Transition to siblinghood in a wild chacma baboon population

Axelle Delaunay [a, *] , Alice Baniel [b] , Jules Dezeure [a] , Alecia J. Carter [c] ,
Guy Cowlishaw [d] , Marie J. E. Charpentier [a, 1] , Elise Huchard [a, 1]

[a] Institute of Evolutionary Science of Montpellier (ISEM), Univ Montpellier, CNRS, IRD, Montpellier, France
[b] Institute for Advanced Study in Toulouse (IAST), Université Toulouse 1 Capitole, Toulouse, France
[c] Department of Anthropology, University College London, London, U.K.
[d] Institute of Zoology, Zoological Society of London, London, U.K.

ARTICLE INFO

In monotocous mammals (i.e. where females produce one offspring at a time), most juveniles will experience the birth of a younger sibling in their life. Transition to siblinghood (TTS) has rarely been studied in primates, although it reflects the last step in the shift of maternal investment from one offspring to the next and could thus represent a critical moment for mother−offspring conflict and sibling competition. Here, we used behavioural data on juvenile primates that had recently experienced, or not, the birth of a younger sibling to investigate changes in mother−juvenile relationships during TTS in a wild population of chacma baboons, *Papio ursinus*. We show that (1) mother−juvenile spatial associations remained stable; (2) mothers did not decrease their probability of initiating proximity or affiliation with their juvenile; and (3) juveniles initiated proximity and affiliation more frequently towards their mothers, and showed more signs of anxiety, after the birth of their younger sibling. Taken together, these findings suggest that juveniles with a younger sibling solicit their mother more often and seek more maternal attention than juveniles without. Overall, mother−offspring conflict could extend into the postweaning period, during which more subtle maternal resources, such as maternal attention, could be at stake in competitive sibling relationships.

© 2023 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Parental investment is defined as any type of investment a parent can provide to its offspring that will enhance the offspring's fitness at the cost of the parent's future reproduction (Trivers, 1972). In a seminal paper, Trivers (1974) argued that natural selection should favour, in offspring, the expression of traits favouring the monopolization of parental resources, above the level that parents may be willing to provide. This difference in the optimal amount of parental investment is triggered by an asymmetry in genetic relatedness between the different family members: an offspring is twice as related to itself as it is to its siblings, while a parent is equally related to all offspring. This genetic conflict of interest is predicted to trigger conflicts over the amount and duration of parental investment, not only between parents and offspring, but also between siblings, which should all try to maximize their share of parental investment until the costs for their siblings decrease their own inclusive fitness.

Sibling competition has found empirical support in a wide range of taxa from insects to mammals (see for reviews: Mock & Parker 1998; Drummond, 2006) where it can largely impact offspring's development, with long-term consequences in three areas: morphology (e.g. insects: Schrader et al., 2018; birds: de Kogel & Prijs, 1996; mammals: Fisher et al., 2018; Hofer & East, 2008), physiology (e.g. birds: Drummond & Rodríguez, 2013; Nettle et al., 2015; Verhulst et al., 2006; mammals: Fey & Trillmich, 2008; Guenther & Trillmich, 2015; Stauffer et al., 2018) and behaviour (e.g. birds: Bebbington et al., 2017; Ekman et al., 2002; mammals: Guenther & Trillmich, 2015; Hudson et al., 2011) and even lead to siblicide (e.g. birds: Braun & Hunt, 1983; Fujioka, 1985; Lougheed & Anderson, 1999; mammals: Andersen et al., 2011; Hofer & East, 2008). However, our understanding of family competition suffers from a taxonomic bias: most studies have focused on brood- or litter-rearing species (especially in mammals, see for reviews: Drummond, 2006; Hudson & Trillmich, 2008; Roulin & Dreiss, 2012). Most of the theoretical models and evolutionary hypotheses have thus been developed for same-age siblings and within-brood competition (Hudson & Trillmich, 2008), leaving the competition between siblings of different ages virtually unstudied.

In long-lived species, such as monotocous mammals, which generally produce and nurse one offspring at a time (Altmann, 1980; Clutton-Brock et al., 1983), siblings could compete for resources other than milk (Hudson & Trillmich, 2008), meaning that sibling competition can last beyond weaning age. In these species, offspring may form long and enduring bonds with their mother that can extend far beyond independency (e.g. yellow baboons, *Papio cynocephalus*: Silk, Alberts, et al., 2006; Silk, Altmann, et al., 2006; Asian elephants, *Elephas maximus*: Lynch et al., 2019; red deer, *Cervus elaphus*: Clutton-Brock et al., 1982) killer whales, *Orcinus orca*: Weiss et al., 2023, and exhibit a period of postweaning juvenility, during which they keep benefiting from maternal care such as social support, facilitated access to food or protection against predators (Clutton-Brock, 1991). Maternal presence during the postweaning developmental period improves offspring growth (e.g. chimpanzees, *Pan troglodytes*: Samuni et al., 2020), and increases future reproductive success and longevity (chimpanzees: Crockford et al., 2020, Stanton et al., 2020; bonobos, *Pan paniscus*: Surbeck et al., 2011; red deer: Andres et al., 2013), potentially through prolonged access to such forms of maternal care. Monopolizing such resources might be advantageous for offspring, and could thus induce competition between siblings.

In line with this, several empirical studies show that sibling competition can have substantial fitness consequences in monotocous species. In Galapagos fur seals, *Arctocephalus galapagoensis*, and sea lions, *Zalophus wollebaeki*, calves whose mother is still nursing the older sibling experience reduced growth and increased mortality risk (Trillmich & Wolf, 2008). In rhesus macaques, *Macaca mulatta*, short interbirth intervals reduce the survival to adulthood for the older offspring and the survival to weaning for the younger one (Lee et al., 2019). In female yellow baboons, having a close-in-age younger sibling nearly doubles the mortality risk during adulthood (Tung et al., 2016). Moreover, this effect has intergenerational consequences because adult females whose mother had a close-in-age younger sibling further experienced higher offspring mortality (Zipple et al., 2019). In humans as well, short interbirth intervals increase offspring mortality risk (Conde-Agudelo et al., 2006; Rutstein, 2005; Wendt et al., 2012). Overall, these studies show that the dilution of maternal care between different-age offspring has fitness costs, setting the conditions under which sibling competition over access to maternal resources should evolve.

Regarding the behavioural mechanisms at play, while many primate studies have focused on mother—offspring conflicts during the weaning period or around a mother's cycle resumption (Barrett & Henzi, 2000; Bateson, 1994; reviewed in Maestripieri, 2002), the birth of a younger sibling has been somewhat overlooked. This is striking as the arrival of a younger sibling is the last step in the mother's shift from her current offspring to the next one and could thus represent a critical moment for both mother—offspring conflict and sibling competition. A few studies on captive or free-ranging cercopithecines showed that the birth of a younger sibling induces an abrupt decrease in time spent in contact with, or in proximity to, the mother and in the rate of mother—offspring interactions, primarily driven by the juvenile itself (Devinney et al., 2001; DiGregorio et al., 1987; Holman & Goy, 1988; Schino & Troisi, 2001). Maternal rejection and aggression also increased, often associated with signs of stress and 'depression' in the offspring (Bolwig, 1980; Devinney et al., 2001; DiGregorio et al., 1987; Holman & Goy, 1988). In bonobos, juveniles face an increase in cortisol and a decrease in neopterin levels that can last more than 6 months after the birth of their younger sibling (Behringer et al., 2022). The behavioural transition to siblinghood has been more thoroughly studied in humans: it is often characterized by a decrease in maternal care and in the rate of mother—offspring interactions, an increase in the rate of confrontational behaviour with the mother and a reversal in who initiates most interactions, with children (instead of mothers) becoming the primary initiators (Dunn et al., 1981; Dunn & Kendrick, 1980; Stewart et al., 1987; Volling, 2012). Children can also show signs of distress and exhibit more demanding behaviours (Dunn et al., 1981; Volling, 2012). Finally, a striking aspect emerging from the human literature is the high interindividual variability in children's behavioural adjustment to the birth of a sibling (Dunn et al., 1981; Volling, 2012, 2017). Poor behavioural adjustment (e.g. higher frequency of tantrums and jealousy events towards the younger sibling) is associated, possibly causally, with lower quality relationships between siblings later in life (Brody, 1998; Pike et al., 2005), which could potentially be costly as siblings' relationships and support during adulthood can promote fitness (Pollet & Hoben, 2011).

In this study, we investigated changes in mother—juvenile relationships following the birth of a younger sibling in a wild chacma baboon population, *Papio ursinus*. Baboons typically live in matrilineal, multimale—multifemale societies, where females are philopatric and males disperse from their natal group around the age of 7—8 years (Cheney et al., 2004). Females maintain hierarchical and differentiated social bonds and give birth to one offspring every 2 years on average (Cheney et al., 2004; Dezeure, Baniel, et al., 2021), an interbirth interval somewhat closer to human traditional societies than to great apes (Kramer, 2005). Offspring have a long developmental period and weaning occurs gradually during the second year of life (Carboni et al., 2022; Dezeure, Baniel, et al., 2021), which is characterized by elevated infant mortality (Altmann & Alberts, 2003a). Unweaned infants are sometimes targets of infanticide in this species, with minimal risks to weaned, older offspring (Palombit et al., 2000). In baboons, as in most primates, mothers form long-lasting bonds with their offspring, which facilitate the transition to feeding autonomy (e.g. Lynch et al., 2020) and subsequently translate into preferential grooming relationships and occasional support during conflicts as long as offspring remain in their natal group. All these resources likely increase offspring survival, as observed in chimpanzees (Nakamura et al., 2014; Stanton et al., 2020), and may generate competition among siblings. Specifically, maternal support often allows younger sisters to outrank their older sisters, which suggests that, for a female, having a younger sister could induce lifetime costs through the loss of maternally transmitted social capital (Pereira, 1989).

In three social groups of chacma baboons from Namibia, we investigated immediate changes in the mother—juvenile relationship during the transition to siblinghood (hereafter, TTS), by comparing mother—juvenile interactions among juveniles with no younger sibling and those of comparable ages that recently experienced the birth of a younger sibling. First, we predicted (P1.1) that the amount and quality of affiliative relationships, specifically grooming interactions, between the mother and the juvenile would decrease after the birth of a new infant, with (P1.2) a shift in patterns of initiations of such interactions, from mostly mother-initiated before the birth of the sibling to mostly juvenile-initiated interactions afterwards, as found in humans. Second, we predicted that juveniles (P2.1) would associate less often with their mother, and (P2.2) would become primarily responsible for initiating and maintaining spatial proximity to their mother after the birth of a younger sibling. Third, we predicted (P3) that juveniles that had recently experienced the birth of a younger sibling would exhibit more self-directed behaviours, generally indicating anxiety (Castles et al., 1999; Maestripieri et al., 1992; Palagi & Norscia, 2011).

METHODS

Study Site and Population

We studied wild chacma baboons living in Tsaobis Nature Park, on the edge of the Namib Desert (22°23′S, 15°44′E), Namibia. We collected data on three well-habituated troops (J, L and M, the latter a fission group from J since 2016) over three observational periods: July–August 2017, September–December 2018 and April–July 2019. The groups were followed every day from dawn to dusk by observers on foot, collecting demographic, life history and behavioural data. All individuals, including infants, are individually recognizable (Huchard et al., 2013).

Individual Data

Individual birth dates were assessed with certainty when field observers were present during the birth ($N = 10$ offspring), or were estimated using two different methods, depending on the available information: (1) infant's coloration using a standardized, validated protocol, when the infant was not fully grey when first observed ($N = 16$, median date uncertainty $= 41$ days, see Dezeure, Dagorrette, et al., 2021), (2) otherwise, mother's reproductive states in the previous months ($N = 32$, median date uncertainty $= 18$ days). Overall, age uncertainty in our sample ranged from 0 to 130 days (median $= 10$ days).

Female parity was known from life history records and was defined as primiparous (between the birth of the first-born offspring and the second one), or multiparous (after the birth of the second offspring). Female dominance ranks were calculated separately for each group and each year, using ad libitum data and focal observations of agonistic and approach–avoidance interactions: supplants, displacements, attacks, chases and threats (Huchard et al., 2010). We computed a linear hierarchy using Matman 1.1.4 (Noldus Information Technology, 2013), and transformed it into a proportional hierarchy with relative ranks (i.e. absolute rank divided by number of adult females in a group), assigning each female one relative rank per year, ranging from 0 (low-ranking) to 1 (high-ranking). We used proportional ranks rather than simple ordinal ranks because they allow us to control for group size across different social groups and/or observational periods. Proportional ranks have recently been shown to better predict some female traits associated with reproductive pace (Levy et al., 2020), and could thus better predict patterns of maternal care during the postweaning period.

Behavioural Observations and Sample Selection

We collected 1401 h of focal observations from 71 offspring born to 37 females (mean $\pm$ SD $= 19.7 \pm 9.9$ h of observation per individual, range 1.3–38.6 h) using 20 min long focal observations ($N = 57.6 \pm 27.9$ focal observations per individual, $N = 4086$ in total). Focal individuals were aged from 1 to 34 months old (mean $\pm$ SD $= 16.1 \pm 8.7$ months old). Focal observations were spread equally across the day (split evenly into four 3 h time blocks), and focal individuals were chosen randomly and sampled no more than once per half-day. We recorded the duration and direction of grooming interactions with the mother and the occurrence of self-scratches, a self-directed behaviour generally indicating anxiety. Maintenance of spatial proximity was assessed by recording every close approach or leave (to and from 1 m) between the focal individual and its mother. In addition, we collected scans during focal observations every 5 min (i.e. up to five scans for each 20 min focal observation, resulting in 20 182 scans in total across 4086 focal observations), and recorded whether the mother was in sight, and if yes, her distance to the focal individual. If the mother was out of sight, observers indicated the number of metres around the focal individual for which they could guarantee that the mother was not in sight (range 1–100 m). Other cases where visibility was too obstructed (e.g. when the focal individual was in sight but in a dense bush) were recorded as missing data.

In this study, we aimed to characterize the immediate behavioural response to the birth of a younger sibling. To do so, we used a cross-sectional approach, comparing juveniles that recently experienced, within the last 3 months, the birth of a younger sibling to juveniles of similar ages that did not. Juveniles that had experienced the birth of a sibling in the more distant past were excluded from this study. This 3 months window was chosen to maximize our chances of detecting changes in behaviour that immediately follow the birth of an infant, i.e. reasonably close to the birth event while still ensuring a decent sample size of observations. In our sample of focal observations, juveniles that had recently experienced the birth of a younger sibling were 17–29 months old. Therefore, we restricted our data set to any juvenile in this age range (17–29 months) that had either no younger sibling ($N = 28$) or a younger sibling born within the last 3 months ($N = 18$). Individuals that were followed both before and after the birth of their younger sibling were included in each group, respectively. We collected a total of 1525 focal observations and 7581 scan observations on 38 individuals (eight individuals were observed both with and without a younger sibling).

Statistical Models

Mother–juvenile grooming relationships

To test predictions P1.1 and P1.2, we used focal data during which we recorded the duration and direction of each grooming event. First, for each observation, we recorded whether the focal juvenile groomed its mother at least once (binary: yes/no, model 1), and whether it received grooming from its mother (binary: yes/no, model 2). The probability of giving or receiving grooming from the mother during a focal observation (models 1 and 2, respectively) was modelled with two generalized linear mixed models (GLMMs) with a binomial error structure. Second, we extracted the total duration (s) the juvenile spent grooming its mother (model 3) or being groomed by its mother (model 4) during a focal observation. We ran two GLMMs with a negative binomial distribution and a log-link function.

Mother–juvenile spatial proximity

To test prediction P2.1, we used scan data to estimate how often a juvenile was found in close proximity to its mother. For each scan observation (recorded every 5 min), we recorded whether the focal juvenile was in proximity (1) or not (0) to its mother. We considered two distinct ranges of proximity: within 1 m (model 5) and 5 m (model 6) of the mother. We ran two GLMMs with a binomial error structure.

Second, to test prediction P2.2 and characterize juveniles' responsibility in the maintenance of spatial association with their mother, we used focal observation data. For each focal observation, we established whether the juvenile initiated an approach to, or a leave from, its mother within a circle of 1 m radius (1) or not (0) (models 7 and 8, respectively). We then determined whether the juvenile received an approach or a leave from its mother (1) or not (0) (models 9 and 10, respectively). We ran four GLMMs with a binomial error structure. In addition, we computed 'Hinde's index' for each mother–juvenile dyad, calculated as the percentage of approaches minus the percentage of leaves initiated by the juvenile (Hinde & Atkinson, 1970). This index ranges from -100 (the mother is fully responsible for maintaining proximity) to $+100$ (the juvenile is fully responsible for maintaining proximity). We calculated

one index per dyad for each observational period (i.e. field season) and for each 'sibling status' (i.e. experienced TTS or not). When the focal juvenile experienced TTS during the period, we computed the Hinde's index before and after the birth event. We then tested whether the average Hinde's index for a given sibling status differed from zero using a one-sample Student's t test ($N = 13$ indices on juveniles with a younger sibling, $N = 22$ on juveniles without a younger sibling). We also tested whether the average Hinde's index differed between juveniles with or without a sibling using a linear model ($N = 34$ indices across both groups). For each test, if a dyad had several indices (because it was observed during two different observational periods or because a sibling was born during a given period, $N = 28$ individuals with one index, $N = 9$ with two indices and $N = 1$ with three indices), we randomly selected one of them to avoid pseudoreplication.

Juvenile self-directed behaviour

To monitor the anxiety level of juveniles, we calculated the number of self-scratches per focal observation and ran a GLMM with a negative binomial distribution and a log-link function (model 11).

Fixed and random effects

For each GLMM, we tested the effect of having recently experienced the birth of a younger sibling (yes/no), as well as the following control variables: focal juvenile's sex, age (in months), birth rank (first-born versus later born), and maternal rank. We also tested the interaction terms between the recent birth of a younger sibling and the focal juvenile's age and sex (except for model 3 because of a limited and unbalanced sample size) because mother-offspring relationships and, thus, juveniles' reaction to TTS may differ between the sexes and change with age. We further included three additional fixed effects as controls: (1) group identity, to account for potential differences between groups; (2) in binomial models, duration of the focal observation (s; except models 5 and 6 using scan data) or, in negative binomial models, the log-transformed duration of focal observation as an offset; and (3) in model 11, year of observation because preliminary analyses showed that this variable had a strong effect only on self-scratch frequency.

We included the focal juvenile identity as a random effect in all models to control for repeated focal observations within juveniles. In models 5 and 6, we initially fitted the focal observation identity as a random effect to account for the nonindependence of multiple scan observations within the same focal observation. However, adding this random effect caused convergence problems. We therefore restricted our data set to two scans per focal observation, which were separated by >15 min and for which the mother—focal juvenile distance was documented ('out of sight' or 'in sight' with the approximated distance; missing data were removed). We therefore assumed that such scans were independent from each other and omitted the 'focal observation' random effect from our models to facilitate model convergence.

In the linear model analysing Hinde's index, because of limited sample size ($N = 34$), we only included the three following explanatory variables to avoid overparameterization: presence of a younger sibling, focal juvenile's sex and age (average age in months across the observational period).

The structure of each model, the different fixed and random effects and sample sizes are summarized in Appendix Table A1.

Note that several other variables could account for some variability in mother—juvenile relationships throughout the TTS, such as the mother's reproductive stage or the presence or number of older siblings. In the first case, pregnant mothers may reduce their level of care, but it was impossible to test with this cross-sectional design because mother's reproductive stage was correlated with the presence of a younger sibling (i.e. mothers of juveniles with a younger sibling are all lactating, while mothers of those without are either cycling or pregnant). In the latter case, older nonadult siblings may represent potential compensatory social partners, or may alternatively contribute to the dilution of the level of maternal care received by each sibling. Therefore, we reran all models with the number of older immature siblings as an additional fixed factor, setting the maximum age threshold at 4 years old for older siblings, as some females can reach menarche at this age in our population (results are presented in Appendix Tables A2—A7). This additional control variable was never found to exert a significant effect on our response variables, and did not improve our model fits, so we present the results without it in the main text.

Statistical analysis

All statistical analyses were conducted using the R Studio software (version 4.0.2, R Core Team, 2020). We ran mixed models using the function 'glmer' from the lme4 package (Bates et al., 2015) for binomial models and 'glmmTMB' from the glmmTMB package (Brooks et al., 2017) for Poisson and negative binomial models. To control for the focal juvenile's age in all analyses, we started by investigating the developmental pattern of each response variable, i.e. the shape of its relationship with age. To do so, we ran generalized additive mixed models (GAMMs), using the 'gam' function of the mgvc package (Wood, 2003), and fitted univariate models using a smoothing function, a linear function and a second- or third-degree polynomial function to model the effect of age (offsets and random effects were also included). We then compared model fits and selected the models with the lowest AIC (Zuur et al., 2009). Linear, first-order functions of age produced the best fit to all types of data analysed, so we subsequently used linear regression between the response variable and age. When we obtained singular fits, we confirmed the results by running a Bayesian approach, using the 'bglmer' function from the blme package (Dorie et al., 2021). When a Poisson model was overdispersed, we compared its fit with a type I negative binomial model and a type II negative binomial model and selected the model with the lowest Akaike's information criterion (AIC; Zuur et al., 2009). Following this test, models 3 and 4 were run with a type I negative binomial distribution and model 11 was run with a type II negative binomial distribution. All quantitative variables were z-transformed (mean = 0; SD = 1) using the 'scale' function from the car package (Fox & Weisberg, 2019) to facilitate model convergence, as well as to compare effect sizes across estimates (Harrison et al., 2018). To diagnose the presence of multicollinearities, we calculated the variance inflation factor (VIF) for each predictor in each model using the 'vif' function from the car package (Fox & Weisberg, 2019). VIFs were <2 in all cases, suggesting that multicollinearities did not impact coefficients' estimation in our models. To test the significance of fixed factors for each model, we used the likelihood ratio test (LRT) and associated P values computed by the 'drop1' function and calculated the 95% Wald confidence intervals. Nonsignificant interactions were removed from the full model to limit the risk of overparameterization and facilitate the interpretation of simple effects. Finally, we assessed the significance of our full model by comparing its fit to the equivalent null model (intercept only model, including the random effects) using an LRT. We further checked the distribution of the residuals using 'simulateResiduals' from the DHARMa package (Hartig & Lohse, 2021).

Ethical Note

This study was strictly observational and relied on behavioural data collected noninvasively on animals well habituated to human observers. Our research procedures were evaluated and approved by

the Ethics Committee of the Zoological Society of London and adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching. This research was carried out with the permission of the Namibian Ministry of Environment and Tourism (MET), the Ministry of Land Reform and the National Commission on Research, Science and Technology. Our research was conducted under MET permit numbers 2303/2017, RPIV00392018/2019.

RESULTS

Mother–Juvenile Grooming Relationships

We first investigated whether a juvenile's grooming relationship with the mother was affected by the birth of a younger sibling (P1.1 and P1.2). Both the probability and the duration of grooming received from the mother were independent from the birth of a younger sibling (probability: odds ratio, OR = 0.89; duration: mean ± SD = 36.5 ± 13.8 s per observation; Tables 1 and 2, Fig. 1b, d). In contrast, juveniles with a younger sibling had a significantly higher probability of grooming their mother (OR = 1.71; mean probability ± SD with a sibling: 0.10 ± 0.07; without a sibling: 0.05 ± 0.04) and spent significantly more time grooming their mother (20.9 ± 17.3 s per focal observation for juveniles with a sibling versus 9.1 ± 7.2 for those without; Tables 1 and 2, Fig. 1a, c). Juvenile males had a significantly lower probability of grooming their mother and spent less time doing so than juvenile females (OR = 0.22, Tables 1 and 2). In contrast, the probability and duration of grooming received from the mother was independent of juveniles' sex (Tables 1 and 2). The probability of grooming the mother and its duration both increased significantly with age (an increase in 1 SD in age increased grooming likelihood by 49%, OR = 1.49, Tables 1 and 2), while the probability of receiving grooming from the mother and its duration tended to decrease with juvenile age (OR = 0.84, Tables 1 and 2).

Mother–Juvenile Spatial Proximity

Mother–juvenile proximity was not influenced by the birth of a younger sibling (P2.1): juveniles with or without a younger sibling had the same probability of being within 1 m or 5 m of their mother during a scan observation (OR = 0.92 and 1.12, respectively, Table 3). Males were significantly less likely to be within 1 m or 5 m of their mother than females (OR = 0.53 and 0.72, respectively, Table 3). Juveniles born to higher-ranking females were significantly more likely to be within 5 m of their mother (OR = 1.21, Table 3). Overall, juveniles were significantly less likely to be within 1 m or 5 m of their mother as they grew older (OR = 0.81 and 0.80, respectively, Table 3).

Juveniles that had recently experienced the birth of a younger sibling were, however, significantly more likely to approach (OR = 1.74, mean probability ± SD = 0.24 ± 0.06 for juveniles with a sibling versus 0.18 ± 0.05 for juveniles without) and leave (OR = 1.71, mean probability ± SD = 0.20 ± 0.05 for juveniles with a sibling versus 0.14 ± 0.05 for juveniles without) their mother than juveniles that did not yet have a younger sibling (P2.2, Table 4, Fig. 2a, b). Males were significantly less likely to leave their mother than females (OR = 0.66), while juveniles born to high-ranking females were significantly more likely to approach and leave their mother (OR = 1.19 and 1.21, respectively, Table 4). Overall, the probability of approaching and leaving the mother decreased with age (OR = 0.81 and 0.83, Table 4).

The probability of being approached by the mother (P2.2) was also influenced by the interaction between the sex of the focal juvenile and the birth of a younger sibling: juvenile females with a younger sibling were less likely to be approached by their mother (mean probability ± SD = 0.05 ± 0.02) than those without a sibling (0.08 ± 0.04), while males with a younger sibling were more likely to be approached by their mother (0.08 ± 0.02) than those without a sibling (0.05 ± 0.04, Table 5, Fig. 2c). Juveniles born to high-ranking females were also significantly more likely to be approached by their mother than those born to low-ranking females (OR = 1.74, Table 5). The probability of being left by the mother was not influenced by the birth of a younger sibling, and our model did not differ from the null model ($\chi^2 = 13.90$, $P = 0.084$; Table 5, Fig. 2d).

Finally, average Hinde's indices were positively and significantly different from zero both for juveniles with (one-sample t test: $N = 13$, $t = 6.2$, $P < 0.001$) and without (one-sample t test: $N = 22$,

Table 1
Results of the mixed models analysing the probability of a juvenile grooming (model 1) or receiving (model 2) grooming from its mother during a focal observation

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P
				2.5%	97.5%		
Model 1: probability of grooming the mother	Intercept		−2.524	−3.063	−1.985	—	—
	Presence of a younger sibling (No)	Yes	**0.539**	**0.023**	**1.054**	**4.107**	**0.043**
	Juvenile's age		**0.397**	**0.117**	**0.678**	**9.026**	**0.003**
	Juvenile's sex (Female)	Male	**−1.476**	**−2.106**	**−0.846**	**20.622**	**<0.001**
	Juvenile's birth rank (Later born)	First-born	0.184	−0.534	0.901	0.246	0.620
	Mother's rank		0.060	−0.222	0.342	0.171	0.679
	Troop (J)	L	0.133	−0.491	0.758	3.294	0.193
		M	−0.889	−2.035	0.257		
	Focal observation duration		0.065	−0.137	0.266	0.394	0.530
Full −Null model comparison: $x^2_2 = 46.605$, $P < 0.001$ (AIC full = 711.11, AIC null = 741.71)							
Model 2: probability of being groomed by the mother	Intercept		−1.632	−1.993	−1.270	—	—
	Presence of a younger sibling (No)	Yes	−0.114	−0.495	0.268	0.350	0.554
	Juvenile's age		−0.179	−0.371	0.013	3.693	0.055
	Juvenile's sex (Female)	Male	−0.234	−0.601	0.133	1.828	0.176
	Juvenile's birth rank (Later born)	First-born	−0.189	−0.679	0.301	0.603	0.437
	Mother's rank		−0.017	−0.199	0.166	0.042	0.838
	Troop (J)	L	0.099	−0.306	0.504	5.373	0.068
		M	−0.638	−1.291	0.016		
	Focal observation duration		0.141	−0.009	0.292	3.515	0.061
Full-Null model comparison: $x^2_2 = 17.211$, $P = 0.028$ (AIC full = 1252.8, AIC null = 1254.0)							

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 1525 focal observations on 38 juveniles ($N = 18$ with a younger sibling, $N = 28$ without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant.

Table 2
Results of the mixed models analysing the grooming time (s) given to the mother (model 3) or received from the mother (model 4) by the juvenile during a focal observation

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P
				2.5%	97.5%		
Model 3: time spent grooming the mother	Intercept		−4.460	−5.147	−3.773	–	–
	Presence of a younger sibling (No)	Yes	**0.519**	**0.032**	**1.007**	**4.284**	**0.038**
	Juvenile's age		**0.394**	**0.128**	**0.660**	**9.957**	**0.002**
	Juvenile's sex (Female)	Male	**−1.454**	**−2.068**	**−0.840**	**21.161**	**<0.001**
	Juvenile's birth rank (Later born)	First-born	0.147	−0.540	0.834	0.172	0.678
	Mother's rank		0.061	−0.212	0.334	0.187	0.665
	Troop (J)	L	0.152	−0.448	0.752	3.544	0.170
		M	−0.879	−2.002	0.244		
Full-Null model comparison: $x_2^2 = 48.106$, $P < 0.001$ (AIC full = 2135.7, AIC null = 2169.8)							
Model 4: time spent being groomed by the mother	Intercept		−3.357	−3.793	−2.922	–	–
	Presence of a younger sibling (No)	Yes	−0.126	−0.459	0.207	0.552	0.458
	Juvenile's age		−0.167	−0.338	0.003	3.650	0.056
	Juvenile's sex (Female)	Male	−0.229	−0.546	0.087	1.902	0.168
	Juvenile's birth rank (Later born)	First-born	−0.171	−0.589	0.247	0.667	0.414
	Mother's rank		−0.015	−0.171	0.142	0.033	0.855
	Troop (J)	L	**0.142**	**−0.209**	**0.493**	**6.098**	**0.047**
		M	**−0.615**	**−1.206**	**−0.024**		
Full-Null model comparison: $x_2^2 = 14.867$, $P = 0.038$ (AIC full = 4368.7, AIC null = 4369.6)							

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and *P* values of the predictors were estimated using 1525 focal observations on 38 juveniles (*N* = 18 with a younger sibling, *N* = 28 without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant.

$t = 3.8$, $P < 0.001$) a younger sibling, indicating that juveniles were more responsible than their mother for maintaining their close proximity. The average Hinde's index did not differ between both groups (*N* = 34, *t* = 1.131, *P* = 0.267), meaning that juveniles were equally primarily responsible for maintaining close proximity to their mother whether they had a younger sibling or not (P2.2).

Juvenile Self-directed Behaviour

Finally, juveniles' self-scratch frequency was significantly influenced by the interaction between sibship status and age (P3). Self-scratch frequency generally decreased with age but less so for juveniles that had a younger sibling compared to those with no younger sibling (Table 6, Fig. 3). Juveniles born to higher-ranking females tended to have a lower self-scratch frequency than juveniles born to lower-ranking females (Table 6).

DISCUSSION

This study investigated changes in mother−juvenile relationships during the transition to siblinghood in young chacma baboons. First, we showed that, contrary to our predictions, mothers did not reduce their investment in terms of grooming and proximity following the birth of a new infant, as their grooming probability and duration (P1.1), and their probability of initiating and staying in close proximity to their older juveniles remained stable (P2.1 and P2.2). Second, we showed that juveniles with a younger sibling increased their responsibility in the maintenance of grooming and spatial relationships with their mother. Indeed, they groomed twice as often and twice as long (P1.2), and approached and left their mother a third more often (P2.2), even though they spent on average the same amount of time in close proximity to her as juveniles with no younger sibling. Third, signs of anxiety decreased more slowly with age for juveniles with a younger sibling compared to juveniles of similar age without a sibling (P3). Here, we discuss the implications of our findings for the understanding of mother−offspring conflict and sibling competition in primates.

Baboon mothers did not reduce their level of maternal investment in terms of grooming and proximity following the birth of a

new infant, while their older offspring initiated interactions more often. These results contradict previous studies on TTS in macaques, which reported an abrupt decrease in maternal grooming, time spent in close proximity and maternal approaches (Devinney et al., 2001; Holman & Goy, 1988; Schino & Troisi, 2001; Singh & Sachdeva, 1977; but see DiGregorio et al., 1987). In these macaques, these changes were also driven by the juveniles themselves, as they decreased the rate at which they initiated interactions with their mother (Devinney et al., 2001; Holman & Goy, 1988; Schino & Troisi, 2001; Singh & Sachdeva, 1977). These differences with our findings could relate to several, nonmutually exclusive factors. First, the macaque studies were conducted on captive populations (from free ranging to laboratory housing). Captivity and provisioning could affect mother−offspring relationships and specifically accelerate maternal reproductive pace (Altmann & Alberts, 2003b). Second, and perhaps because of their different environments, young macaques were on average 12 months old at the birth of their younger sibling, while young chacma baboons were on average 23 months old in this study. Although this age difference is partly due to species differences in reproductive pace, it may also reflect differences in juveniles' independence. Indeed, juvenile macaques were still nursing in the few months preceding the birth of their siblings, while our study subjects had stopped suckling long before their sibling was born (Dezeure, Baniel, et al., 2021). In addition, isotopic analyses showed that milk intake ceases around 12 months in our study population (Carboni et al., 2022). Subsequently, weaning and the birth of a younger sibling were simultaneous and impossible to disentangle in the macaque studies, while we were able to measure the effects of TTS on mother−offspring relationships independently of weaning.

Our results recall previous findings in human studies. Indeed, in western industrialized societies, children become more responsible for initiating interactions with their mother, including more demanding and clinging behaviour and more signs of anxiety (Dunn et al., 1981; Dunn & Kendrick, 1980; Stewart et al., 1987; Volling, 2012), following the birth of a sibling. Yet, in humans, as in captive macaques, this pattern is associated with a decrease in maternal care and an increase in maternal rejections. The lack of changes in maternal behaviour we observed in our study may be expected in natural populations, as mothers may space births in a
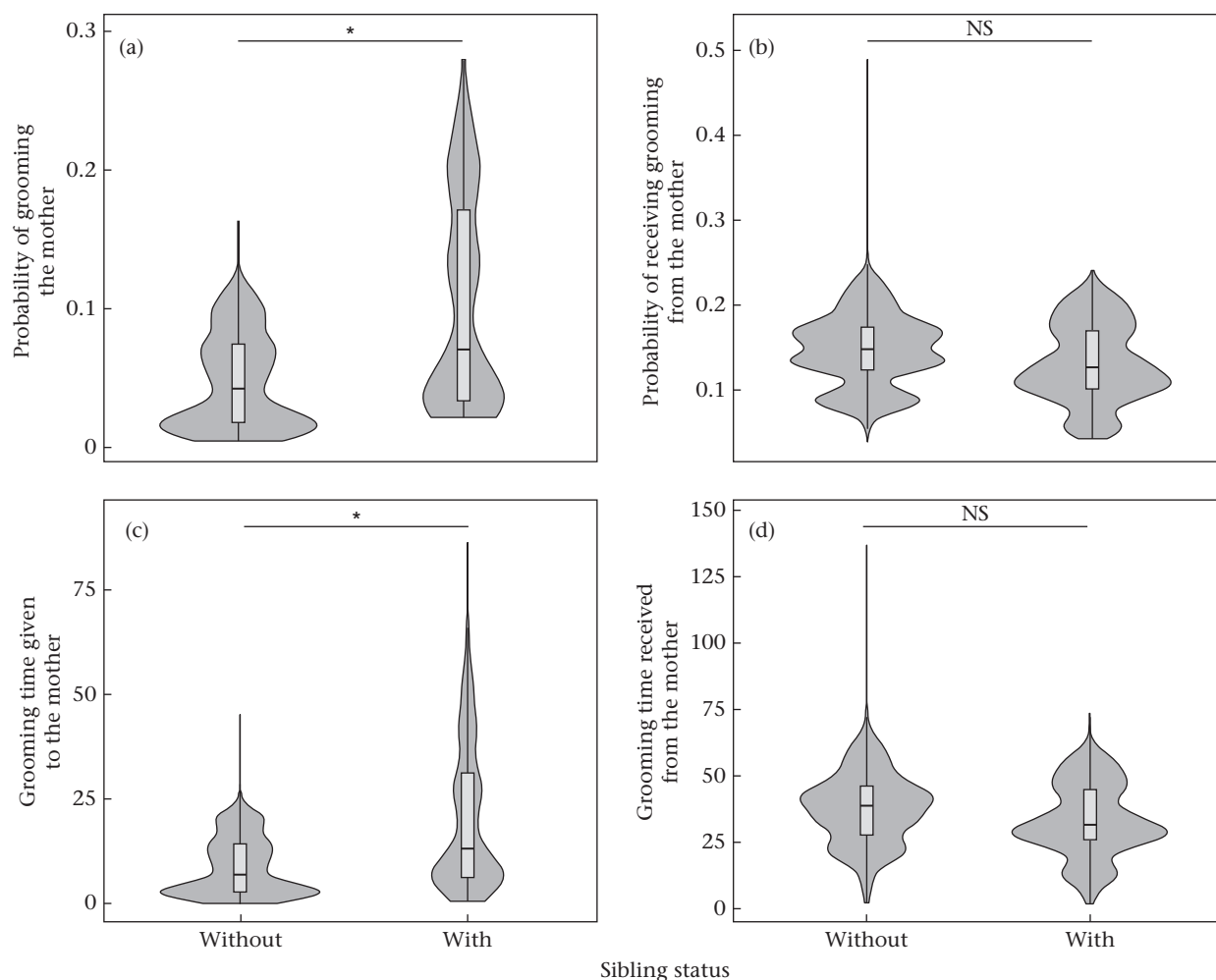
Figure 1. Influence of the birth of the younger sibling on mother—juvenile grooming interactions. 'Sibling status' refers to whether juveniles have recently experienced the birth of a younger sibling ('With') or not ('Without'). (a) Predicted probability that a juvenile grooms its mother during a focal observation depending on its 'sibling status'. (b) Predicted probability that a juvenile is groomed by its mother depending on its 'sibling status'. (c) Predicted grooming time (s) given by a juvenile to its mother during a focal observation depending on its 'sibling status'. (d) Predicted grooming time (s) received by a juvenile from its mother during a focal observation depending on its 'sibling status'. The violin plots show the distribution of the fitted values and the box plots show the median of the distribution of the fitted values (black horizontal bar), the 25th and 75th quartiles (bottom and top of the boxes, respectively) and the whiskers include a maximum of 1.5 times the interquartile range. The effect of the predictor 'Presence of a younger sibling' and the associated P values are shown. *$P < 0.05$.

way that allows them to provide the care needed by their offspring at different stages of their lives. When a newborn arrives, older juveniles are fully weaned and lactation may not substantially affect the mothers' ability to maintain their relationship with their juvenile offspring via proximity, grooming, co-feeding and occasional acts of social support. Thus, adjustments in maternal behaviour after the birth of new infants may be relatively small, contrasting with patterns reported in (at least some) human societies, where mothers care for multiple dependent offspring at the same time. Overall, studies across species and populations may reveal how flexible maternal strategies are, and the associated range of juveniles' behavioural reactions to TTS, widening our understanding of family ecology.

Although juvenile baboons with and without a younger sibling received as much care from their mother, juveniles with a younger sibling approached, left and initiated grooming with their mother more often than those without. These results may first reflect their attraction to the newborn, which is commonly observed across primate species, where nonmother individuals, mainly females, frequently touch or handle newborns (Dunayer & Berman, 2018; Hrdy, 1976; Meredith, 2015). Nonmother females often access the

infant by initiating grooming with the mother, resulting in new mothers receiving increased levels of grooming and attention (Caselli et al., 2021; Frank & Silk, 2009; Henzi & Barrett, 2002; Jiang et al., 2019). However, if the increase in juveniles' initiation of interactions with their mother was exclusively triggered by infant attraction, we would expect juvenile females to initiate more interactions with their mother than males following the birth of a younger sibling, which was not supported by our results. Moreover, when approaching their mother, juveniles immediately interacted with their younger sibling in only 13% of cases, while they interacted with their mother in 35% of cases (see Appendix). Overall, these results suggest that infant handling was not the primary motivation for juveniles to approach their mother.

Second, such behavioural changes driven by juveniles may reflect changes in the mother—offspring relationship following TTS, which may contribute to the acceleration of a juvenile's developmental trajectory. Juveniles may develop greater independence and autonomy following their sibling's birth, thus increasing their own responsibility in maintaining the mother—offspring spatial and grooming relationships. TTS may also translate into a rescheduling of mother—juvenile interactions, where juveniles would be

Table 3
Results of the mixed models analysing the probability of a juvenile being within 1 m (model 5) or within 5 m (model 6) from its mother during a scan observation

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P
				2.5%	97.5%		
Model 5: probability of being within 1 m from the mother	Intercept		−1.913	−2.238	−1.588	–	–
	Presence of a younger sibling (No)	Yes	−0.080	−0.427	0.266	0.405	0.524
	Juvenile's age		**−0.208**	**−0.383**	**−0.033**	**5.480**	**0.019**
	Juvenile's sex (Female)	Male	**−0.629**	**−0.970**	**−0.288**	**13.242**	**<0.001**
	Juvenile's birth rank (Later born)	First-born	−0.240	−0.693	0.213	1.161	0.281
	Mother's rank		0.103	−0.064	0.271	1.810	0.179
	Troop (J)	L	−0.015	−0.397	0.367	2.623	0.269
		M	−0.412	−0.978	0.154		
Full-Null model comparison: $x_2^2 = 27.008$, $P < 0.001$ (AIC full = 1607.7, AIC null = 1620.7)							
Model 6: probability of being within 5 m from the mother	Intercept		−1.695	−1.967	−1.423	–	–
	Presence of a younger sibling (No)	Yes	0.115	−0.175	0.405	0.632	0.427
	Juvenile's age		**−0.223**	**−0.365**	**−0.081**	**10.120**	**0.001**
	Juvenile's sex (Female)	Male	**−0.331**	**−0.598**	**−0.064**	**5.432**	**0.020**
	Juvenile's birth rank (Later born)	First-born	0.036	−0.320	0.392	0.040	0.842
	Mother's rank		**0.189**	**0.055**	**0.323**	**6.408**	**0.011**
	Troop (J)	L	0.034	−0.283	0.352	5.178	0.075
		M	0.443	0.074	0.812		
Full-Null model comparison: $x_2^2 = 25.398$, $P < 0.001$ (AIC full = 2195.2, AIC null = 2206.6)							

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 2562 and 2532 scan observations, respectively, on 38 juveniles (N = 18 with a younger sibling, N = 28 without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant.

Table 4
Results of the mixed models analysing the probability of a juvenile approaching (model 7) or leaving (model 8) its mother within 1 m during a focal observation

| Response variable	Fixed factor	Levels	Estimate	CI		LRT	P
				2.5%	97.5%		
Model 7: probability of approaching the mother	Intercept		−1.572	−1.906	−1.237	–	–
	Presence of a younger sibling (No)	Yes	**0.552**	**0.225**	**0.879**	**10.628**	**0.001**
	Juvenile's age		**−0.207**	**−0.374**	**−0.039**	**5.864**	**0.015**
	Juvenile's sex (Female)	Male	−0.160	−0.479	0.159	0.973	0.324
	Juvenile's birth rank (Later born)	First-born	−0.099	−0.540	0.342	0.197	0.657
	Mother's rank		**0.175**	**0.019**	**0.330**	**4.430**	**0.035**
	Troop (J)	L	**−0.123**	**−0.502**	**0.257**	**7.373**	**0,025**
		M	**0.571**	**0.113**	**1.029**		
	Focal observation duration		**0.139**	**0.003**	**0.275**	**4.148**	**0.042**
Full-Null model comparison: $x_2^2 = 26.202$, $P < 0.001$ (AIC full = 1505.2, AIC null = 1515.4)							
Model 8: probability of leaving the mother	Intercept		−1.726	−2.087	−1.365	–	–
	Presence of a younger sibling (No)	Yes	**0.538**	**0.186**	**0.891**	**9.402**	**0.002**
	Juvenile's age		**−0.185**	**−0.366**	**−0.003**	**4.534**	**0.033**
	Juvenile's sex (Female)	Male	**−0.421**	**−0.770**	**−0.072**	**6.168**	**0.013**
	Juvenile's birth rank (Later born)	First-born	−0.089	−0.565	0.388	0.099	0.753
	Mother's rank		**0.194**	**0.024**	**0.364**	**5.493**	**0.019**
	Troop (J)	L	**−0.119**	**−0.521**	**0.284**	**9.065**	**0.011**
		M	**0.665**	**0.173**	**1.157**		
	Focal observation duration		0.069	−0.075	0.213	0.916	0.338
Full-Null model comparison: $x_2^2 = 25.193$, $P = 0.001$ (AIC full = 1340.8, AIC null = 1350.0)							

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 1525 focal observations on 38 juveniles (N = 18 with a younger sibling, N = 28 without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant.

conditioned to request maternal care only in convenient times so that it does not interfere with infant care (in a similar manner to the rescheduling during the weaning period proposed by Altmann, 1980; Bateson, 1994). Finally, juveniles may solicit their mother more frequently to seek maternal attention and obtain the same 'presibling arrival' level of care, if the birth of a younger sibling leads to lower maternal responsiveness and greater mother−offspring conflict over maternal care. Although most studies on primates have focused on mother−offspring conflicts during weaning or when mothers resume cycling (Maestripieri, 2002), which often manifest through highly conspicuous tantrums (Barrett & Henzi, 2000), conflicts can arise at other developmental stages (Bateson, 1994) and over any type of maternal

investment that can be monopolized. As infants grow older and stop throwing tantrums (as was the case in our study baboons), mother−offspring conflict could be expressed through more subtle behaviours, such as who takes the responsibility in maintaining spatial proximity, or other signs of anxiety, such as self-directed behaviours (Maestripieri, 2002).

This increased mother−offspring conflict likely translates into sibling rivalry, which could be mediated, at a proximate level, by jealousy, and may explain the increase in juveniles' initiation of association and grooming with the mother. Jealousy is a complex emotional state that arises in a social triangle that consists of the jealous individual (here, the older sibling), a beloved (here, the mother) and a rival (here, the younger infant), and is elicited when
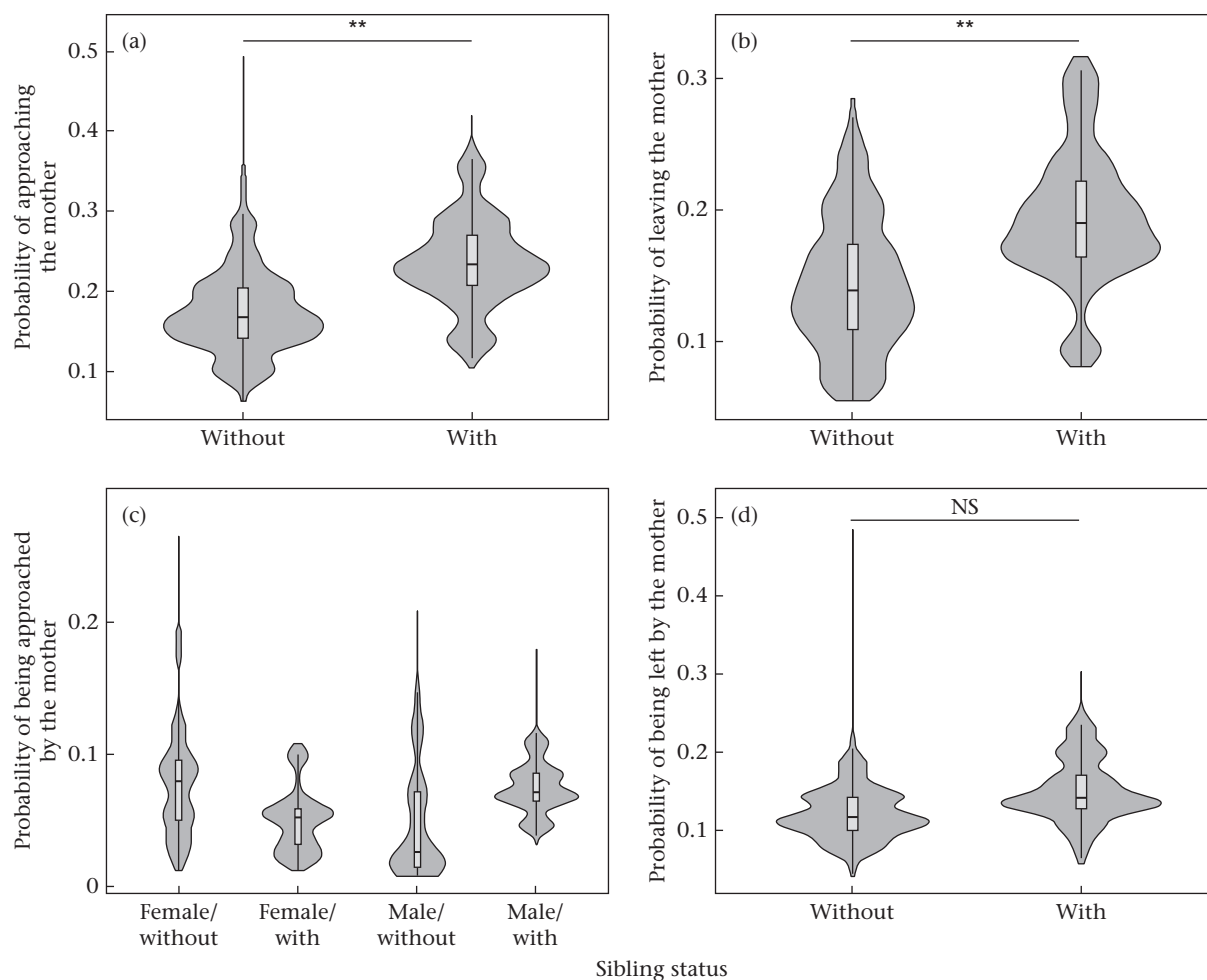
Figure 2. Influence of the birth of the younger sibling on mother–juvenile spatial association (within 1 m). 'Sibling status' refers to whether juveniles have recently experienced the birth of a younger sibling ('With'), or not ('Without'). (a) Predicted probability that a juvenile approaches its mother during a focal observation depending on its 'sibling status'. (b) Predicted probability that a juvenile leaves its mother depending on its 'sibling status'. (c) Predicted probability that a juvenile is approached by its mother depending on its 'sibling status' and sex. (d) Predicted probability that a juvenile is left by its mother depending on its 'sibling status'. The violin plots show the distribution of the fitted probabilities. The box plots show the median of the distribution of the fitted values (black horizontal bar), the 25th and 75th quartiles (bottom and top of the boxes, respectively) and the whiskers include a maximum of 1.5 times the interquartile range. The effect of the predictor 'Presence of a younger sibling' and the associated P values are shown. **$P < 0.01$. In (c) the predicted values of the model include a significant interaction between sibling status and juvenile's sex (model 8) but post hoc pairwise mean comparisons were not significant.

the jealous individual perceives the relationship between their beloved and a rival as a threat to their own bond with the beloved one (Volling et al., 2010, 2014). Children undergoing TTS display two main types of jealous reactions when their mother interacts with their sibling: negative/distress behaviours (protesting, disrupting the interactions, directing aggression at the mother) and social approach behaviours (e.g. watching, maintaining proximity and seeking comfort; Volling et al., 2014). The latter category, social approach, could match the behavioural patterns observed in this study. In humans, sibling jealousy is generally considered as a form of competition for parental attention (Volling et al., 2010), a behaviour that is generally not recognized as a form of parental care per se in other species but could be adaptive where parental attention improves offspring survival by preventing risks such as accidents or predation, or by promoting information transmission. In nonhuman primates, maternal attention could be a form of maternal care that siblings could compete over, but whether juveniles that attract more maternal attention experience fitness benefits (such as a greater probability of securing maternal support during conflicts, protection against predators, etc.) remains to be tested.

Finally, further dimensions of TTS should be investigated to foster its description in monotocous species. In modern societies, children's adjustment to TTS is highly variable and is associated with several traits such as children's sex, age, personality or their attachment style (Dunn et al., 1981; Volling, 2012, 2017; Volling et al., 2014). Insecurely attached or younger children typically show more negative reactions to the birth of a younger sibling (Dunn et al., 1981; Volling, 2017). Maternal traits, such as maternal style, could also influence how juvenile primates cope with TTS (Fairbanks, 1996; Maestripieri, 2018). Moreover, throughout this transition, mother and offspring are generally part of a larger social system not restricted to their dyad. In humans, which are often described as communal or cooperative breeders (Mace & Sear, 2005), the presence of other kin such as the father, grandmother and older siblings can also influence how children cope with this transition by developing strong bonds with others to compensate for the weakening of the maternal bond (Gottlieb & Mendelson, 1990; Legg et al., 1974; Stewart et al., 1987; Volling et al., 2014). This could also be the case in baboons to some extent, as juvenile primates primarily associate with their siblings, and can keep

Table 5
Results of the mixed models analysing the probability of a juvenile being approached (model 9) or left (model 10) within 1 m by its mother during a focal observation

Response variable	Fixed factors	Levels	Estimate	CI		LRT	P
				2.5%	97.5%		
Model 9: probability of being approached by the mother	Intercept		−3.177	−3.758	−2.596	–	–
	Presence of a younger sibling (No)	Yes	−0.512	−1.201	0.177	–	–
	Juvenile's age		0.050	−0.211	0.311	0.100	0.752
	Juvenile's sex (Female)	Male	−0.557	−1.189	0.075	–	–
	Juvenile's birth rank (Later born)	First-born	0.233	−0.448	0.914	0.484	0.486
	Mother's rank		**0.556**	**0.286**	**0.827**	**18.123**	**<0.001**
	Troop (J)	L	**0.792**	**0.203**	**1.382**	**17.726**	**<0.001**
		M	**1.430**	**0.743**	**2.117**		
	Focal observation duration		0.156	−0.062	0.373	1.943	0.163
	Presence of a younger sibling (No)*Juvenile's sex (Female)	Yes, Male	**1.138**	**0.156**	**2.119**	**6.070**	**0.014**
Full-Null model comparison: $x_2^2 = 30.352$, $P < 0.001$ (AIC full = 712.29, AIC null = 724.65)							
Model 10: probability of being left by the mother	Intercept		−1.919	−2.295	−1.544	–	–
	Presence of a younger sibling (No)	Yes	0.254	−0.121	0.629	1.751	0.186
	Juvenile's age		−0.134	−0.325	0.056	1.943	0.163
	Juvenile's sex (Female)	Male	−0.273	−0.638	0.093	2.034	0.154
	Juvenile's birth rank (Later born)	First-born	−0.370	−0.893	0.153	2.066	0.151
	Mother's rank		0.011	−0.169	0.190	0.014	0.907
	Troop (J)	L	0.171	−0.260	0.602	1.531	0.465
		M	0.339	−0.203	0.882		
	Focal observation duration		**0.188**	**0.028**	**0.347**	**5.557**	**0.018**
Full-Null model comparison: $x_2^2 = 13.902$, $P = 0.084$ (AIC full = 1197.5, AIC null = 1195.4)							

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 1525 focal observations on 38 juveniles ($N = 18$ with a younger sibling, $N = 28$ without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant. Whenever an interaction is significant, LRT and P values for the simple predictors are not shown.

Table 6
Results of the mixed models analysing the frequency of self-scratches during a focal observation (model 11)

Fixed factor	Levels	Estimate	CI		LRT	P
			2.5%	97.5%		
Intercept		−5.814	−5.966	−5.661	–	–
Presence of a younger sibling (No)	Yes	0.040	−0.102	0.183	–	–
Juvenile's age		−0.110	−0.197	−0.023	–	–
Juvenile's sex (Female)	Male	0.050	−0.082	0.182	0.536	0.464
Juvenile's birth rank (Later born)	First-born	−0.105	−0.286	0.075	1.266	0.260
Mother's rank		−0.065	−0.132	0.001	3.498	0.061
Troop (J)	L	**0.008**	**−0.138**	**0.154**	**10.806**	**0.005**
	M	**−0.358**	**−0.565**	**−0.150**		
Year (2017)	2018	**−0.317**	**−0.518**	**−0.115**	**14.086**	**0.001**
	2019	**0.085**	**−0.059**	**0.228**		
Presence of a younger sibling (No)*juvenile's age	Yes	**0.166**	**0.036**	**0.296**	**5.873**	**0.015**
Full-Null model comparison: $x_2^2 = 26.07$, $P = 0.004$ (AIC full = 7158.1, AIC null = 7164.1)						

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 1525 focal observations on 38 juveniles ($N = 18$ with a younger sibling, $N = 28$ without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant. Whenever an interaction is significant, LRT and P values for the simple predictors are not shown.

benefitting from their father's presence as long as they co-reside (Charpentier et al., 2008; Lynch et al., 2020).

Our study is among the first to investigate behavioural changes in mother−juvenile relationships following the birth of a new sibling in wild nonhuman primates. In chacma baboons, the birth of a newborn does not translate into decreased maternal affiliation or association towards the older sibling, but it does push juveniles to increase solicitations towards their mother and seems to generate anxiety, which overall suggests that juveniles have to make more effort to maintain the same level of attention and care from their mother. From an ultimate perspective, these results raise the important question of the adaptive significance of maternal attention that siblings seem to compete over. From a proximate perspective, the juveniles' behavioural changes reported here may resemble the jealous reactions commonly observed in young humans during TTS and may thus offer a relevant context to study emotional development in young primates. Finally, our results, which are distinct from findings in captive primates, show both similarities to and differences from human patterns. As such, they emphasize the need to investigate broader aspects of this intriguing developmental milestone in the wild and across populations and species showing a diversity of life histories and ecologies.
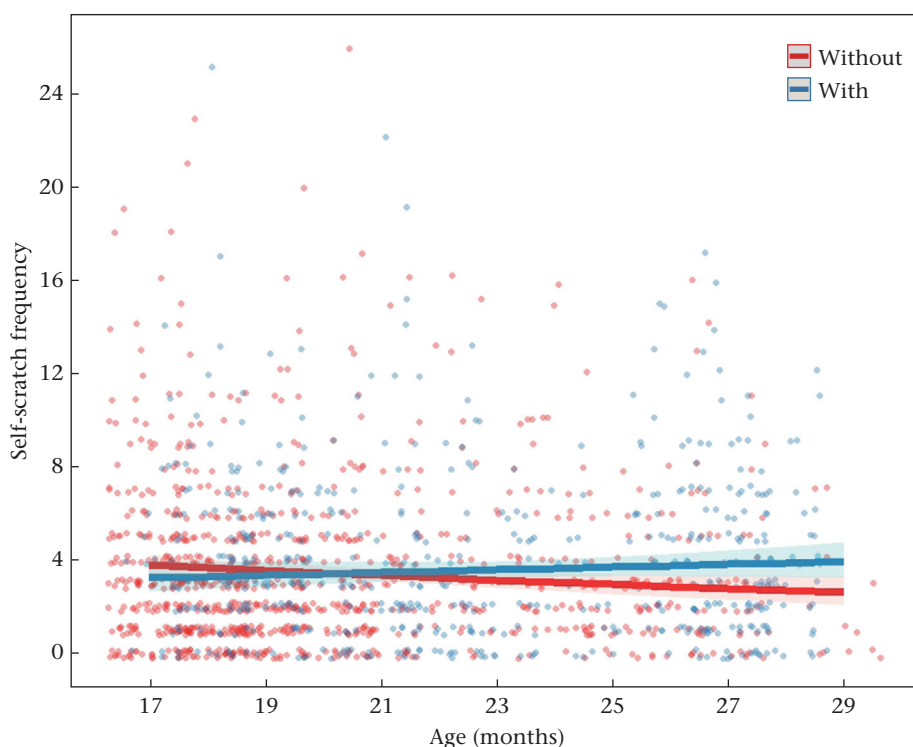
Figure 3. Variation in the frequency of self-scratches according to juvenile's age and the birth of a younger sibling. 'With' refers to juveniles that recently experienced the birth of a younger sibling. 'Without' refers to juveniles that did not experience the birth of a younger sibling. Dots represent the model's adjusted predicted values, and the curves show the linear predicted fit from the corresponding mixed model. Predicted values were computed using the function 'ggeffect' from the ggeffect package, averaging the values of all the other variables in the model. The darker area around each curve represents the 95% confidence interval of the fitted curve.

Author Contributions

A.D., M.J.E.C. and E.H. conceptualized the ideas and designed the methodology; A.B., A.D. and J.D. collected the data; A.J.C., G.C. and E.H. led project administration; A.D. formatted and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability

Data sets and scripts used in this study are available at https://gitlab.com/AxelleDelaunay/transition-to-siblinghood-in-a-wild-chacma-baboon-population.

Declaration of Interest

None.

References

Altmann, J. (1980). *Baboon mothers and infants*. University of Chicago Press.
Altmann, J., & Alberts, S. C. (2003a). Intraspecific variability in fertility and offspring survival in a nonhuman primate: Behavioural control of ecological and social sources. In K. W. Wachter, & R. A. Bulatao (Eds.), *Offspring: Human fertility behavior in biodemographic perspective*. National Academies Press. https://www.ncbi.nlm.nih.gov/books/NBK97280/
Altmann, J., & Alberts, S. C. (2003b). Variability in reproductive success viewed from a life-history perspective in baboons. *American Journal of Human Biology, 15*(3), 401–409. https://doi.org/10.1002/ajhb.10157
Andersen, I. L., Nævdal, E., & Bøe, K. E. (2011). Maternal investment, sibling competition, and offspring survival with increasing litter size and parity in pigs (*Sus scrofa*). *Behavioral Ecology and Sociobiology, 65*(6), 1159–1167. https://doi.org/10.1007/s00265-010-1128-4
Andres, D., Clutton-Brock, T. H., Kruuk, L. E. B., Pemberton, J. M., Stopher, K. V., & Ruckstuhl, K. E. (2013). Sex differences in the consequences of maternal loss in a long-lived mammal, the red deer (*Cervus elaphus*). *Behavioral Ecology and Sociobiology, 67*(8), 1249–1258. https://doi.org/10.1007/s00265-013-1552-3
Barrett, L., & Henzi, S. P. (2000). Are baboon infants Sir Phillip Sydney's offspring? *Ethology, 106*(7), 645–658. https://doi.org/10.1046/j.1439-0310.2000.00577.x
Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01
Bateson, P. (1994). The dynamics of parent-offspring relationships in mammals. *Trends in Ecology & Evolution, 9*(10), 399–403. https://doi.org/10.1016/0169-5347(94)90066-3

Bebbington, K., Kingma, S. A., Fairfield, E. A., Spurgin, L. G., Komdeur, J., & Richardson, D. S. (2017). Consequences of sibling rivalry vary across life in a passerine bird. *Behavioral Ecology, 28*(2), 407–418. https://doi.org/10.1093/beheco/arw167

Behringer, V., Berghänel, A., Deschner, T., Lee, S. M., Fruth, B., & Hohmann, G. (2022). Transition to siblinghood causes a substantial and long-lasting increase in urinary cortisol levels in wild bonobos. *eLife, 11*, Article e77227. https://doi.org/10.7554/eLife.77227

Bolwig, N. (1980). Early social development and emancipation of *Macaca nemestrina* and species of Papio. *Primates, 21*(3), 357–375. https://doi.org/10.1007/BF02390466

Braun, B. M., & Hunt, G. L., Jr. (1983). Brood reduction in black-legged Kittiwakes. *Auk, 100*(2), 469–476. https://doi.org/10.1093/auk/100.2.469

Brody, G. H. (1998). Sibling relationship quality: Its causes and consequences. *Annual Review of Psychology, 49*(1), 1–24. https://doi.org/10.1146/annurev.psych.49.1.1

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal, 9*(2), 378–400.

Carboni, S., Dezeure, J., Cowlishaw, G., Huchard, E., & Marshall, H. H. (2022). Stable isotopes reveal the effects of maternal rank and infant age on weaning dynamics in wild chacma baboons. *Animal Behaviour, 193*, 21–32. https://doi.org/10.1016/j.anbehav.2022.08.010.

Caselli, M., Zanoli, A., Palagi, E., & Norscia, I. (2021). Infant handling increases grooming towards mothers in wild geladas (*Theropithecus gelada*). *Behavioural Processes, 192*, Article 104501. https://doi.org/10.1016/j.beproc.2021.104501

Castles, D. L., Whiten, A., & Aureli, F. (1999). Social anxiety, relationships and self-directed behaviour among wild female olive baboons. *Animal Behaviour, 58*(6), 1207–1215. https://doi.org/10.1006/anbe.1999.1250

Charpentier, M. J. E., Horn, R. C. V., Altmann, J., & Alberts, S. C. (2008). Paternal effects on offspring fitness in a multimale primate society. *Proceedings of the National Academy of Sciences, 105*(6), 1988–1992. https://doi.org/10.1073/pnas.0711219105

Cheney, D. L., Seyfarth, R. M., Fischer, J., Beehner, J., Bergman, T., Johnson, S. E., Kitchen, D. M., Palombit, R. A., Rendall, D., & Silk, J. B. (2004). Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *International Journal of Primatology, 25*(2), 401–428. https://doi.org/10.1023/B:IJOP.0000019159.75573.13

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton University Press. https://www.degruyter.com/document/doi/10.1515/9780691206981/html.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer: Behavior and ecology of two sexes*. University of Chicago Press.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1983). The costs of reproduction to red deer hinds. *Journal of Animal Ecology, 52*(2), 367–383. https://doi.org/10.2307/4560

Conde-Agudelo, A., Rosas-Bermúdez, A., & Kafury-Goeta, A. C. (2006). Birth spacing and risk of adverse perinatal outcomes: A meta-analysis. *JAMA, 295*(15), 1809–1823. https://doi.org/10.1001/jama.295.15.1809

Crockford, C., Samuni, L., Vigilant, L., & Wittig, R. M. (2020). Postweaning maternal care increases male chimpanzee reproductive success. *Science Advances, 6*(38), eaaz5746. https://doi.org/10.1126/sciadv.aaz5746

Devinney, B. J., Berman, C. M., & Rasmussen, K. L. R. (2001). Changes in yearling rhesus monkeys' relationships with their mothers after sibling birth. *American Journal of Primatology, 54*(4), 193–210. https://doi.org/10.1002/ajp.1030

Dezeure, J., Baniel, A., Carter, A., Cowlishaw, G., Godelle, B., & Huchard, E. (2021). Birth timing generates reproductive trade-offs in a non-seasonal breeding primate, 1950 *Proceedings of the Royal Society B: Biological Sciences, 288*, Article 20210286. https://doi.org/10.1098/rspb.2021.0286.

Dezeure, J., Dagorrette, J., Baniel, A., Carter, A. J., Cowlishaw, G., Marshall, H. H., Martina, C., Raby, C. L., & Huchard, E. (2021). Developmental transitions in body color in chacma baboon infants: Implications to estimate age and developmental pace. *American Journal of Physical Anthropology, 174*(1), 89–102. https://doi.org/10.1002/ajpa.24118

DiGregorio, G., Suomi, S. J., Eisele, C. E., & Chapman, S. A. (1987). Reactions of nuclear-family-reared rhesus macaques to the births of younger siblings. *American Journal of Primatology, 13*(3), 231–253. https://doi.org/10.1002/ajp.1350130303

Dorie, V., Bates, D., Maechler, M., Bolker, B., & Walker, S. (2021). blme: Bayesian linear mixed-effects models [Computer software] https://CRAN.R-project.org/package=blme.

Drummond, H. (2006). Dominance in vertebrate broods and litters. *Quarterly Review of Biology, 81*(1), 3–32. https://doi.org/10.1086/503922

Drummond, H., & Rodríguez, C. (2013). Costs of growing up as a subordinate sibling are passed to the next generation in blue-footed boobies. *Journal of Evolutionary Biology, 26*(3), 625–634. https://doi.org/10.1111/jeb.12087

Dunayer, E. S., & Berman, C. M. (2018). Infant handling among primates. *International Journal of Comparative Psychology, 31*. https://escholarship.org/uc/item/45w0r631.

Dunn, J., & Kendrick, C. (1980). The arrival of a sibling: Changes in patterns of interaction between mother and first-born child. *Journal of Child Psychology and Psychiatry, 21*(2), 119–132. https://doi.org/10.1111/j.1469-7610.1980.tb00024.x

Dunn, J., Kendrick, C., & MacNamee, R. (1981). The reaction of first-born children to the birth of a sibling: Mothers' reports. *Journal of Child Psychology and Psychiatry, 22*(1), 1–18. https://doi.org/10.1111/j.1469-7610.1981.tb00527.x

Ekman, J., Eggers, S., & Griesser, M. (2002). Fighting to stay: The role of sibling rivalry for delayed dispersal. *Animal Behaviour, 64*(3), 453–459. https://doi.org/10.1006/anbe.2002.3075

Fairbanks, L. A. (1996). Individual differences in maternal style: Causes and consequences for mothers and offspring. *Advances in the Study of Behavior, 25*, 579–611. https://doi.org/10.1016/S0065-3454(08)60343-5

Fey, K., & Trillmich, F. (2008). Sibling competition in guinea pigs (*Cavia aperea f. Porcellus*): Scrambling for mother's teats is stressful. *Behavioral Ecology and Sociobiology, 62*(3), 321–329. https://doi.org/10.1007/s00265-007-0419-x

Fisher, H. S., Hook, K. A., Weber, W. D., & Hoekstra, H. E. (2018). Sibling rivalry: Males with more brothers develop larger testes. *Ecology and Evolution, 8*(16), 8197–8203. https://doi.org/10.1002/ece3.4337

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Frank, R. E., & Silk, J. B. (2009). Grooming exchange between mothers and non-mothers: The price of natal attraction in wild baboons (*Papio anubis*). *Behaviour, 146*(7), 889–906.

Fujioka, M. (1985). Sibling competition and siblicide in asynchronously-hatching broods of the cattle egret *Bubulcus ibis*. *Animal Behaviour, 33*(4), 1228–1242. https://doi.org/10.1016/S0003-3472(85)80183-4

Gottlieb, L. N., & Mendelson, M. J. (1990). Parental support and firstborn girls' adaptation to the birth of a sibling. *Journal of Applied Developmental Psychology, 11*(1), 29–48. https://doi.org/10.1016/0193-3973(90)90030-N

Guenther, A., & Trillmich, F. (2015). Within-litter differences in personality and physiology relate to size differences among siblings in cavies. *Physiology & Behavior, 145*, 22–28. https://doi.org/10.1016/j.physbeh.2015.03.026

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ, 6*, Article e4794. https://doi.org/10.7717/peerj.4794

Hartig, F., & Lohse, L. (2021). *DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models* [Computer software] https://CRAN.R-project.org/package=DHARMa.

Henzi, S. P., & Barrett, L. (2002). Infants as a commodity in a baboon market. *Animal Behaviour, 63*(5), 915–921. https://doi.org/10.1006/anbe.2001.1986

Hinde, R. A., & Atkinson, S. (1970). Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. *Animal Behaviour, 18*, 169–176. https://doi.org/10.1016/0003-3472(70)90087-4

Hofer, H., & East, M. L. (2008). Siblicide in Serengeti spotted hyenas: A long-term study of maternal input and cub survival. *Behavioral Ecology and Sociobiology, 62*(3), 341–351. https://doi.org/10.1007/s00265-007-0421-3

Holman, S. D., & Goy, R. W. (1988). Sexually dimorphic transitions revealed in the relationships of yearling rhesus monkeys following the birth of siblings. *International Journal of Primatology, 9*(2), 113–133. https://doi.org/10.1007/BF02735732

Hrdy, S. B. (1976). Care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Advances in the Study of Behavior, 6*, 101–158. https://doi.org/10.1016/S0065-3454(08)60083-2

Huchard, E., Alvergne, A., Féjan, D., Knapp, L. A., Cowlishaw, G., & Raymond, M. (2010). More than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma baboons. *Behavioral Ecology and Sociobiology, 64*(5), 769–781. https://doi.org/10.1007/s00265-009-0894-3

Huchard, E., Charpentier, M. J., Marshall, H., King, A. J., Knapp, L. A., & Cowlishaw, G. (2013). Paternal effects on access to resources in a promiscuous primate society. *Behavioral Ecology, 24*(1), 229–236. https://doi.org/10.1093/beheco/ars158

Hudson, R., Bautista, A., Reyes-Meza, V., Montor, J. M., & Rödel, H. G. (2011). The effect of siblings on early development: A potential contributor to personality differences in mammals. *Developmental Psychobiology, 53*(6), 564–574. https://doi.org/10.1002/dev.20535

Hudson, R., & Trillmich, F. (2008). Sibling competition and cooperation in mammals: Challenges, developments and prospects. *Behavioral Ecology and Sociobiology, 62*(3), 299–307. https://doi.org/10.1007/s00265-007-0417-z

Jiang, Q., Xia, D.-P., Wang, X., Zhang, D., Sun, B.-H., & Li, J.-H. (2019). Interchange between grooming and infant handling in female Tibetan macaques (*Macaca thibetana*). *Zoological Research, 40*(2), 139–145. https://doi.org/10.24272/j.issn.2095-8137.2018.049

de Kogel, C. H., & Prijs, H. J. (1996). Effects of brood size manipulations on sexual attractiveness of offspring in the zebra finch. *Animal Behaviour, 51*(3), 699–708. https://doi.org/10.1006/anbe.1996.0073

Kramer, K. L. (2005). Children's help and the pace of reproduction: Cooperative breeding in humans. *Evolutionary Anthropology: Issues, News, and Reviews, 14*(6), 224–237. https://doi.org/10.1002/evan.20082

Lee, D. S., Ruiz-Lambides, A. V., & Higham, J. P. (2019). Higher offspring mortality with short interbirth intervals in free-ranging rhesus macaques. *Proceedings of the National Academy of Sciences, 116*(13), 6057–6062. https://doi.org/10.1073/pnas.1817148116

Legg, C., Sherick, I., & Wadland, W. (1974). Reaction of preschool children to the birth of a sibling. *Child Psychiatry and Human Development, 5*(1), 3–39. https://doi.org/10.1007/BF01441311

Levy, E. J., Zipple, M. N., McLean, E., Campos, F. A., Dasari, M., Fogel, A. S., Franz, M., Gesquiere, L. R., Gordon, J. B., Grieneisen, L., Habig, B., Jansen, D. J., Learn, N. H., Weibel, C. J., Altmann, J., Alberts, S. C., & Archie, E. A. (2020). A comparison of dominance rank metrics reveals multiple competitive landscapes in an animal

society. *Proceedings of the Royal Society B: Biological Sciences, 287*(1934), Article 20201013. https://doi.org/10.1098/rspb.2020.1013

Lougheed, L. W., & Anderson, D. J. (1999). Parent blue-footed boobies suppress siblicidal behavior of offspring. *Behavioral Ecology and Sociobiology, 45*(1), 11—18. https://doi.org/10.1007/s002650050535

Lynch, E. C., Johnson, C. A., Lynch, R. F., Rothman, J. M., Fiore, A. D., & Palombit, R. A. (2020). Mothers and fathers improve immature baboon foraging success. *Behaviour, 157*(5), 387—414. https://doi.org/10.1163/1568539X-bja10006

Lynch, E. C., Lummaa, V., Htut, W., & Lahdenperä, M. (2019). Evolutionary significance of maternal kinship in a long-lived mammal. *Philosophical Transactions of the Royal Society B: Biological Sciences, 374*(1780), Article 20180067. https://doi.org/10.1098/rstb.2018.0067

Mace, R., & Sear, R. (2005). Are humans cooperative breeders? In E. Voland, A. Chasiotis, & W. Schiefenhoevel (Eds.), *Grandmotherhood: The evolutionary significance of the second half of female life* (pp. 143—159). Rutgers University Press.

Maestripieri, D. (2002). Parent—offspring conflict in primates. *International Journal of Primatology, 23*(4), 923—951. https://doi.org/10.1023/A:1015537201184

Maestripieri, D. (2018). Maternal influences on primate social development. *Behavioral Ecology and Sociobiology, 72*(8), 130. https://doi.org/10.1007/s00265-018-2547-x

Maestripieri, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: Displacement activities as an indicator of emotions in primates. *Animal Behaviour, 44*(5), 967—979. https://doi.org/10.1016/S0003-3472(05)80592-5

Meredith, S. L. (2015). Anchoring the clade: Primate-wide comparative analysis supports the relationship between juvenile interest in infants and adult patterns of infant care. *Folia Primatologica, 86*(1—2), 117—123. https://doi.org/10.1159/000368356

Mock, D. W., & Parker, G. A. (1998). *The evolution of sibling rivalry*. Oxford University Press.

Nakamura, M., Hayaki, H., Hosaka, K., Itoh, N., & Zamma, K. (2014). Brief Communication: Orphaned male Chimpanzees die young even after weaning. *American Journal of Physical Anthropology, 153*(1), 139—143. https://doi.org/10.1002/ajpa.22411

Nettle, D., Monaghan, P., Gillespie, R., Brilot, B., Bedford, T., & Bateson, M. (2015). An experimental demonstration that early-life competitive disadvantage accelerates telomere loss. *Proceedings of the Royal Society B: Biological Sciences, 282*(1798), Article 20141610. https://doi.org/10.1098/rspb.2014.1610

Palagi, E., & Norscia, I. (2011). Scratching around stress: Hierarchy and reconciliation make the difference in wild brown lemurs (*Eulemur fulvus*). *Stress, 14*(1), 93—97. https://doi.org/10.3109/10253890.2010.505272

Palombit, R. A., Cheney, D. L., Fischer, J., Johnson, S., Rendall, D., Seyfarth, R. M., & Silk, J. B. (2000). Male infanticide and defense of infants in chacma baboons. In C. P. van Schaik, & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 123—152). Cambridge University Press. https://doi.org/10.1017/CBO9780511542312.008.

Pereira, M. E. (1989). Agonistic interactions of juvenile Savanna baboons. *Ethology, 80*(1—4), 152—171. https://doi.org/10.1111/j.1439-0310.1989.tb00736.x

Pike, A., Coldwell, J., & Dunn, J. F. (2005). Sibling relationships in early/middle childhood: Links with individual adjustment. *Journal of Family Psychology, 19*(4), 523—532. https://doi.org/10.1037/0893-3200.19.4.523

Pollet, T. V., & Hoben, A. D. (2011). An evolutionary perspective on siblings: Rivals and resources. In T. K. Shackelford, & C. Salmon (Eds.), *The Oxford handbook of evolutionary family psychology* (pp. 128—148). Oxford University Press.

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Roulin, A., & Dreiss, A. N. (2012). Sibling competition and cooperation over parental care. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 133—149). Oxford University Press.

Rutstein, S. O. (2005). Effects of preceding birth intervals on neonatal, infant and under-five years mortality and nutritional status in developing countries: Evidence from the demographic and health surveys. *International Journal of Gynecology & Obstetrics, 89*(S1), S7—S24. https://doi.org/10.1016/j.ijgo.2004.11.012

Samuni, L., Tkaczynski, P., Deschner, T., Löhrrich, T., Wittig, R. M., & Crockford, C. (2020). Maternal effects on offspring growth indicate post-weaning juvenile dependence in chimpanzees (*Pan troglodytes verus*). *Frontiers in Zoology, 17*(1), 1. https://doi.org/10.1186/s12983-019-0343-8

Schino, G., & Troisi, A. (2001). Relationship with the mother modulates the response of yearling Japanese macaques (*Macaca fuscata*) to the birth of a sibling. *Journal of Comparative Psychology, 115*(4), 392—396. https://doi.org/10.1037/0735-7036.115.4.392

Schrader, M., Jarrett, B. J. M., & Kilner, R. M. (2018). Parental care and sibling competition independently increase phenotypic variation among burying beetle siblings. *Evolution, 72*(11), 2546—2552. https://doi.org/10.1111/evo.13607

Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology, 61*(2), 197—204. https://doi.org/10.1007/s00265-006-0250-9

Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology, 61*(2), 183—195. https://doi.org/10.1007/s00265-006-0249-2

Singh, M., & Sachdeva, R. (1977). Behaviour of juvenile bonnet monkey before and after his mother gives birth to a new baby. *Primates, 18*(3), 605—610. https://doi.org/10.1007/BF02383138

Stanton, M. A., Lonsdorf, E. V., Murray, C. M., & Pusey, A. E. (2020). Consequences of maternal loss before and after weaning in male and female wild chimpanzees. *Behavioral Ecology and Sociobiology, 74*(2), 22. https://doi.org/10.1007/s00265-020-2804-7

Stauffer, J., Panda, B., & Ilmonen, P. (2018). Telomere length, sibling competition and development of antioxidant defense in wild house mice. *Mechanisms of Ageing and Development, 169*, 45—52. https://doi.org/10.1016/j.mad.2017.10.002

Stewart, R. B., Mobley, L. A., van Tuyl, S. S., & Salvador, M. A. (1987). The firstborn's adjustment to the birth of a sibling: A longitudinal assessment. *Child Development, 58*(2), 341—355. https://doi.org/10.2307/1130511

Surbeck, M., Mundry, R., & Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proceedings of the Royal Society B: Biological Sciences, 278*(1705), 590—598. https://doi.org/10.1098/rspb.2010.1572

Trillmich, F., & Wolf, J. B. W. (2008). Parent—offspring and sibling conflict in Galápagos fur seals and sea lions. *Behavioral Ecology and Sociobiology, 62*(3), 363—375. https://doi.org/10.1007/s00265-007-0423-1

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136—179). Aldine. http://joelvelasco.net/teaching/3330/trivers72-parentalinvestment.pdf.

Trivers, R. L. (1974). Parent-offspring conflict. *Integrative and Comparative Biology, 14*(1), 249—264. https://doi.org/10.1093/icb/14.1.249

Tung, J., Archie, E. A., Altmann, J., & Alberts, S. C. (2016). Cumulative early life adversity predicts longevity in wild baboons. *Nature Communications, 7*(1), 1. https://doi.org/10.1038/ncomms11181

Verhulst, S., Holveck, M.-J., & Riebel, K. (2006). Long-term effects of manipulated natal brood size on metabolic rate in zebra finches. *Biology Letters, 2*(3), 478—480. https://doi.org/10.1098/rsbl.2006.0496

Volling, B. L. (2012). Family transitions following the birth of a sibling: An empirical review of changes in the firstborn's adjustment. *Psychological Bulletin, 138*(3), 497—528. https://doi.org/10.1037/a0026921

Volling, B. L. (2017). Xi. General discussion: Children's adjustment and adaptation following the birth of a sibling. *Monographs of the Society for Research in Child Development, 82*(3), 142—158. https://doi.org/10.1111/mono.12317

Volling, B. L., Kennedy, D. E., & Jackey, L. M. H. (2010). The development of sibling jealousy. In S. L. Hart, & M. Legerstee (Eds.), *Handbook of jealousy: Theory, research, and multidisciplinary approaches* (pp. 387—417). Wiley Blackwell. https://doi.org/10.1002/9781444323542.ch17.

Volling, B. L., Yu, T., Gonzalez, R., Kennedy, D. E., Rosenberg, L., & Oh, W. (2014). Children's responses to mother—infant and father—infant interaction with a baby sibling: Jealousy or joy? *Journal of Family Psychology, 28*(5), 634—644. https://doi.org/10.1037/a0037811

Weiss, M. N., Ellis, S., Franks, D. W., Nielsen, M. L. K., Cant, M. A., Johnstone, R. A., Ellifrit, D. K., Balcomb, K. C., & Croft, D. P. (2023). Costly lifetime maternal investment in killer whales. *Current Biology, 33*(4), 744—748. https://doi.org/10.1016/j.cub.2022.12.057.

Wendt, A., Gibbs, C. M., Peters, S., & Hogue, C. J. (2012). Impact of increasing interpregnancy interval on maternal and infant health. *Paediatric and Perinatal Epidemiology, 26*(s1), 239—258. https://doi.org/10.1111/j.1365-3016.2012.01285.x

Wood, S. N. (2003). Thin plate regression splines. *Journal of the Royal Statistical Society: Series B (Statistical Methodology), 65*(1), 95—114. https://doi.org/10.1111/1467-9868.00374

Zipple, M. N., Archie, E. A., Tung, J., Altmann, J., & Alberts, S. C. (2019). Intergenerational effects of early adversity on survival in wild baboons. *eLife, 8*, Article e47433. https://doi.org/10.7554/eLife.47433

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer.

Appendix

To estimate whether juveniles were approaching their mother to access the newborn, we used focal data on the 18 juveniles that experienced the birth of a younger sibling within the last 3 months. Each time the juvenile approached its mother within 1 m, we calculated whether the juvenile initiated an interaction with the newborn and/or the mother (yes = 1, no = 0) within 1 min following the approach, or until one of them left if a leave happened less than 1 min after the approach. We considered the following interactions: grooming, playing (with the newborn only), affiliative and aggressive interactions. For interactions with the newborn, we considered only the interactions initiated by the juvenile because young baboon infants tend to touch or climb on individuals interacting with their mother. For interactions with the mother, we considered interactions initiated both by the juvenile and its mother. We then calculated the percentage of approaches followed by an interaction with the newborn (whether the juvenile interacted with the newborn only or both with the mother and the newborn) or with the mother (the juvenile interacted with the mother only).

Table A1
Summary of all models included in the study

Model number	Response variable	Model type	Sample size (no. of observations/ no. of juveniles)	Fixed effects	Random effects	Offset
1	Probability of grooming the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
2	Probability of being groomed by the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
3	Total time grooming the mother	Negative binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop	Juvenile identity	Focal duration
4	Total time being groomed by the mother	Negative binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop	Juvenile identity	Focal duration
5	Probability of being within 1 m from the mother	Binomial GLMM	2562/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop	Juvenile identity	NA
6	Probability of being within 5 m from the mother	Binomial GLMM	2532/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop	Juvenile identity	NA
7	Probability of approaching the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
8	Probability of leaving the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
9	Probability of being approached by the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration, presence of a younger sibling*juvenile's sex	Juvenile identity	NA
10	Probability of being left by the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
11	Frequency of self-scratches	Negative binomial GLMM	1523/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, year, presence of a younger sibling*juvenile's age	Juvenile identity	Focal duration

Table A2
Results of the mixed models analysing the probability of a juvenile grooming (model A1) or receiving (model A2) grooming from its mother during a focal observation

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P
				2.5%	97.5%		
Model A1: probability of grooming the mother	Intercept		−2.522	−3.071	−1.973	−	−
	Presence of a younger sibling (No)	Yes	0.542	0.001	1.082	3.829	0.050
	Juvenile's age		**0.395**	**0.077**	**0.712**	**6.344**	**0.012**
	Juvenile's sex (Female)	Male	**−1.477**	**−2.109**	**−0.845**	**20.623**	**<0.001**
	Juvenile's birth rank (Later born)	First-born	0.175	−0.690	1.039	0.153	0.695
	Mother's rank		0.060	−0.222	0.343	0.172	0.678
	Number of immature older siblings		−0.006	−0.357	0.344	0.001	0.971
	Troop (J)	L	0.132	−0.495	0.759	3.228	0.199
		M	−0.893	−2.059	0.273		
	Focal observation duration		0.065	−0.137	0.266	0.391	0.532
Full-Null model comparison: $x_2^2 = 46.607$, $P < 0.001$ (AIC full = 713.11, AIC null = 741.11)							
Model 1-Model A1 comparison: $x_2^2 = 0.0013$, $P = 0.971$ (AIC Model 1 = 711.11, AIC Model A1 = 713.11)							
Model A2: probability of being groomed by the mother	Intercept		−1.648	−2.018	−1.277	−	−
	Presence of a younger sibling (No)	Yes	−0.137	−0.537	0.263	0.476	0.490
	Juvenile's age		−0.154	−0.387	0.079	1.854	0.173
	Juvenile's sex (Female)	Male	−0.229	−0.596	0.137	1.770	0.183
	Juvenile's birth rank (Later born)	First-born	−0.118	−0.734	0.498	0.125	0.723
	Mother's rank		−0.021	−0.205	0.162	0.066	0.798
	Number of immature older siblings		0.048	−0.209	0.305	0.168	0.682
	Troop (J)	L	0.107	−0.299	0.512	4.428	0.109

Table A2 (*continued*)

Response variable	Fixed factor	Levels	Estimate	CI 2.5%	97.5%	LRT	P
		M	−0.596	−1.285	0.093		
	Focal observation duration		0.142	−0.009	0.292	3.545	0.060

Full-Null model comparison: $X_2^2 = 17.379$, P < 0.043 (AIC full = 1254.6, AIC null = 1254.0)
Model 2-Model A2 comparison: $X_2^2 = 0.168$, P = 0.682 (AIC Model 2 = 1252.8, AIC Model A1 = 1254.6)

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 1525 focal observations on 38 juveniles (N = 18 with a younger sibling, N = 28 without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant.

Table A3
Results of the mixed models analysing the grooming time (s) given to the mother (model A3) or received from the mother (model A4) by the juvenile during a focal observation

Response variable	Fixed factor	Levels	Estimate	CI 2.5%	97.5%	LRT	P
Model A3: time spent grooming the mother	Intercept		−4.459	−5.153	−3.765	−	−
	Presence of a younger sibling (No)	Yes	**0.521**	**0.009**	**1.032**	**3.978**	**0.046**
	Juvenile's age		**0.393**	**0.094**	**0.691**	**7.097**	**0.008**
	Juvenile's sex (Female)	Male	**−1.455**	**−2.071**	**−0.838**	**21.161**	**<0.001**
	Juvenile's birth rank (Later born)	First-born	0.143	−0.683	0.969	0.112	0.738
	Mother's rank		0.061	−0.213	0.335	0.188	0.665
	Number of immature older siblings		−0.003	−0.335	0.329	0.000	0.985
	Troop (J)	L	0.152	−0.451	0.754	3.466	0.177
		M	−0.881	−2.024	0.262		
Full-Null model comparison: $x_2^2 = 48.106$, P < 0.001 (AIC full = 2137.7, AIC null = 2169.8) Model 3-Model A3 comparison: $x_2^2 = 0.0003$, P = 0.986 (AIC Model 3 = 2135.7, AIC Model A3 = 2137.7)							
Model A4: time spent being groomed by the mother	Intercept		−3.375	−3.814	−2.936	−	−
	Presence of a younger sibling (No)	Yes	−0.153	−0.500	0.194	0.749	0.387
	Juvenile's age		−0.137	−0.342	0.067	1.730	0.188
	Juvenile's sex (Female)	Male	−0.226	−0.540	0.088	1.869	0.172
	Juvenile's birth rank (Later born)	First-born	−0.084	−0.613	0.445	0.098	0.754
	Mother's rank		−0.020	−0.176	0.137	0.063	0.803
	Number of immature older siblings		0.058	−0.164	0.280	0.262	0.609
	Troop (J)	L	0.151	−0.197	0.499	5.062	0.080
		M	−0.566	−1.181	0.048		

Full-Null model comparison: $x_2^2 = 15.129$, P = 0.057 (AIC full = 4370.4, AIC null = 4369.6)
Model 4-Model A4 comparison: $x_2^2 = 0.262$, P = 0.609 (AIC Model 4 = 4368.7, AIC Model A4 = 4370.4)

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 1525 focal observations on 38 juveniles (N = 18 with a younger sibling, N = 28 without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant.

Table A4
Results of the mixed models analysing the probability for a juvenile to be within 1 m (model A5) or within 5 m (model A6) from its mother during a scan observation

Response variable	Fixed factor	Levels	Estimate	CI 2.5%	97.5%	LRT	P
Model A5: probability of being within 1 m from the mother	Intercept		−1.896	−2.227	−1.566	−	−
	Presence of a younger sibling (No)	Yes	−0.049	−0.417	0.319	0.182	0.670
	Juvenile's age		**−0.240**	**−0.453**	**−0.027**	**4.948**	**0.026**
	Juvenile's sex (Female)	Male	**−0.636**	**−0.979**	**−0.292**	**13.418**	**<0.001**
	Juvenile's birth rank (Later born)	First-born	−0.325	−0.879	0.230	1.368	0.242
	Mother's rank		0.106	−0.062	0.274	1.854	0.173
	Number of older immature siblings		−0.061	−0.288	0.166	0.251	0.617
	Troop (J)	L	−0.021	−0.407	0.364	2.875	0.237
		M	−0.461	−1.057	0.134		
Full-Null model comparison: $x_2^2 = 27.259$, P < 0.001 (AIC full = 1609.4, AIC null = 1620.7) Model 5-Model A5 comparison: $x_2^2 = 0.251$, P = 0.617 (AIC Model 5 = 1607.7, AIC Model A5 = 1609.4)							
Model A6: probability of being within 5 m from the mother	Intercept		−1.682	−1.961	−1.403	−	−
	Presence of a younger sibling (No)	Yes	0.155	−0.164	0.474	0.968	0.325
	Juvenile's age		**−0.256**	**−0.432**	**−0.080**	**9.135**	**0.003**
	Juvenile's sex (Female)	Male	**−0.338**	**−0.610**	**−0.065**	**5.508**	**0.019**

Table A4 (*continued*)

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P
				2.5%	97.5%		
	Juvenile's birth rank (Later born)	First-born	−0.046	−0.485	0.394	0.042	0.838
	Mother's rank		**0.190**	**0.054**	**0.326**	**6.387**	**0.011**
	Number of immature older siblings		−0.064	−0.256	0.128	0.439	0.508
	Troop (J)	L	0.024	−0.303	0.351	3.255	0.196
		M	0.388	−0.023	0.800		

Full-Null model comparison: $x_2^2 = 25.837$, $P = 0.001$ (AIC full = 2196.7, AIC null = 2206.6)
Model 5-Model A5 comparison: $x_2^2 = 0.439$, $P = 0.508$ (AIC Model 6 = 2195.2, AIC Model A6 = 2196.7)

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 2562 and 2532 scan observations, respectively, on 38 juveniles ($N = 18$ with a younger sibling, $N = 28$ without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant.

Table A5
Results of the mixed models analysing the probability of a juvenile approaching (model A7) or leaving (model A8) its mother within 1 m during a focal observation.

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P
				2.5%	97.5%		
Model A7: probability of approaching the mother	Intercept		−1.606	−1.943	−1.270	−	−
	Presence of a younger sibling (No)	Yes	**0.503**	**0.163**	**0.844**	**8.293**	**0.004**
	Juvenile's age		−0.161	−0.356	0.034	2.655	0.103
	Juvenile's sex (Female)	Male	−0.149	−0.463	0.165	0.874	0.350
	Juvenile's birth rank (Later born)	First-born	0.036	−0.490	0.562	0.018	0.894
	Mother's rank		**0.170**	**0.016**	**0.323**	**4.257**	**0.039**
	Number of immature older siblings		0.096	−0.123	0.315	0.734	0.392
	Troop (J)	L	**−0.104**	**−0.477**	0.270	**8.063**	**0,018**
		M	**0.662**	**0.168**	**1.157**		
	Focal observation duration		**0.141**	**0.005**	**0.277**	**4.275**	**0.039**

Full-Null model comparison: $x_2^2 = 26.936$, $P = 0.001$ (AIC full = 1506.5, AIC null = 1515.4)
Model 7-Model A7 comparison: $x_2^2 = 0.0003$, $P = 0.734$ (AIC Model 7 = 1505.2, AIC Model A7 = 1506.5)

Model A8: probability of leaving the mother	Intercept		−1.778	−2.144	−1.413	−	−
	Presence of a younger sibling (No)	Yes	**0.468**	**0.101**	**0.835**	**6.758**	**0.009**
	Juvenile's age		−0.116	−0.327	0.096	1.426	0.232
	Juvenile's sex (Female)	Male	**−0.407**	**−0.752**	**−0.062**	**5.915**	**0.015**
	Juvenile's birth rank (Later born)	First-born	0.120	−0.452	0.692	0.223	0.637
	Mother's rank		**0.187**	**0.019**	**0.356**	**5.244**	**0.022**
	Number of immature older siblings		0.152	−0.088	0.393	1.691	0.194
	Troop (J)	L	**−0.100**	**−0.497**	0.296	**10.745**	**0.005**
		M	**0.803**	**0.269**	**1.338**		
	Focal Observation duration		0.073	−0.071	0.217	1.039	0.308

Full-Null model comparison: $x_2^2 = 26.884$, $P = 0.002$ (AIC full = 1341.1, AIC null = 1350.0)
Model 8-Model A8 comparison: $x_2^2 = 1.691$, $P = 0.196$ (AIC Model 8 = 1340.8, AIC Model A8 = 1341.1)

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 1525 focal observations on 38 juveniles ($N = 18$ with a younger sibling, $N = 28$ without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant.

Table A6
Results of the mixed models analysing the probability of a juvenile being approached (model A9) or being left (model A10) within 1 m by its mother during a focal observation

Response variable	Fixed factors	Levels	Estimate	CI		LRT	P
				2.5%	97.5%		
Model A9: probability of being approached by the mother	Intercept		−3.163	−3.749	−2.577	−	−
	Presence of a younger sibling (No)	Yes	−0.498	−1.191	0.195	−	−
	Juvenile's age		0.017	−0.292	0.325	0.006	0.941
	Juvenile's sex (Female)	Male	−0.585	−1.234	0.064	−	−
	Juvenile's birth rank (Later born)	First-born	0.145	−0.659	0.949	0.155	0.694
	Mother's rank		**0.565**	**0.290**	**0.840**	**18.241**	**<0.001**
	Number of immature older siblings		−0.075	−0.438	0.289	0.141	0.707
	Troop (J)	L	**0.807**	**0.210**	**1.404**	**15.725**	**<0.001**
		M	**1.378**	**0.645**	**2.111**		
	Focal observation duration		0.154	−0.064	0.372	1.893	0.169
	Presence of a younger sibling (No)* Juvenile's sex (Female)	Yes, Male	**1.190**	**0.171**	**2.210**	**6.184**	**0.013**

Full-Null model comparison: $X_2^2 = 30.493$, $P < 0.001$ (AIC full = 714.15, AIC null = 724.65)
Model 9-Model A9 comparison: $X_2^2 = 0.141$, $P = 0.707$ (AIC Model 9 = 712.29, AIC Model A9 = 714.15)

Model A10: probability of being left by the mother	Intercept		−1.977	−2.355	−1.599	−	−
	Presence of a younger sibling (No)	Yes	0.175	−0.213	0.563	0.779	0.377
	Juvenile's age		−0.055	−0.281	0.172	0.225	0.636
	Juvenile's sex (Female)	Male	−0.253	−0.612	0.107	1.788	0.181
	Juvenile's birth rank (Later born)	First-born	−0.147	−0.763	0.470	0.222	0.638
	Mother's rank		0.000	−0.178	0.178	0.000	0.998
	Number of immature older siblings		0.157	−0.096	0.411	1.482	0.223
	Troop (J)	L	0.204	−0.214	0.623	2.578	0.276
		M	0.481	−0.095	1.057		
	Focal observation duration		**0.190**	**0.031**	**0.349**	**5.726**	**0.017**

Full-Null model comparison: $X_2^2 = 15.384$, $P = 0.081$ (AIC full = 1198.0, AIC null = 1195.4)
Model 10-Model A10 comparison: $X_2^2 = 1.482$, $P = 0.223$ (AIC Model 10 = 1197.5, AIC Model A10 = 1198.0)

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 1525 focal observations on 38 juveniles ($N = 18$ with a younger sibling, $N = 28$ without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant. Whenever an interaction is significant, LRT and P values for the simple predictors are not shown.

Table A7
Results of the mixed models analysing the frequency of self-scratches during a focal observation (model A11)

Fixed factor	Levels	Estimate	CI		LRT	P
			2.5%	97.5%		
Intercept		−5.813	−5.971	−5.656	−	−
Presence of a younger sibling (No)	Yes	0.041	−0.113	0.194	−	−
Juvenile's age		−0.110	−0.209	−0.012	−	−
Juvenile's sex (Female)	Male	0.050	−0.083	0.182	0.529	0.467
Juvenile's birth rank (Later born)	First-born	−0.106	−0.325	0.112	0.880	0.348
Mother's rank		−0.065	−0.132	0.001	3.476	0.062
Number of older immature siblings		−0.001	−0.090	0.089	0.000	0.989
Troop (J)	L	**0.008**	**−0.140**	**0.156**	**9.775**	**0.008**
	M	**−0.358**	**−0.578**	**−0.138**		
Year (2017)	2018	**−0.316**	**−0.519**	**−0.114**	**13.809**	**0.001**
	2019	**0.085**	**−0.060**	**0.230**		
Presence of a younger sibling (No)*juvenile's age	Yes	**0.166**	**0.036**	**0.296**	**5.866**	**0.015**

Full-Null model comparison: $X_2^2 = 26.07$, $P = 0.006$ (AIC full = 7160.1, AIC null = 7164.1)
Model 11-Model A11 comparison: $X_2^2 = 0.0002$, $P = 0.989$ (AIC Model 11 = 7158.1, AIC Model A11 = 7160.1)

Estimates, 95% confidence intervals (CI), likelihood ratio test (LRT) statistics and P values of the predictors were estimated using 1525 focal observations on 38 juveniles ($N = 18$ with a younger sibling, $N = 28$ without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provide Akaike information criterion (AIC) values to clarify which model performed best when the full−null model comparison was significant. Whenever an interaction is significant, LRT and P values for the simple predictors are not shown.