Early-life paternal relationships predict adult female survival in wild baboons

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ABSTRACT

Parent-offspring relationships can have profound effects on offspring behavior, health, and fitness in adulthood. These effects are strong when parents make heavy investments in offspring care. However, in some mammals, including several species of carnivores, rodents, and primates, fathers live and socialize with offspring, but paternal care *per se* is subtle or indirect. Do these limited father-offspring relationships also affect later-life outcomes for offspring? Working in a well-studied baboon population where males contribute little direct offspring care, we found that juvenile female baboons who had stronger paternal relationships, or who resided longer with their fathers, led adult lives that were 2-4 years longer than females with weak or short paternal relationships. This pattern did not differ between females who experienced high versus low levels of early-life adversity; hence, paternal relationships were equally protective in both harsh and benign early environments. Males' relationships were strongest with juvenile females they were most likely to have sired and when males had few mating opportunities. Hence, father-daughter relationships may be constrained by male mating effort. Because survival predicts female fitness, fathers and their daughters may experience selection to engage socially and stay close in daughters' early lives.

Keywords: paternal care, parental care, mammals, early-life effects, fathers, adult survival

1. INTRODUCTION

In humans and other mammals, social environments are powerful determinants of individual health, survival, and fitness [1]. Social relationships in early life are especially important, both because of their immediate benefits to offspring—such as opportunities to learn social skills, gain resources, or receive protection—and also because these relationships have lasting consequences for adult health and survival [2]. Maternal relationships are especially well-studied in this regard [3-11], and across mammals, maternal loss and the quality of maternal care have lasting consequences for offspring gene regulation, stress reactivity, social integration, and adult survival [3-12].

But what about relationships with fathers? Early-life paternal social effects have received less attention, in part because it is rare for male mammals to make substantial investments in offspring care [13, 14]. However, in species with caring males, early-life father-offspring relationships can have profound effects on offspring in adulthood. In humans, paternal absence in childhood is linked to lower income, poorer health, and higher mortality risk [e.g., 15, 16-19]. In rodents with biparental care, fathers affect the complexity of offspring social environments, with consequences for neurological development and adult behavior [20, 21]. Yet mammal species with caring males are rare. In a wider (but still unusual) set of group-living mammals, fathers live and even socialize with offspring, but paternal care is subtle and often indirect [13, 22]. These species include several carnivores and equids, as well as gorillas, chimpanzees, baboons, and other primates [13, 17, 23-29]. Whether these more limited early-life paternal relationships have long-term consequences for offspring is largely unknown.

Here we test if early-life paternal relationships predict adult survival for female baboons—a species where fathers and their juvenile offspring may co-reside and interact, but where mothers provide all essential care [30, 31]. Baboons are useful for testing these relationships for three reasons. First, many baboons live in polygynandrous mating systems where paternity certainty is incomplete, yet adult males often interact with their offspring and engage in some forms of offspring care, including carrying and supporting offspring in conflicts [30, 32-38]. Further, lactating female baboons sometimes form close social bonds (i.e., "primary associations") with particular males, and these relationships are better explained by parenting than mating effort [33-35, 39-41], as male primary associates typically do not sire their female associate's next infant [34, but see 35]. Male primary associates are also disproportionately the fathers of their female partner's current infant, intervene on behalf of females and their infants in conflicts, and may buffer infants from rough handling [30, 32-38, 42].

Second, proximity to adult males and/or paternal presence in early life have developmental and social consequences for young baboons. For instance, proximity to adult males, including fathers and non-fathers, increases the complexity of the social environment for infants [43]. Paternal presence is also correlated with earlier sexual maturity in daughters [32] and predicts stronger social bonds between paternal half-siblings [44].

Third, adult lifespan, our outcome of interest, explains 80%-90% of the variance in lifetime reproductive success for female baboons in our population [7, 45, 46]. Hence, if early-life paternal relationships influence daughters' lifespans, they are likely to have important consequences for fitness. Males and their daughters may therefore experience selection to form and maintain early-life social relationships with one another, and male care may meet the criteria for "true" parental care (i.e., care that improves offspring and male fitness [14]).

Working in the Amboseli baboon population in Kenya [47], we pursued three objectives to understand whether and how fathers influence daughters' lifespans. First, we measured patterns of grooming and co-residency between juvenile females and their fathers. Social bonds are often developed and maintained through grooming, a primary affiliative behavior in many social species, including baboons [48-50]. We measured co-residency because father-offspring pairs who live together for longer have more time to interact (co-residency varies because males may disperse or die during their daughters' juvenile years).

Second, we tested whether juvenile females who had stronger grooming relationships or longer co-residency with their fathers exhibit higher adult survival than females who had weak paternal grooming relationships or short co-residency periods. In the Amboseli baboons, adult female longevity is also predicted by an accumulation of harsh conditions in early life, including drought, maternal loss, or having a low-ranking or socially isolated mother [7, 45, 51]. Hence, we also tested if early-life relationships with fathers protect daughters from the negative effects of cumulative early-life adversity.

Third, we tested why some fathers are more likely to groom or have longer co-residency with their daughters than others. We predicted that males would have stronger relationships with their daughters when they had high paternity certainty (e.g., spent more time mate guarding his daughter's mother when his daughter was conceived) and when reproductive tradeoffs were favorable (e.g., when the male had few current mating opportunities). Together, our results support the importance of early-life paternal relationships to adult female baboons, lending context to paternal effects on adult outcomes and the evolution of mammalian parental care.

2. METHODS

(a) Study population and subjects

Our subjects were wild baboons studied by the Amboseli Baboon Research Project (ABRP) in the Amboseli ecosystem, Kenya [47]. This population is admixed between yellow and anubis baboons (*Papio cynocephalus* and *P. anubis*), with majority yellow ancestry [52, 53]. ABRP observers collect behavioral and demographic data year-round on a near-daily basis, and all study animals are known through visual recognition. Our analyses centered on 216 female baboons that: (i) survived the first 4 years of life, encompassing the juvenile period for females [median age at menarche in Amboseli = 4.5 years; 54]; (ii) had known mothers and fathers assigned using demographic and genetic data (see below); and (iii) had complete information on their experience of six sources of early-life adversity that together predict adult mortality [7, 51]: maternal loss, low maternal dominance rank, maternal social isolation, early-life drought, a close-in-age younger sibling, or large group size (see below). The females in our study were born into 13 different social groups, which are the fission or fusion products of two original study groups, first studied in 1971 and 1981.

(b) Assigning maternities and paternities

The 216 female subjects were born to 117 mothers and sired by 102 fathers. Maternities were known from near-daily demographic records. Paternity assignments were based on microsatellite genotypes from at least six microsatellite loci and demographic records used to identify an initial pool of candidate fathers. These methods are described in detail in previous studies [30, 55-57], but briefly, microsatellite genotypes for juvenile females, mothers, and potential fathers were analyzed in the likelihood-based paternity assignment program CERVUS [58, 59]. We first included all potential fathers residing in the mother's group at the time of conception (potential fathers are any male in the adult male hierarchy), and then expanded the set of potential fathers to include all adult, ranked males in the population. These two sets of analyses identified the same father in all but one case. In this case, we assigned paternity the sire who was seen consorting with the mother (the other potential sire lived in a different group and was never seen consorting the mother). Levels of confidence for all CERVUS analyses were set at 95%, and paternity assignments were robust across three rates of error, 1%, 5%, and 10% [30, 55-57].

(c) Measuring grooming and co-residency between juvenile females and adult males

We defined co-residency as the cumulative number of days each juvenile female lived in the same group with her genetically confirmed father during the first 4 years of her life.

Following [6, 51, 60, 61], we measured annual pairwise grooming relationships for each year of the female's life, using the "dyadic sociality index" (DSI). DSI provides a numeric score for each juvenile female's dyadic relationship strength with individual adult males, scaled to be directly comparable to all other juvenile female-male pairs in the population in a given year of the female's life, birthday to birthday. We calculated three types of DSI scores for juvenile females, which differed in the males included in the calculations: DSI_{all} measured dyadic relationships between juvenile females and all adult males who lived in her group for ≥30 days in the year in question, including her father (i.e., "co-resident" males); $DSI_{paternal}$ measured dyadic relationships between juvenile females and their fathers; and $DSI_{non\text{-}paternal}$ measured dyadic relationships between juvenile females and all co-resident males, excluding her father.

Because the ABRP only systematically collects focal animal samples on adult females and juveniles, and these data are sparse, DSI scores rely on grooming interactions collected via "representative interaction sampling" [6, 51, 60, 61]. During this sampling, observers record all grooming interactions between any interactants in their line of sight while simultaneously conducting random-order, 10-minute focal animal samples. These data are collected while observers continuously move throughout the group during focal sampling [6, 61], and prior work in our population finds that the resulting relative grooming frequencies are correlated with hourly rates of grooming from focal animal sampling [60].

From these data, we calculated each dyad's log-transformed daily rate of grooming in a given year. Because dyads living in small groups experienced more intense representative interaction sampling than those in large groups, we accounted for differences in "observer effort" by regressing each dyad's log-transformed daily rate of grooming against a measure of observer effort in that year: the number of focal animal samples per adult female per observation day for that group during the year in question. The resulting residuals were z-scored within years to estimate the DSI. Negative DSI scores were dyads who groomed less than was typical in that year; positive DSI scores were dyads who groomed more than was typical in that year. Note that the $DSI_{paternal}$ score would be the same for a juvenile female who had no observed grooming with her father, whether they lived in the same group or not. We distinguish between these conditions by including both $DSI_{paternal}$ and co-residency in our models of adult female survival (see below).

Our third objective required us to test why some fathers are more likely to groom their daughters than other males. For these analyses we compiled data on the presence or absence of male grooming directed to their daughters, in a given juvenile female year of life (contingent on ≥30 days of co-residency).

(d) Measuring early-life adversity

To test if fathers moderate early-life effects on female mortality, we measured early-life adversity using a cumulative adversity index developed in prior studies [6, 7, 45, 51, 62]. This index sums the presence of six sources of early-life adversity: (1) drought in the first year of life (<200 mm of annual rainfall); (2) maternal death in the first four years of life; (3) being born into a large group as an index of realized resource competition (group size in the top quartile; ≥36 adults); (4) the birth of a close-in-age younger sibling that may divert maternal resources (interbirth interval in the shortest quartile, <1.5 years after the focal female's own birth); (5) being born to a mother whose ordinal social dominance rank is in the bottom quartile for the population; and (6) being born to a mother who is in the top quartile for social isolation over the first 2 years of the juvenile's life, measured based on an overall index of her involvement in grooming [7]. For each of the 216 juvenile females, we summed the number of these conditions that applied, resulting in a final index that could range from zero to six. No subject experienced more than four sources of adversity (20.3% of the 216 females experienced 0 sources of adversity; 40.2% experienced 1 source; 24.1% experienced 2 sources; 11.6% experienced 3 sources, and 3.7% experienced 4 sources).

(e) Measuring predictors of father-daughter grooming and co-residency

For our third objective, we tested why some fathers are more likely to groom their juvenile daughters than other fathers. For a sub-set of variables, we also tested whether they explained the duration of father-daughter co-residency. Our sample sizes for these analyses were smaller than the 216 females in the first two objectives because we lacked information on some variables (see below).

Male ordinal dominance rank determines male priority of access to mates in our population, and mating opportunities could impose a tradeoff on time spent grooming offspring [63]. In Amboseli, male ranks are calculated monthly based on decided dyadic agonistic encounters between adult males [64].

The *daily rate of fertile females* in the group could also influence a male's mating opportunities and impose a tradeoff on grooming offspring. This variable was calculated as the average daily

196 number of peri-ovulatory females in the group in a given juvenile female-year on the days the male
197 was resident in the group [65]. Peri-ovulatory periods are inferred from continuous records of sexual
198 skin swellings that increase in size during the follicular phase and decrease during the luteal phase
199 [65].

200 The *proportion of the mother's available consort time the male obtained* during the 5-day peri-ovulatory
201 period when the focal female was conceived predicts paternity [66] and possibly male paternity
202 certainty. Hence, we summed all observed consort time that a mother had with any adult male
203 within 5 days before the likely conception date of the focal female and calculated the proportion of
204 this consort time that was monopolized by the male in question. Conception dates were calculated
205 as described previously based on obvious signs of female reproductive state [65, 67]. For 31 of the
206 216 females, no males were observed consorting the focal female's mother during her conceptive
207 period. We excluded these 31 females because failing to observe a consort is much more likely to be
208 caused by sparse behavioral sampling than the true absence of mate guarding.

209 *The number of potential fathers* present in the group at the juvenile female's conception could
210 influence male paternity certainty [56, 68]. This variable was calculated as the number of adult
211 ranked males present in the group during the 5-day peri-ovulatory period when the female was
212 conceived.

213 Following [34, 35], males who *sired the juvenile's mother's previous or subsequent offspring* might be
214 more likely to groom their daughters if "primary associates" represent male mating effort. To test
215 this possibility, we identified all cases in which the focal female's father sired their mother's previous
216 or subsequent offspring. Including this variable led to further reductions in sample size because
217 there were 42 cases where the paternity of either the female's mother's previous or subsequent
218 infant was unknown.

219 The *number of offspring the male had in the group (i.e., co-resident offspring-years)* could influence his
220 likelihood of remaining in his daughter's group. This variable was calculated, for each father, as the
221 number of his juvenile offspring that were alive in the group in a given juvenile female-year, scaled
222 for days of co-residency. This variable may underestimate the male's true count of living juvenile
223 offspring because paternity is often missed for the youngest offspring (we generally obtain the first
224 fecal sample between 6 and 18 months of age).

225 The female's experience of *cumulative early-life adversity* (ELA), could also influence paternal
226 investment. Cumulative ELA was calculated as the sum of the 6 conditions a female experienced
227 prior to age 4 years (see above).

228 *Paternal age and the ages of daughters and their mothers* were known from near daily demographic
229 records. All 216 daughters had ages accurate within a few days. Of the 102 fathers, 43 (42.2%) were
230 born into the study population and their ages were accurate within a few days. For the remaining 59
231 fathers (57.8%), their ages were estimated to within a few years by comparing them to known-age
232 males from the population [69]. For the mothers, 101 (86.3%) had ages accurate within a few days,
233 14 (12.0%) had ages accurate within 3 months, and 2 (1.7%) had ages accurate within 3 years.
234 For our model of why some fathers groom their daughters more than others, *we also modeled*
235 *observer effort*, measured as the number of focal animal samples we collected per female-day (see
236 above).
237
238 **(f) Statistical Analyses**
239 Most analyses were performed in R 4.4.0 using the packages lme4 [70], lmerTest [71], lmtest
240 [72], MuMIn [73], rptR [74], and survival [75]. We use an AICc-based information theoretic
241 approach to test our hypotheses. See the GitHub repository cited in our data statement for a full list
242 of packages.
243
244 *Objective 1: Characterizing patterns of grooming and co-residency between juvenile females, their fathers, and other*
245 *adult males*
246 To measure grooming relationships between juvenile females and adult males, we calculated,
247 in each female-year (i) the average number of adult males each female groomed with, and (ii) the
248 percentage of grooming interactions she initiated with adult males (N=216 females; from 0 to 4
249 years of age). To test if female age predicted grooming initiation with males (both fathers and non-
250 fathers), we ran a binomial LMM where the response variable measured whether grooming with
251 adult males was initiated by females (1) or not (0), as a function of female age in each year of the
252 juvenile period. Female identity was modeled as a random effect. To test if DSI_{all} was stronger
253 between father-daughter pairs than other male-female pairs we compared Akaike information
254 criteria (AICc) scores between two LMMs of juvenile females' DSI_{all} scores: one that only included
255 juvenile female age (0-4 years of age), and one that included juvenile female age and whether the
256 male was the female's father. Female identity was a random effect.
257
258 *Objective 2: Testing if paternal co-residency and social bonds predict adult female survival*

To test if females who have longer juvenile co-residency or stronger paternal grooming relationships exhibit higher adult survival than females who had short paternal co-residency or weak paternal grooming relationships, we ran a series of Cox proportional hazards models where the response variable was each female's age at death or censorship, contingent on survival to her 4th year of life (N=216 females; 124 censored values). Models were fit using coxph in the survival package [75]. We tested which variables best explained variation in adult female mortality risk based on AICc, including each female's: (i) average $DSI_{paternal}$ scores across the first four years of her life (because grooming patterns change with juvenile female age, these values were z-scored across females, within a year of life); (ii and iii) average $DSI_{non\text{-}paternal}$ or DSI_{all} (also z-scored and averaged across the first four years of life); (iv) cumulative years of co-residency with her father in the first four years of life; and (v) cumulative early-life adversity score.

To test if the effects of early-life adversity on adult female survival are moderated by paternal grooming or co-residency, we added an interaction effect between females' early-life adversity scores and (vi) their average annual $DSI_{paternal}$ scores, and (vii) their cumulative years of paternal co-residency.

We also tested if juvenile females with strong paternal grooming bonds are socially well-connected with females and males in adulthood. If so, early-life relationships between female baboons and their fathers might be important for later life survival because they influence female social connectivity in adulthood, which predicts adult female survival in this population [51, 60, 61]. Social connectivity was calculated as a social connectedness index (SCI), which reflects the total amount of grooming the female, as an adult, gave and received with other adult females (SCI_F) and adult males (SCI_M) in her group [51, 60, 61]. For these analyses, we first ran an LMM testing if females with stronger mean $DSI_{paternal}$ scores in the first 4 years of life had stronger SCI_F and SCI_M scores in adulthood, controlling for her age and dominance rank and modeling female identity as a random effect. We then ran a series of survival models to test if the association between $DSI_{paternal}$ and adult female survival is attenuated by adding SCI_F and SCI_M to the model. The sample size for these models was 194 females because adult social connectedness information was missing for 22 females.

Objective 3: Testing the predictors of father-daughter grooming and co-residency

To test why some fathers are more likely to groom their daughters than others, we ran a binomial LMM where the response variable was whether a given father was observed to groom (1)

291 or did not groom (0) his daughter in each of the first four years of her life, contingent on ≥30 days
292 of co-residency. We used AICc to evaluate the predictive power of several fixed effects. These
293 predictors included three indicators of a male's mating opportunities in that year: (i) the father's
294 average dominance rank in that year, (ii) the average number of fertile (i.e., peri-ovulatory) females in
295 the group each day in that year, (iii) and the number of other adult males (i.e., potential fathers) in
296 the group at the daughter's conception. As an indicator of paternity certainty, we used (iv) the
297 proportion of observed consort time between the male and the focal female's mother during the 5-
298 day period when the female was conceived. As an indicator of whether male grooming of his
299 daughter functioned as a form of mating effort with her mother, we included whether the father
300 sired either the mother's (v) prior or (vi) subsequent offspring. Because a male might invest less in
301 any given daughter when he has many offspring, we controlled for (vii) the number of juvenile
302 paternal offspring the father had in the group in that year ("co-resident offspring years"). We also
303 controlled for (viii) the daughter's cumulative ELA score, (ix-xi) the ages of the juvenile, the father,
304 and the mother at the start of the year, and (xii) observer effort. Paternal identity was included a
305 random effect (N=379 father-years involving 70 fathers and 130 juvenile females). We also
306 performed a parallel analysis for all co-resident males (i.e., not just father-daughter pairs), which
307 included a binary fixed effect for if the adult male was the father (N=6,324 father-years involving
308 288 males and 184 juvenile females with ≥30 days of co-residency).
309 To test why some fathers have longer co-residencies with their daughters than others, we ran
310 an LMM where the response variable was the number of days the father resided in the same group
311 as his daughter in the first four years of her life. The fixed effects: (i) the father's dominance rank in
312 the month co-residency ended; (ii) the daily rate of fertile females in the group in the month co-
313 residency ended; (iii) the proportion of consort time the male had with the female's mother; (iv) the
314 number of other adult males (i.e., potential fathers) in the group at the daughter's conception; (v)
315 whether the father sired the mother's previous offspring (subsequent offspring was excluded
316 because only males with long co-residencies could sire future offspring); (vi) the number of juvenile
317 paternal offspring the father had in the group in the year the co-residency ended (co-resident
318 offspring years); and (vii) the daughter's cumulative ELA score; and (viii-ix) the father's and
319 mother's ages in the month co-residency ended (juvenile age was excluded because it was colinear
320 with the duration of co-residency). Paternal identity was included as a random effect (N=166 co-
321 residencies involving 86 fathers and 166 juvenile females).

322 Before performing our analyses, we checked for multicollinearity using variance inflation
323 factor (VIF) analysis adapted for lmer models [76]. No variables had VIF >2.5.
324
325 **3. RESULTS**
326 **(a) Objective 1: Patterns of co-residency and grooming between juvenile females and their**
327 **fathers**
328 The median co-residency between the 216 daughters and their fathers was 33 months (**Fig.**
329 **1A**; range=0-48 months). More than a third of these females (n=80; 37%) lived in the same group
330 with their father for ≥3 of their juvenile years. For the remaining 63% of females (n=136), their
331 fathers either left the group or died sometime between their conception and 3 years of age (**Fig. 1A**).
332 Thirteen females (6%) never co-resided with their fathers because the male dispersed or died
333 between the focal female's conception and birth.
334 Grooming between juvenile females, their fathers, and other adult males changed in
335 frequency and directionality across females' juvenile years. From birth to 4 years of age, females
336 groomed with an increasing number of adult males (β=0.35; p<0.001) and were more likely to
337 initiate grooming with adult males (**Fig. 1B**: binomial LMM: β=1.00; p<0.001). In the first year of
338 life, however, 18.2% of grooming interactions with adult males were initiated by the females, and
339 each female groomed with 1.15 adult males on average (range=1-3 males). By the 4th year of life,
340 females had, on average, 1.54 male grooming partners (range=1-6 males), and 83% of these
341 interactions were initiated by the female.
342 Consistent with prior evidence that males and their offspring have differentiated
343 relationships [30, 32-36], daughters' DSI_{all} values were stronger with their fathers than with other co-
344 resident adult males (**Table 1;** ΔAICc for a model with and without "male is the father"=175.82).
345 However, a visualization of DSI_{all} values between juvenile females and their fathers and between
346 juvenile females and non-paternal males shows that some juvenile females also groom adult males
347 who are not their fathers, and these bonds are sometimes strong (**Fig. S1**).
348
349 **Table 1.** LMM explaining dyadic bond strength between juvenile females and all co-resident adult males in a
350 given year (N=10,833 DSI_{all} values between 216 females and 297 males, including 90 fathers).

Term	*β (SE)*	t	df	Interpretation
Age of juvenile female	0.152 (0.010)	14.289	10133.1	↑juvenile age ↑bond strength
Male is the father	0.696 (0.042)	13.550	10105.4	male is father ↑bond strength

351

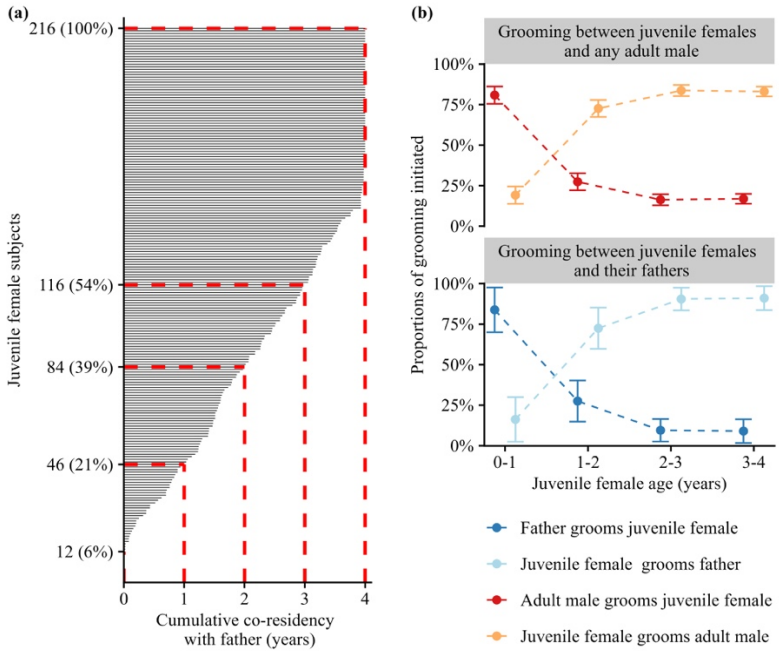


Figure 1. Co-residency and grooming directionality between juvenile females, their fathers, and other adult males. **(A)** Cumulative paternal co-residency (x-axis) for 216 juvenile females (y-axis). Each black bar represents the cumulative duration of time one female lived in the same group with her father. Red dashed lines demarcate the percentages of females who resided with their fathers for 1, 2, 3 or 4 years. **(B)** The average proportion of grooming interactions initiated by juvenile females (top: dark blue; bottom: red) or adult males (top: light blue; bottom: orange) as a function of female age. Top panel shows grooming initiation for fathers; bottom panel shows grooming initiation with all adult males.

(b) Objective 2: Early-life grooming and co-residency with fathers predicts adult female survival

We next tested whether daughters' early-life relationships with their fathers predicted their adult survival. We found that juvenile females who had strong $DSI_{paternal}$ scores with their fathers, or who had long co-residency with their fathers, or both, led longer adult lives than females with weaker paternal relationships (**Fig. 2**; **Table 2**). In support, the top three models predicting adult female survival included either the female's average $DSI_{paternal}$ score in the first four years of life, the duration of co-residency with her father, or both (**Fig. 2**; **Table 2 rows A-C**). $DSI_{paternal}$ and co-residency were positively correlated with each other (**Fig. S2**; β =0.142, p<0.001), consistent with the idea that father-daughter pairs who co-reside for longer will also have stronger grooming relationships. Models that included either one or both variables were interchangeable in their ability

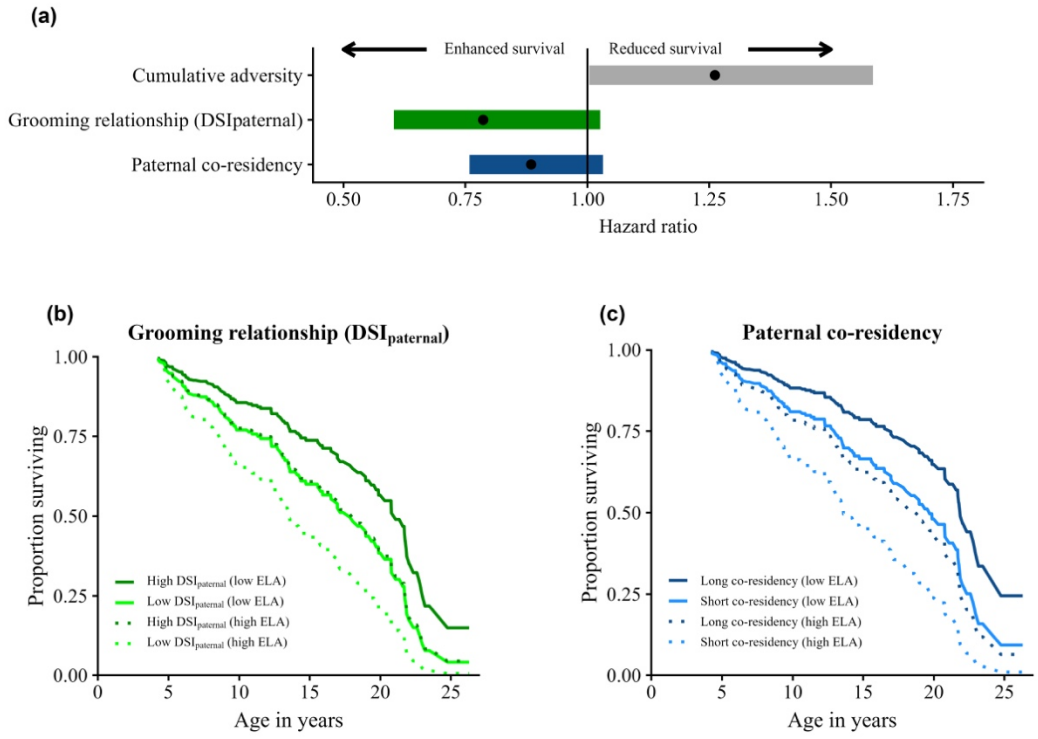
372 to explain adult female mortality (**Table 2 rows A-C;** range in ΔAICc=0.31-1.28). This effect was
373 specific to $DSI_{paternal}$: strong relationships during the juvenile period with adult males in general
374 (DSI_{all}), or with non-fathers ($DSI_{non\text{-}paternal}$), did not predict adult survival (**Table 2 rows A-C** versus
375 **rows D, F, and G**).
376 Early-life adversity (ELA) also predicted adult female mortality (**Table 2 all models,** [7,
377 51]), but the models that included $DSI_{paternal}$ and/or co-residency were a better fit to the data than a
378 model that only included ELA (**Table 2 rows A-C vs row E**; range in ΔAICc=3.228-4.56). We
379 therefore asked whether relationships with fathers predicted adult female survival more so for
380 females who experienced harsh early-life circumstances. We found little evidence for an interaction
381 effect between female ELA and either $DSI_{paternal}$ or paternal co-residency (range in ΔAICc=1.66-3.57;
382 **Table S1**). Hence, paternal relationships are not especially beneficial to high-adversity females.
383 However, paternal relationships could still buffer females against some costs of ELA. Indeed,
384 females who experienced three or more sources of adversity and were in the top quartile of paternal
385 co-residency appear to survive as long as those who experienced just one source of adversity but had
386 short paternal co-residency (**Fig. 2C**). For females who experienced one source of ELA, having a
387 mean $DSI_{paternal}$ score in the top quartile for the population predicted a median difference in survival
388 of 1.8 years compared to females in the bottom quartile (**Fig. 2B**). Females who experienced one
389 source of ELA and lived with their fathers for all 4 years were predicted to live 2.6 years longer than
390 females who only lived with their father for 1 year (**Fig. 2C**). Females who experienced 3 or more
391 sources of ELA were predicted to live 4.3-4.6 years longer if they co-resided with their father for 4
392 years versus 1 year or had grooming relationships with their fathers in the top versus bottom quartile
393 (**Figs. 2B and 2C**).
394 We wondered whether some of the survival effects we observed could be explained by adult
395 females' social bonds with either sex in adulthood, both of which predict adult female survival [51,
396 60, 61, 77]. We found that females who had stronger average $DSI_{paternal}$ scores across the first 4 years
397 of life also had strong social bonds with adult males in adulthood (SCI_M; **Table S2**). Females who
398 had stronger average $DSI_{paternal}$ scores also had stronger social bonds with adult females in adulthood,
399 but in only one of the three best-supported models (SCI_F; **Table S2**). In support of the idea that
400 $DSI_{paternal}$, SCI_F, and SCI_M all contribute to adult mortality risk, four of the seven best-fitting models
401 in **Table S3** included a metric of adult social connectedness (SCI_F, SCI_M, or both; **Table S3 models**
402 **3, 4, 6 and 7**), while six of the best seven models included $DSI_{paternal}$, paternal co-residency, or both
403 (**Table S3 models 1-6**).

404 **Table 2.** Results from seven alternative Cox proportional hazards models (n=216 females with 124 censored
405 values) showing predictors of adult female survival. Each cell shows the variable's hazard ratio (and 95%
406 confidence interval). Models are ordered by AICc. No model violated the proportional hazards assumption.

Model	Cumulative ELA	Mean $DSI_{paternal}$	Years of co-residency with father	Mean $DSI_{non\text{-}paternal}$	Mean DSI_{all}	AICc	ΔAICc
A	1.262 (1.004-1.586)	0.787 (0.603-1.026)	0.885 (0.759-1.032)	-	-	810.67	0.00
B	1.278 (1.016-1.608)	0.738 (0.573-0.951)	-	-	-	810.98	0.31
C	1.25 (0.995-1.571)	-	0.84 (0.725-0.973)	-	-	811.95	1.28
D	1.277 (1.014-1.608)	0.743 (0.576-0.959)	-	0.92 (0.675-1.255)	-	812.84	2.17
E	1.273 (1.012-1.601)	-	-	-	-	815.23	4.56
F	1.27 (1.008-1.6)	-	-	0.88 (0.648-1.195)	-	816.65	5.98
G	1.273 (1.01-1.604)	-	-	-	0.82 (0.616-1.092)	815.48	4.82

407

408



409

410 **Figure 2. Juvenile females' paternal grooming relationships and co-residency predict their adult**
411 **survival. (A)** Estimates from the time-to-event effects on the hazard of death in adult female baboons.
412 Effects and 95% CI are from **row A in Table 2**, the model that had the lowest AICc and that includes mean
413 $DSI_{paternal}$ (green), paternal co-residency (blue) and early-life adversity (grey). **(B)** Predicted survival curves

414 showing the effects of juvenile females' mean $DSI_{paternal}$ and early-life adversity (ELA) on adult female
415 survival (predictions from model B in Table 2). Dark green lines are females in the top quartile of $DSI_{paternal}$
416 scores; light green lines show females in the bottom quartile of $DSI_{paternal}$. Solid lines show females who
417 experienced one source of ELA; dashed lines show females who experienced 3 sources of ELA. **(C)**
418 Predicted survival curves showing the effects of juvenile females' duration of co-residency with their fathers
419 and early-life adversity on adult female survival (predictions from model C in **Table 2**). Dark blue lines show
420 females who lived with tsheir father for 1 year; light blue lines show females who lived with their fathers for
421 all 4 juvenile years. Solid lines show females who experienced one source of ELA; dashed lines show females
422 who experienced three sources of ELA.
423

424 **(c) Objective 3: Fathers are more likely to groom and live with their daughters when**
425 **paternity is more certain and reproductive opportunities are limited**

426 Father-daughter relationships should be stronger when males have greater paternity certainty
427 and fewer reproductive opportunities. In support, males were more likely to groom their daughters
428 in a given year if the male was low-ranking, if there were relatively few cycling females in the group
429 that year (i.e., few reproductive opportunities), and if the male had a higher proportion of consort
430 time with the female's mother during the cycle the daughter was conceived (i.e., higher paternity
431 certainty; **Table 3**; **Table S4**). Notably, we found that having more offspring in the group predicted
432 more grooming, suggesting that males may increase their overall grooming time with juveniles if they
433 have many offspring (**Table 3; Table S4**). Males who groomed their daughters were not more likely
434 to sire the mother's previous or next infant (**Table 3; Table S4**), consistent with the idea that
435 grooming males are not investing in mating effort with the juvenile's mother [33, 35, 36]. A similar
436 subset of these variables also explained whether adult males had a grooming interaction with a
437 juvenile female, regardless of whether the male was the father (**Table S5**), suggesting that a male's
438 rank and mating behavior at the time of an infant's conception may influence his behavior towards
439 that infant, regardless of whether he is the father.

440 A slightly different set of variables predicted the duration of co-residency between fathers
441 and their daughters (**Table 4; Table S6**). Fathers and daughters had longer co-residencies if the
442 male was older, the mother was older, if there were more cycling females in the group, and if the
443 male had more offspring in the group. Co-residencies also tended to be longer if the male had a
444 prior offspring with the female's mother.
445

446 **Table 3.** Model averaged estimates (*β*), standard errors (*SE*), and z-values for the seven best-supported
447 GLMMs predicting the probability that a male groomed (1) or did not groom (0) his juvenile daughter in a
448 given year of her life (N=379 father-years years involving 70 fathers and 130 juvenile females). Variables in
449 bold appeared in all seven best-supported models (**Table S4**).

Term*	*β (SE)*	z-value	interpretation
Father's average ordinal rank	**0.185 (0.064)**	**2.868**	**higher ordinal rank ↓grooming**
Daily rate of fertile females	**-8.290 (2.425)**	**3.406**	**↑fertile females ↓grooming**
Proportion of consort time	**2.334 (0.901)**	**2.581**	**↑consort time ↑grooming**
Father sired the mother's next offspring	-0.949 (0.969)	0.975	Future offspring ↓grooming
Father sired the mother's previous offspring	-0.378 (1.001)	0.376	Previous offspring ↓grooming
Father's co-resident offspring-years	**0.235 (0.049)**	**4.822**	**↑co-resident offspring ↑grooming**
Daughter's cumulative adversity score	-0.416 (0.391)	1.061	↑adversity ↓grooming
Juvenile age	**0.778 (0.178)**	**4.362**	**↑juvenile age ↑grooming**
Paternal age	0.241 (0.201)	1.195	↑male age ↑grooming
Maternal age	0.035 (0.097)	0.364	↑maternal age ↑grooming
Observer effort	**1.462 (0.247)**	**5.903**	**↑effort ↑grooming**

450

451 **Table 4.** Model averaged estimates (*β*), standard errors (*SE*), and z-values for the five best-supported LMMs
452 predicting the duration of father-daughter co-residency during the daughter's 4-year juvenile period (N=166
453 co-residencies between 166 juvenile females and 86 fathers). Variables in bold appeared in all five best-
454 supported models (**Table S6**).

Term*	*β (SE)*	z-value	interpretation
Daily rate of fertile females	1.963 (1.030)	1.892	↑fertile females ↑co-residency
Father sired the mother's previous offspring	-0.535 (0.239)	2.226	had offspring ↑co-residency
Father's co-resident offspring-years	0.116 (0.036)	3.228	↑offspring ↑ co-residency
Paternal age	**0.160 (0.043)**	**3.672**	**↑male age ↑co-residency**
Maternal age	0.064 (0.020)	3.086	↑maternal age ↑co-residency

455

456

457 **4. DISCUSSION**

458 In many group-living mammals, males selectively interact with and provide low-cost forms
459 of care to offspring [13, 22]. The selective pressures shaping these behaviors, and their importance
460 to offspring health and survival, have received considerable attention in baboons [27, 30, 32-42].
461 Here we report that the strength of early-life paternal social relationships predicts meaningful
462 differences in adult survival for female baboons in Amboseli, Kenya. These differences are on the

463 order of 2-4 years for females in the top versus bottom quartile for paternal grooming or co-
464 residency—effect sizes that are comparable to those for other major predictors of adult survival in
465 Amboseli baboons, such as social isolation and early-life adversity [7, 61, 78]. This result joins prior
466 evidence for early-life paternal effects in baboons, including the observations that paternal presence
467 predicts earlier sexual maturity in daughters [32] and stronger social bonds between paternal half-
468 siblings [44]. These early-life paternal effects may also be important in other mammal species that
469 have subtle or indirect forms of paternal care [13, 17, 23-29]; hence, such effects may be more
470 powerful and widespread than is currently appreciated.
471
472 **(a) What mechanisms explain early-life paternal social effects on female survival?**
473 The two measures of father-offspring relationships we focused on—co-residency and
474 grooming—are not themselves parental care, raising the question: how do these measures lead to
475 early-life paternal effects? One possibility is that father-daughter grooming and co-residency are
476 correlated with other male care behaviors, which in turn, directly benefit their daughter's health and
477 longevity. For instance, male baboons sometimes intervene on behalf of offspring in conflicts and
478 buffer offspring and their mothers from negative interactions with other group members, including
479 threats from infanticidal males [79-81]. These behaviors may reduce injury risk, improve offspring
480 and maternal health, and ultimately affect offspring survival in adulthood [7, 62].
481 However, early-life relationships with fathers do not necessarily have direct, causal effects on
482 offspring health and survival. Another possibility is that the strength of father-offspring
483 relationships reflects daughters' own phenotypic quality, which in turn, partly or completely explains
484 the relationship between these traits and female survival. Under this scenario, strong, healthy
485 juvenile females may build and maintain strong relationships with their fathers in early life, and also
486 lead long, healthy adult lives. In support, father-daughter grooming relationships are largely
487 maintained by daughters, not their fathers. Paternal effects may also be mediated by male health if
488 paternal health affects offspring health, even in the absence of a direct relationship between fathers
489 and offspring (through e.g., epigenetic marks or semen quality [18, 82]). Under this scenario, fathers
490 who are in good condition produce healthy offspring, are less likely to disperse from groups where
491 they fathered offspring, and are more socially engaged, including with their daughters. Such effects
492 could create a correlation between father-offspring social relationships and offspring health and
493 survival that is not directly causal.

494 Early-life paternal relationships could promote offspring social development [43], which in
495 turn might affect survival via the established relationship between adult social connectedness and
496 longevity [83]. In support, the juvenile females in our study were more socially connected in
497 adulthood—especially to adult males—if they had stronger grooming relationships with their
498 fathers. However, juvenile grooming with non-paternal males did not predict adult female survival—
499 only grooming with fathers was protective. Further, paternal relationships predict adult survival,
500 even controlling for adult social connectedness. Hence, the paternal effects we observed likely
501 emerge from something more than adult social connectedness, and social connectedness to *all* males
502 is likely not beneficial to females in the juvenile period, as it is in adulthood.
503 Much remains unknown about the mechanisms connecting father-daughter relationships to
504 adult female longevity. One important next step is to test whether father-daughter grooming
505 relationships are linked to more direct forms of care (e.g., carrying, agonistic support). We also do
506 not yet know if fathers help their offspring survive the *juvenile* period, prior to adulthood. Further,
507 data on daughters' phenotypic quality and health in early life and adulthood are needed to test
508 whether daughters with stronger paternal relationships are healthier and if so, which mechanisms
509 mediate that effect (e.g., paternal care leading to offspring health, biological embedding of early
510 experience, healthy females have more energy to pursue paternal bonds etc.).
511
512 **(b) Do male baboons experience selection to provide parental care?**
513 If male care has direct effects on daughters' lifespans and fitness, then our results help
514 illuminate the evolution of paternal care. In Amboseli, adult female longevity is the largest
515 contributor to female fitness for baboons, explaining ~80-90% of individual variation in adult
516 female lifetime reproductive success [7, 45, 46]. Because female baboons typically produce one
517 offspring every two years [84], the increased years of survival predicted by paternal co-residency or
518 grooming could translate to 1-2 additional offspring over these females' lifespans. As such, fathers
519 and their juvenile daughters may experience selection to stay close and form lasting relationships.
520 However, male baboons are most likely to invest in social bonds with offspring when the
521 reproductive tradeoffs are favorable [85-87]. For instance, the males in our population were more
522 likely to groom their daughters when they had cues of paternity certainty—such as consorting with
523 her mother—and few current mating opportunities. In practice, this meant that males were more
524 likely to groom their daughters when they were low-ranking (because low-ranking males have low
525 mating success) and/or when there were few fertile females in the group.

If males experience selection to remain in the same group with their daughters, the risk of inbreeding could increase. Indeed, the duration of father-daughter co-residency in our data indicates that baboons do experience this risk: 18% of females will co-reside with their father for some time period in adulthood [88]. However, even when fathers and daughters live together, mate guarding between father-daughter pairs in Amboseli is exceptionally rare [88]. Hence, father-daughter social relationships likely do not lead to costs of inbreeding for males or their daughters, and these relationships may in fact allow fathers and daughters to recognize each other and avoid mating.

We also found that males were more likely to have strong grooming relationships with their daughters and co-reside with their daughters if the male had more offspring in the group ("co-resident offspring years" in Tables 3 and 4). Hence, having more offspring does not appear to lead to a dilution in males' tendencies to socialize with their daughters. While more research is needed to understand how being born into a large cohort of paternal siblings shapes baboons' developmental environments, the lack of a dilution effect is consistent with the idea that, to the degree to which father-daughter grooming reflects parental care, most forms of parenting for male baboons are low effort, even if they carry substantial benefits to offspring.

These observations, together with the survival patterns we observed, suggest that baboon mothers may experience selection to increase males' paternity certainty. Doing so would be advantageous to females if a prospective male sire meets other criteria for being a caring male (e.g., he sired a cohort of paternal siblings in the group). Selection for paternity certainty may also contribute to the evolution of sexual swellings in female baboons, which provide reliable signals of female ovulation and conception [35, 36, 65, 89, 90].

(c) How do early-life paternal relationships interact with other early-life conditions?

We found little evidence for an interaction between females' experiences of early-life adversity and the strength of their paternal relationships. As such, females who experienced harsh conditions in early life did not experience stronger survival benefits from paternal relationships than females who grew up in benign early-life environments. Hence, baboon fathers do not seem to actively fill deficits in their daughters' early environments. However, despite the lack of an interaction effect, fathers may sometimes play important roles in buffering their daughters against the survival effects of early-life adversity. For instance, high-adversity females who have strong paternal grooming relationships or long paternal co-residency seem to survive just as long as low-adversity females with weak paternal relationships. These results parallel those for the effects of

adult social connectedness and fecal glucocorticoid hormones in our population, both of which also have strong effects on adult survival, but appear to be mostly independent of early-life adversity [51, 78]. Hence, our data support the existence of multiple paths for mitigating early-life effects, including paternal relationships.

ACKNOWLEDGEMENTS

We are grateful to Jeanne Altmann for stewarding the ABRP and in designing many of its data collection protocols. We acknowledge support from the National Science Foundation and the National Institutes of Health, currently through R01AG071684, R01AG075914, R01AG053330, R01AG053308, and R61AG078470. We thank the Max Planck Institute for Evolutionary Anthropology, Duke University, and the University of Notre Dame for financial and logistical support. In Kenya, our research was approved by the Wildlife Research Training Institute, Kenya Wildlife Service, the National Commission for Science, Technology, and Innovation, and the National Environment Management Authority. We also thank the University of Nairobi, the Kenya Institute of Primate Research, the National Museums of Kenya, the members of the Amboseli-Longido pastoralist communities, the Enduimet Wildlife Management Area, and Ker & Downey Safaris for their cooperation and assistance in the field. We thank T. Wango and V. Oudu for their assistance in Nairobi. The ABRP database is managed by J. Gordon and W. Wilbur, with contributions from N. Learn and K. Pinc. This research was approved by the IACUC at Duke University, University of Notre Dame, and the Ethics Council of the Max Planck Society. For further acknowledgments please visit http://amboselibaboons.nd.edu/acknowledgements/.

DATA STATEMENT

Our data are publicly available on Zenodo at https://doi.org/10.5281/zenodo.14590285. Our code is available on GitHub at https://github.com/david-awam-jansen/BaboonPaternalRelationshipsSurvival

REFERENCES

[1] Snyder-Mackler, N., Burger, J.R., et al. 2020 Social determinants of health and survival in humans and other animals. *Science* **368**, 6493.

[2] Curley, J.P. & Champagne, F.A. 2023 Shaping the development of complex social behavior. *Ann N Y Acad Sci* **1530**, 46-63.

[3] Goldenberg, S.Z. & Wittemyer, G. 2018 Orphaning and natal group dispersal are associated with social costs in female elephants. *Animal Behaviour* **143**, 1-8.

592 [4] Goldenberg, S.Z. & Wittemyer, G. 2017 Orphaned female elephant social bonds reflect lack of
593 access to mature adults. *Scientific Reports* **7**.
594 [5] Kalcher-Sommersguter, E., Preuschoft, S., et al. 2015 Early maternal loss affects social
595 integration of chimpanzees throughout their lifetime. *Scientific Reports* **5**.
596 [6] Rosenbaum, S.R., Zeng, S., et al. 2020 Social bonds do not mediate the relationship between
597 early adversity and adult glucocorticoids in wild baboons. *Proceedings of the National Academy of Sciences*
598 **117**, 20052-20062.
599 [7] Tung, J., Archie, E.A., et al. 2016 Cumulative early adversity predicts longevity in wild baboons.
600 *Nature Communications* **7**, 11181.
601 [8] Stanton, M.A., Lonsdorf, E.V., et al. 2020 Consequences of maternal loss before and after
602 weaning in male and female wild chimpanzees. *Behavioral Ecology and Sociobiology*.
603 [9] Parker, J.M., Webb, C.T., et al. 2021 Poaching of African elephants indirectly decreases
604 population growth through lowered orphan survival. *Current Biology* **31**, 4156-+.
605 [10] Sear, R. & Mace, R. 2008 Who keeps children alive? A review of the effects of kin on child
606 survival. *Evolution and Human Behavior* **29**, 1-18.
607 [11] Lahdenpera, M., Mar, K.U., et al. 2016 Short-term and delayed effects of mother death on calf
608 mortality in Asian elephants. *Behav Ecol* **27**, 166-174.
609 [12] Patterson, S.K., Strum, S.C., et al. 2022 Early life adversity has long-term effects on sociality and
610 interaction style in female baboons. *Proc Biol Sci* **289**, 20212244.
611 [13] Kleiman, D. & Malcolm, J. 1981 The evolution of male parental investment in mammals. In
612 *Parental Care in Mammals* (eds. D. Gubernick & P. Klopfer), pp. 347–387. New York, Plenum Press.
613 [14] Clutton-Brock, T.H. 1991 *The evolution of parental care*. Princeton, Princeton University Press.
614 [15] Smith, K.R., Hanson, H.A., et al. 2014 Survival of offspring who experience early parental
615 death: early life conditions and later-life mortality. *Soc Sci Med* **119**, 180-190.
616 [16] Feldman, R. 2023 Father contribution to human resilience. *Development and Psychopathology* **35**,
617 2402-2419.
618 [17] Gettler, L.T., Boyette, A.H., et al. 2020 Broadening Perspectives on the Evolution of Human
619 Paternal Care and Fathers' Effects on Children. *Annu Rev Anthropol*.
620 [18] Watkins, A.J., Rubini, E., et al. 2020 Paternal programming of offspring health. *Early Hum Dev*
621 **150**, 105185.
622 [19] Todd, N., Valleron, A.J., et al. 2017 Prenatal loss of father during World War One is predictive
623 of a reduced lifespan in adulthood. *Proc Natl Acad Sci U S A* **114**, 4201-4206.
624 [20] Braun, K. & Champagne, F.A. 2014 Paternal influences on offspring development: behavioural
625 and epigenetic pathways. *J Neuroendocrinol* **26**, 697-706.
626 [21] Dimofski, P., Meyre, D., et al. 2021 Consequences of Paternal Nutrition on Offspring Health
627 and Disease. *Nutrients* **13**.
628 [22] Clutton-Brock, T. 2016 *Mammal Societies*, Wiley Blackwell.
629 [23] Rosenbaum, S. & Silk, J.B. 2022 Pathways to paternal care in primates. *Evol Anthropol* **31**, 245-
630 262.
631 [24] Sandel, A.A., Langergraber, K.E., et al. 2020 Adolescent male chimpanzees (*Pan troglodytes*) form
632 social bonds with their brothers and others during the transition to adulthood. *American Journal of*
633 *Primatology* **82**.
634 [25] Rosenbaum, S., Silk, J.B., et al. 2011 Male-immature relationships in multi-male groups of
635 mountain gorillas (Gorilla beringei beringei). *Am J Primatol* **73**, 356-365.
636 [26] de Bruin, R., Ganswindt, A., et al. 2016 From killer to carer: steroid hormones and paternal
637 behaviour. *Afr Zool* **51**, 173-182.
638 [27] Maestripieri, D. 1998 The evolution of male-infant interactions in the tribe Papionini (Primates:
639 Cercopithecidae). *Folia Primatol (Basel)* **69**, 247-251.

[28] Ostner, J., Vigilant, L., et al. 2013 Stable heterosexual associations in a promiscuous primate. *Animal Behaviour* **86**, 623-631.
[29] Rosenbaum, S., Vigilant, L., et al. 2018 Caring for infants is associated with increased reproductive success for male mountain gorillas. *Scientific Reports* **8**, 15223.
[30] Buchan, J.C., Alberts, S.C., et al. 2003 True paternal care in a multi-male primate society. *Nature* **425**, 179-181.
[31] Altmann, J. 1980 *Baboon Mothers and Infants*. Cambridge, MA, Harvard University Press.
[32] Charpentier, M.J., Van Horn, R.C., et al. 2008 Paternal effects on offspring fitness in a multimale primate society. *Proc Natl Acad Sci U S A* **105**, 1988-1992.
[33] Nguyen, N., Van Horn, R.C., et al. 2009 "Friendships" between new mothers and adult males: adaptive benefits and determinants in wild baboons (Papio cynocephalus). *Behavioral Ecology and Sociobiology* **63**, 1331-1344.
[34] Silk, J.B., Stadele, V., et al. 2020 Shifts in Male Reproductive Tactics over the Life Course in a Polygynandrous Mammal. *Curr Biol* **30**, 1716-1720 e1713.
[35] Stadele, V., Roberts, E.R., et al. 2019 Male-female relationships in olive baboons (Papio anubis): Parenting or mating effort? *J Hum Evol* **127**, 81-92.
[36] Stadele, V., Vigilant, L., et al. 2021 Extended male–female bonds and potential for prolonged paternal investment in a polygynandrous primate (Papio anubis). *Animal Behaviour*.
[37] Huchard, E., Alvergne, A., et al. 2010 More than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma baboons. *Behavioral Ecology and Sociobiology* **64**, 769-781.
[38] Moscovice, L.R., Di Fiore, A., et al. 2010 Hedging their bets? Male and female chacma baboons form friendships based on likelihood of paternity. *Animal Behaviour* **79**, 1007-1015.
[39] Smuts, B.B. 1985 *Sex and Friendship in Baboons*. New York, Aldine Transaction.
[40] Palombit, R.A., Seyfarth, R.M., et al. 1997 The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Animal Behavior* **54**, 599-614.
[41] Lemasson, A., Palombit, R.A., et al. 2008 Friendships between males and lactating females in a free-ranging group of olive baboons (Papio hamadryas anubis): evidence from playback experiments. *Behavioral Ecology and Sociobiology* **62**, 1027-1035.
[42] Moscovice, L.R., Heesen, M., et al. 2009 Paternity alone does not predict long-term investment in juveniles by male baboons. *Behav Ecol Sociobiol* **63**, 1471-1482.
[43] Zipple, M.N., Southworth, C.A., et al. 2024 Infant spatial relationships with adult males in a wild primate: males as mitigators or magnifiers of intergenerational effects of early adversity? *bioRxiv*.
[44] Lynch, E.C., Di Fiore, A., et al. 2017 Fathers enhance social bonds among paternal half-siblings in immature olive baboons (Papio cynocephalus). *Behavioral Ecology and Sociobiology* **71**, 120.
[45] Weibel, C.J., Tung, J.T., et al. 2020 Accelerated reproduction is not an adaptive response to early life adversity in wild baboons. *Proceedings of the National Academy of Sciences* **117**, 24909-24919.
[46] McLean, E.M., Archie, E.A., et al. 2019 Lifetime Fitness in Wild Female Baboons: Trade-Offs and Individual Heterogeneity in Quality. *American Naturalist* **194**, 745-759.
[47] Alberts, S.C. & Altmann, J. 2012 The Amboseli Baboon Research Project: Themes of continuity and change. In *Long-term field studies of primates* (eds. P. Kappeler & D.P. Watts), pp. 261-287, Springer Verlag.
[48] Silk, J.B., Altmann, J., et al. 2006 Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology* **61**, 183-195.
[49] Mitani, J.C. 2009 Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour* **77**, 633-640.
[50] Schino, G. & Aureli, F. 2008 Grooming reciprocation among female primates: a meta-analysis. *Biol Letters* **4**, 9-11.

[51] Lange, E.C., Zeng, S., et al. 2023 Early life adversity and adult social relationships have independent effects on survival in a wild primate. *Sci Adv* **9**, eade7172.
[52] Wall, J.D., Schlebusch, S.A., et al. 2016 Genome-wide ancestry and divergence patterns from low-coverage sequencing data reveal a complex history of admixture in wild baboons. *Mol Ecol* **25**, 3469-3483.
[53] Vilgalys, T.P., Fogel, A.S., et al. 2022 Selection against admixture and gene regulatory divergence in a long-term primate field study. *Science* **377**, 635-641.
[54] Onyango, P.O., Gesquiere, L.R., et al. 2013 Puberty and dispersal in a wild primate population. *Hormones and Behavior* **64**, 240-249.
[55] McLean, E.M., Moorad, J.A., et al. 2023 Genetic variance and indirect genetic effects for affiliative social behavior in a wild primate. *Evolution* **77**, 1607-1621.
[56] Alberts, S.C., Buchan, J.C., et al. 2006 Sexual selection in wild baboons: from mating opportunities to paternity success. *Anim Behav* **72**, 1177-1196.
[57] Van Horn, R.C., Buchan, J.C., et al. 2007 Divided destinies: group choice of female savannah baboons during social group fission. *Behavioral Ecology and Sociobiology* **61**, 1823-1837.
[58] Kalinowski, S.T., Taper, M.L., et al. 2007 Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**, 1099-1006.
[59] Marshall, T.C., Slate, J., et al. 1998 Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* **7**, 639-655.
[60] Archie, E.A., Tung, J., et al. 2014 Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society* **281**, 20141261.
[61] Campos, F.A., Villavicencio, F., et al. 2020 Social bonds, social status and survival in wild baboons: a tale of two sexes. *Philos Trans R Soc Lond B Biol Sci* **375**, 20190621.
[62] Zipple, M.N., Archie, E.A., et al. 2019 Intergenerational effects of early adversity on survival in wild baboons. *eLife* **8**, e47433.
[63] Alberts, S.C., Watts, H.E., et al. 2003 Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Animal Behaviour* **65**, 821-840.
[64] Gordon, J.B., Jansen, D., et al. 2023 Ordinal dominance rank assignments: Protocol for the Amboseli Baboon Research Project. (
[65] Gesquiere, L.R., Wango, E.O., et al. 2007 Mechanisms of sexual selection: sexual swellings and estrogen concentrations as fertility indicators and cues for male consort decisions in wild baboons. *Hormones and Behavior* **51**, 114-125.
[66] Alberts, S.C., Buchan, J.C., et al. 2006 Sexual selection in wild baboons: from mating opportunities to paternity success. *Animal Behaviour* **72**, 1177-1196.
[67] Beehner, J.C., Onderdonk, D.A., et al. 2006 The ecology of conception and pregnancy failure in wild baboons. *Behavioral Ecology* **17**, 741-750.
[68] Altmann, J., Alberts, S.C., et al. 1996 Behavior predicts genetic structure in a wild primate group. *Proceedings of the National Academy of Sciences* **93**, 5797-5801.
[69] Alberts, S.C., Archie, E.A., et al. 2024 Monitoring guide for the Amboseli Baboon Research Project: http://amboselibaboons.nd.edu/downloads/.
[70] Bates, D., Maechler, M., et al. 2014 lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-5. In *http://CRAN.R-project.org/package=lme4* (
[71] Kuznetsova, A., Brockhoff, P.B., et al. 2017 lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software* **82**, 1-26.
[72] Zeileis, A. & Hothorn, T. 2002 Diagnostic Checking in Regression Relationships. *R News* **2**, 7–10.
[73] Barton, K. 2023 R Package: MuMIn: Multi-model inference (1.47.5). (

[74] Stoffel, M.A., S., N., et al. 2017 rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution* **8**, 1639-1644.
[75] Therneau. 2014 A Package for Survival Analysis in S. R package version 2.37-7, http://CRAN.R-project.org/package=survival. (
[76] Belsley, D.A., Kuh, E., et al. 1980 *Regression Diagnostics; Identifying Influence Data and Source of Collinearity*. New York, Wiley.
[77] Silk, J.B., Beehner, J.C., et al. 2010 Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology* **20**, 1359-1361.
[78] Tung, J., Lange, E.C., et al. 2023 Social and early life determinants of survival from cradle to grave: A case study in wild baboons. *Neurosci Biobehav Rev* **152**, 105282.
[79] Palombit, R.A. 2003 Male infanticide in wild savanna baboons: adap- tive significance and intraspecific variation. In *Sexual selection and reproductive competition in primates: new perspectives and directions* (ed. C.B. Jones), pp. 367-411, American Society of Primatologists.
[80] Collins, D.A., Busse, C.D., et al. 1984 Infanticide in two populations of savanna baboons. In *Infanticide: comparative and evolutionary perspectives* (eds. G. Hausfater & S. Hrdy), pp. 193–216. New York, Hawthorne.
[81] Zipple, M.N., Grady, J.H., et al. 2017 Conditional fetal and infant killing by male baboons. *Proc Biol Sci* **284**.
[82] Sabei, L., Bernardino, T., et al. 2023 Life experiences of boars can shape the survival, aggression, and nociception responses of their offspring. *Front Anim Sci* **4**.
[83] Silk, J.B. 2012 The adaptive value of sociality. In *Evolution of Primate Societies* (eds. J.C. Mitani, J. Call, P. Kappeler, R. Palombit & J.B. Silk), pp. 552-564. Chicago, University of Chicago Press.
[84] Gesquiere, L.R., Altmann, J., et al. 2018 Interbirth intervals in wild baboons: Environmental predictors and hormonal correlates. *Am J Phys Anthropol* **166**, 107-126.
[85] Trivers, R.L. 1972 Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871-1971* (Aldine Press.
[86] Stiver, K.A. & Alonzo, S.H. 2009 Parental and Mating Effort: Is There Necessarily a Trade-Off. *Ethology* **115**, 1101–1126.
[87] Kokko, H. & Jennions, M.D. 2008 Parental investment, sexual selection and sex ratios. *J Evol Biol* **21**, 919-948.
[88] Galezo, A.A., Nolas, M.A., et al. 2022 Mechanisms of inbreeding avoidance in a wild primate. *Curr Biol* **32**, 1607-1615 e1604.
[89] Alberts, S.C. & Fitzpatrick, C.L. 2012 Paternal care and the evolution of exaggerated sexual swellings in primates. *Behavioral Ecology*.
[90] Nunn, C.L. 1999 The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Anim Behav* **58**, 229-246.