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Sex Differences in the Development of Aggressive Behavior in Rhesus Macaques (*Macaca mulatta*)

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Abstract Aggressive behavior plays a central role in primate life, having a crucial effect on their reproductive performance and survival and possibly affecting the formation and maintenance of social bonds. Although aggressive behavior might serve a different function in males and females, and sex differences in aggressive behavior seem to emerge early during development, very few studies have investigated whether aggressive patterns follow different developmental trajectories in male and female primates. However, the developmental perspective is crucial to understanding when differences in adults' aggression emerge and which factors trigger them. We here analyzed aggressive interactions in rhesus macaques from birth to sexual maturation (before male dispersal), including male and female focal subjects. We further considered the partner's sex, age, and rank, as well as maternal and paternal kinship, and used powerful multivariate statistical analysis. The probability to initiate aggression was largely similar for both sexes and throughout development. Both males and females were more aggressive toward partners of the same sex and similar age. In contrast, the probability of receiving aggression mostly differed between sexes across development and depended on the social context. The probability of receiving aggression increased through development. Finally, important developmental changes appeared between 2 and 3 yr of age, indicating that this period is crucial for the development of adult social roles. Our results suggest that aggressive behavior largely serves a similar function for

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both sexes during the first years of development, only partially anticipating adult aggressive patterns.

Keywords Aggression · Ontogeny · Social bonding · Sociality · Social relationship

Introduction

From early on, researchers have recognized the central role that aggressive behavior plays in primate life (Bernstein 1976; Bernstein and Gordon 1974; Deag 1977; Hall 1964; Lorenz 1966; Tinbergen 1968). Primates are extremely social animals, and most of them live in groups. This is generally considered an evolutionary compromise between the high fitness benefits that group living provides, mainly against predation and infanticide, and the competition costs that it unavoidably imposes (Dunbar 1988; Janson and Van Schaik 1988; Silk 2007; Van Schaik 1983; Van Schaik and Kappeler 1997; Walters and Seyfarth 1987). Group-living primates therefore compete for access to resources such as food, water, resting spots, or mates, and aggression might be essential to determine which individuals will have access to these resources (Bernstein and Gordon 1974; Honess and Marin 2006).

The occurrence of aggression enhances stress levels, and having to deal with aggression might have crucial consequences on individuals' fitness and survival (Crockford *et al.* 2008; Honess and Marin 2006; Wittig *et al.* 2015). Further, intragroup aggression often involves several individuals, so that physiological stress may not be limited to the initial recipient of the aggression and can therefore have negative consequences on the fitness and survival of all group members (Ha *et al.* 2011; Wittig *et al.* 2015). Therefore, aggression is usually categorized as socio-negative interactions that have a mostly negative impact on social relationships (Crockford *et al.* 2012; Fraser *et al.* 2008; Nakamichi 2001; Worlein *et al.* 1988).

Despite the evident negative effects that aggression exerts on primates, some researchers have also highlighted the positive role that aggression might have. Aggression can indeed have a positive effect on socialization processes among primates, e.g., by modifying others' inappropriate social behavior (Bernstein and Ehardt 1985a, b, 1986) and producing cohesive forces within a social group (Bercovitch *et al.* 1987; Bernstein and Gordon 1974; de Waal 1989). The frequency of aggressive interactions is also often higher in dyads having stronger affiliative relationships (Bernstein and Ehardt 1986; Kulik *et al.* 2015; Widdig *et al.* 2002, 2006; *cf.* Silk *et al.* 1981, 2004), suggesting that aggressive and affiliative behaviors might be different expressions of the same social relationship, and both need to be included when assessing the quality and strength of social relationships (Fraser *et al.* 2008). Importantly, individuals that have strong social relationships, i.e., social bonds (Silk 2007), spend more time together and might more often engage in aggressive behavior simply because closer proximity may create more opportunities for conflict.

One question that has been addressed in primates is whether aggressive behavior serves a different function in males and females. Among primates, females generally require a higher energetic intake to supply the costs of maternal care (Trivers 1972), and females are generally assumed to compete with each other mainly for resources other than mates (Silk *et al.* 1981). In the wild, for example, availability and distribution of food influences agonistic interactions among both philopatric and dispersing females (Van Schaik 1989; Wrangham 1980; Hanuman langurs, *Presbytis entellus*: Koenig *et al.* 1998; spider monkeys, *Ateles hybridus*: Abondano and Link 2012). Aggression among females frequently occurs during feeding competition, e.g., Assamese macaques (*Macaca assamensis*: Heesen *et al.* 2014), and probably reflects a response to competition over food resources, e.g., spider monkeys (Asensio *et al.* 2008).

Males also compete for resources such as food or water and, as among females, competition levels and frequency of aggressive interactions vary depending on food availability (Honess and Marin 2006; Silk and Boyd 1983). However, aggression among males also frequently occurs in a mating context. As predicted by the theory of sexual selection (Darwin 1871), males invest less than females in their offspring and compete with each other for access to females (Trivers 1972). In Assamese macaques, for example, males have higher physiological stress levels in the breeding season due to the increased levels of male–male competition and aggression (Ostner *et al.* 2008; *cf.* for a lack of difference in ring-tailed lemurs, *Lemur catta:* Gould *et al.* 2005; and rhesus macaques, *Macaca mulatta:* Higham *et al.* 2012). Moreover, males are more often involved in aggressive behavior during intergroup encounters than females (Japanese macaques, *Macaca fuscata*: Majolo *et al.* 2005). Males might therefore experience especially intense competition over resources and will often be involved in aggressive interactions (Mitchell 1979; chimpanzees, *Pan troglodytes*: Muller and Mitani 2005; Wilson and Wrangham 2003; rhesus macaques: Reinhardt 1987; Japanese macaques: Alexander and Roth 1971; Eaton *et al.* 1981; grivets, *Chlorocebus aethiops*: Bramblett 1980).

Aggressive interactions also frequently occur between males and females (Abondano and Link 2012; Campbell 2003; Fedigan and Baxter 1984; Link *et al.* 2009; Slater *et al.* 2008, 2009; Van Roosmalen and Klein 1988). However, male aggression to females does not necessarily reflect competition over food resources and might also be part of male reproductive strategies. According to some authors, male aggression to females might represent an indirect form of sexual coercion or ritualized courtship, with males using aggression to achieve reproductive success (Japanese macaques: Barrett *et al.* 2002; Eaton *et al.* 1981; spider monkeys: Fedigan and Baxter 1984; Link *et al.* 2009; Slater *et al.* 2008; chimpanzees: Feldblum *et al.* 2014; *cf.* rhesus macaques: Bercovitch *et al.* 1987).

A second question is whether sex differences in aggression patterns might reflect differences in the life histories of males and females (Silk *et al.* 1981). Juvenile females, for instance, usually remain in their natal group, where they will feed and breed, and may therefore present more potential competition over scarce resources (Dittus 1979; Silk *et al.* 1981). Individuals might thus reduce future competition by diminishing the viability of young females (Dittus 1979; Silk and Boyd 1983), so that females might tend to receive more aggression than males by other troop members, e.g., Japanese macaques (Eaton *et al.* 1986), toque macaques (*Macaca sinica*: Dittus 1977, 1979), and bonnet macaques (*Macaca radiata*: Silk *et al.* 1981). Although some studies have failed to document sex differences in aggressive behavior, e.g., green monkeys (*Cercopithecus aethiops sabaeus*: Raleigh *et al.* 1979), blue monkeys (*Cercopithecus mitis stuhlmanni*: Cords *et al.* 2010; Ekernas and Cords 2007), and Japanese macaques (Eaton *et al.* 1986), other studies found sex differences in aggression, with males being involved in more aggression than females (baboons, *Papio species*: Owens 1975; Young *et al.* 1982; talapoin monkeys, *Myopithecus talapoin*: Wolfheim 1977).

Sex differences in aggressive behavior are found in several mammals before sexual maturation (Archer and Côté 2005). The early emergence of aggressive behavior might serve several functions, including the practice of aggressive strategies that may prove valuable in adulthood, and provide the long-term advantage of dominance being partially acquired before maturation and the immediate advantage of gaining access to resources (Archer 1994; Archer and Côté 2005). If the resources needed vary through development in a different way between sexes, it comes as no surprise that sex differences in aggressive behavior might vary during individuals' development, reflecting differences in male and female life histories (Silk *et al.* 1981). In several species, for example, males experienced higher rates of aggression from other group members than females around sexual maturation (Pereira and Fairbanks 1993; white-handed gibbons, *Hylobates lar*: Carpenter 1940; rhesus macaques: Altmann 1962; Wilson and Boelkins 1970; Kulik *et al.* unpubl. data; red howlers, *Alouatta sara*: Crockett and Pope 1993; Hanuman langurs: Borries 2000; Rajpurohit and Sommer 1993; blue monkeys: Rudran 1978; *cf.* Pusey and Packer 1987). In Japanese macaques, juveniles show no sex differences in aggressive behavior, but males become much more aggressive than females in adulthood (Eaton *et al.* 1986). In young primates, therefore, sex differences in aggressive behavior do not necessarily anticipate adult patterns (Cords *et al.* 2010; Raleigh *et al.* 1979; Wolfheim 1977), as juvenile behavior may reflect the immediate needs of this age, which might differ from those of adults (Cords *et al.* 2010).

Although aggressive behavior likely differs between sexes and these differences may change through time, very few studies, to our knowledge, have so far systematically analyzed how sex differences in aggressive behavior develop through ontogeny. However, the developmental approach is crucial to understand when adult social roles are established during primate development and to gain a better insight into the factors that might trigger their emergence. One study investigated the development of sex differences in captive patas monkeys (*Erythrocebus patas:* Rowell and Chism 1986). In their third year of life, females increased the frequency of aggression given and were more often involved in aggressive interactions than males. Moreover, males were mostly aggressive toward other males, and females toward females and immatures, while aggression between males and females ware rare. Another study investigated aggression and kinship in captive rhesus monkeys for 17 mo across different sex and age classes (Bernstein and Ehardt 1986). This study showed that females are mainly aggressive toward kin throughout their lives, while the relative frequency of male aggression involving kin decreased through development, supporting the hypothesis that aggression has a positive effect by modifying others' social behavior. Finally, a study on wild blue monkeys briefly analyzed sex differences in aggressive behavior, showing that younger and older juveniles received a comparable rate of aggression, regardless of their sex (Cords *et al.* 2010).

The main focus of these previous studies, however, was the development of sex differences in affiliative behavior, and they provided very little information on sex differences in the development of aggressive behavior. In addition, the first two studies were conducted on captive populations, where subjects have little opportunities to avoid aggression by moving away, and cannot thus be generalized to wild individuals (*cf.* Boesch 2007; Call and Tomasello 1996). Furthermore, statistical constraints did not allow any of these studies to determine exactly when sex differences in aggressive behavior appear during ontogeny. Moreover, although aggressive behavior in nonhuman primates varies depending on the social context (Cords *et al.* 2010), no study has so far analyzed how sex differences in aggression change from birth to maturation while taking into account partners' sex, age, rank, and kinship.

The aim of this study was therefore to investigate whether aggressive patterns follow different developmental trajectories in male and female rhesus macaques, depending on the social context. We conducted our study in a semi-free-ranging population of rhesus macaques in Cayo Santiago, Puerto Rico. Rhesus macaques live in multimale, multifemale groups, in which females are philopatric (Gouzoules and Gouzoules 1987) and males disperse at puberty (Colvin 1983; Lindburg 1969). Given the complexity of their social life and the abundance of aggressive behavior typically happening in this species (de Waal and Luttrell 1989; de Waal and Johanowicz 1993; Thierry 1990; Thierry *et al.* 2004), rhesus macaques are an ideal model to study how sex differences in aggressive behavior emerge during ontogeny.

Based on the literature reviewed in the preceding text, we predicted that aggressive behavior gradually differs between sexes over the course of development, with males experiencing generally more intense competition and thus being more often involved in aggressive interactions as compared to females from early on. We also hypothesized that the development of sex differences in aggressive behavior strongly depends on the social context. In particular, we predicted focal subjects to be more aggressive with partners having the same sex and a similar age. We also predicted that females are more aggressive with maternally related animals, as compared to males, especially around maturation, given that females, but not males, will remain in the natal group and compete over the same resources. Finally, we predicted that high-ranking individuals would initiate more aggression than low-ranking conspecifics, which should receive more aggression. The developmental perspective allowed us to detect whether sex differences in aggressive behavior are present since birth or develop through time as a function of the social context and the experience acquired.

Materials and Methods

Study Population and Subjects

We conducted the study from October 2004 to August 2008 on the rhesus macaque population of Cayo Santiago, a 15.2-ha island offshore Puerto Rico. All monkeys living on the island are direct descendants of the 409 founder animals captured in different places in India in 1938 (Rawlins and Kessler 1986). However, pedigree data show no evidence of inbreeding over time, despite the fact that no other monkeys have been added to the population except through natural births (Widdig *et al.* unpubl. data). The Caribbean Primate Research Center (CPRC) manages the whole population, which is partly provisioned but spends *ca*. 50% of its feeding time on natural vegetation (Marriott *et al.* 1989). CPRC census takers have continuously recorded demographic data since 1956, including the date of birth and date of death of focal subjects, sex, group membership, the number of maternal kin, and male dispersal. Females' interbirth interval in this population is *ca.* 1 yr and females mostly give birth to a single offspring (Rawlins and Kessler 1986). Infants can be assigned to nonoverlapping birth cohorts (which comprise all infants born in a given mating season), but infants from the same cohort can differ up to 6 mo in age. In captivity, female rhesus macaques reach sexual maturation between 2.5 and 3.5 yr of age (Zehr *et al.* 2005) and males between 3 and 3.5 yr of age (Dixson and Nevison 1997). In our study population, the youngest reported mother was 2.9 yr old (Bercovitch and Berard 1993) and the youngest sire was 3.8 yr old (Bercovitch *et al.* 2003), although interindividual variation in sexual maturation is high (Bercovitch and Goy 1990). Males leave their natal group between 3 and 5.5 yr of age (median age = 4.5 yr; Berard 1990).

During the study period, our study troop (group R) consisted of 78.5 ± 5.8 (mean ± SD) adult females and 47.9 ± 7.1 (mean ± SD) adult males across study years. Starting immediately after birth, we followed all 55 focal subjects (26 females and 29 males) born in the birth cohort 2005 (hereafter focal subjects). A total of 28 focal subjects (15 females, 13 males) survived until they reached maturation and the study was completed, while 13 died during the study period for unknown reasons and 16 were removed by the CPRC due to colony management. Over the entire study period group R consisted of a total of 522 potential social partners for our focal subjects (hereafter focal partners). All group members, including focal subjects, were recognized on an individual basis using natural markings and tattoos. All of them were included until their death. Importantly, the modeling procedure we used allowed us to appropriately address differences in the number of focal subjects through time.

Although the population of rhesus macaques in Cayo Santiago is partly provisioned (Marriott *et al.* 1989) and lacking predation, it still provides an appropriate setup to study the development of aggression, for several reasons (Widdig *et al.* 2015a). Males on Cayo Santiago migrate to different groups and females can exert some mate choice, so the scenario closely resembles the natural one. Moreover, macaques can avoid aggressions by moving away from challengers. Therefore, this population constitutes a unique opportunity to combine detailed demographic and genetic data with long-term behavioral data collected in an almost natural situation.

Behavioral Data

Using focal animal sampling (Altmann 1974), we conducted a total of 3543 observational hours over the entire study period, resulting in 64.4 ± 37.3 h (mean ± SD; range 8.3–95.3 h) per focal subject. Sampling was not completely balanced over the 4 yr. However, our modeling procedure allowed us to appropriately address these differences across the study period. We recorded no more than one 20-min sample per day and focal subject, with focal observations being evenly distributed over the day and balanced weekly among subjects. During each sample we continuously recorded affiliative and aggressive interactions between the focal subject and all other group members, including both physical aggression (push, hit, grab, bite, attack) and nonphysical aggression (stare, head-bobbing, vocal/open mouth threat, lunge, charge, chase, following Widdig *et al.* 2002). We excluded aggressive interactions between mothers and their offspring because of their special relation, which would probably hide other patterns in aggressive behavior (Bernstein and Ehardt 1986), and we analyzed them separately in another study focusing on the development of mother–offspring relationships (Kulik *et al.* unpubl. data). Given that the proportion of physical and nonphysical aggression was quite similar for both initiated and received aggression (proportion of nonphysical aggression initiated: 63.5%; received: 69.7%), that we were mostly interested in the difference between initiated and received aggression, and that separate analyses for both aggression types would have excessively increased the complexity of our analyses (probably making our models unstable), we pooled physical and nonphysical aggression and analyzed them together. For each interaction involving the focal subject we also recorded whether the mother of the focal subject was present within a 2 m range of the focal subject or not. Finally, we collected *ad libitum* data (Altmann 1974) on displacement, aggression, or submission among adult males and females to construct dominance hierarchies. A. Widdig, D. Langos, and two field assistants collected the data. We tested interobserver reliability (which ranged between 90% and 97%) by having each field assistant conduct simultaneous focal samples with A. Widdig or D. Langos, respectively (Kaufman and Rosenthal 2009). We used Psion Workabout^{TM} handhelds and processed the collected data with Observer (version 5.0).

Parentage Assignment and Determination of Kinship

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

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

Establishing Dominance Hierarchies

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

Data Analyses

We used generalized linear mixed models (GLMMs; Baayen 2008) to analyze which factors affect the ontogeny of aggression in immature rhesus macaques. We calculated two models with an identical set of predictors but different response variables: one based on the aggression initiated by the focal subject and one on the aggression received by the focal subject. Data preparation included several steps. First, we determined the frequency of aggression, differentiating those initiated by the focal subject from those received by the focal subject, separately for each day and for each dyad involving a focal subject and any of the individuals present in our study group based on the demographic records. We further differentiated between interactions that occurred when the mother was within 2.0 m of the focal subject and those that occurred when the mother was more than 2.0 m away. As most of the derived frequency values were zero and therefore a Poisson model would not have been valid, we transformed these values into a binary variable to treat the data with a binomial error structure, setting all values >0 to 1. The data reduction resulting by this step affected only a small proportion of the data, as the number of days in which an initiated or received aggression occurred more than once constituted only a minor part of the full data set (initiated = 0.46%, received = 1.26%). We then calculated the frequency of all these daily values over 3-mo periods (determined based on the focal subject age), leading to a total of 301,694 data points, i.e., including one data point per quarter for each potential focal subject–partner dyad per mother-presence condition.

To model the probability of aggression, we used the number of days with aggressive interactions vs. the number of days without aggressive interactions for each 3-mo period as two separate variables that we set as the response (binomial response in two vectors). This was necessary due to the large number of data points and the limited calculation capacity. To analyze whether focal subjects' aggressive behavior toward group members varied through ontogeny, we included the subject age (averaged over the 3-mo period) in our model as test predictor. Moreover, for each subject we included squared age (as the relation between subject age and aggression was expected to be nonlinear), sex (as we were interested in sex differences) and rank (as focal dominance status might influence patterns of aggression). For social partners we included partner's rank, age difference between focal subject and partner (as age peers might likely compete over the same resources: Widdig *et al.* 2001), and kin relation between focal subject and partner (i.e., maternal kin, paternal kin, nonkin). As a control variable we included mother's presence, as mothers can influence the behavior of focal subjects, e.g., by exerting control over social partners (Langos *et al.* 2013). We also included sex ratio, group size (averaged over the 3-mo period) and number of maternal kin (up to the grandparent generation, 10.72 ± 6.55; mean ± SD) as control variables, as they have been shown to affect focal subjects' social behavior (Berman *et al.* 1997). Finally, we included the identity of both focal subject and partner as random effects in the model. We did not control for proximity because although aggression necessitates close proximity, close proximity does not automatically lead to aggression and aggression thus provides different information about social relationships than proximity *per se*.

We expected several interactions between these main effects to be significant, as the study explored aggressive behavior over a long time frame, from birth to maturation of focal subjects. Specifically, we included six three-way interactions, each of them including the focal subject's age/age squared (to explore ontogenetic changes in aggressive behavior) and the focal subject's sex. As the third variable in the three-way interactions, we included 1) partner's sex, 2) age difference between subject and partner, 3) partner's rank, 4) subject's rank, 5) kin relation between subject and partner, or 6) mother's presence, which was included as a control and not interpreted (*cf.* Mundry 2014), as each of these variables might affect aggressive behavior in primates, e.g., rank (Lambert 2005; Pereira and Kappeler 1997; Silk *et al.* 1981), sex (Dittus 1977, 1979; Eaton *et al.* 1986; Silk *et al.* 1981), age (Bernstein and Ehardt 1985c, 1986; Campbell 2006; Valero *et al.* 2006; Widdig *et al.* 2001), and kin (Bernstein and Ehardt 1986; Glick *et al.* 1986; Janus 1991a; Widdig *et al.* 2002). To achieve a valid model we also included all the two-way interactions covered by these interactions.

As our dataset was likely to show temporal autocorrelation; i.e., residuals of data points recorded closer to one another in time could be more similar to one another than data points recorded further apart, the assumption of independent residuals might be violated and the model might thus become less reliable. We therefore included two autocorrelation terms, one for the focal subject and one for the partner, to clearly account for temporal autocorrelation in the data (for more details, see the Electronic Supplementary Material). Before running the model, we z-transformed all the covariates (including the autocorrelation term) to a mean of 0 and a standard deviation of 1 (Schielzeth 2010). We fitted the models in R (version 3.0.2; R Core Team, 2014) using the function "lmer" from the R package "lme4" (Bates *et al.* 2011). The models revealed the probabilities of aggression (initiated or received, respectively), as we modeled the proportions of days with aggression out of the total of all possible days. The GLMM was fitted with binomial error structure and logit link function. For each model, we determined the statistical significance of the full model by comparing its fit with that of the null model (comprising the control variables and the random effects and the autocorrelation terms), using a likelihood ratio test (LRT; Dobson 2002) available as R function "anova," package "stats." We also tested all terms in the models for their statistical significance by running additional LRTs, comparing the fit of the full model with that of a reduced model lacking the particular term of interest but comprising all the other terms. When interactions were not significant, we removed them from the model to reliably interpret the lower terms included. Such removal was done only if the full-null model comparison revealed significance (Barr *et al.* 2013; Schielzeth and Forstmeier 2009).

We also calculated variance inflation factors (VIFs; Quinn and Keough 2002) by running models without the random effects, to check that the model assumptions were satisfied. The results revealed that collinearity was not an issue (largest VIF = 1.78). VIFs were determined using the function "vif" of the R package "car" (Fox and Weisberg 2011). We considered P-values ≤ 0.05 to be significant. Although the incorporation of random slopes into the model and a model stability estimation would reveal more reliable P-values (Barr *et al.* 2013), computational power leading to the unfeasible calculation time of *ca.* 400 d led us to decline this approach.

Results

Overall, we were able to extract a total of 3522 aggressive interactions (0.33 ± 0.76; mean ± SD per focal subject and day) between the focal subjects and their partners over the study period. In particular, we observed 1184 aggressive behaviors initiated (0.11 ± 0.4; mean ± SD per focal subject and day) and 2338 aggressive behaviors received by focals (0.22 ± 0.58; mean ± SD per focal subject and day).

Null vs. full model comparisons revealed that the set of predictor variables used had a clear influence on the respective behavioral responses for each of our two models (LRT for aggression initiated: $\chi^2 = 1776.6$, d.f. = 47, $P < 0.001$; aggression received : $\chi^2 = 2215.9$, d.f. = 47, $P < 0.001$). The full results of each model are reported in Electronic Supplementary Material Tables SI and SII.

Effect of Partner's Sex

Initiating We found a significant three-way interaction (hereafter three-way IA) of focal subject age, focal subject sex, and partner's sex for aggression initiated by the focal subject (LRT: $\chi^2 = 434.16$, d.f. = 2, $P < 0.001$). Female focal subjects were more likely to initiate aggression than males until 3 yr of age, and then less likely with male and female partners. However, female focal subjects were more aggressive than males with female partners over the whole period. Male focal subjects were more likely to initiate aggression than females until 2 yr, and then became strongly less likely afterwards. Male focal subjects were more aggressive toward female partners than males in the first 18 mo of life, but were more likely to target male partners thereafter (Fig. 1a).

Receiving We also found a significant three-way IA of focal subject age, focal subject sex, and partner's sex for aggression received by the focal subject (LRT: $\chi^2 = 27.236$, d.f. = 2, $P < 0.001$). Female focal subjects received increasingly more aggression from females than females until 3 yr of age and then received more aggression from males. The picture for males is quite different: male focal subjects received more aggression from females than females only in the first year. After that they were slowly less likely to receive aggression from females, while they were strongly more likely to receive aggression from males until 2.5 yr, and then also became less likely (Fig. 1b) as compared to females.

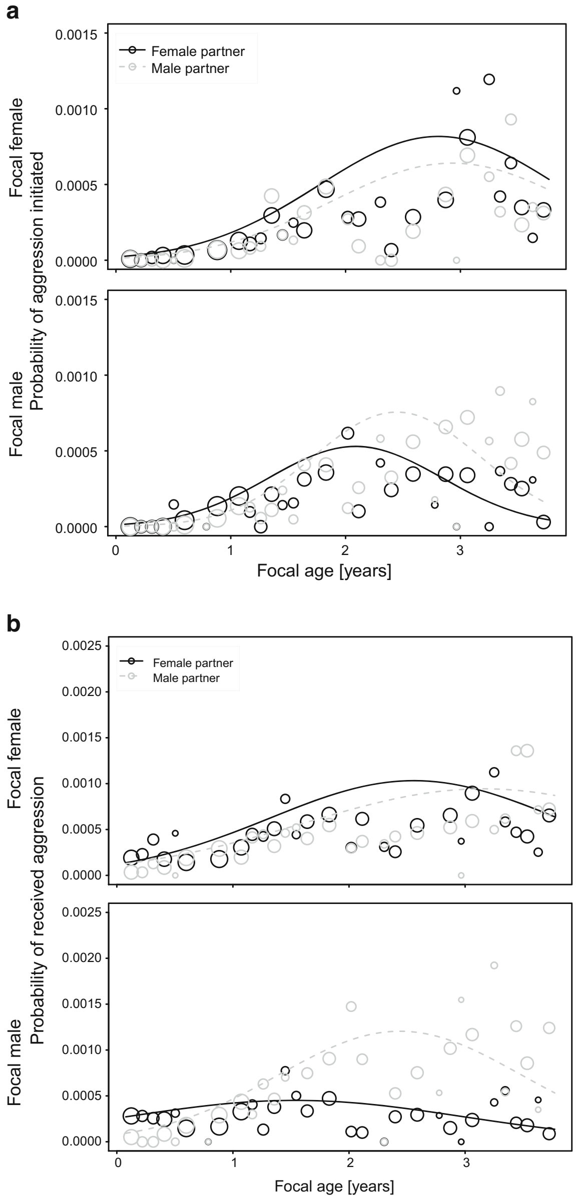


Fig. 1 **a** Development of sex differences in aggression initiated by focal subjects of both sexes, in rhesus macaques on Cayo Santiago (October 2004–August 2008). The lines represent the calculated model and the circles the binned and averaged observed values. The area of the circles corresponds to the respective sample size. **b** The development of sex differences in aggression received from partners of different sex, in rhesus macaques on Cayo Santiago (October 2004–August 2008). Details in **a**.

Effect of Age Difference Between Focal Subject and Partner

Initiating Depending on the age difference between focal subject and social partner, male and female focal subjects had a different probability of initiating aggression throughout ontogeny (two-way IA focal subject's sex*age difference, LRT: $\chi^2 = 12.243$, d.f. = 2, $P < 0.001$). In particular, focal subjects mostly initiated aggression toward age peers, regardless of their actual age, and this was more pronounced for male focal subjects than for female focal subjects (Fig. 2a).

Receiving Aggression received depended on focal sex and age as well as on the age difference between focal subject and social partner (three-way IA focal subject's age* focal subject's sex*age difference LRT: $\chi^2 = 14.572$, d.f. = 2, $P = 0.001$). In particular, female focal subjects were more likely to receive aggression than male focal subjects as

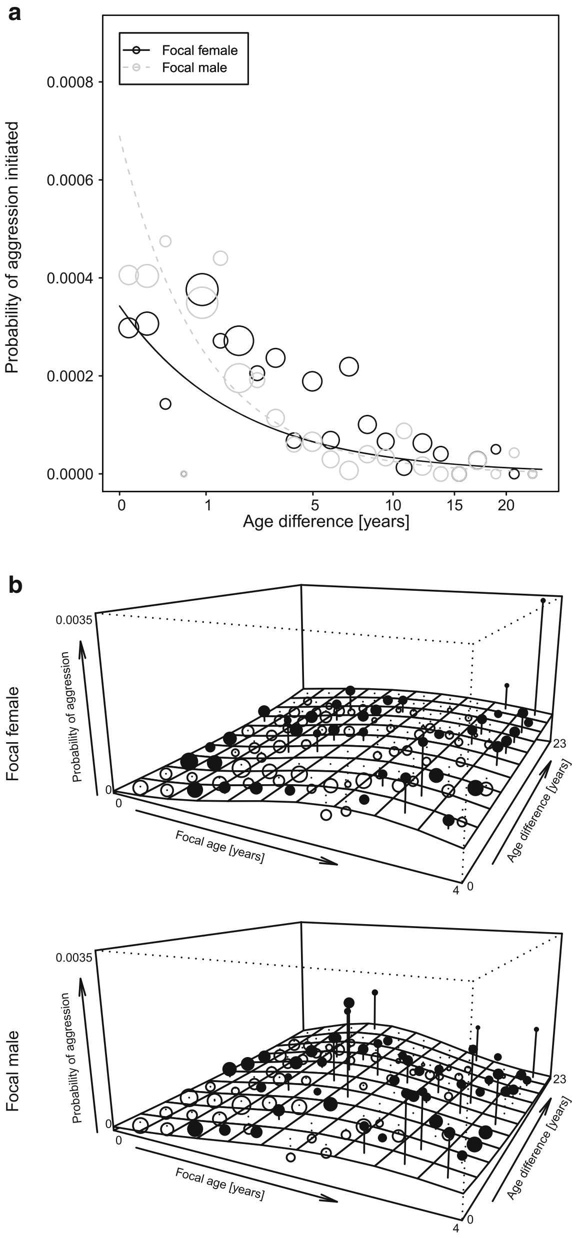


Fig. 2 **a** Development of sex differences in aggression initiated, depending on the age difference between focal subject and partner, in rhesus macaques on Cayo Santiago (October 2004–August 2008). Details in Fig. 1a. **b** Development of sex differences in aggression received, depending on the age difference between focal subject and partner, in rhesus macaques on Cayo Santiago (October 2004–August 2008). The points represent the mean response for each cell. White points have a mean below and black points have a mean above the plane representing the model; the area of the circles corresponds to the respective sample size.

they got older, independently of their age difference toward the aggressor. In contrast, male focal subjects received more aggression from older partners than female focal subjects in the first 2 yr, and after that from age peers (Fig. 2b).

Effect of Focal Subject's Rank

Initiating Focal subjects initiated aggression depending on their rank, but independently of their sex and age (main effect subject's rank: LRT: $\chi^2 = 14.303$, d.f. = 1, $P < 0.001$); i.e., the effect of the focal subject's rank was the same for males and females throughout the first four years, with high-ranking focal subjects being more aggressive than low-ranking focal subjects (Fig. 3a).

Receiving Focal subjects received aggression depending on their rank and age, but independently of their sex (two-way IA focal subject's age* focal subject's rank: LRT: $\chi^2 = 5.700$, d.f. = 2, $P = 0.058$). In particular, younger focal subjects received less aggression, independently of their rank. While getting older, focal subjects (and

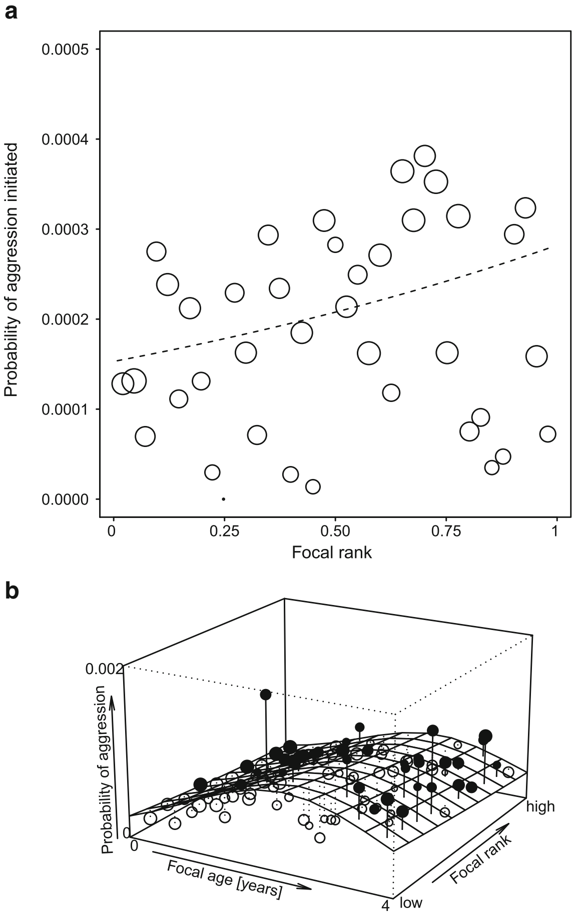


Fig. 3 **a** Effect of focal subject's rank on the probability of initiated aggression, in rhesus macaques on Cayo Santiago (October 2004-August 2008). Details in Fig. 1a. **b** Effect of focal subject's rank on the development of aggression received, in rhesus macaques on Cayo Santiago (October 2004–August 2008). Details in Fig. 2b.

especially low-ranking ones) were more likely to receive aggression until the second year of life. After the second year, focal subjects (and especially high-ranking ones) became slowly less likely to receive aggressions (Fig. 3b).

Effect of Partner's Rank

Initiating Focal subjects initiated aggression depending on the partner's rank but independently of the focal subject's age and sex (main effect partner's rank: LRT: $\chi^2 = 26.955$, d.f. = 1, $P < 0.001$); i.e., the effect of the partner's rank was the same for males and females throughout the first 4 yr, with low-ranking partners receiving more aggression from focal subjects than high-ranking partners (Fig. 4a).

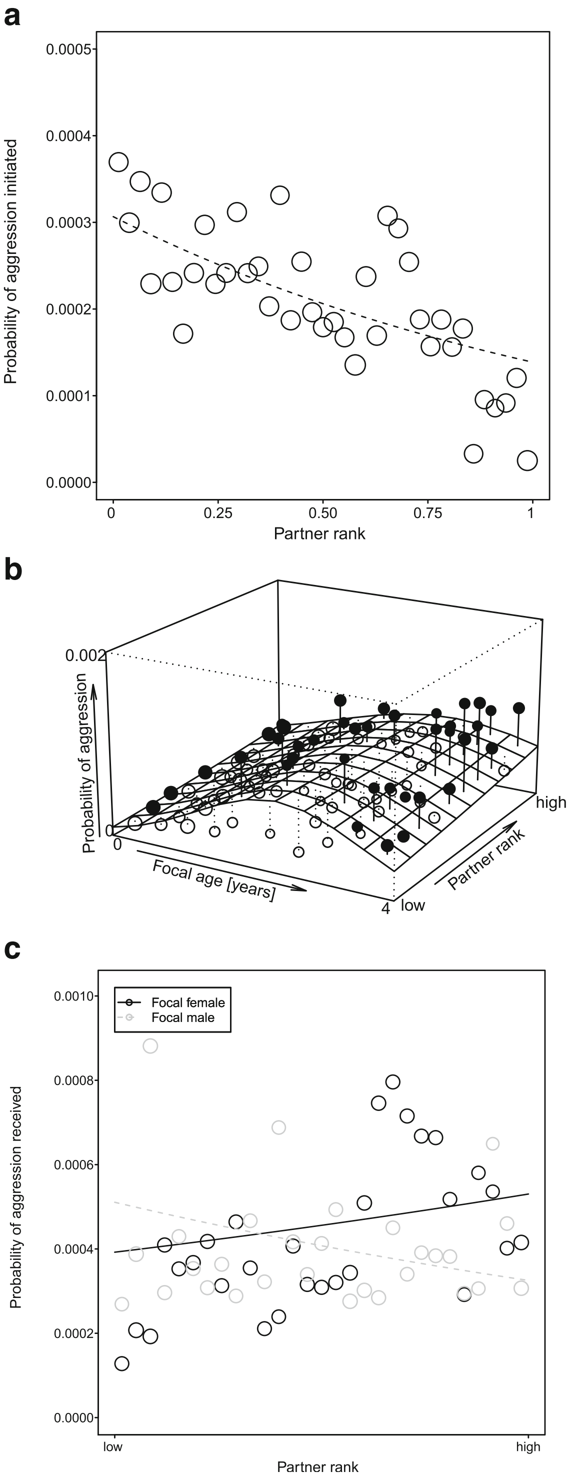
Receiving Focal subjects received aggression depending on the partner's rank and the focal subject's age (two-way IA focal subject's age*partner's rank: LRT: $\chi^2 = 9.121$, d.f. = 2, $P = 0.010$), as well as on the partner's rank and the focal subject's sex (two-way IA focal subject's sex*partner's rank: LRT: $\chi^2 = 23.054$, d.f. = 2, $P < 0.001$). In particular, young focal subjects received little aggression. When getting older, both low- and high-ranking partners became more likely to receive aggression up to the second year of life. After the second year, focal subjects (and slightly more low-ranking than high-ranking ones) became less likely to receive aggression (Fig. 4b). Moreover, female focal subjects received more aggression from high-ranking partners than low-ranking partners, while male focal subjects received more aggression from low-ranking partners than high-ranking partners (Fig. 4c).

Effect of Kinship

Initiating Focal subjects initiated aggression depending on kinship, but independently of the focal subject's age and sex (main effect kinship LRT: $\chi^2 = 26.955$, d.f. = 1, $P < 0.001$; Fig. 5a); i.e., the effect of kinship on aggression initiated by the focal subject was the same for males and females throughout the first 4 yr of life. In particular, focal subjects initiated aggression toward maternal kin more frequently than toward paternal kin and nonkin, but there was no statistically significant difference between aggression toward paternal kin and nonkin ($P = 0.374$; see Table SI).

Receiving Focal subjects received aggression depending on kinship and the focal subject's age (two-way IA focal subject's age*kinship: LRT: $\chi^2 = 52.246$, d.f.=4, $P < 0.001$). In particular, focal subjects were more likely to receive aggression from maternal kin until one and a half years of age, and then strongly less likely. In contrast, they were more likely to receive aggression from paternal kin and nonkin until 3 yr of age, and then slightly less likely (Fig. 5b).Moreover, we found that focal subjects received aggression depending on kinship and the focal subject's sex (two-way IA focal subject's sex*kinship: LRT: $\chi^2 = 8.226$, d.f. = 2, $P = 0.016$). Female and male focal subjects mostly received aggression from maternal kin. In particular, males received slightly more aggression from maternal and paternal kin, but females slightly more from nonkin (Fig. 5c). Accordingly, we found a small effect that males seems to receive more aggression from paternal kin than nonkin compared to females ($P = 0.021$; see Table SII).

Fig. 4 **a** Development of aggression initiated by the focal subject, depending on the partner's rank, in rhesus macaques on Cayo Santiago (October 2004–August 2008). Details in Fig. 1a. **b** The development of aggression received, depending on the partner's rank, in rhesus macaques on Cayo Santiago (October 2004–August 2008). Details in Fig. 2b. **(c)** Development of sex differences in aggression received, depending on the partner's rank, in rhesus macaques on Cayo Santiago (October 2004–August 2008). Details in Fig. 2b.



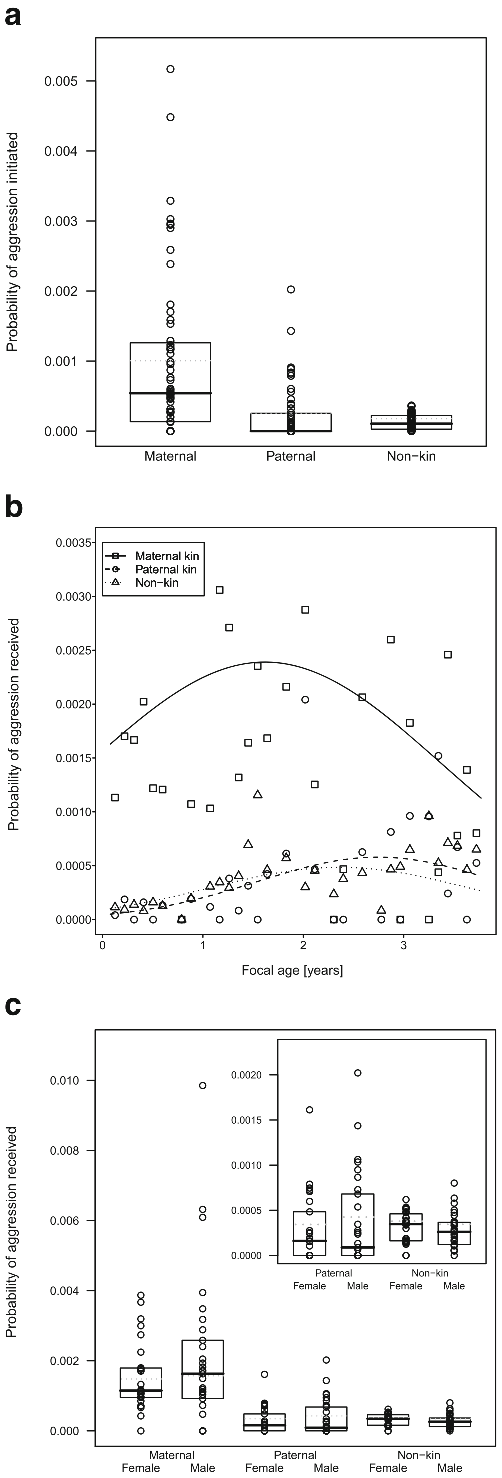


Fig. 5 **a** Probabilities of aggression initiated, depending on kinship, in rhesus macaques on Cayo Santiago (October 2004–August 2008). Details in Fig. 1a. **b** Development in aggression received, depending on kinship, in rhesus macaques on Cayo Santiago (October 2004–August 2008). Details in Fig. 1a. **(c)** Development of sex differences in aggression received, depending on kinship, in rhesus macaques on Cayo Santiago (October 2004–August 2008). Boxes represent the first to third quartile of observed values, solid lines show the median, dashed lines show the values fitted by the model, and each circle represents a data point for a focal subject. **a** Comparison over all three kin categories. **b** Detail showing only comparison between paternal kin and nonkin.

Discussion

The results of our study revealed sex differences and similarities in the development of aggressive behavior in rhesus macaques. The probability of initiating aggression was similar for both sexes throughout development, with some exceptions. In contrast, the probability of receiving aggression mostly differed between sexes but generally increased through development depending on the social context. As predicted, males and females were preferentially aggressive toward partners of the same sex and a similar age. Aggression was mostly directed toward immature partners. As predicted, high-ranking individuals initiated more aggression than low-ranking ones, which received most aggression in both sexes and throughout development. Aggression mostly involved maternal kin and, in contrast to our prediction, this was also true for both sexes throughout development. Finally, important developmental changes in aggressive behavior appeared between 2 and 3 yr of age.

In contrast to our prediction, we found no consistent sex differences in terms of general frequency of aggression initiated, suggesting that males and females younger than 4 yr of age initiate aggression at similar frequencies, although in part directed toward different partners. Focal subjects' age also played a minor role in the probability of being aggressive, suggesting that being aggressive has a similar function during the first years of development. Our results are in line with a study on Japanese macaques showing that sex differences in aggressive behavior are absent in juveniles and appear only in adulthood (Eaton *et al.* 1986). Furthermore, in our study the probability of initiating aggression was the same across development in most social contexts: both high-ranking males and females were more aggressive than low-ranking ones, especially toward low-ranking partners and maternal kin. However, there was one exception: although females directed more aggression toward other females throughout development, males did so in the first 18 mo and then initiated more aggression toward male partners. Importantly, these results also confirm our prediction that aggression is directed mostly toward those social partners of the same sex and a similar age, as they are more likely to compete for the same resources. Our results show that aggressive behavior in rhesus macaques varies with the partner's sex and the age of the individuals involved in the interaction. This flexibility in aggressive behavior might result in a better ability to compete with others. Therefore, it might be especially crucial for male primates, as aggressive behavior might be part of males' reproductive success by, for example, increasing their monopolization potential (Barrett *et al.* 2002; Eaton *et al.* 1981; Fedigan and Baxter, 1984; Link *et al.* 2009; Slater *et al.* 2008).

However, these results are also consistent with the hypothesis that aggression is directed mostly toward those social partners with which individuals have the strongest affiliative bonds (Bernstein and Ehardt, 1986; Kulik *et al.* 2015; Widdig *et al.* 2002, 2006). In primates, females usually form the strongest social bonds with other females, e.g., rhesus macaques (Kapsalis and Berman 1996), vervets (*Cercopithecus aethiops*: Seyfarth 1980), capuchins (*Cebus capucinus*: Perry 1996), and savannah baboons (Seyfarth 1976; Silk *et al.* 1999), and males with males (red colobus, *Colobus badius*: Struhsaker and Leland, 1976; spider monkeys: Slater *et al.* 2009; muriquis, *Brachyteles arachnoids hypoxanthus*: Strier *et al.* 2002; chimpanzees: Arnold and Whiten 2003; Gilby and Wrangham 2008; Goodall, 1986; Lonsdorf *et al.* 2014; Nishida 1979; Watts 2000a,b; Wrangham *et al.* 1992). Moreover, males share a closer proximity with age peers around maturation, with which they are likely to be closely related owing to high male reproductive skew (Widdig 2013) and are likely to disperse together from their natal group (Albers and Widdig 2013). Finally, males also preferentially direct affiliative behaviors toward females early in development and later on toward males (Kulik *et al.* 2015), further suggesting that the distribution of affiliative and aggressive behaviors partly follows similar patterns. Although in this study we conducted no direct analyses to test the link between affiliative and aggressive behaviors at the dyadic level, it is evident that classes of individuals, e.g., males, maternal kin, and younger individuals, largely share the same preferences when interacting with other classes of individuals both via aggressive and affiliative behaviors (*cf.* Kulik *et al.* 2015). Possibly the distribution of aggressive behavior reflects the association patterns in the social group, with most aggressive interactions taking place between individuals that are often in close proximity and have strong affiliative bonds. At this point, our data do not allow us to draw any conclusions on whether aggression has a mainly negative or positive social function. However, they seem to confirm that aggressive and affiliative behaviors both represent two essential aspects of social relationships (Fraser *et al.* 2008).

Throughout development, both sexes initiated the most aggression toward maternal kin and also received the most aggression from maternal kin. This comes as no surprise, as social interactions are generally stronger among maternal kin (Widdig 2007, 2013), aggression more often involves kin (Bernstein and Ehardt 1986; Glick *et al.* 1986; Janus 1991b; Widdig *et al.* 2002, 2006; *cf.* Silk *et al.* 1981), and females are especially aggressive to maternal kin throughout their lives, at least in rhesus macaques (Bernstein and Ehardt 1986). In addition, we found that male focals had a slightly higher probability of exchanging aggression with paternal kin than with nonkin as compared to female focals. This is in line with previous findings on the same population, showing that males at maturation aggressively interact with paternal kin almost as much as with maternal kin (Widdig *et al.* 2015b). This is interesting, as affiliative behaviors are also often skewed in favor of paternal kin from an early age (Charpentier *et al.* 2007), confirming that the distribution of affiliative and aggressive behaviors follow a similar pattern. In contrast to our prediction, males were as aggressive as females toward maternal kin throughout development, although only females remain in their natal group and have a higher chance to compete with maternal kin over the same resources. These results support the suggestion that being aggressive might largely serve a similar function for both sexes during the first years of development, and juvenile aggressive behavior does not necessarily anticipate adult patterns (Cords *et al.* 2010; Eaton *et al.* 1986; Raleigh *et al.* 1979; Wolfheim 1977). Whereas affiliative behavior allows individuals to construct lasting relationships over long time frames (Kulik *et al.* 2015), aggressive behavior might serve more immediate functions, i.e., to solve contingent conflictual situations, and thus fail to completely anticipate future patterns of interactions.

As predicted, and in line with previous studies, high-ranking individuals initiated more aggression than low-ranking conspecifics, which received more aggression (Lambert 2005; Lambert and Whitham 2001; Pereira and Kappeler 1997; Silk *et al.* 1981). It is likely that high-ranking individuals have a higher probability of winning aggressive interactions (*cf.* Markham *et al.* 2015), and might thus more frequently initiate aggression. This was true for both sexes and throughout development, suggesting that rhesus macaques can differentiate partners depending on their rank from very early on. In contrast, a recent analysis of the development of sex differences in affiliative behavior in the same population of rhesus macaques showed that very young monkeys do not seem to differentiate affiliation partners based on their rank, and possibly acquire this ability only as they get older (Kulik *et al.* 2015). The present results, however, conflict with this conclusion, and suggest that monkeys possess this ability very early. It is possible that individuals' motivation to differentiate ranks among social partners is stronger during aggressive than affiliative interactions, as directing aggression unintentionally toward higher-ranking conspecific can be quite costly.

In general, the probability of receiving aggression differed between sexes and across development, strongly depending on the social context. In general, the probability of receiving aggression increased through development. This is in contrast to other studies showing that the most frequent targets of aggression are usually younger individuals (Bernstein and Ehardt 1985c, 1986; Campbell 2006; Sapolsky 2005; Valero *et al.* 2006), or that the rate of aggression received does not change through development (Cords *et al.* 2010). However, only few primate studies, such as ours, considered aggression received from birth to maturation. In rhesus macaques, it seems possible that the probability of receiving aggression is close to zero around birth, as infants' interactions with others and potentially conflictual situations are still extremely limited. In the following months, rhesus monkeys increase their rate of interactions with social partners (Kulik *et al.* 2015), and the probability of receiving aggression is thus higher. Studies that do not include the initial phases of infants' development might not capture this change, and instead simply detect the decrease in rate of received aggression that likely takes place during adulthood when focal subjects have become older and less vulnerable and might be avoided as targets of aggression. This possibility is supported by the finding that individuals of both sexes initially received most aggression from females and only later from males, suggesting that aggression is usually directed toward immatures by social partners who can clearly outcompete them. Moreover, older female partners were more aggressive toward young male focal subjects as compared to female focal subjects of the same age. This is in line with other findings that mothers in the same population target their sons more often than their daughters during their first year of life (Kulik *et al.* unpubl. data), possibly as a behavioral mechanism to edge the young males out of the family. However, future studies should test these hypotheses in more detail.

This study confirms the existence of an important developmental change in social behavior happening in rhesus macaques between 2 and 3 yr of age (Kulik *et al.* 2015). The probability of initiating aggression, for example, had a peak around 3 yr of age in females, and 2 yr in males. Kulik and colleagues (2015) suggested that around an age of 2 yr rhesus macaques might experience a "social revolution," in which sex differences in social behavior become stronger and crucial changes allow individuals to best prepare for their sex-specific social role (Koyama 1985; Nakamichi 1989; Roney and Maestripieri 2005; Suomi 2005). This study provides further evidence for that and extends this "social revolution" to aggressive behaviors.

In the future, more studies should be conducted to carefully disentangle the interplay of aggressive and affiliative behaviors in the development of primate social relationships. In particular, we will need to investigate the extent to which aggression exerts positive and negative effects on primate life, e.g., on fitness, and whether aggression is frequently directed toward preferred social partners because they compete for the same resources, form the strongest affiliative bonds, or simply are closer in space. Moreover, it will be interesting to explore the level of correlation between aggression given and received, analyzing how it varies across pairs of individuals. Future studies will also need to analyze in more detail whether physical and nonphysical forms of aggression follow the same developmental trajectory, and whether similar results will be found in wild populations of other species, including both female and male philopatric species. The developmental approach allows us to explore when differences in sociality emerge across individuals and classes of individuals, how these differences develop, and which factors trigger their emergence.

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