

# Transition to siblinghood in a wild chacma baboon population

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## 1 Transition to siblinghood in a wild chacma baboon population

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### 20 HIGHLIGHTS

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We examine the transition to siblinghood in wild chacma baboons

- Maternal behaviour does not change following the birth of a younger sibling
- But juveniles solicit their mother more often, and show more signs of anxiety
- These results suggest that weaned siblings may compete for maternal attention

### 25 ABSTRACT

26 In monotocous mammals (i.e. where females produce one offspring at a time), most juveniles 27 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 28 29 investment from one offspring to the next and could thus represent a critical moment for mother-offspring conflict and sibling competition. Here, we use behavioural data on juvenile 30 primates who recently experienced, or not, the birth of a younger sibling to investigate 31 32 changes in mother-juvenile relationships during TTS in a wild population of chacma baboons 33 (*Papio ursinus*). We show that (1) mother-juvenile spatial association remained stable; (2) mothers did not decrease their probability to initiate proximity or affiliation with their 34 35 juvenile; and (3) juveniles initiated proximity and affiliation more frequently toward their mothers, and showed more signs of anxiety after the birth of their younger sibling. Taken 36 together, these findings suggest that juveniles with a younger sibling solicit their mother more 37 38 often and seek more maternal attention than juveniles without. Overall, mother-offspring 39 conflict could extend in the post-weaning period, during which more subtle maternal resources, such as maternal attention, could be at stake in sibling competitive relationships. 40

41 KEYWORDS

Maternal behaviour; mother-offspring bonds; mother-offspring conflicts; sibling birth; sibling
 rivalry; sibship

### 44 INTRODUCTION

Parental investment is defined as any type of investment a parent can provide to its offspring 45 46 that will enhance the offspring's fitness at the cost of the parent's future reproduction (Trivers, 47 1972). In a seminal paper, Trivers argued that natural selection should favour, in offspring, the expression of traits favouring the monopolisation of parental resources, above the level that 48 parents may be willing to provide (Trivers, 1974). This difference in the optimal amount of 49 50 parental investment is triggered by an asymmetry in genetic relatedness between the different family members: an offspring is twice as related to himself as it is to its siblings, while 51 a parent is equally related to all offspring. This genetic conflict of interest is predicted to trigger 52 53 conflicts over the amount and duration of parental investment, not only between parents and offspring, but also between siblings, who should all try to maximize their share of parental 54 55 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 56 to mammals (see for reviews: Mock et Parker 1998; Drummond 2006) where it can largely 57 58 impact offspring's development, with long-term consequences in three areas: morphology 59 (e.g. insects: Schrader et al., 2018; birds: de Kogel and Prijs, 1996; mammals: Fisher et al., 60 2018; Hofer and East, 2008), physiology (e.g. birds: Drummond and Rodríguez, 2013; Nettle et al., 2015; Verhulst et al., 2006; mammals: Fey and Trillmich, 2008; Guenther and Trillmich, 61 2015; Stauffer et al., 2018) and behaviour (e.g. birds: Bebbington et al., 2017; Ekman et al., 62 2002; mammals: Guenther and Trillmich, 2015; Hudson et al., 2011) and even lead to siblicide 63 (e.g. birds: Braun and Hunt, 1983; Fujioka, 1985; Lougheed and Anderson, 1999; mammals: 64

Andersen et al., 2011; Hofer and East, 2008). However, our understanding of family competition suffers from a taxonomic bias: most studies have focused on brood or litterrearing species (especially in mammals, see for reviews: Drummond 2006, Hudson et Trillmich 2008, Roulin et 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.

72 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 73 compete for different resources than milk (Hudson & Trillmich, 2008), meaning that sibling 74 competition can last beyond weaning age. In those species, offspring may form long and 75 76 enduring bonds with mother that can extend far beyond independency (e.g. yellow baboons, 77 Papio cynocephalus: Silk et al., 2006b, 2006a; Asian elephants, Elephas maximus: Lynch et al., 2019; red deer, Cervus elaphus: Clutton-Brock et al., 1982), and exhibit a period of post-78 79 weaning juvenility, during which they keep benefiting from maternal care such as social support, facilitated access to food, or protection against predators (Clutton-Brock, 1991). 80 Maternal presence during the post-weaning developmental period improves offspring growth 81 (e.g. chimpanzees, Pan troglodytes: Samuni et al. 2020), and increases future reproductive 82 success and longevity (chimpanzees: Crockford et al., 2020, Stanton et al. 2020; bonobos, Pan 83 paniscus: Surbeck et al., 2011; red deer: Andres et al., 2013), potentially through a prolonged 84 access to such forms of maternal care. Monopolising such resources might be advantageous 85 86 for offspring, and could thus induce competition between siblings.

In line with this, several empirical studies show that sibling competition can have 87 substantial fitness consequences in monotocous species. In Galapagos fur seals 88 (Arctocephalus galapagoensis) and sea lions (Zalophus wollebaeki), calves whose mother is 89 still nursing the older sibling experience a reduced growth and increased mortality risk 90 91 (Trillmich & Wolf, 2008). In rhesus macaques (Macaca mulatta), short interbirth intervals 92 reduce the survival to adulthood for the older offspring and the survival to weaning for the 93 younger one (Lee et al., 2019). In female yellow baboons, having a close-in-age younger sibling 94 nearly doubles the mortality risk during adulthood (Tung et al., 2016). Moreover, this effect 95 has intergenerational consequences because adult females whose mother had a close-in-age 96 younger sibling further experienced higher offspring mortality (Zipple et al., 2019). In humans (Homo sapiens) as well, short interbirth intervals increase offspring mortality risk (Conde-97 98 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 99 conditions under which sibling competition over access to maternal resources should evolve. 100

101 Regarding the behavioural mechanisms at play, while many primate studies have 102 focused on mother-offspring conflicts during the weaning period or around a mother's cycle 103 resumption (Barrett and Henzi, 2000; Bateson, 1994; reviewed in Maestripieri, 2002), the birth 104 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 105 could thus represent a critical moment for both mother-offspring conflict and sibling 106 107 competition. A few studies led on captive or free-ranging cercopithecines showed that the 108 birth of a younger sibling induces an abrupt decrease in time spent in contact or in proximity 109 to the mother and in the rate of mother-offspring interactions, primarily driven by the juvenile 110 itself (Devinney et al., 2001; DiGregorio et al., 1987; Holman & Goy, 1988; Schino & Troisi,

111 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; 112 Holman & Goy, 1988). In bonobos, juveniles face an increase in cortisol and a decrease in 113 114 neopterin levels that can last more than six months after the birth of their younger sibling 115 (Behringer et al., 2022). The behavioural transition to siblinghood has been more thoroughly 116 studied in humans: it is often characterized by a decrease in maternal care and in the rate of 117 mother-offspring interactions, an increase in the rate of confrontational behaviour with the 118 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., 119 120 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 121 122 human literature is the high inter-individual variability in children's behavioural adjustment to 123 the birth of a sibling (Dunn et al., 1981; Volling, 2012, 2017). Poor behavioural adjustment (e.g. higher frequency of tantrums and jealousy events toward the younger sibling) is 124 associated, possibly causally, with lower quality relationships between siblings later in life 125 126 (Brody, 1998; Pike et al., 2005), which could potentially be costly as siblings' relationships and 127 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 two 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). 135 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 136 elevated infant mortality (Altmann & Alberts, 2003a). Unweaned infants are sometimes 137 138 targets of infanticide in this species, with minimal risks to weaned, older offspring (Palombit 139 et al., 2000). In baboons, like in most primates, mothers form long-lasting bonds with their 140 offspring, which facilitate the transition to feeding autonomy (e.g. Lynch et al., 2020) and 141 subsequently translate into preferential grooming relationships and occasional support during 142 conflicts as long as offspring remain in their natal group. All these resources likely increase 143 offspring survival, as observed in chimpanzees (Nakamura et al., 2014; Stanton et al., 2020), 144 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 145 146 younger sister could induce lifetime costs through the loss of maternally-transmitted social 147 capital (Pereira, 1989).

148 In three social groups of chacma baboons from Namibia, we investigated immediate 149 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 150 151 those of comparable ages who recently experienced the birth of a younger sibling. First, we 152 predicted (P1.1) that the amount and quality of affiliative relationships, specifically grooming 153 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-154 155 initiated before the birth of the sibling, to mostly juvenile-initiated interactions afterwards, as 156 found in humans. Second, we predicted that juveniles (P2.1) would associate less often with 157 their mother, and (P2.2) would become primarily responsible for initiating and maintaining 158 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).

### 162 METHODS

### 163 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).

### 171 Individual data

172 Individual birth dates were assessed with certainty when field observers were present during 173 the birth (N = 10 offspring), or were estimated using two different methods, depending on the 174 available information: (i) infant's coloration using a standardized, validated protocol, when 175 the infant was not fully grey when first observed (N = 16, median date uncertainty = 41 days, 176 see (Dezeure, Dagorrette, et al., 2021)), (ii) mother's reproductive states in the previous 177 months otherwise (N = 32, median date uncertainty = 18 days). Overall, age uncertainty in our 178 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 181 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-182 avoidance interactions: supplants, displacements, attacks, chases and threats (Huchard et al., 183 2010). We computed a linear hierarchy using Matman 1.1.4 (Noldus Information Technology, 184 185 2013), and transformed it into a proportional hierarchy with relative ranks (i.e. absolute rank 186 divided by number of adult females in a group), assigning each female one relative rank per 187 year, ranging from 0 (low-ranking) to 1 (high-ranking). We used proportional ranks rather than 188 simple ordinal ranks because they allow to control for group size across different social groups and/or observational periods. Proportional ranks have recently been shown to better predict 189 190 some female traits associated with reproductive pace (Levy et al., 2020), and could thus better predict patterns of maternal care during the post-weaning period. 191

### 192 Behavioural observations and sample selection

We collected 1401 hours of focal observations from 71 offspring born to 37 females (mean ± 193 194 SD =  $19.7 \pm 9.9$  h of observation per individual, range 1.3-38.6 h) using 20-min long focal 195 observations ( $N = 57.6 \pm 27.9$  focal observations per individual, N = 4086 in total). Focal 196 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 3h time blocks), and 197 focal individuals were chosen randomly and sampled no more than once per half-day. We 198 recorded the duration and direction of grooming interactions with the mother and the 199 200 occurrence of self-scratches, a self-directed behaviour generally indicating anxiety. 201 Maintenance of spatial proximity was assessed by recording every close approach or leave (to 202 and from 1m) between the focal individual and its mother. In addition, we collected scans 203 during focal observations every five minutes (i.e., up to 5 scans for each 20-min focal

204 observation, resulting in 20182 scans in total across 4086 focal observations), and recorded 205 whether the mother was in sight, and if yes, her distance to the focal. If the mother was out 206 of sight, observers indicated the number of meters around the focal individual for which they 207 could guarantee that the mother was not in sight (range: 1-100 m). Other cases where visibility 208 was too obstructed (e.g. when focal was in sight but in a dense bush) were recorded as missing 209 data.

210 In this study, we aimed to characterize the immediate behavioural response to the 211 birth of a younger sibling. To do so, we used a cross-sectional approach, comparing juveniles 212 who recently experienced, within the last three months, the birth of a younger sibling to juveniles of similar ages who did not yet. Juveniles who had experienced the birth of a sibling 213 214 in the more distant past were excluded from this study. This 3-months window was chosen to 215 maximize our chances to detect changes in behaviour that immediately follow the birth of an 216 infant, i.e. reasonably close to the birth event while still ensuring a decent sample size of 217 observations. In our sample of focal observations, juveniles who had recently experienced the 218 birth of a younger sibling were 17- to 29-month-old. Therefore, we restricted our dataset to any juvenile in this age range (17-29 months), who either had no younger sibling (N = 28), or 219 a younger sibling born within the last three months (N = 18). Individuals who were followed 220 221 both before and after the birth of their younger sibling were included in each group 222 respectively. We collected a total of 1525 focal observations and 7581 scan observations on 38 individuals (8 individuals were observed both with and without a younger sibling). 223

224 Statistical models

### 225 Mother-juvenile grooming relationships

226 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 227 focal juvenile groomed its mother at least once (binary: yes/no - model 1), and whether it 228 received grooming from its mother (binary: yes/no - model 2). The probability to give or to 229 230 receive grooming from the mother during a focal observation (models 1 and 2, respectively) 231 was modelled with two generalised linear mixed models (GLMMs) with a binomial error 232 structure. Second, we extracted the total duration (in seconds) the juvenile spent grooming 233 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. 234

#### 235 <u>Mother-juvenile spatial proximity</u>

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

241 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 242 243 each focal observation, we established whether the juvenile initiated an approach to, or a 244 leave from its mother within a circle of 1m-radius (1) or not (0) (models 7 and 8, respectively). 245 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 246 structure. In addition, we computed 'Hinde's Index' for each mother-juvenile dyad, calculated 247 as the percentage of approaches minus the percentage of leaves initiated by the juvenile 248

249 (Hinde & Atkinson, 1970). This index ranges from -100 (the mother is fully responsible for 250 maintaining proximity) to +100 (the juvenile is fully responsible for maintaining proximity). We 251 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 252 the period, we computed the Hinde's index before and after the birth event. We then tested 253 254 if the average Hinde's Index for a given sibling status differed from zero using a one-sample 255 Student's t-test (*N* = 13 indices on juveniles with a younger sibling, *N* = 22 on juveniles without 256 a younger sibling). We also tested whether the average Hinde's Index differed between juveniles with or without sibling using a linear model (N = 34 indices across both groups). For 257 258 each test, if a dyad had several indices (because it was observed during two different 259 observational periods or because a sibling was born during a given period -N = 28 individuals 260 with 1 index, N = 9 with 2 indices and N = 1 with 3 indices), we randomly selected one of them to avoid pseudoreplication. 261

### 262 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).

### 266 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 sex, age (in months), birth rank (first-born vs later-born), and maternal rank. We also tested the interaction terms between the recent birth of a younger sibling and the focal juvenile age and sex (except for model 3 because of a limited and unbalanced sample size). 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 (in seconds) (except
models 5-6 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.

277 We included the focal juvenile identity as a random effect in all models to control for 278 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 non-independence of multiple scan 279 observations within a same focal observation. However, adding this random effect caused 280 convergence problems. We therefore restricted our dataset to two scans per focal 281 observation, which were separated by >15 minutes and for which the mother-focal juvenile 282 283 distance was documented ("out of sight" or "in sight" with the approximated distance; missing 284 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 285 286 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 over-parametrisation: 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 summarised in Table A1.

293 Note that several other variables could account for some variability in mother-juvenile 294 relationships throughout the TTS, such as the mother's reproductive stage or the presence or 295 number of older siblings. In the first case, pregnant mothers may reduce their level of care but 296 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 297 sibling are all lactating, while mothers of those without are either cycling or pregnant). In the 298 299 latter case, older non-adult siblings may represent potential compensatory social partners, or 300 may alternatively contribute to dilute the level of maternal care received by each sibling. 301 Therefore, we re-ran all models with the number of older immature siblings as an additional 302 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, and results are presented in the 303 304 Supplementary Materials (Tables A2 to A7). This additional control variable was never found 305 to exert a significant effect on our response variables, and did not improve our model fits, so 306 we present the results without it in the main text.

#### 307 <u>Statistical analysis</u>

308 All statistical analyses were conducted using the R Studio software (version 4.0.2). We ran mixed models using the function "glmer" from the lme4 package (Bates et al., 2015) for 309 binomial models and "glmmTMB" from the glmmTMB package (Brooks et al., 2017) for 310 311 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 312 313 shape of its relationship with age. To do so, we ran generalized additive mixed models 314 (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 315 316 polynomial function to model the effect of age (offsets and random effects were also 317 included). We then compared model fits and selected the models with the lowest AIC (Zuur et 318 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. 319 When we obtained singular fits, we confirmed the results by running a Bayesian approach, 320 using the "bglmer" function from the blme package (Dorie et al., 2021). When a Poisson model 321 322 was overdispersed, we compared its fit with a type-I negative binomial model and a type-II 323 negative binomial model and selected the model with the lowest AIC (Zuur et al., 2009). 324 Following this test, models 3 and 4 were run with a type-I negative binomial distribution and 325 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 & 326 327 Weisberg, 2019) in order to facilitate model convergence, as well as to compare effect sizes across estimates (Harrison et al., 2018). To diagnose the presence of multicollinearities, we 328 329 calculated the variance inflation factor (VIF) for each predictor in each model using the "vif" 330 function from the car package (Fox & Weisberg, 2019). VIFs were inferior to 2 in all cases, suggesting that multicollinearities did not impact coefficients' estimation in our models. To 331 test the significance of fixed factors for each model, we used the likelihood ratio test (LRT) and 332 associated p-values computed by the "drop1" function, and calculated the 95% Wald 333 334 confidence intervals. Non-significant interactions were removed from the full model to limit 335 the risk of over-parametrisation and facilitate the interpretation of simple effects. Finally, we 336 assessed the significance of our full model by comparing its fit to the equivalent null model (intercept only model, including the random effects) using a likelihood-ratio test. We further 337 checked the distribution of the residuals using "simulateResiduals" from the DHARMa package 338 339 (Hartig & Lohse, 2021).

340 Ethical Note

341 This study was strictly observational and relied on behavioural data collected noninvasively 342 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 343 ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching. This 344 345 research was carried out with the permission of the Namibian Ministry of Environment and 346 Tourism (MET), the Ministry of Land Reform, and the National Commission on Research, 347 Science and Technology. Our research was conducted under MET permit numbers 2303/2017, RPIV00392018/2019. 348

349 **RESULTS** 

### 350 Mother-juvenile grooming relationships

351 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 352 353 grooming received from the mother were independent from the birth of a younger sibling (probability: Odds Ratio – OR - = 0.89, duration: mean  $\pm$  SD = 36.5  $\pm$  13.8 seconds per 354 observation; Tables 1 and 2, Fig. 1b, 1d). In contrast, juveniles with a younger sibling had a 355 356 significantly higher probability (OR = 1.71; mean probability  $\pm$  SD with a sibling:  $0.10 \pm 0.07$  vs 357 without a sibling:  $0.05 \pm 0.04$ ), and spent significantly more time grooming their mother (20.9)  $\pm$  17.3 seconds per focal observation for juveniles with a sibling vs. 9.1  $\pm$  7.2 for those without; 358 359 Tables 1 and 2, Fig. 1a, 1c). Juvenile males had a significantly lower probability, and spent less time grooming their mother than juvenile females (OR = 0.22, Tables 1 and 2). In contrast, the 360 probability and duration of grooming received from the mother was independent of juveniles' 361 362 sex (Tables 1 and 2). The probability to groom the mother and its duration both significantly increased with age (an increase in one standard deviation in age increased grooming likelihood 363

by 49%, OR = 1.49, Tables 1 and 2), while the probability to receive a grooming from the mother and its duration tended to decrease with juvenile age (OR = 0.84, Tables 1 and 2).

366 Mother-juvenile spatial proximity

367 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 to be within 1m or 5m of their 368 mother during a scan observation (OR = 0.92 and 1.12 respectively, Table 3). Males were 369 370 significantly less likely to be within 1m or 5m of their mother than females (OR = 0.53 and 0.72 respectively, Table 3). Juveniles born to higher-ranking females were significantly more likely 371 372 to be within 5m of their mother (OR = 1.21, Table 3). Overall, juveniles were significantly less 373 likely to be within 1m or 5m of their mother as they grew older (OR = 0.81 and 0.80 respectively, Table 3). 374

375 Juveniles who had recently experienced the birth of a younger sibling were, however, 376 significantly more likely to approach (OR = 1.74, mean probability  $\pm$  SD = 0.24  $\pm$  0.06 for 377 juveniles with a sibling vs.  $0.18 \pm 0.05$  for juveniles without) and leave (OR = 1.71, 0.20 \pm 0.05) for juveniles with a sibling vs.  $0.14 \pm 0.05$  for juveniles without) their mother than juveniles 378 379 who did not yet have a younger sibling (P2.2, Table 4, Fig 2a, 2b). Males were significantly less 380 likely to leave their mother than females (OR = 0.66), while juveniles born to high-ranking 381 females were significantly more likely to approach and leave their mother (OR = 1.19 and 1.21 respectively, Table 4). Overall, the probability to approach and to leave the mother decreased 382 with age (OR = 0.81 and 0.83, Table 4). 383

The probability of receiving an approach from 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  $\pm$  SD = 0.05  $\pm$  0.02) than those without a sibling (0.08  $\pm$  0.04), while males with a younger sibling were more likely to be approached by their mother (0.08  $\pm$  0.02) than those without a sibling (0.05  $\pm$  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 lowranking females (OR = 1.74, Table 5). The probability to be 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*<sup>2</sup> = 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 a younger sibling (one-sample t-test, N = 13, t = 6.2, P < 0.001) and without (one-sample t-test, N = 22, t = 3.8, P < 0.001), indicating that juveniles were more responsible than their mother for maintaining their close spatial proximity. The average Hinde's index was not different between both groups (N = 34, t = 1.131, P = 0.267), meaning that juveniles were equally primarily responsible for maintaining close spatial proximity with their mother whether they had a younger sibling or not (P2.2).

### 401 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 who 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).

### 407 DISCUSSION

408 This study investigated changes in mother-juvenile relationships during the transition to 409 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 410 birth of a new infant, as their grooming probability and duration (P1.1), and their probability 411 412 to initiate and stay in close spatial proximity with their older juveniles remained stable (P2.1 413 and P2.2). Second, we showed that juveniles with a younger sibling increased their 414 responsibility in the maintenance of grooming and spatial relationships with their mother. 415 Indeed, they groomed two times more often and two times longer (P1.2), and approached 416 and left their mother a third more often (P2.2), even though they spent on average the same 417 amount of time in close spatial proximity with her than juveniles with no younger sibling. Third, signs of anxiety decreased more slowly with age for juveniles with a younger sibling 418 419 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 420 421 primates.

422 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 423 interactions more often. These results contradict previous studies on TTS in macaques, which 424 425 reported an abrupt decrease in maternal grooming, time spent in close spatial proximity and 426 maternal approaches (Devinney et al., 2001; Holman and Goy, 1988; Schino and Troisi, 2001; Singh and Sachdeva, 1977 but see DiGregorio et al., 1987). In these macaques, these changes 427 were also driven by the juveniles themselves, who decreased the rate at which they initiated 428 429 interactions with their mother (Devinney et al., 2001; Holman & Goy, 1988; Schino & Troisi, 430 2001; Singh & Sachdeva, 1977). These differences with our findings could relate to several, non-mutually exclusive factors. First, the macaque studies were conducted on captive 431

432 populations (from free-ranging to laboratory housing). Captivity and provisioning could affect 433 mother-offspring relationships and specifically accelerate maternal reproductive pace (Altmann & Alberts, 2003b). Second, and perhaps because of their different environments, 434 young macaques were on average 12 months old at the birth of their younger sibling, while 435 436 young chacma baboons were on average 23 months old in this study. Although this age 437 difference is partly due to species differences in reproductive pace, it may also reflect 438 differences in juveniles' independence. Indeed, juvenile macaques were still nursing in the few 439 months preceding the birth of their siblings, while our study subjects had stopped suckling 440 long before their sibling was born (Dezeure, Baniel, et al., 2021). In addition, isotopic analyses 441 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 442 443 impossible to disentangle in the macaque studies, while we were able to measure the effects of TTS on mother-offspring relationships independently of weaning. 444

445 Our results recall previous findings in human studies. Indeed, in western industrialised 446 societies, children became more responsible for initiating interactions with their mother, 447 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 448 449 sibling. Yet, in humans – as in captive macaques – this pattern was associated with a decrease 450 in maternal care and an increase in maternal rejections. The lack of changes in maternal behaviour we observe in our study may be expected in natural populations, as mothers may 451 space births in a way that allows them to provide the care needed by their offspring at 452 453 different stages of their lives. When a newborn arrives, older juveniles are fully weaned and 454 lactation may not substantially affect mothers' ability to maintain their relationship with their 455 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.

461 Although juvenile baboons with and without a younger sibling received as much care 462 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 463 attraction to the newborn, which is commonly observed across primate species, where non-464 mother individuals, mainly females, frequently touch or handle newborns (Dunayer & 465 Berman, 2018; Hrdy, 1976; Meredith, 2015). Non-mother females often access the infant by 466 467 initiating grooming with the mother, resulting in new mothers receiving increased levels of 468 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 469 470 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 471 472 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 473 474 with their mother in 35% of cases (see Appendix 1). Overall, these results suggest that infant handling was not the primary motivation for juveniles to approach their mother. 475

Second, such behavioural changes driven by juveniles may reflect changes in motheroffspring relationship following TTS, which may contribute to accelerate a juvenile's developmental trajectory. They may develop greater independence and autonomy following 479 their sibling's birth, thus increasing their own responsibility in maintaining the motheroffspring spatial and grooming relationships. TTS may also translate into a rescheduling of 480 mother-juvenile interactions, where juveniles would be conditioned to request maternal care 481 only in convenient times so that it does not interfere with infant care (in a similar manner to 482 483 the rescheduling during the weaning period proposed by (Altmann, 1980; Bateson, 1994)). 484 Finally, juveniles may solicit their mother more frequently to seek maternal attention and 485 obtain the same 'pre-sibling arrival' level of care, if the birth of a younger sibling leads to lower 486 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 487 mothers resume cycling (Maestripieri, 2002), which often manifest through highly 488 conspicuous tantrums (Barrett & Henzi, 2000), conflicts can arise at other developmental 489 490 stages (Bateson, 1994) and over any type of maternal investment that can be monopolised. 491 As infants grow older and stop throwing tantrums (as was the case of our study baboons), 492 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-493 494 directed behaviours (Maestripieri, 2002).

495 This increased mother-offspring conflict likely translates into sibling rivalry, which 496 could be mediated, at a proximate level, by jealousy, and may explain the increase in juveniles' 497 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 498 499 beloved (here, the mother), and a rival (here, the younger infant), and is elicited when the 500 jealous individual perceives the relationship between their beloved and a rival as a threat to 501 their own bond with the beloved one (Volling et al., 2010, 2014). Children undergoing TTS 502 display two main types of jealous reactions when their mother interacts with their sibling:

503 negative/distress behaviours (protesting, disrupting the interactions, directing aggression at 504 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 505 the behavioural patterns observed in this study. In humans, sibling jealousy is generally 506 507 considered as a form of competition for parental attention (Volling et al., 2010), a behaviour 508 that is generally not recognized as a form of parental care *per se* in other species but could be 509 adaptive where parental attention improves offspring survival by preventing risks such as 510 accidents or predation, or by promoting information transmission. In non-human primates, 511 maternal attention could be a form of maternal care that siblings could compete over, but this 512 would require testing whether juveniles who attract more maternal attention experience 513 fitness benefits, such as a greater probability to secure maternal support during conflicts, 514 protection against predators, etc.

515 Finally, further dimensions of TTS should be investigated to foster its description in 516 monotocous species. In modern societies, children's adjustment to TTS is highly variable and 517 is associated with several traits such as children's sex, age, personality or their attachment 518 style (Dunn et al., 1981; Volling, 2012, 2017; Volling et al., 2014). Insecurely attached or 519 younger children typically show more negative reactions to the birth of a younger sibling 520 (Dunn et al., 1981; Volling, 2017). Maternal traits, such as maternal style, could also influence 521 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 522 not restricted to their dyad. In humans, which are often described as communal or cooperative 523 524 breeders (Mace & Sear, 2005), the presence of other kin such as the father, grandmother and 525 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 & 526

527 Mendelson, 1990; Legg et al., 1974; Stewart et al., 1987; Volling et al., 2014). This could also 528 be the case in baboons to some extent, as juvenile primates primarily associate with their 529 siblings, and can keep benefitting from their father's presence as long as they co-reside 530 (Charpentier et al., 2008; Lynch et al., 2020).

Our study is among the first to investigate behavioural changes in mother-juvenile 531 532 relationships following the birth of a new sibling in wild nonhuman primates. In chacma 533 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 534 535 towards their mother and seems to generate anxiety, which overall suggests that juveniles 536 have to make more effort to maintain the same level of attention and care from their mother. 537 From an ultimate perspective, these results raise the important question of the adaptive 538 significance of maternal attention that siblings seem to compete over. From a proximate 539 perspective, the juveniles' behavioural changes reported here may resemble the jealous 540 reactions commonly observed in young humans during TTS, and may thus offer a relevant 541 context to study emotional development in young primates. Finally, our results, which are distinct from findings in captive primates, show both similarities and differences to human 542 patterns. As such, they emphasize the need to investigate broader aspects of this intriguing 543 544 developmental milestone in the wild, and across populations and species showing a diversity 545 of life histories and ecologies.

546 DATA AVAILABILITY

547 Data sets and scripts used in this study are available on the following public repository: 548 <u>https://gitlab.com/AxelleDelaunay/transition-to-siblinghood-in-a-wild-chacma-baboon-</u> 549 <u>population</u>

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### 567 **REFERENCES**

568 Altmann, J. (1980). *Baboon Mothers and Infants*. University of Chicago Press.

- 569 Altmann, J., & Alberts, S. C. (2003a). Intraspecific variability in fertility and offspring
- 570 survival in a nonhuman primate : Behavioural control of ecological and social sources.
- 571 In Offspring : Human Fertility Behavior in Biodemographic Perspective. National
- 572 Academies Press (US). https://www.ncbi.nlm.nih.gov/books/NBK97280/

| 573 | Altmann, J., & Alberts, S. C. (2003b). Variability in reproductive success viewed from a life- |
|-----|--|
| 574 | history perspective in baboons. American Journal of Human Biology, 15(3), 401-409.             |
| 575 | https://doi.org/10.1002/ajhb.10157   |

- 576 Andersen, I. L., Nævdal, E., & Bøe, K. E. (2011). Maternal investment, sibling competition,
- 577 and offspring survival with increasing litter size and parity in pigs (*Sus scrofa*).

578 *Behavioral Ecology and Sociobiology*, 65(6), 1159-1167.

579 https://doi.org/10.1007/s00265-010-1128-4

580 Andres, D., Clutton-Brock, T. H., Kruuk, L. E. B., Pemberton, J. M., Stopher, K. V., &

581 Ruckstuhl, K. E. (2013). Sex differences in the consequences of maternal loss in a

582 long-lived mammal, the red deer (*Cervus elaphus*). *Behavioral Ecology and* 

583 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
- 586 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models
- 587 Using lme4. *Journal of Statistical Software*, 67(1), 1.
- 588 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
- 591 Bebbington, K., Kingma, S. A., Fairfield, E. A., Spurgin, L. G., Komdeur, J., & Richardson,
- 592 D. S. (2017). Consequences of sibling rivalry vary across life in a passerine bird.
- 593 *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).
- 595 Transition to siblinghood causes a substantial and long-lasting increase in urinary
- cortisol levels in wild bonobos. *eLife*, *11*, 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. *The 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.,
- 604 Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). GlmmTMB Balances Speed and
- Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling.
- 606 *The R Journal*, 9(2), 378-400.
- 607 Carboni, S., Dezeure, J., Cowlishaw, G., Huchard, E., & Marshall, H. H. (2022). Stable
  608 isotopes reveal the effects of maternal rank and infant age on weaning dynamics in
  609 wild chacma baboons. *Animal Behaviour*.
- 610 Caselli, M., Zanoli, A., Palagi, E., & Norscia, I. (2021). Infant handling increases grooming
- towards mothers in wild geladas (*Theropithecus gelada*). *Behavioural Processes*, 192,
  104501. https://doi.org/10.1016/j.beproc.2021.104501
- 613 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.
- 615 https://doi.org/10.1006/anbe.1999.1250
- 616 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
- 619 Cheney, D. L., Seyfarth, R. M., Fischer, J., Beehner, J., Bergman, T., Johnson, S. E., Kitchen,
- 620 D. M., Palombit, R. A., Rendall, D., & Silk, J. B. (2004). Factors Affecting
- 621 Reproduction and Mortality Among Baboons in the Okavango Delta, Botswana.

- 622 *International Journal of Primatology*, 25(2), 401-428.
- 623 https://doi.org/10.1023/B:IJOP.0000019159.75573.13
- 624 Clutton-Brock, T. H. (1991). The Evolution of Parental Care. In *The Evolution of Parental*625 *Care*. Princeton University Press.
- https://www.degruyter.com/document/doi/10.1515/9780691206981/html
- 627 Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red Deer : Behavior and* 628 *Ecology of Two Sexes*. University of Chicago Press.
- 629 Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1983). The Costs of Reproduction to
- 630 Red Deer Hinds. *Journal of Animal Ecology*, 52(2), 367-383.
- 631 https://doi.org/10.2307/4560
- 632 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
- 635 Crockford, C., Samuni, L., Vigilant, L., & Wittig, R. M. (2020). Postweaning maternal care
- 636 increases male chimpanzee reproductive success. *Science Advances*, *6*(38), eaaz5746.
  637 https://doi.org/10.1126/sciadv.aaz5746
- 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.
- 640 https://doi.org/10.1006/anbe.1996.0073
- 641 Devinney, B. J., Berman, C. M., & Rasmussen, K. L. R. (2001). Changes in yearling rhesus
- 642 monkeys' relationships with their mothers after sibling birth. *American Journal of*
- 643 *Primatology*, 54(4), 193-210. https://doi.org/10.1002/ajp.1030
- 644 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.

646 *Proceedings of the Royal Society B: Biological Sciences*, 288(1950), 20210286.
 647 https://doi.org/10.1098/rspb.2021.0286

648 Dezeure, J., Dagorrette, J., Baniel, A., Carter, A. J., Cowlishaw, G., Marshall, H. H., Martina,

- 649 C., Raby, C. L., & Huchard, E. (2021). Developmental transitions in body color in
- 650 chacma baboon infants : Implications to estimate age and developmental pace.
- 651 *American Journal of Physical Anthropology*, 174(1), 89-102.
- 652 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., functions), D. B. (lme4 non-modular, functions), M. M. (lme4 non-modular,
- functions), B. B. (lme4 non-modular, & functions), S. W. (lme4 non-modular. (2021).
- *blme : Bayesian Linear Mixed-Effects Models* (1.0-5) [Computer software].
- 659 https://CRAN.R-project.org/package=blme
- Drummond, H. (2006). Dominance in Vertebrate Broods and Litters. *The Quarterly Review of Biology*, 81(1), 3-32. https://doi.org/10.1086/503922
- 662 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*,

```
664 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*(0). https://escholarship.org/uc/item/45w0r631
- 667 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*,
- 669 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
- 671 Birth of a Sibling : Mothers' Reports. *Journal of Child Psychology and Psychiatry*,

672 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.
- 675 https://doi.org/10.1006/anbe.2002.3075
- 676 Fairbanks, L. A. (1996). Individual Differences in Maternal Style : Causes and Consequences
- 677 for Mothers and offspring. In J. S. Rosenblatt & C. T. Snowdon (Éds.), *Advances in*

678 *the Study of Behavior* (Vol. 25, p. 579-611). Academic Press.

- 679 https://doi.org/10.1016/S0065-3454(08)60343-5
- 680 Fey, K., & Trillmich, F. (2008). Sibling competition in guinea pigs (*Cavia aperea f.*
- 681 *Porcellus*): Scrambling for mother's teats is stressful. *Behavioral Ecology and*

682 *Sociobiology*, *62*(3), 321-329. https://doi.org/10.1007/s00265-007-0419-x

- 683 Fisher, H. S., Hook, K. A., Weber, W. D., & Hoekstra, H. E. (2018). Sibling rivalry : Males
- 684 with more brothers develop larger testes. *Ecology and Evolution*, 8(16), 8197-8203.
- 685 https://doi.org/10.1002/ece3.4337
- Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (Third). SAGE
  Publications. https://socialsciences.mcmaster.ca/ifox/Books/Companion/
- 688 Frank, R. E., & Silk, J. B. (2009). Grooming Exchange between Mothers and Non-Mothers :
- 689 The Price of Natal Attraction in Wild Baboons (*Papio anubis*). *Behaviour*, *146*(7), 889
  690 -906.
- Fujioka, M. (1985). Sibling competition and siblicide in asynchronously-hatching broods of
- the cattle egret *Bubulcus ibis*. *Animal Behaviour*, *33*(4), 1228-1242.
- 693 https://doi.org/10.1016/S0003-3472(85)80183-4

- Gottlieb, L. N., & Mendelson, M. J. (1990). Parental support and firstborn girls' adaptation to 694
- the birth of a sibling. Journal of Applied Developmental Psychology, 11(1), 29-48. 695 https://doi.org/10.1016/0193-3973(90)90030-N
- 696
- Guenther, A., & Trillmich, F. (2015). Within-litter differences in personality and physiology 697
- relate to size differences among siblings in cavies. Physiology & Behavior, 145, 22-698
- 28. https://doi.org/10.1016/j.physbeh.2015.03.026 699
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. 700
- 701 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, e4794. 702
- https://doi.org/10.7717/peerj.4794 703
- Hartig, F., & Lohse, L. (2021). DHARMa : Residual Diagnostics for Hierarchical (Multi-704
- Level / Mixed) Regression Models (0.3.4) [Computer software]. https://CRAN.R-705 706 project.org/package=DHARMa
- Henzi, S. P., & Barrett, L. (2002). Infants as a commodity in a baboon market. Animal 707 708 *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 709
- 710 mutual proximity, as exemplified by mother-infant relations in rhesus monkeys.
- 711 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 712
- maternal input and cub survival. Behavioral Ecology and Sociobiology, 62(3), 341-713
- 351. https://doi.org/10.1007/s00265-007-0421-3 714
- Holman, S. D., & Goy, R. W. (1988). Sexually dimorphic transitions revealed in the 715
- relationships of yearling rhesus monkeys following the birth of siblings. International 716
- 717 Journal of Primatology, 9(2), 113-133. https://doi.org/10.1007/BF02735732

| 718 | Hrdy, S. B. (1976). Care and Exploitation of Nonhuman Primate Infants by Conspecifics     |
|-----|---|
| 719 | Other Than the Mother. In J. S. Rosenblatt, R. A. Hinde, E. Shaw, & C. Beer (Éds.),       |
| 720 | Advances in the Study of Behavior (Vol. 6, p. 101-158). Academic Press.                   |
| 721 | https://doi.org/10.1016/S0065-3454(08)60083-2   |
| 722 | Huchard, E., Alvergne, A., Féjan, D., Knapp, L. A., Cowlishaw, G., & Raymond, M. (2010).  |
| 723 | More than friends? Behavioural and genetic aspects of heterosexual associations in        |
| 724 | wild chacma baboons. Behavioral Ecology and Sociobiology, 64(5), 769-781.                 |
| 725 | https://doi.org/10.1007/s00265-009-0894-3   |
| 726 | Huchard, E., Charpentier, M. J., Marshall, H., King, A. J., Knapp, L. A., & Cowlishaw, G. |
| 727 | (2013). Paternal effects on access to resources in a promiscuous primate society.         |

728 *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.

- 732 https://doi.org/10.1002/dev.20535
- Hudson, R., & Trillmich, F. (2008). Sibling competition and cooperation in mammals :
- 734 Challenges, developments and prospects. *Behavioral Ecology and Sociobiology*,

735 62(3), 299-307. https://doi.org/10.1007/s00265-007-0417-z

736 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*
- 738 *thibetana*). Zoological Research, 40(2), 139-145. https://doi.org/10.24272/j.issn.2095-
- 739 8137.2018.049

- 740 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.
- 742 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.
- 748 https://doi.org/10.1007/BF01441311
- Levy, E. J., Zipple, M. N., McLean, E., Campos, F. A., Dasari, M., Fogel, A. S., Franz, M.,
- 750 Gesquiere, L. R., Gordon, J. B., Grieneisen, L., Habig, B., Jansen, D. J., Learn, N. H.,
- 751 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.
- 753 *Proceedings of the Royal Society B: Biological Sciences*, 287(1934), 20201013.
- 754 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.
- 757 https://doi.org/10.1007/s002650050535
- Lynch, E. C., Johnson, C. A., Lynch, R. F., Rothman, J. M., Fiore, A. D., & Palombit, R. A.
- 759 (2020). Mothers and fathers improve immature baboon foraging success. *Behaviour*,
  760 *157*(5), 387-414. https://doi.org/10.1163/1568539X-bja10006
- 761 Lynch, E. C., Lummaa, V., Htut, W., & Lahdenperä, M. (2019). Evolutionary significance of
- 762 maternal kinship in a long-lived mammal. *Philosophical Transactions of the Royal*
- 763 *Society B: Biological Sciences*, *374*(1780), 20180067.
- 764 https://doi.org/10.1098/rstb.2018.0067

| 765 | Mace, R., & Sear, R. (2005). Are humans cooperative breeders. Grandmotherhood: The             |
|-----|--|
| 766 | evolutionary significance of the second half of female life, 143-159.                          |
| 767 | Maestripieri, D. (2002). Parent-Offspring Conflict in Primates. International Journal of       |
| 768 | Primatology, 23(4), 923-951. https://doi.org/10.1023/A:1015537201184                           |
| 769 | Maestripieri, D. (2018). Maternal influences on primate social development. Behavioral         |
| 770 | Ecology and Sociobiology, 72(8), 130. https://doi.org/10.1007/s00265-018-2547-x                |
| 771 | Maestripieri, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal :             |
| 772 | Displacement activities as an indicator of emotions in primates. Animal Behaviour,             |
| 773 | 44(5), 967-979. https://doi.org/10.1016/S0003-3472(05)80592-5                                  |
| 774 | Meredith, S. L. (2015). Anchoring the Clade : Primate-Wide Comparative Analysis Supports       |
| 775 | the Relationship between Juvenile Interest in Infants and Adult Patterns of Infant Care.       |
| 776 | Folia Primatologica, 86(1-2), 117-123. https://doi.org/10.1159/000368356                       |
| 777 | Mock, D. W., & Parker, G. A. (1998). The evolution of sibling rivalry. Oxford University       |
| 778 | Press, New York, NY(USA). 464, 1998.   |
| 779 | Nakamura, M., Hayaki, H., Hosaka, K., Itoh, N., & Zamma, K. (2014). Brief                      |
| 780 | Communication : Orphaned male Chimpanzees die young even after weaning.                        |
| 781 | American Journal of Physical Anthropology, 153(1), 139-143.                                    |
| 782 | https://doi.org/10.1002/ajpa.22411   |
| 783 | Nettle, D., Monaghan, P., Gillespie, R., Brilot, B., Bedford, T., & Bateson, M. (2015). An     |
| 784 | experimental demonstration that early-life competitive disadvantage accelerates                |
| 785 | telomere loss. Proceedings of the Royal Society B: Biological Sciences, 282(1798),             |
| 786 | 20141610. https://doi.org/10.1098/rspb.2014.1610   |
| 787 | Palagi, E., & Norscia, I. (2011). Scratching around stress : Hierarchy and reconciliation make |
| 788 | the difference in wild brown lemurs (Eulemur fulvus). Stress, 14(1), 93-97.                    |
| 789 | https://doi.org/10.3109/10253890.2010.505272   |
|     |  |

| 790 | Palombit, R. A., Cheney, D. L., Fischer, J., Johnson, S., Rendall, D., Seyfarth, R. M., & Silk, |
|-----|---|
| 791 | J. B. (2000). Male infanticide and defense of infants in chacma baboons. In C. P. van           |
| 792 | Schaik & C. H. Janson (Éds.), Infanticide by Males and its Implications (1re éd., p. 123        |
| 793 | -152). Cambridge University Press. https://doi.org/10.1017/CBO9780511542312.008                 |
| 794 | Pereira, M. E. (1989). Agonistic Interactions of Juvenile Savanna Baboons. Ethology, 80(1-      |
| 795 | 4), 152-171. https://doi.org/10.1111/j.1439-0310.1989.tb00736.x                                 |
| 796 | Pike, A., Coldwell, J., & Dunn, J. F. (2005). Sibling relationships in early/middle childhood : |
| 797 | Links with individual adjustment. Journal of Family Psychology, 19(4), 523-532.                 |
| 798 | https://doi.org/10.1037/0893-3200.19.4.523  |
| 799 | Pollet, T. V., & Hoben, A. D. (2011). An evolutionary perspective on siblings : Rivals and      |
| 800 | resources. In The Oxford handbook of evolutionary family psychology (p. 128-148).               |
| 801 | Oxford University Press.  |
| 802 | Roulin, A., & Dreiss, A. N. (2012). Sibling competition and cooperation over parental care. In  |
| 803 | The evolution of parental care (p. 133-149). Oxford University Press.                           |
| 804 | Rutstein, S. O. (2005). Effects of preceding birth intervals on neonatal, infant and under-five |
| 805 | years mortality and nutritional status in developing countries : Evidence from the              |
| 806 | demographic and health surveys. International Journal of Gynecology & Obstetrics,               |
| 807 | 89(S1), S7-S24. https://doi.org/10.1016/j.ijgo.2004.11.012                                      |
| 808 | Samuni, L., Tkaczynski, P., Deschner, T., Löhrrich, T., Wittig, R. M., & Crockford, C.          |
| 809 | (2020). Maternal effects on offspring growth indicate post-weaning juvenile                     |
| 810 | dependence in chimpanzees (Pan troglodytes verus). Frontiers in Zoology, 17(1), 1.              |
| 811 | https://doi.org/10.1186/s12983-019-0343-8   |
| 812 | Schino, G., & Troisi, A. (2001). Relationship with the mother modulates the response of         |
| 813 | yearling Japanese macaques (Macaca fuscata) to the birth of a sibling. Journal of               |
|     |   |

- 814 *Comparative Psychology*, *115*(4), 392-396. https://doi.org/10.1037/0735-
- 815 7036.115.4.392
- 816 Schrader, M., Jarrett, B. J. M., & Kilner, R. M. (2018). Parental care and sibling competition
- 817 independently increase phenotypic variation among burying beetle siblings. *Evolution*,
- 818 72(11), 2546-2552. https://doi.org/10.1111/evo.13607
- 819 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.
- 821 Behavioral Ecology and Sociobiology, 61(2), 197-204.
- 822 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-
- 826

- 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.
- 829 https://doi.org/10.1007/BF02383138
- 830 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-
- 833 2804-7
- 834 Stauffer, J., Panda, B., & Ilmonen, P. (2018). Telomere length, sibling competition and
- development of antioxidant defense in wild house mice. *Mechanisms of Ageing and*
- 836 *Development*, 169, 45-52. https://doi.org/10.1016/j.mad.2017.10.002

- 837 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
- 840 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.
- 843 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.
- 846 https://doi.org/10.1007/s00265-007-0423-1
- 847 Trivers, R. L. (1972). *Parental investment and sexual selection*.
- 848 http://joelvelasco.net/teaching/3330/trivers72-parentalinvestment.pdf
- 849 Trivers, R. L. (1974). Parent-Offspring Conflict. *Integrative and Comparative Biology*, 14(1),
- 850 249-264. 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.
- 853 https://doi.org/10.1038/ncomms11181
- 854 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.
- 856 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.
- 859 https://doi.org/10.1037/a0026921

- 860 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 *Handbook of jealousy : Theory, research, and multidisciplinary*
- approaches (p. 387-417). Wiley Blackwell.
- 866 https://doi.org/10.1002/9781444323542.ch17
- Volling, B. L., Yu, T., Gonzalez, R., Kennedy, D. E., Rosenberg, L., & Oh, W. (2014).
- 868 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.
- 870 https://doi.org/10.1037/a0037811
- 871 Wendt, A., Gibbs, C. M., Peters, S., & Hogue, C. J. (2012). Impact of Increasing Inter-
- 872 pregnancy Interval on Maternal and Infant Health. *Paediatric and Perinatal*
- 873 *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:*
- 875 Series B (Statistical Methodology), 65(1), 95-114. https://doi.org/10.1111/1467-
- 876 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*, e47433.
- 879 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* (Vol. 574). Springer.

#### 882 FIGURES

*Figure 1 Influence of the birth of the younger sibling on mother-juvenile grooming interactions.* 883 In all panels, "Sibling status" refers to whether juveniles have recently experienced the birth of 884 a younger sibling ("With"), or not ("Without"). (a) Predicted probability that a juvenile grooms 885 its mother during a focal observation depending on its "sibling status". (b) Predicted 886 probability that a juvenile is being groomed by its mother depending on its "sibling status". (c) 887 Predicted grooming time (in seconds) given by a juvenile to its mother during a focal 888 observation depending on its "sibling status". (d) Predicted grooming time (in seconds) 889 received by a juvenile from its mother during a focal observation depending on its "sibling 890 status". The violin plots show the distribution of the fitted values and the boxplots show the 891 892 median of the distribution of the fitted values (black horizontal bar), the 25th and 75th 893 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" 894 and the associated p-values are shown. "ns": not significant (P>0.05); \*: P<0.05; \*\*: P<0.01; 895 \*\*\*: P <0.001 896



Figure 2: Influence of the birth of the younger sibling on mother-juvenile spatial association 899 (within 1m). In all panels, "Sibling status" refers to whether juveniles have recently experienced 900 the birth of a younger sibling ("With"), or not ("Without"). The four panels show the effect of 901 sibling status on (a) the predicted probability that a juvenile approaches its mother during a 902 focal observation; (b) the predicted probability that a juvenile leaves its mother; (c) the 903 predicted probability that a juvenile is approached by its mother in interaction with juvenile's 904 905 sex; and (d) the predicted probability that a juvenile is left by its mother. The violin plots show 906 the distribution of the fitted probabilities. The boxplots show the median of the distribution of 907 the fitted values (black horizontal bar), the 25th and 75th quartiles (bottom and top of the 908 boxes, respectively) and the whiskers include a maximum of 1.5 times the interguartile range. The effect of the predictor "Presence of a younger sibling" and the associated p-values are 909 shown. "ns": not significant (P>0.05); \* : P <0.05; \*\* : P <0.01; \*\*\* : P <0.001. Note that panel 910 *C* shows the predicted values of the model including a significant interaction between sibling 911 912 status and juvenile's sex (model 8), but post-hoc pairwise mean comparisons were not significant 913





- 916 *Figure 3: Variation in the frequency of self-scratches according to juvenile's age and the birth*
- 917 <u>of a younger sibling.</u> "With" refers to juveniles who recently experienced the birth of a
- 918 younger sibling, "Without" refers to juveniles who did not experience the birth of a younger
- sibling yet. Dots represent the model's adjusted predicted values and the curves show the
- 920 *linear predicted fit from the corresponding mixed model. Predicted values were computed*
- 921 using the function "ggeffect" from the ggeffect package, averaging the values of all the other
- 922 variables in the model. The darker area around each curve represents the confidence interval
- 923 *of the fitted curve*



## 925 TABLES

## 926 Table 1: Determinants of the occurrence of grooming between the mother and the juvenile

| Response variable  |                            | Fixed factor                       | Louolo     | Louale Ectimate |        |        | IDT    | Durahua        |
|--|----------------------------|------------------------------------|------------|-----------------|--------|--------|--------|----------------|
|  |                            | Fixed factor                       | Levels     | Estimate        | 2.5 %  | 97.5 % | LKI    | <i>p-value</i> |
|  | Model 1: Probability to    | Intercept                          |            | -2.524          | -3.063 | -1.985 | -      | -              |
|  | groom the mother           | 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  | 2 204  | 0 102          |
|  |                            |                                    | Μ          | -0.889          | -2.035 | 0.257  | 5.294  | 0.195          |
|  |                            | Focal observation duration         |            | 0.065           | -0.137 | 0.266  | 0.394  | 0.530          |
| Full –Null model comparison: $X_2^2$ = 46.605, <i>P</i> < 0.001 (AIC full = 711.11, AIC null = 741.71) |                            |                                    |            |                 |        |        |        |                |
|  | Model 2: Probability to be | Intercept                          |            | -1.632          | -1.993 | -1.270 | -      | -              |
|  | groomed by the mother      | 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 | 5 272 | 0.068 |
|                                    | М          | -0.638 | -1.291 | 0.016 | 5.575 | 0.008 |
| 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)

927 Table 1: Results of the mixed models analyzing the probability for a juvenile to groom (model 1) or to receive (model 2) a grooming from its mother during a focal observation. Estimates, 95%

928 confidence intervals (CI), 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

929 identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to

930 clarify which model performed best in case the full-null model comparison was significant.

## 932 Table 2: Determinants of the grooming time exchanged between the mother and the juvenile

| Posponso variablo    | Eived factor                            | Lovala                   | Ectimato          | C               | CI        |         | D valua |
|----------------------|---|--------------------------|-------------------|-----------------|-----------|---------|---------|
| Response variable    |   | Levels                   | LStimate          | 2.5 %           | 97.5 %    |         | F-vulue |
| Model 3: Time spent  | Intercept                               |                          | -4.460            | -5.147          | -3.773    | -       | -       |
| grooming the mother  | 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     | 2 5 4 4 | 0.470   |
|                      |   | М                        | -0.879            | -2.002          | 0.244     | 3.544   | 0.170   |
|                      | Full-Null model comparison: $X_2^2 = 4$ | 48.106 <i>, P</i> < 0.00 | 1 (AIC full = 213 | 5.7, AIC null : | = 2169.8) |         |         |
| Model 4: Time spent  | Intercept                               |                          | -3.357            | -3.793          | -2.922    | -       | -       |
| being groomed by the | Presence of a younger sibling (No)      | Yes                      | -0.126            | -0.459          | 0.207     | 0.552   | 0.458   |
| mother               | 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   |

|                                    | М          | -0.615 | -1.206 | -0.024 | 0.050 | 0.047 |
|------------------------------------|------------|--------|--------|--------|-------|-------|
| Troop (J)                          | L          | 0.142  | -0.209 | 0.493  | 6 098 | 0 047 |
| Mother's rank                      |            | -0.015 | -0.171 | 0.142  | 0.033 | 0.855 |
| Juvenile's birth rank (Later-born) | First-born | -0.171 | -0.589 | 0.247  | 0.667 | 0.414 |

Full-Null model comparison:  $X_2^2$  = 14.867, P = 0.038 (AIC full = 4368.7, AIC null = 4369.6)

933 Table 1 : Results of the mixed models analyzing the grooming time (in seconds) given to the mother (Model 3) or received from the mother (Model 4) by the juvenile during a focal observation.

934 Estimates, 95% confidence intervals (CI), 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).

935 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 provided AIC

936 values to clarify which model performed best in case the full-null model comparison was significant.

## 938 Table 3: Determinants of the spatial proximity between the mother and the juvenile

| Response variable    | Fixed factor                               | Levels                   | Estimate         |                 | CI     | LRT    | P-value |
|----------------------|--|--------------------------|------------------|-----------------|--------|--------|---------|
|                      |  |                          |                  | 2.5 %           | 97.5 % |        |         |
| Model 5: Probability | Intercept                                  |                          | -1.913           | -2.238          | -1.588 | -      | -       |
| to be within 1m from | Presence of a younger sibling (No)         | Yes                      | -0.080           | -0.427          | 0.266  | 0.405  | 0.524   |
| the mother           | 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  |        |         |
|                      |  | Μ                        | -0.412           | -0.978          | 0.154  | 2.623  | 0.269   |
|                      | Full-Null model comparison: $X_2^2 = 27.0$ | 08 <i>, P</i> < 0.001 (A | IC full = 1607.7 | , AIC null =162 | 20.7)  |        |         |
| Model 6: Probability | Intercept                                  |                          | -1.695           | -1.967          | -1.423 | -      | -       |
| to be within 5m from | Presence of a younger sibling (No)         | Yes                      | 0.115            | -0.175          | 0.405  | 0.632  | 0.427   |
| the mother           | 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 |       |       |
|               | М | 0.443 | 0.074  | 0.812 | 5.178 | 0.075 |

### Full-Null model comparison: X<sup>2</sup><sub>2</sub> = 25.398, P < 0.001 (AIC full = 2195.2, AIC null = 2206.6)

939 Table 2 : Results of the mixed models analyzing the probability for a juvenile to be within 1 meter (model 5) or within 5 meters (model 6) from its mother during a scan observation. Estimates,

940 95% confidence intervals (CI), 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,

941 N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We
 942 provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

## 944 Table 4: Determinants of proximity maintenance by the juvenile

| Response variable       | Fixed factor                                 | Levels                      | Estimate          | C             |        | LRT    | P-value |
|-------------------------|--|-----------------------------|-------------------|---------------|--------|--------|---------|
|                         |  |                             |                   | 2.5 %         | 97.5 % |        |         |
| Model 7: Probability to | Intercept                                    |                             | -1.572            | -1.906        | -1.237 | -      | -       |
| approach the mother     | 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  | 7 070  | 0.025   |
|                         |  | М                           | 0.571             | 0.113         | 1.029  | 7.373  | 0,025   |
|                         | Focal observation duration                   |                             | 0.139             | 0.003         | 0.275  | 4.148  | 0.042   |
|                         | Full-Null model comparison: $X_2^2 = 26.202$ | 2, <i>P</i> < 0.001 (AIC fu | III = 1505.2, AIC | null = 1515.4 | )      |        |         |
| Model 8: Probability to | Intercept                                    |                             | -1.726            | -2.087        | -1.365 | -      | -       |
| leave the mother        | 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 |
|                                    | М          | 0.665  | 0.173  | 1.157  | 5.005 | 0.011 |
| 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)

945 Table 3 : Results of the mixed models analyzing the probability for a juvenile to approach (model 7) or to leave (model 8) its mother within 1 meter during a focal observation. Estimates, 95%

946 confidence intervals (CI), 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

947 identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to

948 clarify which model performed best in case the full-null model comparison was significant.

## 950 Table 5: Determinants of proximity maintenance by the mother

| Decrease veriable       | Eived factors  | Levels     | Fstimate | CI     |        | IRT    | Duralua |
|-------------------------|--|------------|----------|--------|--------|--------|---------|
| Response variable       | Fixed factors  | Leveis     | Estimate | 2.5 %  | 97.5 % | LKI    | P-value |
| Model 9: Probability to | Intercept  |            | -3.177   | -3.758 | -2.596 | -      | -       |
| be approached by the    | Presence of a younger sibling (No)   | Yes        | -0.512   | -1.201 | 0.177  | -      | -       |
| mother                  | 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  | 47 726 | -0.001  |
|                         |  | М          | 1.430    | 0.743  | 2.117  | 17.726 | <0.001  |
|                         | Focal observation duration   |            | 0.156    | -0.062 | 0.373  | 1.943  | 0.163   |
|                         | Presence of a younger sibling  | Yes, Male  | 1.138    | 0.156  | 2.119  | 6.070  | 0.014   |
|                         | (No)*Juvenile's sex (Female)   |            |          |        |        |        |         |
|                         | Full-Null model comparison: X <sup>2</sup> <sub>2</sub> = 30.352, P < 0.001 (AIC full = 712.29, AIC null = 724.65) |            |          |        |        |        |         |
|                         | Intercept  |            | -1.919   | -2.295 | -1.544 | -      | -       |

|                          | Focal observation duration         |            | 0.188  | 0.028  | 0.347 | 5.557 | 0.018 |
|--------------------------|------------------------------------|------------|--------|--------|-------|-------|-------|
|                          |                                    | М          | 0.339  | -0.203 | 0.882 | 1.331 | 0.405 |
|                          | Troop (J)                          | L          | 0.171  | -0.260 | 0.602 | 1 531 | 0 465 |
|                          | Mother's rank                      |            | 0.011  | -0.169 | 0.190 | 0.014 | 0.907 |
|                          | Juvenile's birth rank (Later-born) | First-born | -0.370 | -0.893 | 0.153 | 2.066 | 0.151 |
|                          | Juvenile's sex (Female)            | Male       | -0.273 | -0.638 | 0.093 | 2.034 | 0.154 |
| be left by the mother    | Juvenile's age                     |            | -0.134 | -0.325 | 0.056 | 1.943 | 0.163 |
| Model 10: Probability to | Presence of a younger sibling (No) | Yes        | 0.254  | -0.121 | 0.629 | 1.751 | 0.186 |

Full-Null model comparison:  $X_2^2$  = 13.902, P = 0.084 (AIC full = 1197.5, AIC null = 1195.4)

951 Table 4 : Results of the mixed models analyzing the probability for a juvenile to be approached (model 9) or left (model 10) within 1 meter by its mother during a focal observation. Estimates,

952 95% confidence intervals (CI), 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

953 identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is

954 significant, LRT and p-values for the simple predictors are not shown. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

### 956 Table 6: Determinants of the juvenile's anxiety

| Eived factor                                      | Lovals     | Ectimato | C      | CI     |        | D value        |
|---|------------|----------|--------|--------|--------|----------------|
|   | Levels     | Estimate | 2.5 %  | 97.5 % |        | <i>F-vulue</i> |
| 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          |
|   | М          | -0.358   | -0.565 | -0.150 | 10.806 | 0.005          |
| Year (2017)                                       | 2018       | -0.317   | -0.518 | -0.115 | 14.096 | 0.001          |
|   | 2019       | 0.085    | -0.059 | 0.228  | 14.086 | 0.001          |
| 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)

Table 5 : Results of the mixed models analyzing the frequency of self-scratches during a focal observation (model 11). Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1523 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is significant, LRT and p-values for the simple predictors are not shown. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

| Model<br>Number | Response variable                             | Model type                | Sample size (number of<br>observations/number of<br>juveniles) | Fixed effects   | Random effects    | Offset         |
|-----------------|---|---------------------------|--|---|-------------------|----------------|
| 1               | Probability to groom the mother               | Binomial GLMM             | 1525/38  | Presence of a<br>younger sibling,<br>juvenile's age,<br>sex and birth<br>rank, maternal<br>rank, troop, focal<br>duration | Juvenile identity | NA             |
| 2               | Probability to be<br>groomed by the<br>mother | Binomial GLMM             | 1525/38  | Presence of a<br>younger sibling,<br>juvenile's age,<br>sex and birth<br>rank, maternal<br>rank, troop, focal<br>duration | Juvenile identity | NA             |
| 3               | Total time grooming the mother                | Negative<br>binomial GLMM | 1525/38  | Presence of a<br>younger sibling,<br>juvenile's age,<br>sex and birth<br>rank, maternal<br>rank, troop                    | Juvenile identity | Focal duration |
| 4               | Total time being<br>groomed by the<br>mother  | Negative<br>binomial GLMM | 1525/38  | Presence of a<br>younger sibling,<br>juvenile's age,<br>sex and birth<br>rank, maternal<br>rank, troop                    | Juvenile identity | Focal duration |

## 961 Table A1: Summary of all models included in the study

| 5 | Probability to be<br>within 1m from the<br>mother | Binomial GLMM | 2562/38 | Presence of a<br>younger sibling,<br>juvenile's age,<br>sex and birth<br>rank, maternal<br>rank, troop, focal<br>duration | Juvenile identity | NA |
|---|---|---------------|---------|---|-------------------|----|
| 6 | Probability to be<br>within 5m from the<br>mother | Binomial GLMM | 2532/38 | Presence of a<br>younger sibling,<br>juvenile's age,<br>sex and birth<br>rank, maternal<br>rank, troop                    | Juvenile identity | NA |
| 7 | Probability to<br>approach the mother             | Binomial GLMM | 1525/38 | Presence of a<br>younger sibling,<br>juvenile's age,<br>sex and birth<br>rank, maternal<br>rank, troop, focal<br>duration | Juvenile identity | NA |
| 8 | Probability to leave<br>the mother                | Binomial GLMM | 1525/38 | Presence of a<br>younger sibling,<br>juvenile's age,<br>sex and birth<br>rank, maternal<br>rank, troop, focal<br>duration | Juvenile identity | NA |
| 9 | Probability to be<br>approached by the<br>mother  | Binomial GLMM | 1525/38 | Presence of a<br>younger sibling,<br>juvenile's age,<br>sex and birth<br>rank, maternal<br>rank, troop, focal             | Juvenile identity | NA |

|    |  |         | duration,<br>presence of a<br>younger                  |
|----|--|---------|--|
|    |  |         | sibling*juvenile's                                     |
|    |  |         | sex  |
| 10 | Probability to be left Binomial GLMM by the mother | 1525/38 | Presence of a Juvenile identity NA<br>younger sibling, |
|    |  |         | juvenile's age,  |
|    |  |         | sex and birth  |
|    |  |         | rank, maternal   |
|    |  |         | rank, troop, focal                                     |
|    |  |         | duration   |
| 11 | Frequency of self- Negative                        | 1523/38 | Presence of a Juvenile identity Focal duration         |
|    | scratch binomial GLMM                              |         | younger sibling,                                       |
|    |  |         | juvenile's age,  |
|    |  |         | sex and birth  |
|    |  |         | rank, maternal   |
|    |  |         | rank, troop  |

## 964 Table A2: Determinants of the occurrence of grooming between the mother and the juvenile

| Posponso variable        | Eived factor  | Lovols                   | Ectimato           | (               | CI              |        | P value        |
|--------------------------|---|--------------------------|--------------------|-----------------|-----------------|--------|----------------|
|                          | FIXEU IACIOI  | Levels                   | Estimate           | 2.5 %           | 97.5 %          |        | <i>r-vuiue</i> |
| Model S1: Probability to | Intercept   |                          | -2.522             | -3.071          | -1.973          | -      | -              |
| groom the mother         | 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           |        |                |
|                          |   | М                        | -0.893             | -2.059          | 0.273           | 3.228  | 0.199          |
|                          | Focal observation duration                              |                          | 0.065              | -0.137          | 0.266           | 0.391  | 0.532          |
|                          | Full-Null model comparison: X <sup>2</sup> <sub>2</sub> | = 46.607 <i>, P</i> < 0. | .001 (AIC full = 7 | '13.11, AIC nul | l = 741.11)     |        |                |
| ז                        | Model 1-Model S1 comparison: $X^2_2 = 0$ .              | 0013, <i>P</i> = 0.971   | . (AIC Model 1 =   | 711.11, AIC M   | odel S1 = 713.1 | .1)    |                |
|                          | Intercept   |                          | -1.648             | -2.018          | -1.277          | -      | -              |

| Mod | del S2: Prol | Model S2: Probability to |     | Presence of a younger sibling (No) | Yes        | -0.137 | -0.537 | 0.263 | 0.476 | 0.490 |
|-----|--------------|--------------------------|-----|------------------------------------|------------|--------|--------|-------|-------|-------|
| be  | groomed      | by                       | the | Juvenile's age                     |            | -0.154 | -0.387 | 0.079 | 1.854 | 0.173 |
| mot | her          |                          |     | 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 | 4 478 | 0 109 |
|     |              |                          |     |                                    | Μ          | -0.596 | -1.285 | 0.093 | 1.120 | 0.100 |
|     |              |                          |     | 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 S2 comparison: $X_{2}^{2}$ = 0.168, P = 0.682 (AIC Model 2 = 1252.8, AIC Model S1 = 1254.6)

965 Table A2: Results of the mixed models analyzing the probability for a juvenile to groom (model 1) or to receive (model 2) a grooming from its mother during a focal observation. Estimates, 95%

966 confidence intervals (CI), 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
 967 identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to

968 clarify which model performed best in case the full-null model comparison was significant.

### 970 Table A3: Determinants of the grooming time exchanged between the mother and the juvenile

| Posnonso variablo    | Eived factor                                | Lovola  | Ectimato          | (             | Cl        |        | D value        |  |  |  |  |
|----------------------|---|---|-------------------|---------------|-----------|--------|----------------|--|--|--|--|
| kesponse variable    | Fixed factor                                | Leveis  | Estimate          | 2.5 %         | 97.5 %    | LNI    | <i>F-vulue</i> |  |  |  |  |
| Model S3: Time spent | Intercept                                   |   | -4.459            | -5.153        | -3.765    | -      | -              |  |  |  |  |
| grooming the mother  | 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     | 2.466  | 0 1 7 7        |  |  |  |  |
|                      |   | М   | -0.881            | -2.024        | 0.262     | 3.466  | 0.177          |  |  |  |  |
|                      | Full-Null model comparison: $X_2^2$ =       | 48.106, <i>P</i> < 0.00   | 1 (AIC full = 213 | 7.7, AIC null | = 2169.8) |        |                |  |  |  |  |
|                      | Model 3-Model S3 comparison: $X_2^2 = 0.00$ | Model 3-Model S3 comparison: $X_2^2 = 0.0003$ , $P = 0.986$ (AIC Model 3 = 2135.7, AIC Model S3 = 2137.7) |                   |               |           |        |                |  |  |  |  |
|                      | Intercept                                   |   | -3.375            | -3.814        | -2.936    | -      | -              |  |  |  |  |
|                      | Presence of a younger sibling (No)          | Yes   | -0.153            | -0.500        | 0.194     | 0.749  | 0.387          |  |  |  |  |

| Model S4: Time spent | Juvenile's age                     |            | -0.137 | -0.342 | 0.067 | 1.730 | 0.188 |
|----------------------|------------------------------------|------------|--------|--------|-------|-------|-------|
| being groomed by the | Juvenile's sex (Female)            | Male       | -0.226 | -0.540 | 0.088 | 1.869 | 0.172 |
| mother               | 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 |
|                      |                                    | Μ          | -0.566 | -1.181 | 0.048 | 5.002 | 0.000 |

Full-Null model comparison:  $X_2^2 = 15.129$ , P = 0.057 (AIC full = 4370.4, AIC null = 4369.6)

Model 4-Model S4 comparison:  $X_{2}^{2} = 0.262$ , P = 0.609 (AIC Model 4 = 4368.7, AIC Model S4 = 4370.4)

971 Table A3: Results of the mixed models analyzing the grooming time (in seconds) given to the mother (Model 3) or received from the mother (Model 4) by the juvenile during a focal observation.

972 Estimates, 95% confidence intervals (CI), 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).

973 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 provided AIC

974 values to clarify which model performed best in case the full-null model comparison was significant.

## 976 Table A4: Determinants of the spatial proximity between the mother and the juvenile

| Response variable     | Fixed factor  | Levels                  | Estimate                 |                          | CI                    | LRT    | P-value |
|-----------------------|---|-------------------------|--------------------------|--------------------------|-----------------------|--------|---------|
|                       |   |                         |                          | 2.5 %                    | 97.5 %                |        |         |
| Model S5: Probability | Intercept   |                         | -1.896                   | -2.227                   | -1.566                | -      | -       |
| to be within 1m from  | Presence of a younger sibling (No)                            | Yes                     | -0.049                   | -0.417                   | 0.319                 | 0.182  | 0.670   |
| the mother            | 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                 |        |         |
|                       |   | Μ                       | -0.461                   | -1.057                   | 0.134                 | 2.875  | 0.237   |
|                       | Full-Null model comparison: $X_2^2 = 27.2$                    | 59, <i>P</i> < 0.001 (A | IC full = 1609.4         | , AIC null = 162         | 20.7)                 |        |         |
| Model S6: Probability | Model 5-Model S5 comparison: $X_2^2 = 0.251$ , P<br>Intercept | ? = 0.617 (AIC N        | odel 5 = 1607.<br>-1.682 | 7, AIC Model S<br>-1.961 | 5 = 1609.4)<br>-1.403 | -      | -       |
| to be within 5m from  | Presence of a younger sibling (No)                            | Yes                     | 0.155                    | -0.164                   | 0.474                 | 0.968  | 0.325   |
| the mother            | 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 |
|------------------------------------|------------|--------|--------|--------|-------|-------|
| 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  |       |       |
|                                    | М          | 0.388  | -0.023 | 0.800  | 3.255 | 0.196 |

Full-Null model comparison:  $X_2^2$  = 25.837, P = 0.001 (AIC full = 2196.7, AIC null = 2206.6)

Model 5-Model S5 comparison:  $X_2^2 = 0.439$ , P = 0.508 (AIC Model 6 = 2195.2, AIC Model S6 = 2196.7)

977 Table A4: Results of the mixed models analyzing the probability for a juvenile to be within 1 meter (model 5) or within 5 meters (model 6) from its mother during a scan observation. Estimates,

978 95% confidence intervals (CI), 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,

979 N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We

980 provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

## 982 Table A5: Determinants of proximity maintenance by the juvenile

| Response variable        | Fixed factor   | Levels                       | Estimate          | C              |        | LRT   | P-value |  |
|--------------------------|--|------------------------------|-------------------|----------------|--------|-------|---------|--|
|                          |  |                              |                   | 2.5 %          | 97.5 % |       |         |  |
| Model S7: Probability to | Intercept  |                              | -1.606            | -1.943         | -1.270 | -     | -       |  |
| approach the mother      | 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  | 8.002 | 0,018   |  |
|                          |  | М                            | 0.662             | 0.168          | 1.157  | 8.063 |         |  |
|                          | Focal observation duration   |                              | 0.141             | 0.005          | 0.277  | 4.275 | 0.039   |  |
|                          | Full-Null model comparison: $X_2^2 = 26.93$  | 86, <i>P</i> = 0.001 (AIC fu | III = 1506.5, AIC | cnull = 1515.4 | )      |       |         |  |
| Ν                        | Model 7-Model S7 comparison: $X_2^2$ = 0.0003, P = 0.734 (AIC Model 7 = 1505.2, AIC Model S7 = 1506.5) |                              |                   |                |        |       |         |  |
|                          | Intercept  |                              | -1.778            | -2.144         | -1.413 | -     | -       |  |

| Model S8: Probability to | Presence of a younger sibling (No) | Yes        | 0.468  | 0.101  | 0.835  | 6.758  | 0.009 |
|--------------------------|------------------------------------|------------|--------|--------|--------|--------|-------|
| leave the mother         | 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 |
|                          |                                    | М          | 0.803  | 0.269  | 1.338  | 10.745 | 0.005 |
|                          | 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 S8 comparison: X<sup>2</sup><sub>2</sub> = 1.691, P = 0.196 (AIC Model 8 = 1340.8, AIC Model S8 = 1341.1)

983 Table A5: Results of the mixed models analyzing the probability for a juvenile to approach (model 7) or to leave (model 8) its mother within 1 meter during a focal observation. Estimates, 95%

984 confidence intervals (CI), 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
 985 identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to

986 clarify which model performed best in case the full-null model comparison was significant.

### 988 Table A6: Determinants of proximity maintenance by the mother

| Despense veriable        | Fixed factors                      | Lovala     | Fatimata | C       | CI     |        | Dualua  |
|--------------------------|------------------------------------|------------|----------|---------|--------|--------|---------|
| Response variable        |                                    | Leveis     | Estimate | 2.5 %   | 97.5 % | LKI    | P-value |
| Model S9: Probability to | Intercept                          |            | -3.163   | -3.749  | -2.577 | -      | -       |
| be approached by the     | Presence of a younger sibling (No) | Yes        | -0.498   | -1.191  | 0.195  | -      | -       |
| mother                   | 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  |
|                          |                                    | М          | 1.378    | 0.645   | 2.111  | 15.725 | <0.001  |
|                          | Focal observation duration         |            | 0.154    | -0.064  | 0.372  | 1.893  | 0.169   |
|                          | Presence of a younger sibling      |            | 1 100    | 0 1 7 1 | 2 210  | C 191  | 0 012   |
|                          | ہ<br>(No)*Juvenile's sex (Female)  | ies, male  | 1.190    | 0.171   | 2.210  | 0.104  | 0.015   |

Full-Null model comparison:  $X_2^2$  = 30.493, P < 0.001 (AIC full = 714.15, AIC null = 724.65)

| Model S10: Probability   | Intercept                          |            | -1.977 | -2.355 | -1.599 | -       | -     |
|--------------------------|------------------------------------|------------|--------|--------|--------|---------|-------|
| to be left by the mother | 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 5 7 9 | 0 276 |
|                          |                                    | Μ          | 0.481  | -0.095 | 1.057  | 2.578   | 0.276 |
|                          | Focal observation duration         |            | 0.190  | 0.031  | 0.349  | 5.726   | 0.017 |

### Model 9-Model S9 comparison: X<sup>2</sup><sub>2</sub> = 0.141, P = 0.707 (AIC Model 9 = 712.29, AIC Model S9 = 714.15)

Full-Null model comparison:  $X_2^2 = 15.384$ , P = 0.081 (AIC full = 1198.0, AIC null = 1195.4)

### Model 10-Model S10 comparison: X<sup>2</sup><sub>2</sub> = 1.482, P = 0.223 (AIC Model 10 = 1197.5, AIC Model S10 = 1198.0)

Table A6: Results of the mixed models analyzing the probability for a juvenile to be approached (model 9) or left (model 10) within 1 meter by its mother during a focal observation. Estimates,
 95% confidence intervals (CI), 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 random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is

992 significant, LRT and p-values for the simple predictors are not shown. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

# 994 Table A7: Determinants of the juvenile's anxiety

| Eived factor                                      | Lovals     | Ectimato | CI     |        | IDT    | Pyalua         |
|---|------------|----------|--------|--------|--------|----------------|
|   | Levels     | Estimate | 2.5 %  | 97.5 % | LNI    | <i>r-vulue</i> |
| 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  | 0.775  | 0.009          |
|   | М          | -0.358   | -0.578 | -0.138 | 5.775  | 0.008          |
| Year (2017)                                       | 2018       | -0.316   | -0.519 | -0.114 | 12 800 | 0.001          |
|   | 2019       | 0.085    | -0.060 | 0.230  | 12.003 | 0.001          |
| 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 S11 comparison: $X_2^2 = 0.0002$ , P = 0.989 (AIC Model 11 = 7158.1, AIC Model S11 = 7160.1)

995 Table A7: Results of the mixed models analyzing the frequency of self-scratches during a focal observation (model S11). Estimates, 95% confidence intervals (CI), LRT statistics and p-values of

the predictors were estimated using 1523 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical
 predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is significant, LRT and p-values for the simple predictors

998 are not shown. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

### 1000 Appendix 1: Test of the newborn attraction hypothesis

1001 To estimate if juveniles were approaching their mother to access the newborn, we used focal 1002 data on the 18 juveniles who experienced the birth of a younger sibling within the last three 1003 months. Each time the juvenile approached their mother within 1m, we calculated whether 1004 the juvenile initiated an interaction with the newborn and/or the mother (yes=1, no=0) within 1005 one minute following the approach, or until one of them left if a leave happened less than one 1006 minute after the approach. We considered the following interactions: grooming, playing (with 1007 the newborn only), affiliative and aggressive interactions. For interactions with the newborn, 1008 we considered only the interactions initiated by the juvenile because young baboon infants 1009 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 1010 1011 calculated the percentage of approach followed by an interaction with the newborn (whether 1012 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). 1013