, *unpublished data*). The present study suggests that paternal bias continues after males disperse from their natal group.

What remains puzzling is that dyads related via both kin lines (maternal and paternal) show the weakest pattern of spatial proximity. Interestingly, these kin dyads belong to the

maternal line from the perspective of individual A with a female as the primary ancestral link, and to the paternal line from the perspective of individual B with a male as the primary ancestral link. In other words, dyads at the parent level were maternal siblings of a different sex. The offspring of each of these related individuals are indeed unlikely to affiliate with one another because males (and their descendants) are not socially linked to their maternal sisters and their offspring. Nevertheless, more research is needed to understand the implications of this kin configuration.

Time since Immigration

In contrast to our prediction, we found no influence of spatial proximity between natal migrants and familiar males over time. This suggests that there is no decline in association between these individuals within the first 5 months of immigration. As natal migrants are in closer spatial proximity to more closely related than to more distantly related or unrelated familiar males and relatedness to unfamiliar individuals is likely to be minimal (see below), this may mean that kinship plays a role for natal migrants during their initial period in the new group.

Limitations of the Study

Further studies would benefit from more detailed behavioral observations to obtain a more complete picture of the dispersal process and to understand whether patterns of spatial proximity indeed reflect affiliative interactions among migrants. Including unfamiliar males with detailed genetic data would enable a better understanding of the role of kinship for recent natal immigrants. However, relatedness to unfamiliar males in the new group may not influence patterns of spatial proximity or affiliation among adolescent immigrants very much. First, owing to lack of familiarity (the most likely mechanism of kin discrimination among maternal kin; Widdig 2007), older and therefore unfamiliar maternal brothers should not play an important role for natal migrants. Second, it is less likely that natal migrants are paternally related to unfamiliar males, unless males successfully reproduce in more than one group through secondary dispersal or extra-group paternity.

Conclusions

Overall, our data suggest that, within the familiar subgroup, kinship potentially influences the spatial proximity patterns of dispersing male rhesus macaques, despite the decrease in kin availability with departure from the natal group and further dilution due to subsequent dispersal. However, bonding with unrelated familiar males might also positively influence immigration, particularly after males have spent some time in their new group. A recent study suggests that male bonding with unrelated males is associated with male fitness. Male Assamese macaques (*Macaca assamensis*) with strong male bonds formed more coalitions and were more likely to gain an increase in dominance and enjoyed higher reproductive success than males with weaker bonds that formed fewer coalitions (Schülke *et al.* 2010). The limited availability of kin, but the need to socially interact with others in the new group, may lead to dispersing males initially affiliating with related individuals and then subsequently with unrelated individuals.

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Fig. 1.

Effect of relatedness coefficients on spatial proximity between natal migrants and familiar males. The size of the circles indicates the number of data points. The dashed line represents the predicted distance.

Fig. 2. Effect of kin category on spatial proximity between natal migrants and familiar males. The size of the circles represents the number of data points. Lines show the respective predicted values.

Table I

Levels of the response variable: Distance categories and corresponding numerical values assigned to each category

Numerical distance category	Description of distance category
0	Body contact with focal individual
1	Within 0.5 m of focal individual, but not in body contact
2	Between 0.5 and 2 m of focal individual
3	Outside 2 m of focal individual