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Toward independence: maternal social status and experience shape mother–infant relationships in mandrills

Berta Roura-Torres^{1,2,3} · Alice Baniel³ · Anna Cryer⁴ · Loïc Sauvadet⁴ · Mélyssa De Pastors⁴ · George Havill⁴ · Mélodie Kreyer⁴ · Jade Meric de Bellefon⁴ · Steven Abaga⁴ · Mélanie Harté⁴ · Peter M. Kappeler^{1,2} · Marie J. E. Charpentier^{3,5}

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Abstract

Mammalian species with slow life histories invest heavily in offspring care to meet offspring nutritional and developmental requirements, typically at significant costs to mothers. While maternal care has been extensively studied, understanding the mechanisms driving variation in mother–offspring relationships during key offspring developmental periods require more comparative data from natural populations. Using eight years of behavioral data, we analyzed mother–offspring interactions in 68 infants born to 46 mothers in wild mandrills (*Mandrillus sphinx*), spanning multiple birth cohorts and the entire first year of infant life, a critical period for individual social and physical development. We found that mothers dynamically adjusted caregiving behavior as infants aged, reducing physical contact while promoting spatial independence and social integration. Maternal traits, such as age, social rank, and reproductive history, shaped maternal phenotypes: high-ranking mothers promoted infant socialization while reducing carrying, and older, multiparous mothers invested more in grooming and physical contact than younger, inexperienced females. Previous infant loss predicted reduced maternal aggression, potentially due to fewer immatures to care for or behavioral adjustments aimed at improving offspring survival. Finally, mothers fostered closer bonds with their daughters while encouraging their sons' independence, possibly resulting in more frequent tantrums observed in males. This sex-biased pattern likely reflects preparation for contrasting life histories between the sexes in this species. By combining extensive longitudinal observations with fine-scale, individual analyses, our study emphasizes the dynamic and multifaceted nature of early mother–offspring interactions and their evolutionary implications in long-lived mammals.

Significance statement

Caring for offspring is energetically costly, requiring mothers to balance their own condition with their infants' needs through flexible behaviors that can also have long-term consequences for offspring development and survival. Using eight years of data on wild mandrills, our study revealed how maternal traits such as age, rank, and reproductive history influence caregiving behavior during the first year of the infant's life. Notably, high-ranking and experienced mothers facilitated their infants' social engagement while fostering independence. The closer bonds observed with daughters and the greater independence encouraged in sons may reflect preparation for their contrasting adult roles (i.e., female philopatry and male natal dispersal). These findings deepen our understanding of the flexibility and evolutionary drivers of maternal care in long-lived mammals, highlighting the complex interplay between maternal behavior, infant needs, and future reproductive success.

Keywords Mother–infant relationships · Maternal investment · Infant development and independence · Mandrill (*Mandrillus sphinx*)

Peter M. Kappeler and Marie J. E. Charpentier contributed equally to this work.

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Extended author information available on the last page of the article

Introduction

Maternal investment during early development has far-reaching consequences for offspring, with pervasive effects that can be observed until adulthood, influencing their behavior, social relationships, health, reproductive success, and mortality risk (Clutton-Brock 1991; Royle et al. 2012). Studies on mother-offspring relationships during early life may inform about the adaptive responses of long-lived animals to challenges from their physical and social environments (Alberts 2019) as well as underlying genetic and maternal effects (Moore et al. 2019). Long-lived animal species generally exhibit slow life histories (Promislow and Harvey 1990), characterized by an extended postnatal period of development and parental investment, which appear to reinforce each other over evolutionary times (Zippel et al. 2024). Mammalian offspring, in particular, rely heavily on their mothers for nourishment, transportation, protection, learning opportunities, and social support (Clutton-Brock 1991). While research on maternal care in mammals is substantial (Lee et al. 1991; van Noordwijk 2012; Liebal et al. 2024), opportunities remain to explore the behavioral outcomes of maternal investment and its dynamics over time, particularly in little studied species.

Mammalian motherhood is inherently costly, as it requires significant physiological and behavioral investments in gestation, lactation, and postnatal care (Clutton-Brock 1991; Weiss et al. 2023). The optimal level of maternal investment sought by offspring typically exceeds what mothers should provide to maximize their lifetime reproductive success, leading to mother-offspring conflict with consequences for both maternal and offspring fitness (Trivers 1974). For example, in many species, the transition from maternal nutritional dependence to independence, known as weaning, represents a typical stage of this conflict (Martin 1984; Lee et al. 1991; Lee 1996). Offspring may require prolonged nursing, whereas mothers may reduce this period of nutritional dependence (Trivers 1974) or alter nursing patterns to minimize interference with other maternal activities (Barrett et al. 1995). These conflicts may generate behavioral manifestations, such as increased maternal rejection or aggression (e.g., in rhesus macaques, *Macaca mulatta*, Simpson et al. 1986), changes in mother-offspring proximity dynamics (e.g., African elephants, *Loxodonta africana*, Lee and Moss 1986), and increased infant soliciting behaviors, such as tantrums (e.g., displays of intense emotional outbursts, typically characterized by behaviors such as loud vocalizations, physical agitation, or aggressive gestures; e.g., humans, *Homo sapiens*, LeVine and LeVine 1988), which affect mother-offspring relationships overall.

Maternal investment can vary flexibly in response to both maternal energetic condition and offspring needs (Smith

2005). Mothers in prime condition generally provide optimal resources to their offspring during development (Martin 1984; Stearns 1992; Lee 1996). For example, in gregarious mammals with female dominance hierarchies, high-ranking mothers often have priority of access to high-quality food sources improving their physiological and body conditions, such as milk production and quality, ultimately enhancing offspring growth (Ellis 1995; Stockley and Bro-Jørgensen 2011; Clutton-Brock and Huchard 2013). Additionally, in matrilineal species, immature offspring often inherit their mothers' social rank, granting differential access to resources during critical stages of development (Holekamp et al. 1996). Consequently, immature mammals born to high-ranking females generally reach weaning sooner without compromising their survival (e.g., red deer, *Cervus elaphus*: Clutton-Brock et al. 1986; spotted hyenas, *Crocuta crocuta*: Holekamp et al. 1996; African wild dogs, *Lycaon pictus*: Creel et al. 1997; chimpanzees, *Pan troglodytes*: Pusey et al. 1997; meta-analysis: Shivani et al. 2022). Beyond these nutritional aspects, dominance status is also a major determinant of females' social life and status. Low-ranking mothers and their offspring generally face greater social risks, with frequent aggression and harassment from social companions (Abbott 1987; Maestripieri 1994; Fairbanks 1996; Clutton-Brock and Huchard 2013). These rank-related differences may profoundly shape mother-offspring relationships. For example, low-ranking mothers often appear both more protective and restrictive with their infants than high-ranking mothers (e.g., White and Hinde 1975; Altmann 1980; Berman 1984). In contrast, in species with more tolerant societies, where social risk is perceived to be lower, maternal protectiveness does not vary with social rank (Maestripieri 1994).

Beyond rank-related differences in energy availability and mobilization, maternal age and experience similarly influence the allocation of resources for offspring care. For example, young and primiparous mothers often reproduce before reaching full adult size, generating trade-offs between the allocation of resources to reproduction *versus* somatic growth (Stearns 1992). Consequently, primiparous mothers may adjust their maternal behaviors to compensate for their limited energy reserves. In chimpanzees, primiparous females nurse and groom their offspring more than multiparous mothers resulting in similar offspring survival outcomes (Stanton et al. 2014). Across several mammalian species, however, older and more experienced mothers generally enjoy greater success in raising offspring (e.g., bighorn sheep, *Ovis canadensis*: Festa-Bianchet 1988; Antarctic fur seals, *Arctocephalus gazella*: Lunn et al. 1994; feral horses, *Equus caballus*: Cameron et al. 2000). One reason is that mothers are expected to progressively increase their investment in their successive offspring because

female reproductive value tends to decline with age (i.e., females have fewer opportunities to reproduce in the future; Clutton-Brock 1984). In addition, maternal experience gained throughout motherhood may allow mothers to target care to the most critical periods of offspring development (Green 1993; Fairbanks 1996; Cameron et al. 2000). In feral horses, for example, age-differentiated maternal behavior is apparent only during the first 20 days of the foal's life, with older mares maintaining closer contact with their foals during this critical period but showing reduced effort thereafter (Cameron et al. 2000). In contrast, adverse maternal experience, such as the death of previous offspring, may disrupt this generalized age-related behavioral pattern (Fairbanks 1988). Vervet monkey (*Cercopithecus aethiops*) mothers who experienced reproductive failure (i.e., pregnancy loss or perinatal infant death) are more protective and attentive to their next offspring (Fairbanks 1988). Similarly, feral horse mares who have lost a foal subsequently increase maternal effort by maintaining closer proximity to their next offspring (Cameron et al. 2000).

Finally, maternal investment is shaped not only by the mother's condition and experience but also by offspring traits, with sex being a key factor influencing the allocation of maternal care because of the differential fitness outcomes of rearing sons *versus* daughters (Clutton-Brock et al. 1981; Fairbanks 1996). In sexually dimorphic mammals, male offspring typically require more maternal resources than female offspring because of greater somatic growth and increased energetic demands associated with male development (Clutton-Brock et al. 1985; Lindström 1999). For example, male African elephant calves suckle more frequently than female calves do (Lee and Moss 1986), and bighorn ewes experience delayed reproduction following the birth and rearing of males (Hogg et al. 1992). In contrast, in group-living matrilineal mammals, where female offspring inherit their mothers' dominance rank and social support from their maternal kin (Holekamp and Smale 1991), investing in females rather than in males may yield greater fitness benefits, particularly for high-ranking females (Silk 1983).

Here, we contributed to this body of research on mother-offspring relationships by studying how the dynamic interplay between multiple maternal and offspring characteristics shape maternal investment, in a natural population of mandrills (*Mandrillus sphinx*), using a large sample of infants spanning several cohorts. Mandrills are particularly interesting to study in this context because of several salient aspects of their biology. First, they live in very large, cohesive social groups composed mainly of adult females, the philopatric sex, and their offspring, whereas males disperse from their natal group around puberty, and immigrant males are nonpermanent residents of these groups (Abernethy et al. 2002; Brockmeyer et al. 2015). Mandrills

form typical matrilineal societies where maternally related females show lifelong preferential associations and sociality (Charpentier et al. 2007, 2020). In these societies, females inherit their mother's dominance rank, with adult daughters commonly positioned below her, following a reverse age hierarchy where younger sisters generally outrank older sisters (Setchell et al. 2002). Dominant matrilines typically enjoy priority of access to nutritional and social resources (Dezeure et al. 2022). As a result, high-ranking females generally have shorter interbirth intervals than low-ranking females (median interbirth interval: 15.0 months versus 22.0 months, respectively; Dezeure et al. 2022). However, because mandrills are seasonal breeders, with most births occurring between November and March (Dezeure et al. 2022), birth spacing varies across females, leading to diverse motherhood profiles. Depending on their reproductive history, females may simultaneously care for one or multiple dependent offspring of different ages. Reproductive patterns observed in this study population lead to an alternation between very large birth cohorts (up to 94) and small ones (5; MJEC unpubl. data). Consequently, the social environment in which infants are born may vary dramatically (*see* also Charpentier et al. 2020). Finally, sexual size dimorphism is extreme in this primate, starting as soon as 12 months of age, with adult male mandrills being more than three times heavier than adult females (Setchell et al. 2001).

Here, we analyzed nine social behavioral variables characterizing mother-infant relationships in wild mandrills, using eight years of continuous observations of 68 infants throughout their critical first year of development. Mandrill infants reach locomotor independence within the first months of life, but they maintain close proximity to their mothers even after weaning, which occurs at approximately eight months of age in captive settings (Setchell et al. 2002). We thus studied typical maternal investment behaviors (nursing, carrying), maternal interactions (grooming, restraining, and aggression), infant soliciting behaviors (tantrums), and mother-infant spatial associations (body contact, indices of proximity initiation and maintenance). We hypothesized that changes in mother-infant relationships as infants age would depend on maternal characteristics, infant traits, and the social environment where infants are born. First, as a consequence of priority access to resources by high-ranking mothers, we predicted that they should cease maternal investment earlier than low-ranking mothers, involving an earlier decline in nursing and carrying, coupled with independence-promoting behaviors, such as less contact seeking and more rejections. In turn, infants born to high-ranking mothers should perform more tantrums than those born to low-ranking mothers as a behavioral manifestation of this earlier decline in maternal investment. Second, we predicted that young, primiparous females and mothers who lost their

previous infant would invest more in their offspring and display more protective behaviors (e.g., increased restraining and contact seeking) than experienced and successful mothers. Moreover, we predicted that female mandrills should foster stronger social bonds (e.g., more grooming) with their philopatric daughters than with their sons. However, we also predicted that mandrill mothers should nurse their sons more than their daughters because of the extreme sexual size dimorphism observed in this species. Finally, in the study population, infants born in large cohorts tend to spend more time playing with their peers compared to those born in small cohorts (BR-T pers. obs.). Thus, we predicted that infants born with numerous peers available to socialize with, would be more independent from their mothers (e.g., less grooming, more disruption of associations initiated by infants) than those born with few age-mates. By documenting longitudinal changes throughout the first year of life in a large sample of infants, we aimed to provide a comprehensive understanding of how maternal investment unfolds during infant development in response to maternal and infant traits.

Materials and methods

Study site and population

The study population consists of a natural social group of mandrills (*Mandrillus sphinx*) fully habituated to human presence, freely roaming Lékédi Park and its surroundings (Bakoumba, Gabon; 2.2642° S, 11.5651° E). This group originated from two release events of 65 captive-bred mandrills from CIRMF (Centre Interdisciplinaire de Recherches Médicales de Franceville) in 2002 and 2006 (Peignot et al. 2008). Soon after their release, founder females reproduced with wild migrant males. By November 2023, the group comprised approximately 300 wild-born individuals, with only four founder females remaining, the oldest being 23 years old at the time of the study. This group has been monitored since 2012, when a long-term field project was initiated to study the socioecology of this species (the “Mandrillus Project”: Poirotte et al. 2017; Charpentier et al. 2020). The birth dates were accurately known for most of the studied individuals born after 2012 and for the individuals born at the CIRMF ($N=68$ infants and 36 mothers; mean \pm SD estimated days from birth date: infants = 2.29 ± 5.40 ; mothers = 47.00 ± 168.96). The age of the remaining individuals ($N=10$ mothers) was estimated on the basis of patterns of tooth eruption and wear (i.e., with age, molars become flatter; Galbany et al. 2014) and an assessment of general body condition (i.e., coloration patterns of the face, hands and feet). Each birth was assigned to a birth

cohort, with the transition date between two cohorts being September 1st following the seasonal birth pattern in this population. We determined the sex of newborns through observations of their genitalia.

Behavioral data

All mandrills from the study group are individually recognizable from the face (e.g., shape, presence of distinctive scars or marks, coloration patterns). Trained field assistants, unaware of the aim of this study, have been collecting daily data on group composition, movements and demography, individual life histories, and social behavior. To minimize observer bias, blinded methods were used when all behavioral data for this study were collected on 68 infants (i.e., individuals aged less than one year) from January 2015 to November 2023 on a daily basis via 5-minute continuous focal sampling (Altmann 1974). During each focal observation, observers recorded all infant activities, including mother-infant interactions. Additionally, we collected up to two scan samples during each focal observation (one at the beginning and one at the end) to estimate the spatial association between the focal infant and its groupmates (i.e., either in body contact, or separated by less than 1 m, or by less than 5 m). We divided the first year of infants’ age into four quarters (90-day periods), and we considered only those infants for whom we collected at least 30 min of focal observations and nine scans per quarter, for at least three out of four quarters, in the following analyses. With these restrictions, we used a total of 346 h of focal observations (mean \pm SD minutes of observation per infant: quarter 1 = 103 ± 59 ; quarter 2 = 87 ± 46 ; quarter 3 = 74 ± 41 ; quarter 4 = 71 ± 36) and 7764 scans (mean \pm SD scan samples per infant: quarter 1 = 36.2 ± 21.1 ; quarter 2 = 32.9 ± 18.6 ; quarter 3 = 28.6 ± 17.9 ; quarter 4 = 27.7 ± 15.9) collected from 34 females and 34 males belonging to six different cohorts and born to 46 different mothers (see Supplementary Table S1).

We focused on nine mother-infant interactions previously described in other primates (i.e., Hinde and Simpson 1975; Altmann 1980; Tanaka 1989; Schino et al. 1995; Maestripieri 1998; Bardi et al. 2001; De Lathouwers and van Elsacker 2004; Verderane and Izar 2019; Arbaiza-Bayona et al. 2022; Table 1). These include typical maternal behaviors, such as nursing (i.e., infant making sustained contact with its mouth to the mother’s nipple) and carrying (i.e., ventral – occasionally dorsal – transport of the infant), both recorded as binary occurrences (presence or absence) during each focal observation to avoid pseudoreplication. We further considered maternal grooming as a total duration (in seconds per focal observation), and recorded the total number of events per focal observation of restraining behaviors (i.e., behaviors limiting infant’s movements, such

Table 1 Statistical results of the full models, including both primiparous and multiparous females

Fixed effects	Level	CI		Estimate	χ^2	<i>P</i>
		2.5%	97.5%			
Nursing						
Infant age		-8.030	-6.283	-7.156	318.618	<0.001
Infant age²		0.465	2.093	1.279	360.520	<0.001
Infant sex	Male (ref: female)	-0.086	0.116	0.015	0.081	0.776
Dominance rank		-0.011	0.098	0.043	2.426	0.119
Maternal parity	Multiparous (ref: primiparous)	-0.219	0.014	-0.102	2.949	0.086
Cohort size		-0.154	0.084	-0.035	0.336	0.562
Full-null model comparison: $\chi^2_2=205.170$, $P<0.001$ (AIC full = 1217.700, AIC null = 1412.900)						
Carrying						
Infant age		-17.576	-14.417	-0.160	391.093	<0.001
Infant age²		-4.051	-1.819	-2.935	512.190	<0.001
Infant sex	Male (ref: female)	-0.184	0.017	-0.084	2.675	0.102
Dominance rank		-0.138	-0.037	-0.087	11.362	0.001
Maternal parity	Multiparous (ref: primiparous)	-0.171	0.059	-0.056	0.908	0.341
Cohort size		-0.104	0.004	-0.050	3.300	0.069
Full-null model comparison: $\chi^2_2=328.520$, $P<0.001$ (AIC full = 1199.100, AIC null = 1473.500)						
Restraining						
Infant age		-1.837	-1.366	-1.601	177.633	<0.001
Infant sex	Male (ref: female)	-0.176	0.435	0.130	0.690	0.406
Dominance rank		-0.297	0.062	-0.117	1.649	0.199
Maternal parity	Multiparous (ref: primiparous)	-0.039	0.693	0.327	3.065	0.080
Cohort size		-0.127	0.677	0.275	1.797	0.180
Full-null model comparison: $\chi^2_2=167.540$, $P<0.001$ (AIC full = 649.150, AIC null = 806.690)						
Aggression						
Infant age		1.776	8.120	4.948	7.416	0.006
Infant age²		-8.299	-2.382	-5.340	19.030	<0.001
Infant sex	Male (ref: female)	-0.503	0.265	-0.119	0.370	0.543
Dominance rank		-0.024	0.396	0.186	3.001	0.083
Maternal parity	Multiparous (ref: primiparous)	-0.493	0.399	-0.047	0.042	0.837
Cohort size		-0.141	0.738	0.299	1.774	0.183
Full-null model comparison: $\chi^2_2=25.363$, $P<0.001$ (AIC full = 609.060, AIC null = 622.420)						
Tantrums						
Infant age		-6.714	-1.375	-4.045	4.712	0.030
Infant age²		-7.841	-2.844	-5.343	22.662	<0.001
Infant sex	Male (ref: female)	0.185	0.921	0.553	8.674	0.003
Dominance rank		-0.013	0.397	0.192	3.375	0.066
Maternal parity	Multiparous (ref: primiparous)	-0.719	0.134	-0.293	1.809	0.179
Cohort size		-0.224	1.036	0.406	1.598	0.206
Full-null model comparison: $\chi^2_2=35.889$, $P<0.001$ (AIC full = 949.84, AIC null = 973.720)						
Grooming						
Infant age		0.120	0.341	0.231	16.801	<0.001
Infant sex	Male (ref: female)	-0.374	0.173	-0.100	0.517	0.472
Dominance rank		0.061	0.336	0.198	8.025	0.005
Maternal parity	Multiparous (ref: primiparous)	0.103	0.725	0.414	6.809	0.009
Cohort size		-0.229	0.450	0.110	0.406	0.524

Table 1 (continued)

Fixed effects	Level	CI		Estimate	χ^2	<i>P</i>
		2.5%	97.5%			
Full-null model comparison: $\chi^2=29.331$, $P<0.001$ (AIC full = -1004.850, AIC null = -985.520)						
Body contact						
Infant age		-9.305	-7.741	-8.523	545.346	<0.001
Infant age²		0.045	1.480	0.762	559.713	<0.001
Infant sex	Male (ref: female)	-0.155	0.081	-0.037	0.378	0.539
Dominance rank		-0.040	0.088	0.024	0.539	0.463
Maternal parity	Multiparous (ref: primiparous)	-0.149	0.130	-0.009	0.017	0.895
Cohort size		-0.135	0.126	-0.004	0.004	0.948
Full-null model comparison: $\chi^2=616.66$, $P<0.001$ (AIC full = 1327.100, AIC null = 1931.700)						
Brown's index						
Infant age		1.784	3.637	2.711	27.203	<0.001
Infant age²		-3.124	-1.472	-2.298	54.791	<0.001
Infant sex	Male (ref: female)	0.022	0.290	0.156	5.193	0.023
Dominance rank		-0.130	0.012	-0.059	2.675	0.102
Maternal parity	Multiparous (ref: primiparous)	-0.187	0.094	-0.047	0.420	0.517
Cohort size		-0.188	0.121	-0.033	0.177	0.674
Full-null model comparison: $\chi^2=66.340$, $P<0.001$ (AIC full = 1083.300, AIC null = 1137.700)						
Hinde's index						
Infant age		-1.568	-0.468	-1.008	13.266	<0.001
Infant age²		0.223	1.296	0.759	21.361	<0.001
Infant sex	Male (ref: female)	-0.171	0.001	-0.082	3.432	0.064
Dominance rank		-0.048	0.043	-0.001	0.003	0.959
Maternal parity	Multiparous (ref: primiparous)	-0.068	0.135	0.037	0.508	0.476
Cohort size		-0.067	0.108	0.023	0.246	0.620
Full-null model comparison: $\chi^2=25.319$, $P<0.001$ (AIC full = 89.562, AIC null = 102.881)						

Note. The Table shows estimates, 95% confidence intervals (CI), chi-square and *P* values for the predictors of the GLMMs and LMMs (Hinde's index), including infant, mother and cohort identities as three random effects. Significant effects are highlighted in bold. Mean \pm SD for infant age: 172.791 \pm 101.413; dominance rank: 0.447 \pm 0.326; cohort size: 38.402 \pm 14.421

as pulling, grabbing, or blocking them from moving away), and maternal aggression (i.e., biting, pushing, hitting, slapping, and grasping). Note that maternal aggression, in our study population, serves primarily as a form of rejection of infants' demands to be carried or to access the nipple (BR-T pers. obs.). We also recorded infant tantrums as a total number of events observed per focal. In mandrills, tantrums are defined by every instance of infant crying (i.e., vocalizations such as screaming, moaning, and gecking; Delaunay et al. 2024). Finally, we studied patterns of mother-infant spatial associations by recording first mother-infant body contacts recorded during scans and by then considering two behaviors recorded during focal observations: approaches (i.e., when an individual moves toward a conspecific, entering a 1-meter-radius circle around the latter) and leaves (i.e., when an individual moves away from a conspecific, exiting a 1-meter-radius circle around the latter). Approaches and leaves were considered both as total number of events observed per focal observation.

Maternal dominance rank was assessed via approach-avoidance interactions among adult females collected ad libitum or during focal observations to compute a hierarchy via normalized David scores (David 1987). We then assigned each female a single relative rank by averaging annual ranks over the study period (since annual ranks were highly correlated across years and observation effort varies yearly; Dezeure et al. 2022), which represented the proportion of females dominated by the focal female. The values ranged from 0 (lowest-ranking females) to 1 (highest-ranking females).

Individual data

We used long-term life history records to calculate the mother's age (in years) at the beginning of each quarter and the infant weighted age for each quarter. The infant's weighted age was computed by averaging the infant's age recorded during each focal observation, weighted by the duration of

that focal observation, across all focal observations. Mothers were further categorized on the basis of their reproductive history. First, they were considered either primiparous, when the focal infant was their first surviving infant, or multiparous otherwise. Second, among multiparous mothers only, we classified them as those whose previous infant either died or survived infancy, i.e. at least 12 months of age. Finally, we determined cohort size as the number of infants born in the same birth cohort as the focal infants but who were alive by the end of each quarter of the study period.

Statistical analyses

We studied nine behaviors per quarter as follows. Events (counts) included the total number of nursing and carrying behaviors recorded across all infant focal observations (with multiple occurrences within a single focal observation counted as one to prevent pseudoreplication), as well as maternal restraining, aggression, and infant tantrum. We calculated the proportion of time mothers spent grooming their infants by dividing the total grooming time by the total observation time, and the proportion of scans in body contact by dividing the total number of times mothers and infants were observed in body contact by the total number of scans performed on the infant (see Supplementary Table S1). To assess which individual of the dyad actively changed proximity, we calculated Brown's index (see Supplementary Table S2) as the total number of approaches and leaves initiated by the mother divided by the total number of approaches and leaves observed within the dyad (Brown 2001). This index ranged from 0 to 1, with values below 0.5 indicating infant responsibility for most of the proximity changes between the dyad and above 0.5 indicating maternal responsibility. We further calculated Hinde's index (see Supplementary Table S3) as the proportion of approaches initiated by the mother minus the proportion of her leaves (Hinde and Atkinson 1970). This index ranged from -1 , indicating that the mother initiated more leaves than approaches, to $+1$, indicating that the mother initiated more approaches than leaves. Together, these indices complement each other: while Hinde's index highlights mothers' role in approaching versus leaving the infant, Brown's index indicates the proportion of total proximity changes initiated by the mother (Arbaiza-Bayona et al. 2022).

For each model performed, we considered the following covariates: infant weighted average age (ranging from 25.6 to 336.6 days) and its quadratic term, infant sex (female versus male), maternal dominance rank (ranging from 0 to 1), maternal parity (primiparous versus multiparous) and cohort size (ranging from 5 to 56). In a second step, we focused on multiparous females and included only the

significant predictors of the previous models along with maternal age (in years) and its quadratic term and the outcome of the previous reproductive event (death of previous infant: yes versus no). Mothers experiencing the death of an infant generally showed larger age gaps between their two last living offspring than other females did. To explore whether changes in mother-infant behaviors were directly related to previous infant death or related to the energy required to take care of close-in-age offspring, we reran the models where the outcome of previous reproduction was significant excluding mothers whose previous infant had died and instead including the length of the interbirth interval (IBI) to the previous living offspring as a fixed effect (see Supplementary Table S7).

In all models, we accounted for observational effort by including the log-transformed observation time as an offset (except for models based on the proportions of grooming and body contact). We further considered infant, mother and birth cohort identities as three random effects to control for pseudoreplication.

For the counts of nursing, carrying, restraining, aggression, and tantrums, we used generalized linear mixed models (GLMMs) with a negative binomial distribution (for overdispersed data typically characterizing social behaviors) and a log-link function. Maternal grooming was modeled with a GLMM with a beta family distribution and a logit link function. For body contacts and Brown's index, we ran two GLMMs with a binomial error structure with a logit link function to study a proportion N/T , where N was the total number of scans in which a given dyad was in body contact (or the total number of approaches and leaves initiated by the mother), and T was the total number of scans (or the total number approaches and leaves observed within the dyad). Finally, we modelled Hinde's index as a linear mixed model (LMM) with a Gaussian error structure, as residuals were normally distributed, with an identity link function.

All statistical analyses were conducted via R Studio software (version 4.2.1; R Core Team 2022). We ran GLMMs with the "glmmTMB" function from the glmmTMB package (Brooks et al. 2017) and LMMs with the "lmer" function from the lme4 package (Bates et al. 2015). We assessed fit singularity via the "check_singularity" function and overdispersion via the "check_overdispersion" function from the performance package (Lüdtke et al. 2021). When modeling negative binomial distributions, we compared their fit with negative binomial type I and II models, selecting the one with the lowest Akaike's information criterion (Zuur et al. 2009). All quantitative predictors were z-transformed (i.e., scaled with a mean of 0 and a standard deviation of 1) to compare effect sizes among estimates and to facilitate model convergence (Harrison et al. 2018). We ensured that the estimation of the coefficients in our models was

not influenced by multicollinearities (all Variance Inflation Factors, VIF, were inferior to 2; Lüdecke et al. 2021). After running full-null (equivalent model without fixed effects) model comparisons, we tested the significance of our fixed factors by running Wald chi-square tests and obtained the associated p values for each model via the “Anova” function from the car package (Fox and Weisberg 2019). We obtained 95% confidence intervals and effect estimates via the function “confint”. Finally, to validate the significance of our models, we checked the distribution of the residuals with the “simulateResiduals” function from the DHARMA package (Hartig and Lohse 2022).

Results

Infant age, or its quadratic term, was a major predictor of all studied behaviors (Table 1; Fig. 1). As infants grew older, rates of nursing, carrying, restraining, and body contact decreased significantly, although not always linearly. In contrast, the amount of time mothers spent grooming overall increased with infant age. Both infant tantrums and the number of maternal aggressions peaked between the second and third quarters. Additionally, we observed a progressive transition in spatial association patterns, with mothers becoming more likely to change proximity (increased

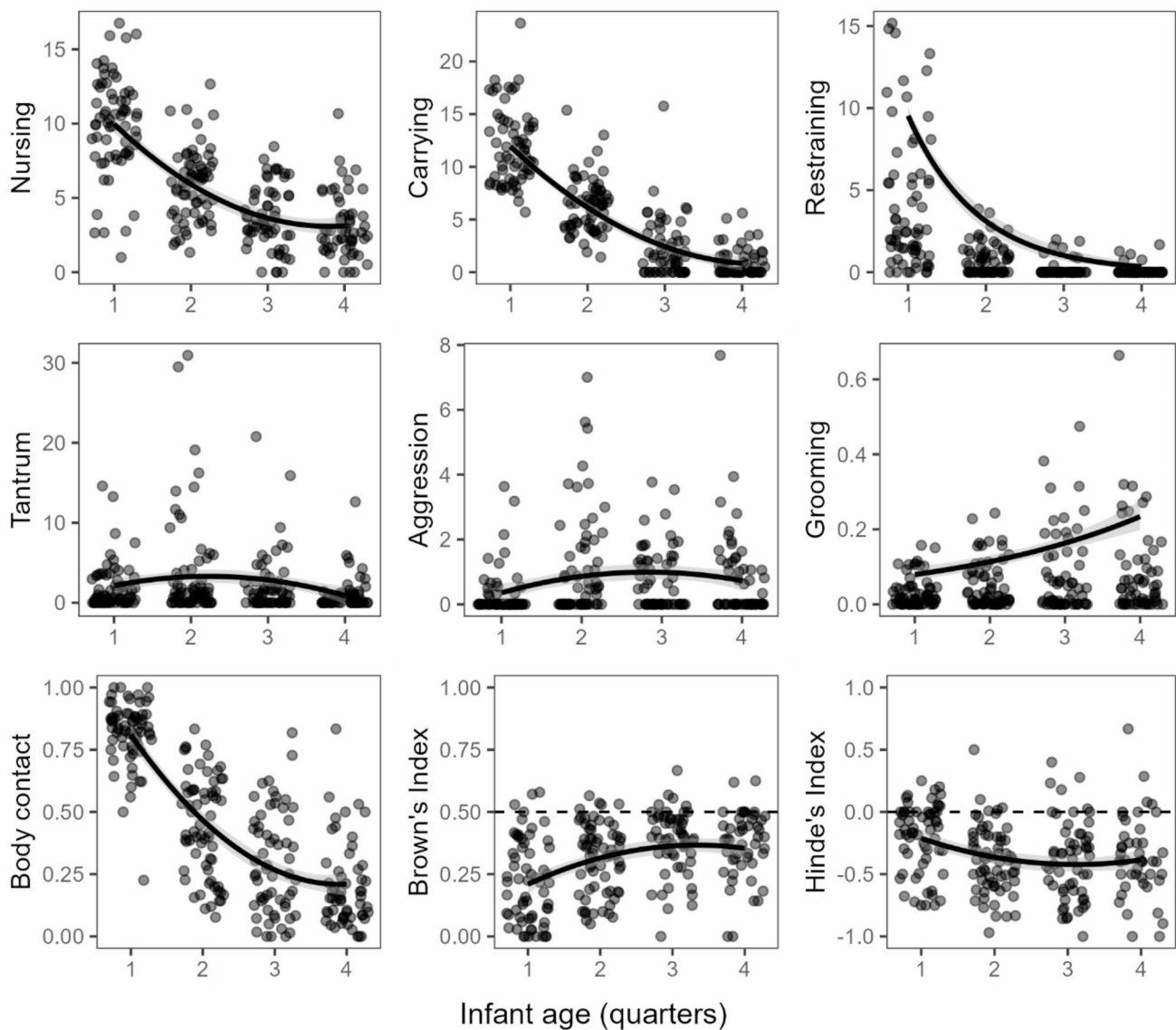


Fig. 1 Behavioral variables studied to characterize mother-infant relationships in mandrills as a function of infant age (for graphical purposes, data were divided into quarters of 90 days). The variables were as follows. Nursing and carrying: proportion of focals with any; restraining, aggression and tantrums: number of events per hour, recorded during all focals; grooming: proportion of focal time mother

groomed her infant; body contact: proportion of scans where mother and infant were in contact (see Table S1, S2, and S3 for full description). Dashed lines represent the transition of responsibility, solid lines indicate fitted regressions, and shaded areas correspond to 95% confidence intervals

Brown's index) and being less responsible for seeking proximity (decreased Hinde's index) to their infants as they aged, although these changes with age were also not linear.

In addition to these age-related effects, maternal dominance rank and reproductive experience both profoundly shaped mother-infant relationships (Tables 1 and 2). First, high-ranking mothers carried their infants less but spent more time grooming them than low-ranking mothers (Fig. 2). Second, primiparous and younger mothers spent less time grooming their infants than did multiparous (Fig. S1) and older (Fig. 3) mothers, the latter also being more frequently in body contact with their infants (Fig. 3). Although maternal aggression was relatively infrequent (0.58 events per hour on average), mothers who lost a previous infant were less aggressive toward their current infant than were those whose previous infant survived (Fig. 4). When we excluded mothers whose previous infant died and included the IBI to the previous living offspring instead, we found that mothers who had spaced births (long IBIs) were less aggressive to their infants than mothers with close-in-age offspring (Fig. S2; Supplementary Table S8). Moreover, mothers changed association patterns more frequently with their sons than with their daughters (Brown's index), meaning that mothers were found less often in close proximity to males than to females, although the proportion of scan spent in body contact was not sex-dependent. Male infants performed more tantrums than females did possibly either as a result of frequent association disruptions initiated by their mother or as a cause of it (Table 1; Fig. 5). Finally, the social environment where infants were born (i.e., cohort size) did not influence mother-infant relationships ($p > 0.05$ in all instances, Table 1).

Discussion

In this study, based on a large sample of infants across eight birth cohorts, we showed that mother-infant relationships in a long-lived primate were shaped by a complex interplay of maternal dominance rank, age, previous reproductive experience, and infant sex. Interestingly, the social environment — specifically, the number of peers born at the same time — did not appear as a critical factor in shaping these relationships, which is not surprising at such a young age. At this stage, mothers are the primary social partners of their offspring, a role that changes rapidly as infants transition to juvenile stages, where interactions with peers become increasingly important (Charpentier et al. 2020). Yet, as infants progress through developmental stages, mother-infant relationship dynamics evolve predictably, with maternal care behaviors decreasing as behaviors promoting independence increased.

These age-related behavioral shifts align with typical patterns of infant development in other mammals (Northern elephant seals, *Mirounga angustirostris*: Reiter et al. 1978; African elephants: Lee and Moss 1986; Sumatran orangutans, *Pongo abelii*: Revathe et al. 2024), which reflects the gradual progression toward autonomy, essential for infants to achieve adequate size and acquire essential skills to survive, but also for mothers to sustain successful future reproduction. Some maternal behaviors, however, did not follow a linear pattern across the first year of life, which suggests that some periods of infancy may be particularly critical for development. In mandrills, indeed, most significant changes in mother-infant relationships occurred between the third and ninth months, with a marked decline in maternal investment (nursing, carrying) alongside peaks in maternal rejection and infant solicitation. Interestingly, this period also roughly corresponds to the critical weaning phase (approximately eight months in captivity; Setchell et al. 2002), when mother-offspring conflicts — often characterized by maternal aggression and infant tantrums — are expected to peak. As mandrill infants transition toward nutritional independence, their decreasing reliance on maternal milk may intensify these behavioral conflicts. In the study population, however, nursing may continue for several months in the absence of a younger sibling (Delaunay et al. 2024), implying that these interactions probably fulfill roles beyond nutrition. Similarly, in wild chimpanzees, nutritional weaning can be completed more than a year before infants stop nipple contact (Bădescu et al. 2017), possibly as a form of comfort nursing without milk transfer (Martin 1984; Reitsema 2012). Such extended nursing behavior in both species may indicate an emotional comfort function, which highlights that the end of weaning does not necessarily mark a definitive end of infant dependency to maternal attention.

Although mother-infant relationships generally stabilized after nine months, with only minor fluctuations, the transition to independence varied with maternal dominance rank. In polygynous species such as mandrills, high-ranking females typically enjoy preferential access to resources, leading to better physical conditions for themselves and their offspring, as well as greater reproductive success. In our study population, for example, high-ranking females produce more offspring on average than low-ranking females (Dezeure et al. 2022). These advantages often result in high-ranking mothers caring for closely spaced immature siblings, which likely explains the reduced frequency of infant carrying compared with low-ranking mothers. This trend mirrors patterns observed in yellow baboons (*Papio cynocephalus*; Altmann and Samuels 1992) and spotted hyenas, where dominant females terminate maternal investment earlier than subordinates (Holekamp et al. 1996; Holekamp and Dionak 2009; East and Hofer 2010).

Table 2 Statistical results of the reduced models, focusing on multiparous females

Fixed effects	Level	CI		Estimate	x^2	<i>P</i>
		2.5%	97.5%			
Nursing						
Infant age		-7.221	-5.182	-6.201	185.077	<0.001
Infant age ²		0.129	1.958	1.044	208.52	<0.001
Maternal age		-0.102	0.024	0.070	1.24	0.265
Death sibling	Yes (ref: no)	-0.096	0.236	0.070	0.68	0.409
Full-null model comparison: $x^2_2=143.400$, $P<0.001$ (AIC full=908.580, AIC null=1043.980)						
Carrying						
Infant age		-17.777	-13.540	-0.157	367.142	<0.001
Infant age ²		-4.607	-1.835	-3.221	319.431	<0.001
Dominance rank		-0.171	-0.040	-0.106	10.041	0.002
Maternal age		-0.050	0.089	0.0198	0.312	0.577
Death sibling	Yes (ref: no)	-0.133	0.246	0.056	0.342	0.559
Full-null model comparison: $x^2_2=263.890$, $P<0.001$ (AIC full=824.130, AIC null=1078.020)						
Restraining						
Infant age		-1.891	-1.291	-1.591	108.286	<0.001
Maternal age		-0.214	0.225	0.005	0.002	0.961
Death sibling	Yes (ref: no)	-0.653	0.426	-0.114	0.170	0.680
Full-null model comparison: $x^2_2=102.85$, $P<0.001$ (AIC full=491.63, AIC null=588.48)						
Aggression						
Infant age		-0.164	6.790	3.313	4.697	0.030
Infant age ²		-9.250	-3.064	-6.157	18.122	<0.001
Maternal age		-0.374	0.126	-0.124	0.943	0.332
Death sibling	Yes (ref: no)	-1.413	-0.053	-0.733	4.467	0.035
Full-null model comparison: $x^2_2=26.180$, $P<0.001$ (AIC full=440.590, AIC null=458.770)						
Tantrums						
Infant age		-6.417	-0.484	-3.451	3.135	0.077
Infant age ²		-6.547	-1.054	-3.800	10.819	0.004
Infant sex	Male (ref: female)	0.171	1.104	0.638	7.176	0.007
Maternal age		-0.119	0.347	0.114	0.923	0.337
Death sibling	Yes (ref: no)	-0.455	0.650	0.097	0.120	0.729
Full-null model comparison: $x^2_2=17.542$, $P=0.004$ (AIC full=689.560, AIC null=697.100)						
Grooming						
Infant age		0.206	0.454	0.330	27.352	<0.001
Dominance rank		0.123	0.434	0.279	12.388	<0.001
Maternal age		0.032	0.312	0.172	5.790	0.016
Death sibling	Yes (ref: no)	-0.281	0.474	0.097	0.253	0.615
Full-null model comparison: $x^2_2=35.104$, $P<0.001$ (AIC full = -707.490, AIC null = -680.380)						
Body contact						
Infant age		-0.595	-0.485	-0.540	371.135	<0.001
Maternal age		0.010	0.141	0.076	5.154	0.023
Death sibling	Yes (ref: no)	-0.097	0.243	0.073	0.713	0.398
Full-null model comparison: $x^2_2=406.230$, $P<0.001$ (AIC full=994.230, AIC null=1394.460)						
Brown's index						
Infant age		1.133	2.992	2.063	18.237	<0.001
Infant age ²		-2.704	-1.041	-1.873	36.424	<0.001
Infant sex	Male (ref: female)	0.001	0.372	0.191	4.280	0.039
Maternal age		-0.138	0.001	-0.064	2.833	0.092
Death sibling	Yes (ref: no)	-0.244	0.131	-0.056	0.347	0.556
Full-null model comparison: $x^2_2=44.110$, $P<0.001$ (AIC full=803.190, AIC null=837.300)						
Hinde's index						
Infant age		-0.101	-0.178	-0.059	7.825	0.005
Maternal age		-0.037	0.073	0.019	0.468	0.494

Table 2 (continued)

Fixed effects	Level	CI		Estimate	χ^2	<i>P</i>
		2.5%	97.5%			
Death sibling	Yes (ref: no)	-0.047	0.239	0.097	2.156	0.142

Full-null model comparison: $\chi^2=9.486$, $P=0.023$ (AIC full=74.875, AIC null=78.361)

Note. The Table shows estimates, 95% confidence intervals (CI), chi-square and *P* values for the predictors of the GLMMs and LMMs (Hinde's index), including infant, mother and cohort identities as three random effects. Significant effects are highlighted in bold. Mean±SD for infant age: 175.040±102.020; dominance rank: 0.477±0.338; cohort size: 36.862±14.734

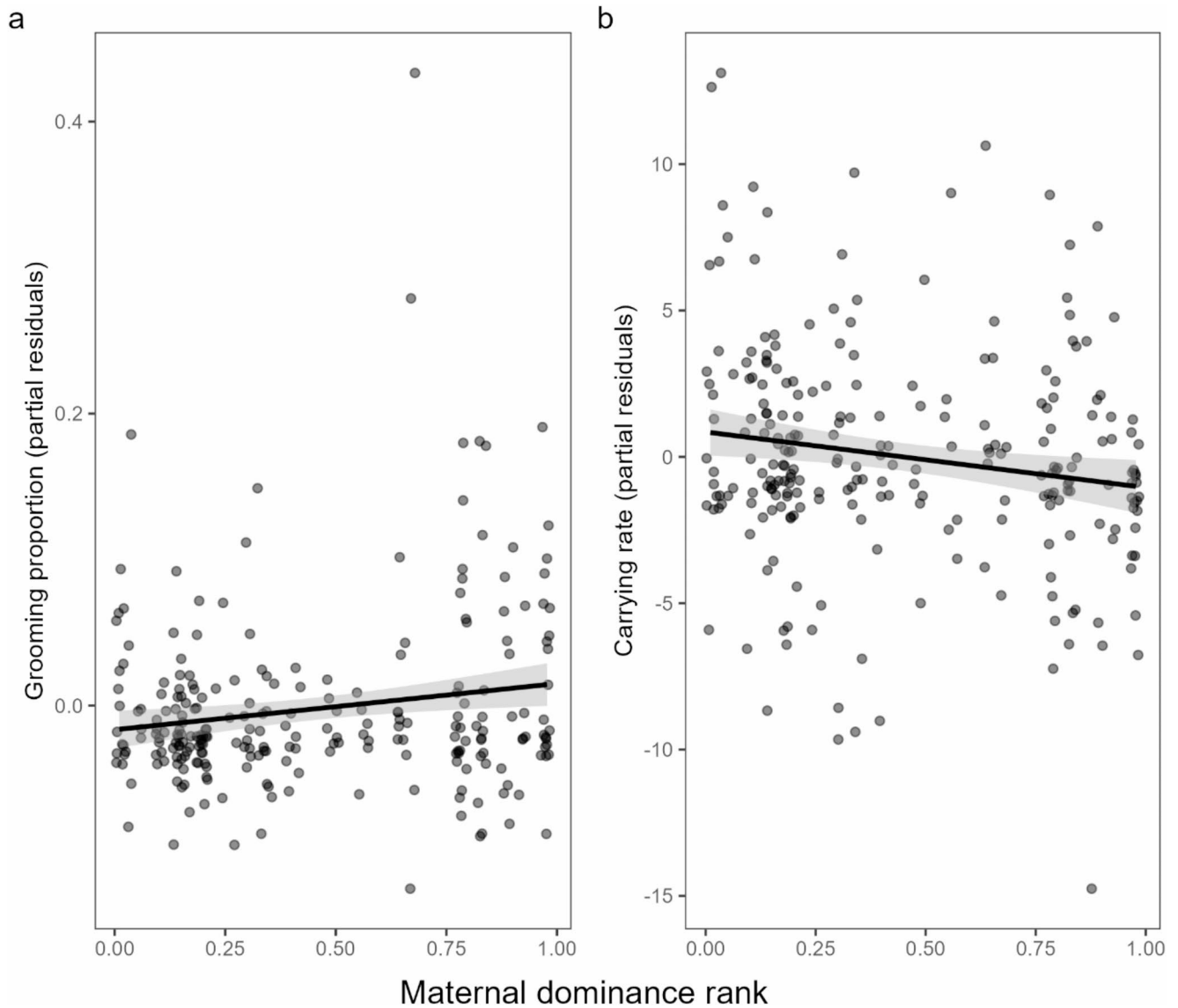


Fig. 2 Partial residuals of **a.** the proportion of time spent grooming per hour and **b.** carrying rates (number of focal observations with at least one event per hour) as a function of maternal dominance rank. Solid

lines indicate fitted regressions, and shaded areas correspond to 95% confidence intervals

Additionally, faster growth in infants born to high-ranking mothers (Setchell et al. 2001) could further accelerate the cessation of maternal carrying. Interestingly, despite having offspring that are often closer in age, high-ranking mandrill mothers spent more time grooming their infants

than low-ranking mothers. Maternal grooming is thought to promote offspring independence while facilitating social development and integration (Meaney 2001). Our findings suggest that high-ranking mothers may use grooming behavior to enhance their offspring's social experience

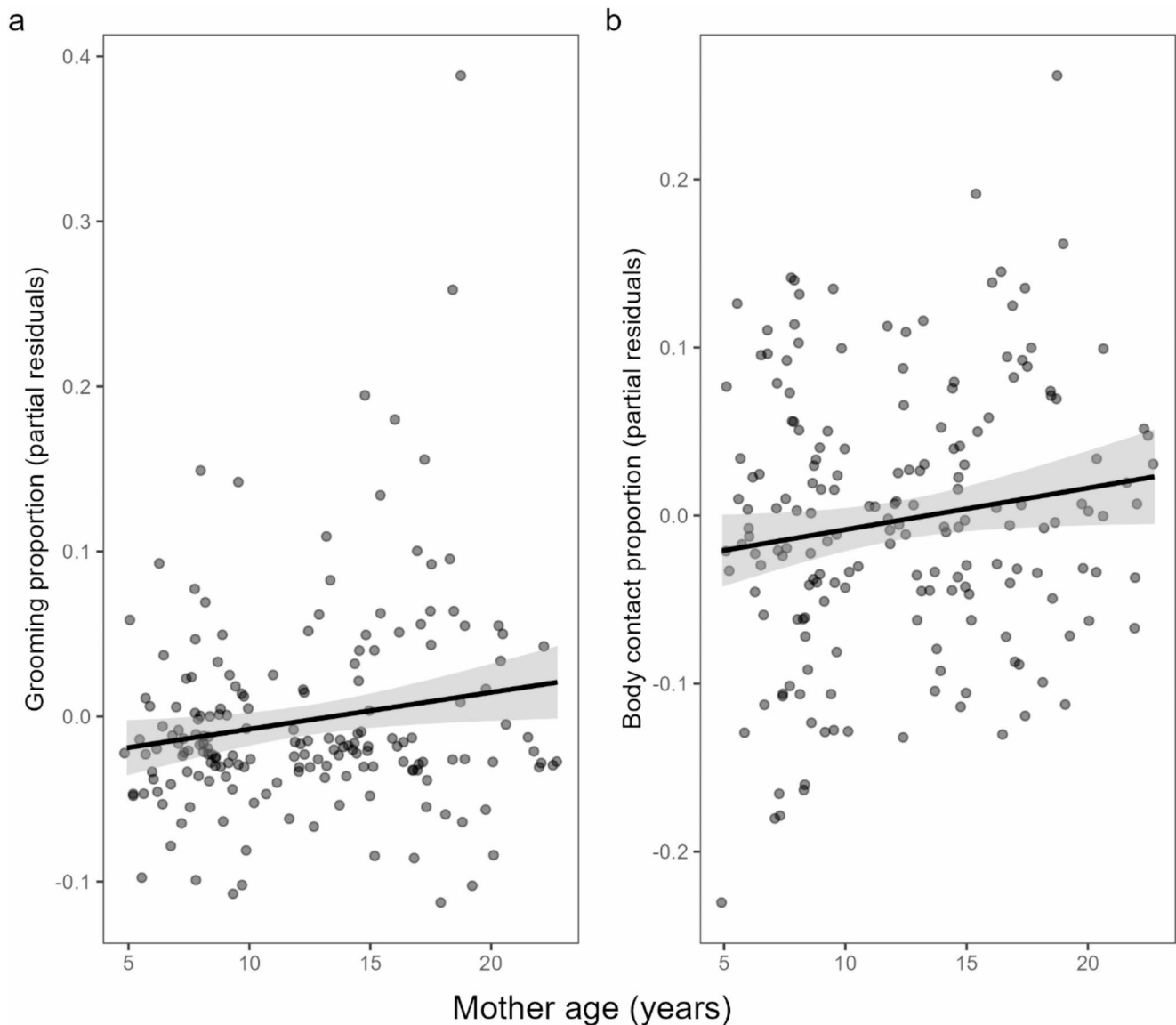


Fig. 3 Partial residuals of **a.** the proportion of time spent grooming per hour and **b.** the probability of body contact (proportion of scans in which the mother and infant were in body contact) as a function of the

mother's age. Solid lines indicate fitted regressions and shaded areas correspond to 95% confidence intervals

during early life, potentially conferring advantages in navigating their complex social environment. This behavioral pattern may reflect the broader reproductive benefits associated with high social rank in mandrills.

Maternal parity and age also emerged as key factors of mother-infant relationships in our study population. Multiparous and older mothers showed higher rates of body contact and spent more time grooming their infants, which are behaviors known to foster infant development and social integration (Maestriperieri et al. 2009). In contrast to findings in other mammals, where primiparous females are often more protective and less rejecting (Clutton-Brock et al. 1982; Fairbanks 1988), we observed that maternal experience in mandrills appears to enhance caregiving skills.

Similarly, in species such as bison (*Bison bison*) and horses, experienced mothers maintain closer contact with offspring during critical preweaning periods, followed by abrupt changes in proximity, suggesting strategic investment during periods of vulnerability (Green 1993; Cameron et al. 2000;). However, maternal behavior is not shaped solely by experience per se. Young mothers, still growing themselves, are likely to face additional nutritional demands that can limit their ability to synchronize activities with their infants (Green 1993). For example, female mandrills typically reproduce before reaching full adult body size (Setchell et al. 2002), and younger individuals spend more time foraging than adults (Nsi Akoue et al. 2017). These factors may

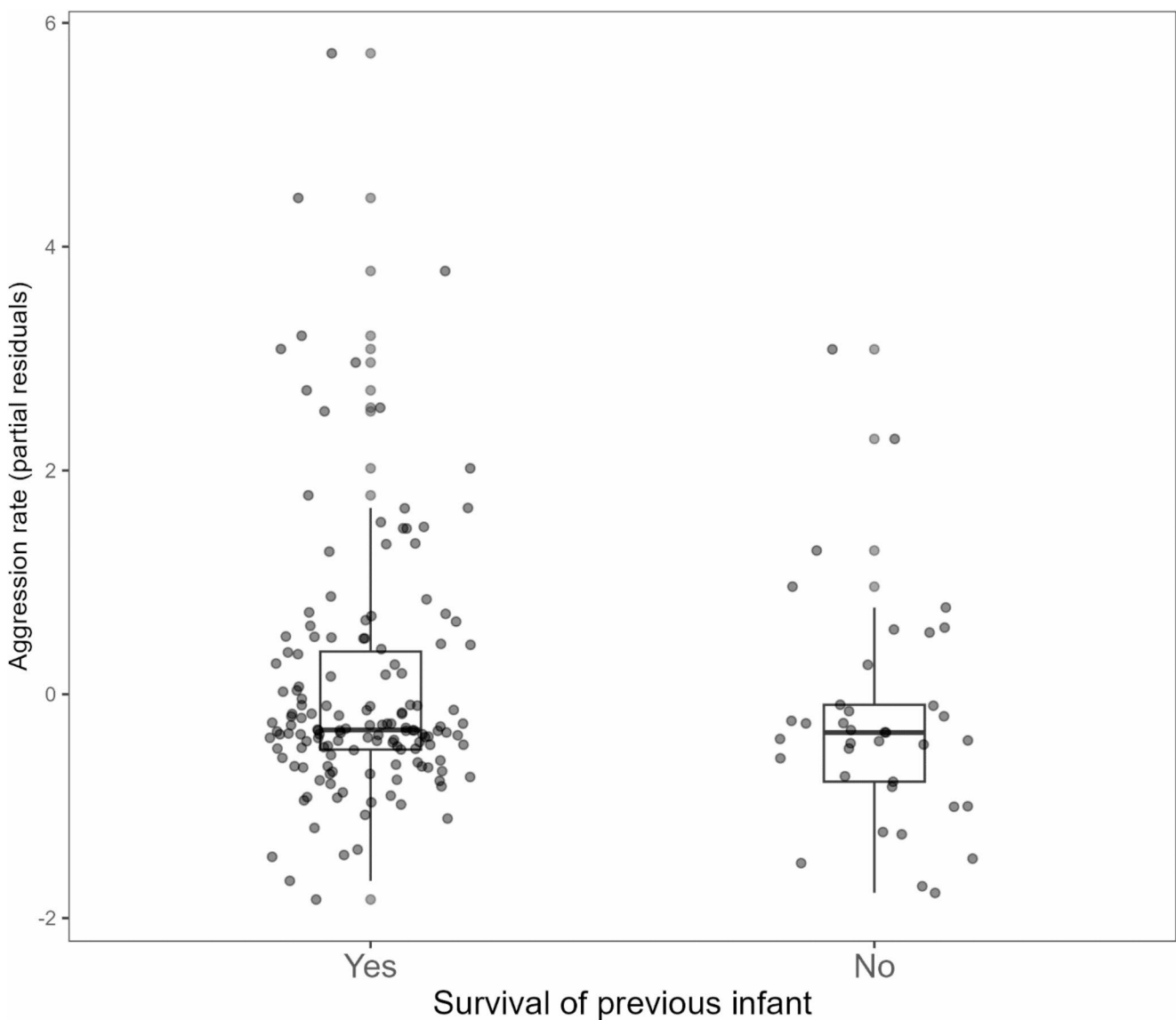


Fig. 4 Partial residuals of maternal aggression rates (number of aggression events per hour) as a function of survival of the previous infant. Boxes represent the interquartile range (IQR), with the lower and upper edges corresponding to the first (Q1) and third (Q3) quartiles,

respectively. The horizontal line within the box indicates the median. Whiskers extend to the smallest and largest values within 1.5 times the IQR from Q1 and Q3

explain the reduced grooming and body contact observed in younger mandrill mothers.

Infant loss and pregnancy failure may, however, alter these rank- and age-related patterns of mother-offspring relationships, as observed in other mammals such as vervet monkeys and horses, where females increase maternal investment following infant loss, probably to secure offspring survival (Fairbanks 1988; Cameron et al. 2000). In mandrills, mothers whose previous infant died were significantly less aggressive toward their next infant. This pattern may reflect not only an adaptive adjustment to increase survival chances but also a reduced need to manage competing demands from multiple close-in-age offspring. Indeed,

mothers of surviving infants often care for another juvenile born in close succession, requiring resource allocation across multiple dependent offspring, which could exacerbate mother-offspring conflicts (Fairbanks 1988). Consistent with this, we found that shorter interbirth intervals between surviving offspring were also associated with increased maternal aggression. Furthermore, the energetic relief provided by the loss of a growing infant might allow mothers to regain a better physical condition, which may result in less frequent displays of rejection or aggression during subsequent caregiving efforts. Distinguishing between these competing hypotheses — adaptive behavioral adjustment *versus* resource reallocation dynamics — lies beyond the

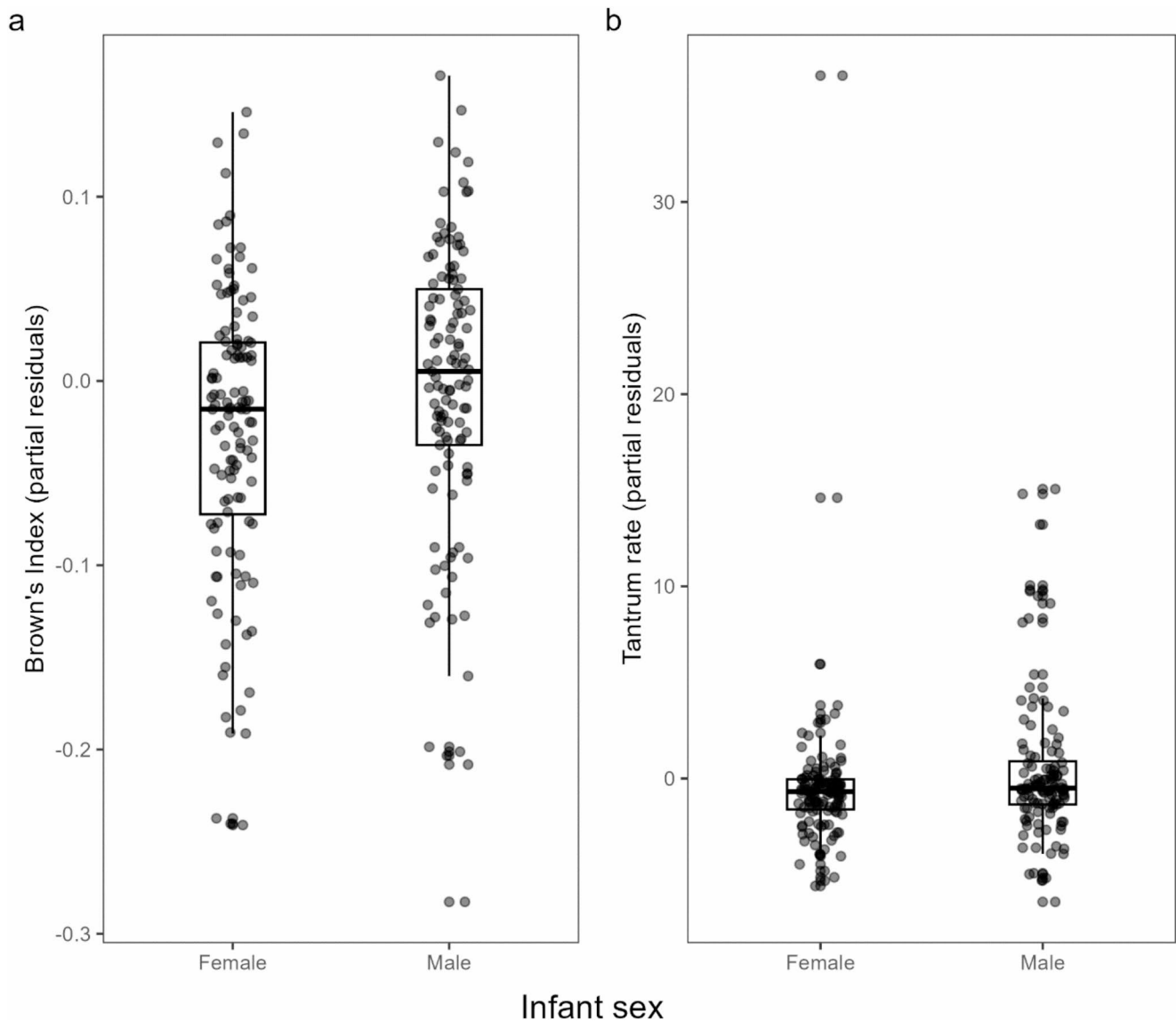


Fig. 5 Partial residuals of **a.** Brown's index and **b.** infant tantrum rates (number of observed events per hour) as a function of infant sex. Dashed lines represent the transition of responsibility. Boxes represent the interquartile range (IQR), with the lower and upper edges corre-

sponding to the first (Q1) and third (Q3) quartiles, respectively. The horizontal line within the box indicates the median. Whiskers extend to the smallest and largest values within 1.5 times the IQR from Q1 and Q3

scope of this study but provides an intriguing avenue for future research, potentially expanding our understanding of maternal strategies in resource allocation and offspring care.

Finally, mandrill mothers were more likely to maintain proximity with their daughters than with their sons, which is consistent with the expected increased maternal investment in the philopatric sex, where reproductive advantages are socially transmitted (Altmann 1980; Hiraiwa-Hasegawa 1993). For example, in chimpanzees, where males are philopatric and mothers can influence their son's reproductive success, male infants are weaned later than females in some populations (Bădescu et al. 2022). Female mandrills are philopatric with lifelong close bonds between mothers and

daughters who inherit their social status (Charpentier et al. 2007, 2020). In this population, juvenile daughters also initiate more grooming with their mothers than juvenile sons (Delaunay et al. 2024). Thus, from an early age, mandrill mothers may foster stronger bonds with their daughters, while encouraging their sons' independence by frequently altering their proximity to them, thereby beginning to prepare them for future natal dispersal. In addition, in highly sexually dimorphic species such as mandrills, where male reproductive skew is high, the advantages provided by sons may be more variable. Overall, daughters may confer greater average fitness advantages than sons due to lifelong social support. The more frequent tantrums observed

in male infants may reflect these sex-biased differences in proximity maintenance. However, similar to other species with pronounced sexual dimorphism (Lee and Moss 1986; Piedrahita et al. 2014; Eckardt et al. 2016), male mandrills grow at a faster rate than females, as early as the first year of life (males: 2.25 kg/year versus females: 1.85 kg/year; Wickings and Dixson 1992). Therefore, males may demand more investment because of their higher growth requirements, which may explain the increased frequency of tantrums observed in these individuals.

In conclusion, this study reveals the complex dynamics of mother–infant relationships in mandrills. While the gradual shift toward infant independence is a common pattern in mammals, mandrills stand out among highly sexually dimorphic species because of the influence of maternal dominance rank and sex-specific investment strategies. Our findings emphasize the critical role of social factors, such as rank inheritance and lifelong social bonds, in shaping maternal behavior and offspring development. Overall, our results underscore the adaptive flexibility of maternal behaviors, demonstrating how maternal care can be fine-tuned to optimize both individual survival and long-term reproductive success in a species with complex social dynamics.

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Author contributions BR-T, MJEC, and PMK conceived the study and design. BR-T, AC, LS, MDP, GH, MK, JMdB, SA and MH collected the behavioral data. BR-T analyzed the data. BR-T, MJEC, and PMK wrote the manuscript with feedback from AB. MJEC and AB manage the long-term project that has generated the data. MJEC and MH manage the associated databases. MJEC and PMK acquired the funding. All authors read and approved the final manuscript.

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Data availability The dataset supporting this article is available as supplementary material.

Declarations

Ethical approval This study was approved by an authorization from the CENAREST Institute (permit number, AR017/22/MESRSTCA//

CENAREST/CG/CST/ CSAR) and followed all applicable international, national, and/or institutional guidelines for the care and use of animals.

Conflict of interest The authors declare that they have no competing interests.

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Authors and Affiliations

Berta Roura-Torres^{1,2,3}  · Alice Baniel³  · Anna Cryer⁴ · Loïc Sauvadet⁴ · Mélyssa De Pastors⁴ · George Havill⁴ · Mélodie Kreyer⁴  · Jade Meric de Bellefon⁴ · Steven Abaga⁴ · Mélanie Harté⁴ · Peter M. Kappeler^{1,2}  · Marie J. E. Charpentier^{3,5} 

✉ Berta Roura-Torres
rouratorresberta@gmail.com

¹ Department of Sociobiology/Anthropology, Institute of Zoology and Anthropology, Johann-Friedrich-Blumenbach, Georg-August University Göttingen, Kellnerweg 6, 37077 Göttingen, Germany

² Behavioral Ecology and Sociobiology Unit, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany

³ ISEM, UMR5554 – University of Montpellier/CNRS/IRD/EPHE, Place Eugène Bataillon (cc065), Montpellier 34095, France

⁴ Projet Mandrillus, Parc de la Lékédi, BP 52, Bakoumba, Gabon

⁵ Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Bücklestraße 5, 78467 Konstanz, Germany