

Sex differences in learning the allocation of social grooming in infant stumptailed macaques

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Summary

Among primates, the intense mother-infant bond provides offspring with a lengthy period for learning from an experienced and reliable demonstrator. Since adult life differs for females and males, the expertise of mother may not be equally useful to both sexes of infant, particularly with regard to social relationships. Here, we report on differences between infant female and male stumptailed macaques in learning how to allocate social grooming, using their mothers as demonstrators. Infant females were significantly more socially precocious than males, starting at early ages to groom mothers. Throughout their first year of life, daughters showed more instances of mirroring mothers' behaviour than sons did. In addition, while grooming on their own, grooming durations of daughters to specific partners was significantly concordant with time devoted by mothers to such recipients. We suggest that daughters learn from their mothers how to distribute grooming amongst social companions, while sons primarily use mother as a secure platform to initiate socializing. These results lend support to the idea that mirroring equates with learning and leads to reinforcement of innate propensities for gender roles in primates.

Keywords: social learning, allogrooming, sexual differences, mother-offspring, stumptailed macaques, intergenerational transmission.

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Introduction

In vertebrates relying on maternal expertise to acquire or reinforce behaviour through social learning is purportedly an adaptive mechanism that ensures survival and enhances fitness by preventing immature subjects from engaging in behaviour that, if attempted by individual trial-error learning, might be deadly or injurious (Galef, 1996; but see Laland, 1996). Keverne et al. (1996) and Broad et al. (2006) have proposed that the mammalian brain evolved to favour mother-offspring attachment (*sensu* Bowlby, 1969, 1973). In primates, learning to make decisions via maternal examples may account for the enlargement of the neocortex (Keverne et al., 1996); a conclusion also reached by Joffe (1997) with regards to the primate extended juvenile period.

Primate mothers are recognized as a main referential model for a diversity of socially learned or reinforced behaviours (Altmann, 1980; Horvat & Kraemer, 1981; Wallen et al., 1981; Fairbanks & McGuire, 1986; Fairbanks, 1989; Berman, 1990, 2004; McGrew, 1992; Tanaka, 1995; Huffman, 1996; de Waal, 1996; Berman et al., 1997; Tanaka, 1998; Berman & Kapsalis, 1999; Drapier & Thierry, 2002; Maestripieri, 2003; Weaver & de Waal, 2003; Lonsdorf et al., 2004; Schino et al., 2004; Weaver et al., 2004; Lonsdorf, 2005, 2006; Suomi, 2005; Maestripieri et al., 2007). Mother-offspring attachment including close proximity provide the confidence and visual opportunities to use mother as a model, even if this might perpetuate behaviour of low efficiency (Tanaka, 1995, 1998; Drapier & Thierry, 2002) or abusive mothering styles prone to reduce fitness (Fairbanks, 1989; Berman, 1990; Maestripieri, 2003; Maestripieri et al., 2007). As infants age, they are able to modify behaviour learned from mothers by using other models such as peers (Wallen et al., 1981; Berman, 1982; Ehardt & Bernstein, 1987; Lee & Johnson, 1992; Huffman, 1996; de Waal, 1996; Suomi, 2005; Leca et al., 2007) or by independent learning (Berman & Kapsalis, 1999). Thus, upon reaching adulthood daughters need not necessarily replicate their mothers' behaviour (Schino et al., 2004).

Despite Altmann's (1980) suggestion that female baboons (and thereby other primate species) may be specially primed to learn social relationships from mothers' behaviour, few studies directly address whether or how offspring sex interacts with the use of mother as a referential model (Rapoport, 1985; McGrew, 1992; Bernstein et al., 1993; Deputte & Quris, 1996; Lonsdorf et al., 2004; Lonsdorf, 2005, 2006). Most of the prior work focuses

on daughters or analyzes and reports sex differences as an intervening variable, rather than being included in hypotheses, even though sex differences in learning abilities during development exist (Bachevalier & Hagger, 1991; Hagger & Bachevalier, 1991).

Sex differences in social development foreshadow immature sex-specific adult life histories (Pereira & Altmann, 1985; Walters, 1987; Hiraiwa-Hasegawa, 1997; Cords, 2000). Primates, like most vertebrates (Morris et al., 2004), are born with a sexually differentiated brain, one proximate mechanism underlying behavioural sex differences (Wallen, 2005). Being born with this sexually differentiated brain allows for learning and the practice of relevant adult behaviour long before facing the demands of reproductive and adult social life. Thus, prenatal differentiation of the brain might fall among what Setchell & Lee (2004) identify as sex-specific developmental pathways arising from age-dependent selection pressures linked to distinct adult reproductive strategies, constrained by time and energy expenditure for both mothers and the developing immatures.

Studies of sex-specific reliance on the maternal expertise necessary to acquire adult competence suggest that differences exist and that these are related to the type of behaviour being learned (McGrew, 1992; Lonsdorf et al., 2004; Agostini & Visalberghi, 2005; Lonsdorf, 2005, 2006; Leca et al., 2007). Since the pioneering study of Sade (1965), immature female rhesus macaques are known to develop social networks similar to those of their mothers (Suomi, 2005). Subsequent studies of kin-biased intergenerational transmission have been mainly female-centred (de Waal, 1996; Schino et al., 2004; capuchins: Perry et al., 2008). While Berman & Kapsalis (1999) found no sex differences in kin biased spacing behaviour in infant and juvenile rhesus monkeys, Cords (2000) found that immature female blue monkeys develop similar allogrooming preferences to those of their mothers, although their sons do not. Berman & Kapsalis (1999) acknowledge that little is still known about the processes involved in developing and perpetuating kin biased (or other social) networks. In addition, development is a period of intense learning across a range of modalities including maternal examples (Berman et al., 1997). All in all, networks or social preferences of yearlings resemble those of their mothers, but this effect is not always seen at later ages. If social risk during infancy influences social learning, then this risk will determine whether or not such resemblance will endure until adulthood.

Our study addresses whether (1) infant stumptailed macaques, *Macaca arctoides*, use mothers as the main model to learn allogrooming (henceforth grooming) preferences (i.e., how much or how often to groom each group member) and (2) if females and males differ in the extent to which they rely on maternal expertise. If infants are able to learn the allocation of grooming from their mother, we predict that they will mirror maternal behaviour (sensu Berman, 2004) to a greater extent than compared to another female that simply keeps close proximity to her mother (i.e., mother's best friend, sensu Silk, 2002). Thus, we expect that infants will show more instances of grooming together and devoting proportionally more time to grooming alongside mothers than with mothers' best friend (prediction 1). Moreover, if mothers are the main social models, we expected that whenever infants groom on their own, they will groom more often and/or for longer times the preferred partners of mothers (prediction 2). In turn, grooming allocation by infants should match the social biases of mothers, such as being kin-biased, rank-biased or showing the same idiosyncratic grooming preferences (prediction 3).

If, as we discuss above, daughters are more disposed than sons to learn from their mothers, the daughters should also be more socially precocious. For instance, daughters should begin to engage in grooming interactions at younger ages (prediction 4). Additionally, daughters should display higher rates of social mirroring (prediction 5) and more concordance with maternal behaviour than will sons (prediction 6). Finally, daughters' social biases would be more akin to those of mothers (prediction 7).

Method

Subjects

We studied 26 captive stumptailed macaques, 14 females and 12 males, from birth until 2 years old. These animals were born at the facilities of the Instituto Nacional de Psiquiatría in Mexico City between 1981 and 1998, to 10 different mothers (Table 1). The stumptailed macaque colony was formed in 1973–1974, and consistently ranged from 27 to 33 animals across all age-sex categories (newborns to adults). Until 1996, animals were kept in three different outdoor groups (each cage 49 m² floor area plus 12 m² of cornices).

Table 1. Demographic characteristics of the sample.

Infant	Mother	Sex of infant	Birth of infant	Parity ^c	Focal samplings (h)	Rank of mother at birth of infant
MG ^a	CA	♀	May 6, 1981	2	84	Dominant
LA ^a	CH	♀	Sep. 6, 1982	2	92	Subordinate
VI ^a	CN	♂	Sep. 13, 1982	6	92	Dominant
LI	CN	♀	Aug. 7, 1984	7	136	Dominant
TA	CA	♂	Aug. 15, 1984	4	136	Dominant
IS	MA	♀	Jun. 14, 1985	1	32	Intermediate
SA	CA	♂	Apr. 23, 1986	5	30	Dominant
NU	CN	♀	Jul. 18, 1986	8	32	Dominant
FR	GR	♂	Dec. 4, 1986	4	31	Dominant
JA	CA	♀	Jul. 2, 1987	6	32	Dominant
CU	TI	♀	Sep. 25, 1987	4	32	Intermediate
PO	CN	♂	Sep. 25, 1987	9	29	Dominant
DW	MA	♂	Dec. 4, 1987	2	31	Intermediate
AU	CA	♀	Feb. 27, 1989	7	32	Dominant
AL	CA	♂	May 3, 1990	8	32	Dominant
ES	TI	♂	May 23, 1990	5	32	Intermediate
SX	CA	♂	Nov. 15, 1991	9	28	Intermediate
R1	NU	♀	May 30, 1992	1	28	Intermediate
R2 ^b	TI	♀	Dec. 1, 1992	7	32	Dominant
JR	AU	♂	Feb. 20, 1994	1	28	Intermediate
GA	TI	♂	May 8, 1994	8	28	Dominant
MN	AU	♀	May 29, 1997	2	32	Intermediate
SO	MA	♀	Jan. 8, 1998	3	32	Subordinate
SE	AU	♂	Jun. 2, 1998	3	30	Dominant
LU	JA	♀	Jun. 8, 1998	3	32	Intermediate
LZ	R1	♀	Nov. 27, 1998	2	30	Subordinate

^a Data from birth were not available.

^b Subject died being 11 months old.

^c Birth number including stillborns.

From April 1996, they were merged into a single group housed in a large outdoor cage (148 m² floor area plus 36 m² of cornices). This provided a more challenging and variable social environment for the macaques. Details on diet, feeding regime and water availability are found in Mondragón-Ceballos (2001).

We also collected data from 10 mothers and 10 additional females as controls (control female models). The control females were the 'best friends' of mothers; chosen as the female with whom the mother exchanged (gave and

received) more than 10% of her total social grooming time (Dunbar, 1983) in the month prior to the birth of the infant being sampled. Whenever a mother had more than one friend, we chose as control female that with the highest percentage of grooming exchanged even if the difference with the next closest one was around or less than 1%. Friendships between female stumptailed macaques are usually life-long and actively maintained, irrespectively of the number of juvenile and adult daughters present (personal observations). Consequently, there were no changes in friendships throughout the study, control females being as constant as mothers were.

In six cases, control females were unrelated to mothers; control females were putative half-sisters of mothers in two cases (born to different, unrelated mothers during the tenure of a same alpha male) while in the remaining two a matriarch and her eldest daughter were control females of each other. The inclusion of related females as controls did not introduce any meaningful bias in analyses. Data collection for infants, mothers and control females was done simultaneously.

We calculated social ranks for every 6-month period using Boyd & Silk's (1983) method for assigning cardinal ranks, based on composite sociomatrices of dyadic agonism given (aggressions and threats) + submissions received. To assign the categorical ranks shown in Table 1, we classified as dominants those females occupying the upper-third positions within the female rank ordering. Intermediates are those in the middle-third positions, and subordinate the females occupying the bottom-third positions. Up to 1.5 years old, we assigned immature stumptailed macaques the same cardinal rank as their mothers; thereafter we incorporated immatures into cardinal rank calculations. In all instances, regardless of their sex, they ranked closely, although not always adjacent, below their mothers.

Behaviour sampling

Data come from ad libitum, focal and instantaneous sampling (Altmann, 1974). Before July 1985, we collected data by daily ad libitum and 1-h focal observations on 6 animals. From July 1985 to December 2001, we collected data on focal animals using video-recording and instantaneous sampling. From July to December 1985, 11 animals were each sampled daily for one hour (between 0800 and 1900 h); from January 1986 onwards focal samples lasted 10 min. All 10-min focal samples were collected by daily recording

(Mondays–Fridays) from 9 randomly chosen animals at randomly selected times between 0800 and 1900 h. This procedure ensured collecting at least two focal samples per animal each week. On two occasions (September 1992 and 1994) three weeks elapsed between successive samples. We took instantaneous scan samples every half-hour from 0700 to 1900 h. In each scan, we recorded activities, interactions, proximity and neighbours from all animals in the colony. Again, besides from the periods mentioned above, gaps in instantaneous scan samples were never longer than 1–2 days, and never skipping more than two consecutive sampling periods within a single day.

Behaviour studied

We define ‘grooming’ as picking through, separating or combing the hair of another animal using fingers or mouth. A grooming bout was defined as any interaction lasting more than 5 s, as shorter interactions are used to request grooming (personal observations). We considered that a grooming bout ended whenever one or both animals involved departed, if actors exchanged roles, or if the interaction was interrupted for more than 20 s before being resumed. Simultaneous mutual grooming (where 2 animals participated together as givers) was considered as a single interaction, but duration of each groomer was recorded separately. We analysed only interactions where offspring, mothers and control females were the givers, but not the recipients, of grooming ($N = 33\,059$). In comparisons of how similar infant grooming was to that of mothers and control females, we divided data into four 6-month age-categories (birth–6 months old; >6 months–1 year; >1 year–1.5 years; and >1.5–2 years old) and used the following indices.

Mirroring

We used 2 behaviours as measures of mirroring mothers and control females (adult females models) grooming behaviour (predictions 1 and 5). (1) The percentage of instances per immature age-category that the adult female model and an immature were recorded simultaneously grooming the same animal. (2) The percentage of time that infants groomed alongside adult female models relative to the total grooming duration ((infant duration/entire grooming session duration) \times 100).

Duration agreement

Duration (in s) of grooming given by an immature to a specific recipient who had also been groomed by the adult female model within the past hour of accumulated focal samples. Unlike mirroring, the infants did not groom together with their adult female models, but groomed on their own (predictions 2 and 6), even though (mainly in the first age-category) mothers could be nearby.

Frequency agreement

Number of grooming bouts given by an immature to a specific recipient who had also been groomed by the adult female model within the past hour of accumulated focal samples. As in duration agreement, grooming was not performed simultaneously with adult females. We considered time and frequency agreement as instances of independently rehearsing learning from adult females (predictions 2 and 6).

Social biases

We used 3 measures of social bias: kin bias, rank bias and idiosyncratic preferences (de Waal, 1996; Schino, 2001; Schino et al., 2004). Bias measures were obtained by regressing the percentage of time allocated to grooming each group member per 6-month period on kin coefficients and cardinal ranks. From these regressions, we determined the unstandardised residuals for kin, rank and remaining individuals so as to assess bias. We performed 2 such multiple regressions, one for infants and the other for adult females. Multiple regressions were done over the entire infant and adult female samples, without distinguishing infants' sex, age or adult female relatedness, so as to ensure that residuals contained variance due to sex, age and relatedness, which could then be explored. Analysing the P-P, Q-Q and residuals vs. independent variables plots confirmed that residuals were not normally distributed and were highly dispersed (when plotted against independent variables). We considered kin coefficients exclusively from the maternal line obtained from genealogical records, as described in López-Vergara et al. (1989). Kin and rank biases and idiosyncratic preferences were used to assess the similarity between infants' networks with those of mothers and control females (predictions 3 and 7).

Analyses

We used the Generalized Linear Mixed Model (GLMM) (McCulloch & Searle, 2001) to assess the effects of sex of infant, adult female model (mother or control female) and age-category on mirroring. We choose GLMM to control for repeated sampling of the same subjects (infants, mothers and control females) and gaps in the sample. Covariance structure of within-subjects effects was modelled as a first-order autoregressive series (AR(1)). We employed the sequential Bonferroni procedure in post-hoc contrasts of significant age effects and interactions.

We performed a series of cross-sectional analyses to assess agreement of grooming frequency and duration between infants and adult female models at the ages-categories above defined. Assessment of grooming frequency and grooming duration matching was done by means of weighted Linear Regressions to control for repeated sampling of subjects. We assigned weights using the clustering procedure described in Manson et al. (2004). Clusters were calculated as the number of times per age category infants and adult female models groomed the same animal, with weights being the inverse of the cluster (e.g., $1/(\text{mother A grooming instances to C} + \text{daughter B grooming instances to C})$). Immature stumptailed macaques that accounted for less than three matching instances per 6-month period were dropped from analyses. As none of our dependent variables were normally distributed, besides from being heteroscedastic, arcsine transformed percentages, logarithmic transformed durations, and square root transformed frequencies were used in GLMM and Linear Regressions analyses.

Finally, we did a series of cross-sectional Generalised Linear Mixed Model Regressions (GLMRs) to estimate matching of infants'-adult female models' kin bias, rank bias and idiosyncratic preferences at different ages. We used van de Pol & Wright (2009) within-subject centring procedure, equations (2) and (3), to distinguish and estimate within- and between-subjects effects, and to assess within- versus between-subjects slope differences. We regressed infants' kin bias, rank bias and unstandardised residuals on within-subject centred mothers' or control females' kin bias, rank bias and unstandardised residuals, respectively. Entering infants, adult females and grooming recipients' identifications into the GLMR was a further control of multilevel aggregation effects. The R 2.5.1 package (Venables et al., 2007) was used to perform all analyses and G*Power 3.1 (Faul et al.,

2007) was used to perform sensitivity and achieved power tests. All tests are two-tailed and the significance level was set at $\alpha \leq 0.05$. For multiple paired contrasts, in addition to the sequential Bonferroni procedure restrictions, we set $1 - \beta \geq 0.84$ for a mean difference to be considered significant.

Results

Age at first grooming

Data from 19 infants (females = 9, males = 10) provided reliable information about the age at which grooming commenced. The first animal groomed by infants was the mother, except for one male whose first grooming was to the group's alpha male. Females tended to start to groom their mother at a younger age than did males (females: mean \pm SE = 74.5 ± 9 days of age; males: 102.4 ± 11.4 days of age; Mann–Whitney $U = 21.5$, $N_1 = 10$, $N_2 = 9$, $p = 0.052$). Similarly, females started grooming other animals at a significant younger age (females: 83 ± 10.7 days; males: 130.2 ± 13 days; $U = 15.5$, $p = 0.01$). Throughout their infancy, females engaged in more grooming interactions than did males (females: 15.8 ± 1.6 bouts/h, males: 11.5 ± 1.6 ; GLMM: $N = 3207$, $F_{1,18.3} = 5.268$, $p = 0.034$, $1 - \beta = 0.78$) and as infants aged, grooming duration increased significantly for both sexes ($F_{3,204.1} = 3.212$, $p = 0.024$, $1 - \beta = 0.87$).

Percentage of instances and proportion of time of grooming together with an adult female

The percentage of instances where offspring and mothers simultaneously groomed the same recipient varied significantly between sexes (GLMM: $N = 208$, $F_{1,19.5} = 15.945$, $p = 0.001$, $1 - \beta = 0.93$) and by age ($F_{3,69.8} = 8.019$, $p < 0.001$, $1 - \beta = 0.99$), with an interaction between sex and age ($F_{3,69.8} = 9.179$, $p < 0.001$, $1 - \beta = 0.95$). The same trends were found for all grooming involving adult female models (sex \times adult female model: $F_{1,34.9} = 14.383$, $p = 0.001$, $1 - \beta = 0.94$; age \times adult female model: $F_{3,80.2} = 3.275$, $p = 0.025$, $1 - \beta = 0.63$; sex \times age \times adult female model: $F_{3,80.5} = 2.746$, $p = 0.048$, $1 - \beta = 0.48$; see Figure 1). Throughout the first and half year of life the percentage of instances daughters groomed alongside mothers was significantly higher than that of sons (Figure 1a); daughters were also in company of control females more than sons until

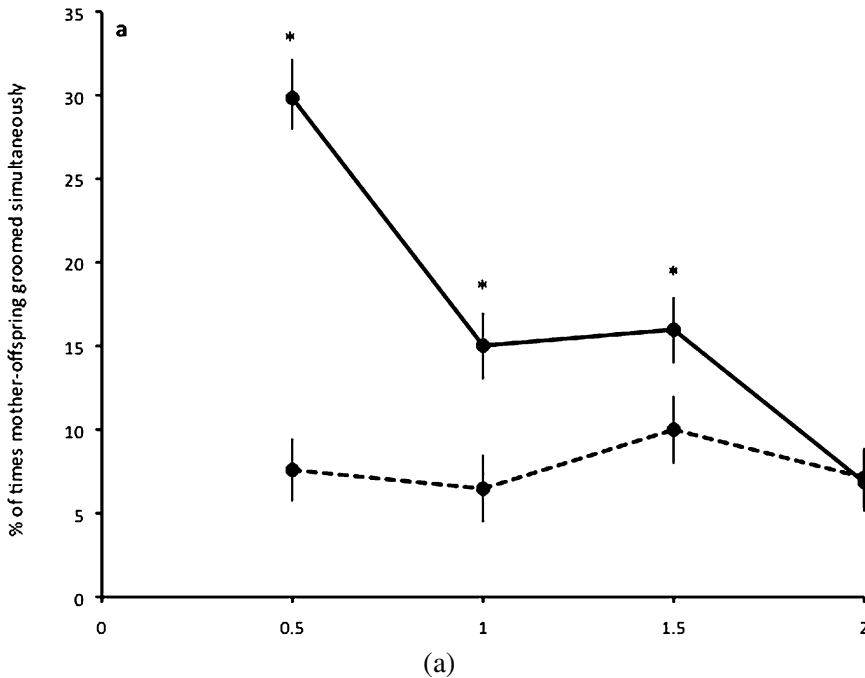


Figure 1. Mean (\pm SEM) percentage of instances daughters (—) and sons (---) groomed together with (a) mothers and (b) control females at different ages. * $p < 0.05$ vs. males (see text for statistical analyses).

one year old (Figure 1b). Up to 6 months of age, the simultaneous grooming percentages of daughters and mothers were significantly higher than these were with control females (means difference = 13.94, $p < 0.0001$, $1 - \beta = 0.85$). Sons, by contrast, scarcely ever groomed simultaneously with mothers or control females nor did they show any trends throughout time.

The percentage of time spent grooming simultaneously with an adult female (mother or control) varied significantly with age (GLMM: $N = 1094$, $F_{3,211.1} = 5.224$, $p = 0.001$, $1 - \beta = 0.95$), with an interaction between adult female model \times age ($F_{3,196.9} = 4.145$, $p = 0.007$, $1 - \beta = 0.91$) and sex of infant \times adult female model \times age ($F_{3,196.9} = 4.559$, $p = 0.004$, $1 - \beta = 0.83$). Figure 2 summarises these complex results. Throughout their first 6 months of life, sons and daughters both spent the majority of time simultaneously grooming alongside their mothers. By one year, both daughters and sons significantly decreased the percentage of time simul-

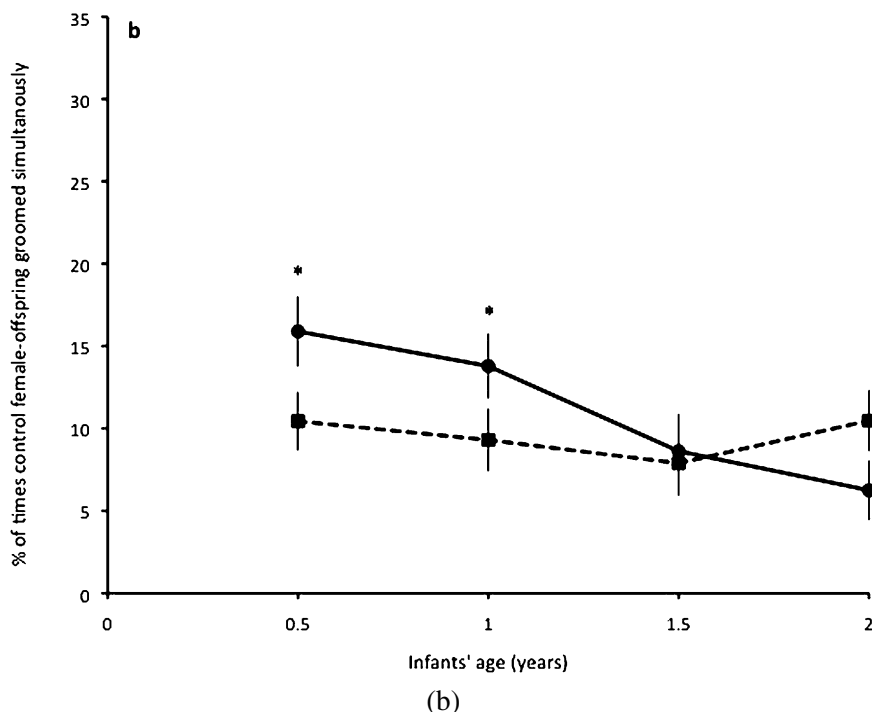


Figure 1. (Continued.)

taneously grooming (diff. = -22.88 , $p < 0.0001$, $1 - \beta = 0.94$). Behaviour of daughters remained constant until 2 years, while at 1.5 years of age, sons significantly increased time spent simultaneously grooming with mothers by comparison to daughters (Figure 2a), and relative to the previous (1.5 vs. 1 year of age: diff. = 22.71 , $p < 0.0001$, $1 - \beta = 0.92$) and subsequent ages (1.5 vs. 2 years of age: diff. = 10.87 , $p < 0.0001$, $1 - \beta = 0.84$). During their first 6 months, daughters and sons spent significantly less time grooming alongside control females than they did alongside their mothers (diff. = -19.94 , $p < 0.0001$, $1 - \beta = 0.89$). Sons showed similar trends until 2 years old (Figure 2b). However, 1.5 years old daughters significantly increased time grooming together with control females when compared with mothers (diff. = 24.64 , $p < 0.0001$, $1 - \beta = 1$), sons (diff. = 15.59 , $p < 0.0001$, $1 - \beta = 0.84$), and the previous age (1.5 vs. 1 year of age: diff. = 26.58 , $p < 0.0001$, $1 - \beta = 1$; Figure 2b).

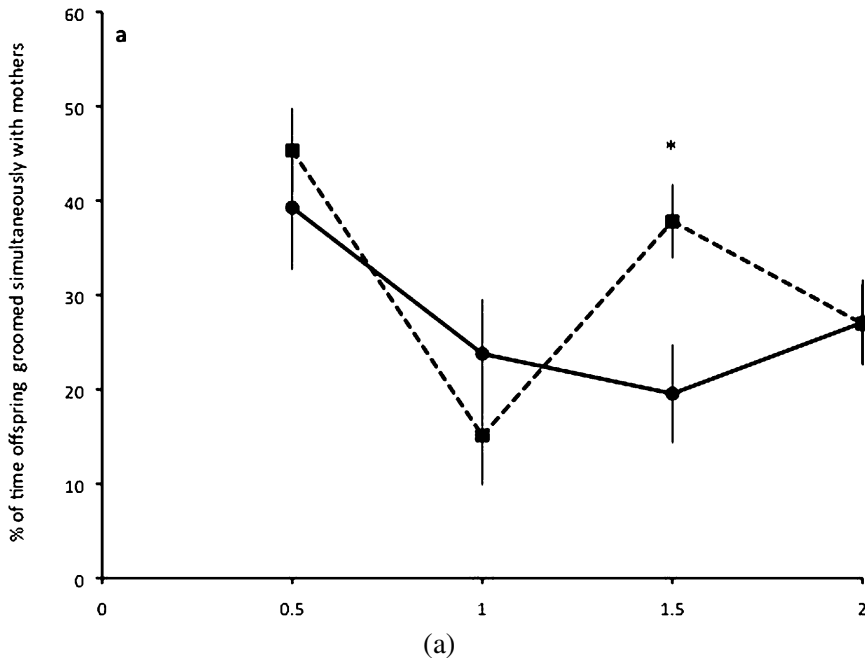


Figure 2. Mean (\pm SEM) percentage of time daughters (—) and sons (---) lasted grooming jointly with (a) mothers and (b) control females. * $p < 0.05$ vs. males (see text for statistical analyses).

Grooming agreement

We found no significant agreement in grooming frequency between immatures of either sex and a control female model. By contrast, daughters' grooming duration was significantly concordant with the grooming durations of their mothers throughout their first six months of life ($a \pm \text{SE} = 0.46 \pm 0.38$, $b = 0.51 \pm 0.22$, $N = 39$, $R^2 = 0.4$, $t_{11} = 2.26$, $p = 0.045$, $1 - \beta = 0.67$; Figure 3a), and continued to be so up to one year of age only ($a = 0.48 \pm 0.41$, $b = 0.44 \pm 0.19$, $N = 60$, $R^2 = 0.38$, $t_{14} = 2.15$, $p = 0.05$, $1 - \beta = 0.77$; Figure 3b). Immature male grooming duration was dissimilar for both mothers and control female models at all ages.

Kin bias, rank bias and idiosyncratic preferences matching

Tables 2–4 summarise results for kin bias, rank bias and idiosyncratic preferences. Daughters at 1.5 years significantly replicated individual maternal kin biases (within-subjects effects: Wald $\chi^2 = 7.322$, $\text{df} = 1$, $p = 0.007$) and

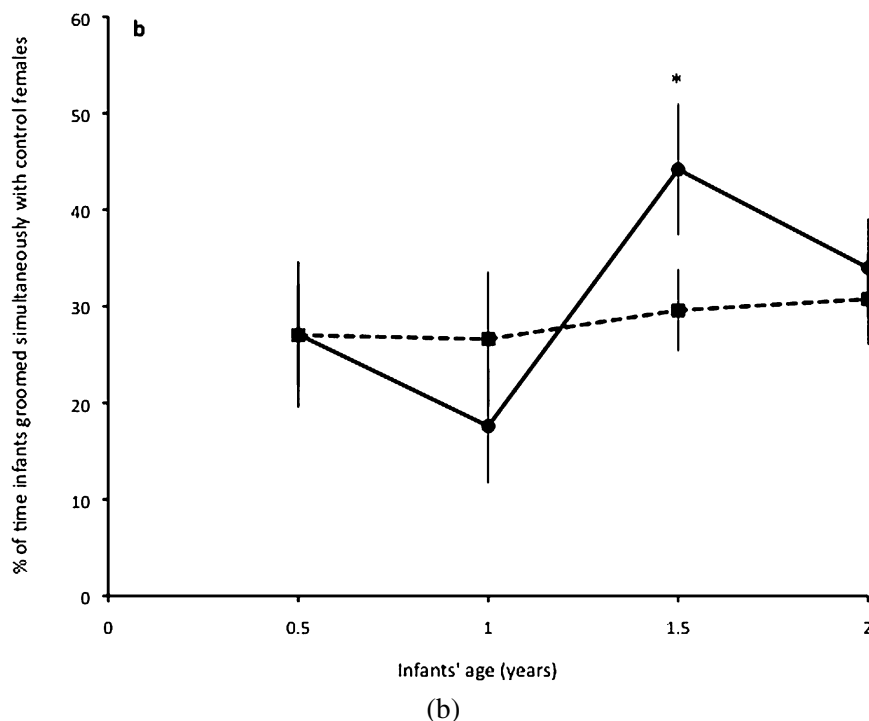


Figure 2. (Continued.)

followed the overall tendency of mothers to allocate more grooming to kin (between-subjects: Wald $\chi^2 = 9.393$, $df = 1$, $p = 0.002$; Table 2). However, within- and between-subjects slopes were significantly different (Wald $\chi^2 = 10.53$, $df = 1$, $p = 0.001$). This last effect is illustrated in Figure 4a where in all 14 cases, the within-subjects slopes match individual maternal kin biases. Ten daughters' within-subjects slopes followed the between-subjects tendency to allocate more grooming time to kin, but there was much variation in the slopes. On the other hand, the within-subjects slopes of 4 daughters showed the opposite trend of allocating more grooming to non-kin. Males at 6 months showed a significant trend to allocate grooming in a similar fashion to control females (between-subjects: Wald $\chi^2 = 5.166$, $df = 1$, $p = 0.023$; Table 2). Nonetheless, they did not match individual females' kin preferences, within-subjects effects being non-significant.

Neither daughters nor sons matched maternal rank biases at any age (Table 3), nor were there immature female rank biases following control models. However, yearling males significantly followed within- (Wald $\chi^2 = 12.725$,

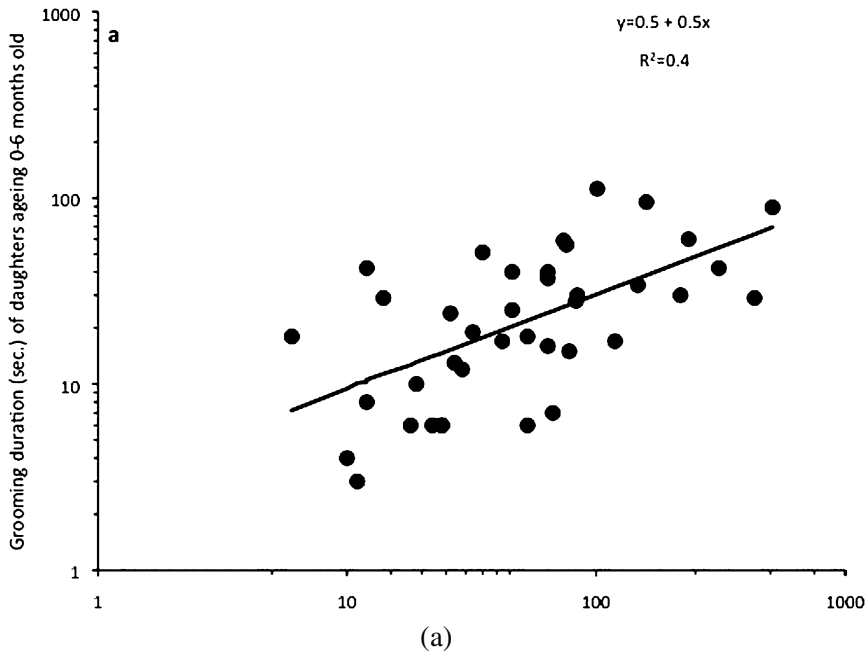


Figure 3. Duration concordance between the grooming bouts of mothers and (a) 6 months old and (b) 1 year old daughters. Each datapoint accounts for the same animal groomed first by the mother and subsequently and independently by her daughter (see Figure 1). Data are shown in a \log_{10} – \log_{10} scale, as these were the data used in analyses (see Methods).

$df = 1$, $p < 0.001$) and between-control females rank bias preferences (Wald $\chi^2 = 13.422$, $df = 1$, $p < 0.001$). In both cases, males showed a tendency to preferentially groom high-ranking animals. Within- and between-subjects slopes were significantly different (Wald $\chi^2 = 5.256$, $df = 1$, $p = 0.022$). Between-slope difference was mainly due to variation in individual slopes ($N = 10$), but also to 2 infant males allocating more grooming to subordinate animals (Figure 4b). In all cases, male immature slopes matched those of control females.

At 6 months of age, daughters' idiosyncratic preferences slopes followed those of mothers (within-subjects: Wald $\chi^2 = 6.119$, $df = 1$, $p = 0.013$; Table 4). They also significantly matched the overall maternal trend to allocate more grooming to preferred partners (between-subjects: Wald $\chi^2 = 9.219$, $df = 1$, $p = 0.002$). Within- and between-subjects slopes were significantly different (Wald $\chi^2 = 3.71$, $df = 1$, $p = 0.05$). In addition to individual differences in slope for 11 daughters, 3 daughters showed trends opposite

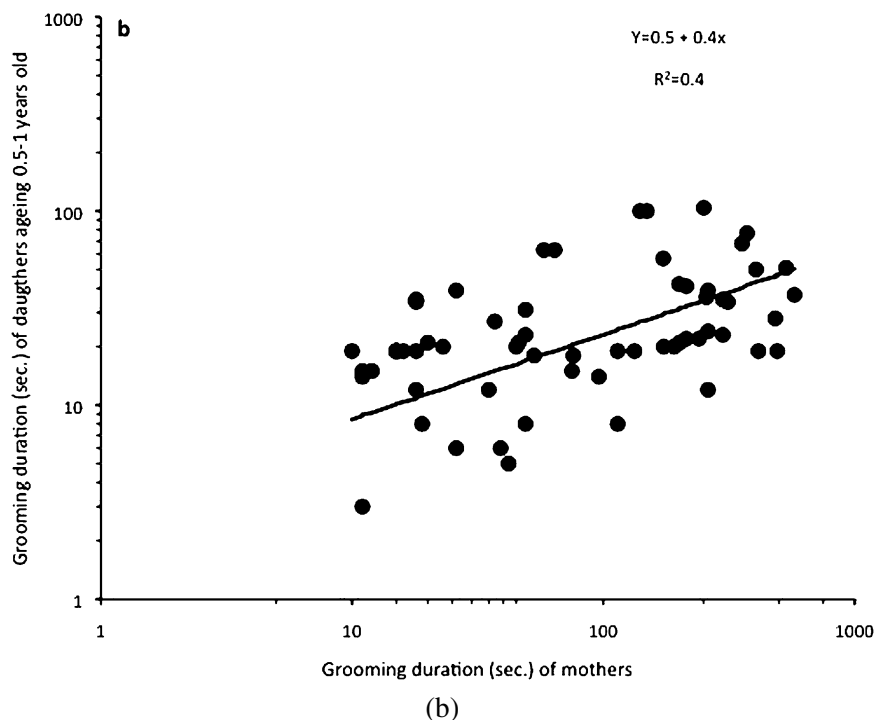


Figure 3. (Continued.)

to their mothers, allocating more grooming to their mothers' less preferred partners (Figure 4c). Sons showed no evidence of matching their mothers' idiosyncratic preferences, although they did followed the general maternal pattern of allocating more grooming to preferred partners at 0.5 (between-subjects: Wald $\chi^2 = 11.787$, $df = 1$, $p = 0.001$), 1 (Wald $\chi^2 = 11.87$, $df = 1$, $p < 0.001$) and 2 years of age (Wald $\chi^2 = 11.87$, $df = 1$, $p < 0.001$). Moreover, male infants also accounted for significant between-subjects effects concerning control females idiosyncratic preferences at 0.5 (Wald $\chi^2 = 4.657$, $df = 1$, $p < 0.031$), 1.5 (Wald $\chi^2 = 18.827$, $df = 1$, $p < 0.001$) and 2 years (Wald $\chi^2 = 7.945$, $df = 1$, $p = 0.005$; Table 4).

Discussion

Our results show that from early infancy, female and male stumptailed macaques follow different development pathways in learning how to allocate

Table 2. Coefficients (\pm SE) from within-subject centred Generalized Linear Mixed Model regressions between mothers and control females kin bias residuals and infants kin bias residuals.

Effect	Mothers		Control females	
	Daughters	Sons	Daughters	Sons
Up to 6 months old				
Intercept	-0.07 ± 0.20	-0.3 ± 0.33	-0.09 ± 0.22	-0.30 ± 0.14
Within-subjects	0.27 ± 0.79	1.6 ± 1.83	0.24 ± 0.69	1.01 ± 0.53
Between-subjects	0.46 ± 0.79	2.10 ± 1.84	0.33 ± 0.71	$1.18 \pm 0.52^*$
Within- vs between-subjects	0.19 ± 0.16	$0.45 \pm 0.08^{**}$	0.08 ± 0.06	$0.17 \pm 0.09^*$
Up to 1 year old				
Intercept	-0.06 ± 0.20	0.28 ± 0.43	0.06 ± 0.16	-0.09 ± 0.10
Within-subjects	0.05 ± 0.82	-1.52 ± 2.31	-0.30 ± 0.52	0.30 ± 0.42
Between-subjects	0.21 ± 0.83	-1.45 ± 2.34	-0.23 ± 0.53	0.43 ± 0.41
Within- vs between-subjects	$0.15 \pm 0.08^*$	0.07 ± 0.29	$0.07 \pm 0.04^*$	$0.12 \pm 0.05^{**}$
Up to 1.5 years old				
Intercept	$-0.27 \pm 0.08^{**}$	-0.37 ± 0.40	-0.15 ± 0.18	-0.13 ± 0.10
Within-subjects	$0.82 \pm 0.30^{**}$	1.41 ± 2.10	0.33 ± 0.59	0.24 ± 0.39
Between-subjects	$0.96 \pm 0.31^{**}$	2.01 ± 2.20	0.53 ± 0.61	0.49 ± 0.39
Within- vs between-subjects	$0.60 \pm 0.18^{**}$	0.15 ± 0.15	$0.19 \pm 0.04^{**}$	$0.25 \pm 0.07^{**}$
Up to 2 years old				
Intercept	0.02 ± 0.12	0.31 ± 0.35	0.00 ± 0.20	-0.16 ± 0.11
Within-subjects	-0.46 ± 0.47	-2.40 ± 1.92	-0.09 ± 0.67	0.39 ± 0.38
Between-subjects	-0.11 ± 0.53	-1.68 ± 1.93	-0.01 ± 0.68	0.64 ± 0.41
Within- vs between-subjects	0.35 ± 0.23	$0.73 \pm 0.09^{**}$	$0.08 \pm 0.04^*$	$0.25 \pm 0.07^{**}$

*: $p < 0.05$; **: $p < 0.01$ based on Wald- χ^2 test (df = 1).

grooming. While mothers were the main source of information, this effect varied between the sexes, and mothers clearly were not the only source.

Our findings suggest that (1) females are more socially precocious than are males, (2) infant female and male stump-tailed macaques choose different models for learning to allocate grooming, (3) females engage in more active learning activities than do males and (4) females learn to be kin-biased while males learn to be rank-biased. Care needs to be taken when interpreting the role of mothers' best friends as a model. In our work these females were chosen to act as a control for mothers' intrinsic (and assumed) importance

Table 3. Coefficients (\pm SE) from within-subject centred Generalized Linear Mixed Model regressions between mothers and control females rank bias residuals and infants rank bias residuals.

Effect	Mothers		Control females	
	Daughters	Sons	Daughters	Sons
Up to 6 months old				
Intercept	-0.01 ± 0.14	-0.08 ± 0.05	0.01 ± 0.06	-0.08 ± 0.07
Within-subjects	-0.20 ± 0.49	0.10 ± 0.30	-0.05 ± 0.18	0.10 ± 0.23
Between-subjects	0.27 ± 0.50	0.43 ± 0.28	0.01 ± 0.18	0.27 ± 0.24
Within- vs between-subjects	$0.48 \pm 0.19^*$	$0.33 \pm 0.06^{**}$	0.05 ± 0.06	$0.17 \pm 0.06^{**}$
Up to 1 year old				
Intercept	0.09 ± 0.18	-0.06 ± 0.04	0.08 ± 0.06	$0.15 \pm 0.03^{**}$
Within-subjects	-0.48 ± 0.72	0.04 ± 0.17	-0.28 ± 0.17	$-0.68 \pm 0.19^{**}$
Between-subjects	-0.30 ± 0.70	0.31 ± 0.25	-0.27 ± 0.17	$-0.51 \pm 0.14^{**}$
Within- vs between-subjects	0.18 ± 0.12	0.27 ± 0.22	0.01 ± 0.03	$0.17 \pm 0.07^*$
Up to 1.5 years old				
Intercept	-0.14 ± 0.09	-0.09 ± 0.05	-0.03 ± 0.08	-0.07 ± 0.05
Within-subjects	-0.04 ± 0.31	-0.04 ± 0.26	0.01 ± 0.24	0.11 ± 0.22
Between-subjects	0.54 ± 0.34	0.44 ± 0.29	0.10 ± 0.22	0.21 ± 0.20
Within- vs between-subjects	$0.58 \pm 0.16^{**}$	$0.48 \pm 0.13^{**}$	$0.09 \pm 0.04^*$	0.10 ± 0.09
Up to 2 years old				
Intercept	-0.11 ± 0.09	-0.03 ± 0.04	-0.06 ± 0.06	-0.03 ± 0.04
Within-subjects	0.14 ± 0.32	-0.23 ± 0.25	0.09 ± 0.21	-0.08 ± 0.17
Between-subjects	0.44 ± 0.38	0.18 ± 0.23	0.16 ± 0.18	0.12 ± 0.14
Within- vs between-subjects	0.30 ± 0.17	0.41 ± 0.11	0.07 ± 0.04	$0.21 \pm 0.07^{**}$

*: $p < 0.05$; **: $p < 0.01$ based on Wald- χ^2 test (df = 1).

as a role model, not as an alternative. Nonetheless, similar to van de Waal et al. (2010) findings in vervet monkeys and as is expected to occur in a female bonded matrifocal species such as the stump-tailed macaque (Fooden, 1990), older females act as a source of social knowledge for infants.

Daughters choose mothers as their model, since for females, social power lies in maintaining intense within-matriline collaboration. Thus, daughters in early infancy (0.5–1 year old) frequently groomed simultaneously with their mothers, allocated grooming durations following maternal durations and displayed the same idiosyncratic partner preferences as did their mothers. Not

Table 4. Coefficients (\pm SE) from within-subject centred Generalized Linear Mixed Model regressions between mothers and control females idiosyncratic preferences and infants idiosyncratic preferences.

Effect	Mothers		Control females	
	Daughters	Sons	Daughters	Sons
Up to 6 months old				
Intercept	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.01	0.01 \pm 0.10
Within-subjects	0.21 \pm 0.08*	0.17 \pm 0.08	0.11 \pm 0.07	0.14 \pm 0.10
Between-subjects	0.39 \pm 0.13**	0.56 \pm 0.11**	0.10 \pm 0.06	0.26 \pm 0.12*
Within- vs between-subjects	0.18 \pm 0.09*	0.40 \pm 0.07**	-0.01 \pm 0.08	0.13 \pm 0.15
Up to 1 year old				
Intercept	0.00 \pm 0.01	-0.01 \pm 0.01	-0.10 \pm 0.01	0.02 \pm 0.01
Within-subjects	0.04 \pm 0.10	0.03 \pm 0.10	0.01 \pm 0.03	0.08 \pm 0.07
Between-subjects	0.13 \pm 0.12	0.72 \pm 0.21**	0.13 \pm 0.06*	0.20 \pm 0.10
Within- vs between-subjects	0.09 \pm 0.15	0.70 \pm 0.21**	0.12 \pm 0.08	0.12 \pm 0.12
Up to 1.5 years old				
Intercept	0.00 \pm 0.01	0.00 \pm 0.00	0.01 \pm 0.00	-0.01 \pm 0.01
Within-subjects	-0.08 \pm 0.05	0.04 \pm 0.05	0.05 \pm 0.05	0.04 \pm 0.05
Between-subjects	0.07 \pm 0.12	0.70 \pm 0.42	0.18 \pm 0.03**	0.31 \pm 0.07**
Within- vs between-subjects	0.15 \pm 0.11	-0.26 \pm 0.21	0.13 \pm 0.06*	0.30 \pm 0.10**
Up to 2 years old				
Intercept	0.00 \pm 0.00	-0.01 \pm 0.00	-0.01 \pm 0.01	0.01 \pm 0.01
Within-subjects	0.14 \pm 0.07	0.02 \pm 0.11	0.09 \pm 0.06	0.07 \pm 0.07
Between-subjects	0.15 \pm 0.07	0.72 \pm 0.23**	0.03 \pm 0.04	0.22 \pm 0.08**
Within- vs between-subjects	0.01 \pm 0.01	0.66 \pm 0.43	-0.06 \pm 0.06	0.16 \pm 0.10

*: $p < 0.05$; **: $p < 0.01$ based on Wald- χ^2 test (df = 1).

only were they learning how to behave as adults, but they were also actively integrating as members of their matriline.

Males, on the other hand, who eventually leave their natal group, require alliances (preferentially with same-sexed peers) to contend with the hazards of adult life, such as acquiring and maintaining a high rank. Therefore, they require a more general knowledge of group social dynamics (e.g., rank-biased interactions) rather than simply their own matriline's particular social traditions or needs. Immature males showed significant between-subjects idiosyncratic preference correlations with mothers throughout most

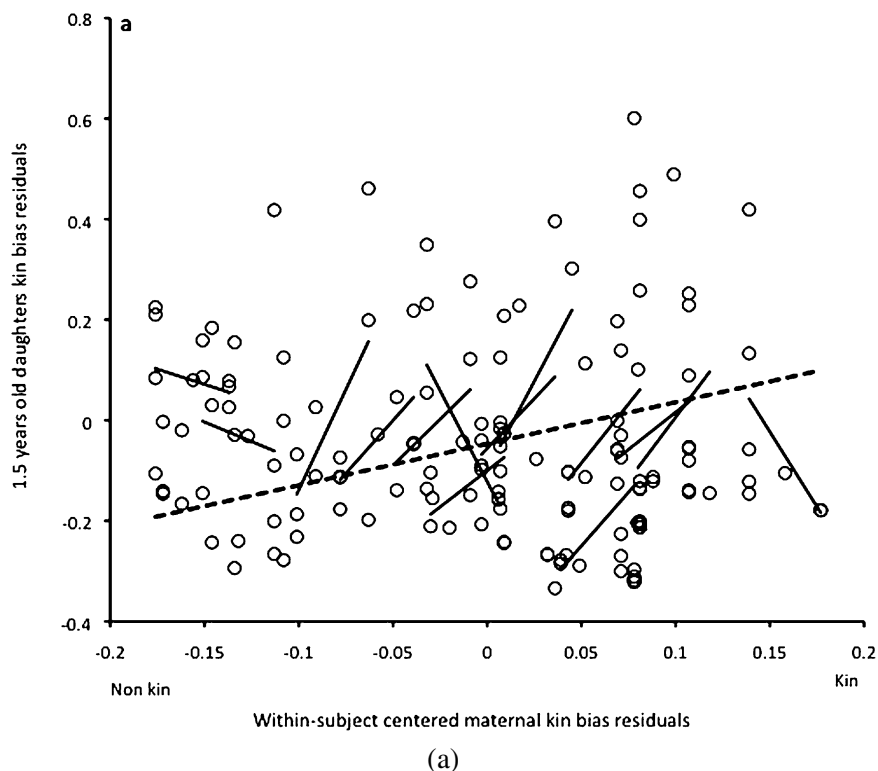


Figure 4. Plots of (a) 1.5 years old daughters' kin bias residuals against within-subject centred maternal kin bias residuals; (b) 1 year old sons' rank bias residuals against within-subject centred control females' rank bias residuals; (c) 6 months old daughters' idiosyncratic preferences against within-subject centred maternal idiosyncratic preferences. Each data point accounts for a same grooming recipient. Dashed lines show the between-subjects regression, and thin black lines the within-immature slopes. The slope trends are shown below the x -axis (a: non kin \rightarrow kin gradient) and (b: dominants \rightarrow subordinates gradient).

of their infancy without ever replicating these (except at 1.5 years when variability increased, although the regression coefficient remained the same). Six-month-old males showed also between-subjects agreement with control females' idiosyncratic preferences. At 1 year of age they showed the same rank bias preferences of control females, while never matching the overall maternal rank-biased grooming preferences. Given close proximity and bond with mothers, control females were chosen as models by males since they provide a knowledgeable and safe model (mothers' friends rarely behave agonistically to infants) from which to learn. However, males never

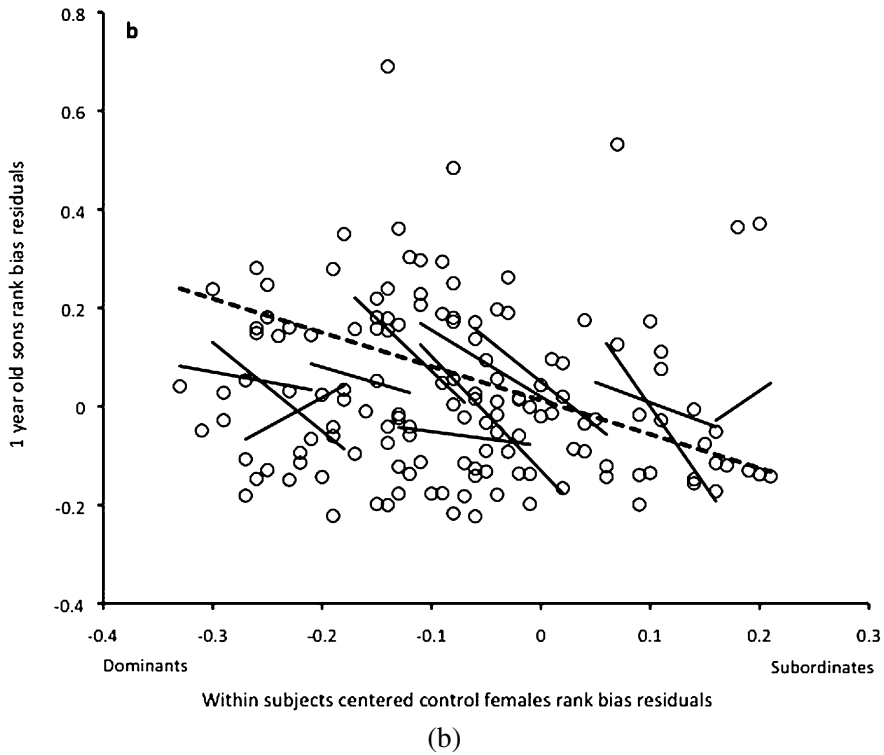


Figure 4. (Continued.)

mirrored control females' behaviour, and our results appear to relate only to observational learning. Observational learning does not require close proximity to the model (e.g., being within arm reach), but can be done from distance (e.g., van de Waal et al., 2010). Thus, resemblance to control females' behaviour does not eliminate the likely possibility that infant males learn to allocate grooming by watching other adult females, older peers, siblings and even adult males. As such, the significant correlations between 1-year-old males and control females rank-biased grooming preferences might not be exclusive, and similar biased correlations might be found by comparing other possible models.

The average inter-birth interval following a surviving infant is 1.7 years (± 0.3 SE) for stump-tailed macaques, with weaning occurring 7–8 months earlier (Nieuwenhuijsen et al., 1985, and colony data). In our sample, by the time infants had reached 1.5 years of age, 25 mothers and 24 control females were either pregnant or had already given birth. Between 1 and 1.5 years

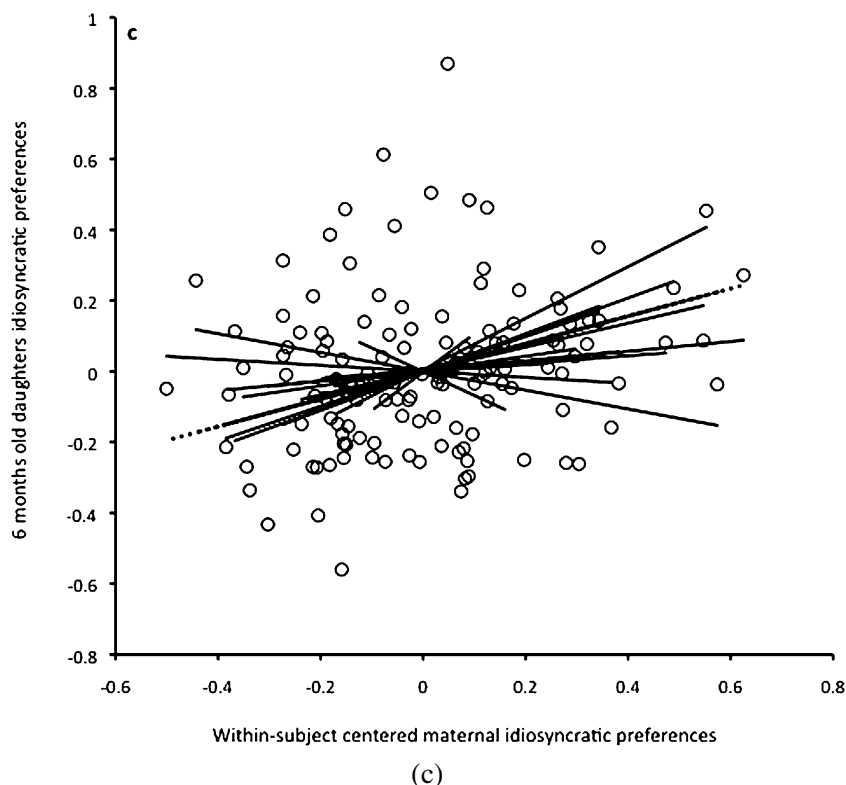


Figure 4. (Continued.)

of age, females increased their time grooming simultaneously with control females and matched maternal kin-biased preferences. Daughters intensified their bonds both with mothers and relatives, and also started mirroring control females behaviour, such as devoting more time grooming alongside them. By the same ages, sons increased time grooming simultaneously with mothers. These trends could be related to weaning, the advent of a new sibling, reduced maternal attention and greater social independence. We suggest that this infant early grooming behaviour relates to maintaining or strengthening social bonds rather than social learning.

Throughout the juvenile period, stumptailed macaques become independent of maternal care, and turn into the most active groomers of the group (particularly females) without reciprocation, and, as in other macaque species (e.g., Bernstein & Ehhardt, 1986), are main targets of aggression. Thus, juvenility is a time when immature female and male stumptailed

macaques actively explore relationships distinct from those of their mothers. Females are socially precocious, and start exploring new relationships earlier than males; 1 and 1.5 years old female infants' idiosyncratic preferences showed significant correlations with between-control females' idiosyncratic preferences, as well as an increasing amount of time simultaneously grooming. Females were paying attention to and rehearsing on their own the control females' grooming choices, but were not copying these. By 2 years, the grooming preferences of immature females showed no correlation with either mothers or control females preferences, perhaps because they were already building new relationships. Male social development lags around 6 months by comparison to that of females, but that at all times they used maternal expertise as a secure platform to socialise.

Our results suggest a sex difference in the attention paid to the attributes of groomees. While infant females pay more attention to kinship, males attend to dominance–subordination relationships. Infant females are not precluded from developing rank-biased grooming preferences; daughters of dominant females tend to develop the same rank biased preferences as those of their mothers (in preparation). Nonetheless our results show that infants are psychologically prepared to attend and interpret social interactions in relation to their own sex-specific adult expectations.

Social learning in immature stump-tailed macaques appears to correspond to the bonding and identification-based observational learning model (de Waal, 2001). Notwithstanding, daughters instead of behaving as passive-attentive apprentices did actively engage and were allowed to practice along with masters and on their own.

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