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 co-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 not especially protective against harsh early environments. Males' relationships were strongest with juvenile females they were most likely to have sired and when males had few current 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 [reviewed in 2]. Maternal relationships are especially well-studied in this regard [3-12], and across mammals, maternal loss and the quality of maternal care can have long-lasting consequences for offspring gene regulation, stress reactivity, social integration, and adult survival [3-9, 11-13].

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 [14, 15]. 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 predicts negative outcomes for adult behavior, income, health, and mortality risk [e.g., 16, 17-20]. In rodents with biparental care, fathers affect the complexity of offspring social environments, with consequences for neurological development and adult behavior [reviewed in 21, 22]. But species in which fathers provide substantial care are unusual among mammals. In a wider (but still unusual) set of group-living mammals, fathers live and even socialize with offspring, but paternal care *per se* is subtle and often indirect [14, 23]. These species include several carnivores and equids, as well as gorillas, chimpanzees, baboons, and other primates [14, 18, 24-30]. 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. Baboons are useful for testing these relationships for three reasons. First, the baboons we studied live in polygynandrous mating systems where paternity certainty is incomplete, yet adult male baboons often maintain proximity to and interact with their offspring [31-38]. 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]. In support, male primary associates typically do not sire their female associate's next infant [34, but see 35]. Furthermore, male primary associates are 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 [31-38, 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 infant baboons [43]. Paternal presence is also correlated with earlier sexual maturity in daughters [31] 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 the lifespan of daughters, they may have important consequences for their daughters' fitness and, by extension, the males themselves. If so, males and their daughters may experience selection to form and maintain early-life social relationships with one another.

Working in the Amboseli baboon population in Kenya [47], we asked whether female baboons who had stronger grooming relationships or longer co-residency with their fathers in early life exhibit higher adult survival. We pursued three objectives. First, we measured patterns of grooming and co-residency between juvenile females and their fathers. We measured grooming because 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 females had stronger grooming relationships or longer co-residency with their fathers in early life exhibit higher adult survival than females who had weak/short paternal grooming or co-residency. In the Amboseli baboons, adult female longevity is also predicted by an accumulation of harsh conditions in early life, such as drought, maternal loss, or having a low-ranking or socially isolated mother [7, 45, 51]. Hence, we also used interaction effects to test if early-life relationships with fathers might 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 she was conceived) and when reproductive tradeoffs are favorable (e.g., when the male had few current mating opportunities). Together, our results support the importance of paternal presence and father-daughter social bonds 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 based on visual recognition. Our analyses centered on 216 female baboons that: (i) survived the first 4 years of life, encompassing most or all of the juvenile period for females [median age at menarche in Amboseli = 4.5 years; 54]; (ii) had known mothers and fathers assigned using combined 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]: early maternal loss, 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 are 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 [32, 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 social 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 males typically identified the same father, but in the few cases where they disagreed, we assigned paternity based on the strength of additional evidence for each father (e.g., geographic distance between the candidates and the mother, male health status, or density of observations on the mother during the window of conception). In all cases, the assigned father resided in same social group as the mother at the time of conception [56]. 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% [32, 55-57].

133

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

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

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

147 The grooming interactions used to calculate the DSI scores were collected via representative
148 interaction sampling. During this sampling, observers moved through the group recording all
149 grooming interactions in their line of sight, while conducting 10-min focal animal follows on a
150 randomized list of females and juveniles [6, 60]. From these data, we calculated each dyad's log-
151 transformed daily rate of grooming in a given year. All log-transformed daily rates were then
152 regressed against a measure of observer effort in that year (the number of focal animal samples per
153 female-day). The resulting residuals were z-scored within years to estimate the DSI. Negative DSI
154 scores reflect dyads who groomed less than was typical in that year; positive DSI scores reflect dyads
155 who groomed more than was typical in that year.

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

160

161 **(d) Measuring early-life adversity**

162 To test if fathers moderate early-life effects on female mortality in adulthood (objective 2),
163 we measured early-life adversity using a cumulative adversity index developed in prior studies [6, 7,
164 45, 51, 61]. 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 of her group; 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 of adversity).

(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).

Paternal age and the ages of daughters and their mothers were known from near daily demographic records. All 216 daughters had ages accurate within a few days. Of the 102 fathers in our data, 43 (42.2%) were born into the study population and their ages were accurate within a few days. For the remaining 59 fathers (57.8%), their ages were estimated to within a few years by comparing them to known-age males from the population [62]. For the mothers, 101 (86.3%) had ages accurate within a few days, 14 (12.0%) had ages accurate within 3 months, and 2 (1.7%) had ages accurate within 3 years.

Male ordinal dominance rank determines male priority of access to mates in our population, and high-ranking males are expected to prioritize mating over parenting effort [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 influence a male's mating opportunities and time spent grooming daughters. This variable was calculated as the average daily number of peri-ovulatory females in the group in a given juvenile female-year on the days the male was resident in the social group [65]. Peri-ovulatory periods are inferred from continuous records of sexual skin swellings that increase in size during the follicular phase and decrease during the luteal phase [65].

The *proportion of the mother's available consort time the male obtained* during the 5-day peri-ovulatory period that led to the focal female's conception could affect male paternity certainty. This measure was calculated by summing all observed consort time that a mother had with any adult male within 5 days before the likely conception date of the focal female. We then calculated the proportion of this consort time that was monopolized by the male in question. Conception dates were calculated as described previously based on obvious signs of female reproductive state [65, 66]. For 31 of the 216 females, no males were observed consorting the focal female's mother; hence analyses with this variable only included 185 females.

The number of potential fathers present in the group at the juvenile female's conception could influence male paternity certainty [56, 67]. This variable was calculated as the number of adult ranked males present in the group during the 5-day peri-ovulatory period when the female was conceived.

Following [34, 35]*, males who sired previous or future offspring of the juvenile female's mother* might be more likely to groom their daughters if "primary associates" represent male mating effort. To test this possibility, we identified all cases in which the focal female's father sired their mother's previous or next offspring (n=185 females; see above). There were 25 cases (13.5%) where the father sired the mother's previous offspring, 131 cases (70.8%) where he did not, 16 cases (8.6%) where the dad was not present, and 13 cases (7%) where the paternity of the mother's previous offspring was unknown. With respect to the mother's next offspring, there were 25 cases (13.5%) where the male sired the mother's next offspring, 115 cases (62.2%) where he did not, 16 cases (8.6%) where the dad was not present, and 29 cases (15.7%) where paternity was unknown. To avoid further reductions in sample size, we imputed the 42 unknown paternities by randomly assigning paternity to one of the adult ranked males present in the group when the female was conceived. We performed these imputations 1000 times and ran our models on each imputed data set. We also repeated our analysis on a smaller "complete cases" data set where paternities for the previous and subsequent offspring were known.

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

229 The female's experience of *cumulative early-life adversity*, could also influence paternal
230 investment. Cumulative adversity was calculated as the sum of the 6 conditions a female might have
231 experienced prior to age 4 years (see above).
232 Finally, for our model of why some fathers groom their daughters more than others, *we also*
233 *modeled observer effort*, measured as the number of focal animal samples we collected per female-day.
234 We considered the effect of observer effort to account for the fact that observers are more likely to
235 observe grooming in groups where we conducted more intensive behavioral observations.
236
237 **(f) Statistical Analyses**
238 Most analyses were performed in R 4.4.0 using the packages lme4 [68], lmerTest [69], lmtest
239 [70], MuMIn [71], rptR [72], and survival [73]. For a full list of packages used in the analysis of this
240 paper see the GitHub repository in our data statement.
241
242 *Objective 1: Characterizing patterns of grooming and co-residency between juvenile females, their fathers, and other*
243 *adult males*
244 To measure grooming relationships between juvenile females and adult males, we calculated,
245 in each female-year (i) the average number of adult males each female groomed with, and (ii) the
246 percentage of grooming interactions she initiated with adult males (N=216 females; from 0 to 4
247 years of age). To test if female age predicted grooming initiation with males (both fathers and non-
248 fathers), we ran a binomial LMM where the response variable measured whether grooming with
249 adult males was initiated by females (1) or not (0), as a function of female age in each year of the
250 juvenile period. Female identity was modeled as a random effect. To test if grooming bonds were
251 stronger between father-daughter pairs than other male-female pairs, we also ran a LMM testing if
252 juvenile females' DSI_{all} scores with all adult, co-resident males, including their fathers, was predicted
253 by whether the male was the female's father or by female age (0 to 4 years of age), again modeling
254 female identity as a random effect.
255
256 *Objective 2: Testing if paternal co-residency and social bonds predict adult female survival*
257 To test if females who have longer juvenile co-residency or stronger grooming relationships
258 with their fathers exhibit higher adult survival than females who had short paternal co-residency or
259 weak paternal grooming relationships, we ran a series of Cox proportional hazards models where the
260 response variable was each female's age at death or censorship, contingent on survival to her 4th year

261 of life (N=216 females; 124 censored values). Models were fit using coxph in the R package survival
262 [73]. We tested which variables best explained variation in adult female mortality risk based on
263 Akaike information criteria (AICc), including each female's: (i) average annual dyadic grooming
264 bond strength with her father ($DSI_{paternal}$) during the first four years of her life (because grooming
265 patterns change with juvenile female age, these strengths were z-scored across females, within age
266 class [i.e., age 0 to 1 years, age 1 to 2 years etc.]); (ii and iii) average annual grooming bond strength
267 with all co-resident adult males, either excluding ($DSI_{non\text{-}paternal}$) or including her father (DSI_{all}; these
268 scores were also z-scored and averaged across the first four years of life); (iv) cumulative years of co-
269 residency with her father in the first four years of life; and (v) cumulative early-life adversity score in
270 the first four years of life.
271 To test if the effects of early-life adversity on adult female survival are moderated by paternal
272 grooming or co-residency, we added an interaction effect between females' early-life adversity scores
273 and (vi) their average annual $DSI_{paternal}$ scores, and (7) their cumulative years of paternal co-residency.
274 We also tested if juvenile females with strong paternal grooming bonds are socially well-
275 connected with females and males in adulthood. If so, early-life relationships between female
276 baboons and their fathers might be important for later life survival because they influence female
277 social connectivity in adulthood. Social connectivity to adult females and males predicts adult female
278 survival in this population [51, 60, 74]. Social connectivity was calculated as a social connectedness
279 index (SCI), which reflects the total amount of grooming the female, as an adult, gave and received
280 with other adult females (SCI_F) and adult males (SCI_M) in her social group [51, 60, 74]. For these
281 analyses, we first ran an LMM testing if females with stronger mean $DSI_{paternal}$ scores in the first 4
282 years of life had stronger SCI_F and SCI_M scores in adulthood, controlling for her age and dominance
283 rank and modeling female identity as a random effect. We then ran a series of survival models to test
284 if the observed association between $DSI_{paternal}$ and adult female survival is attenuated by adding SCI_F
285 and SCI_M to the model. The sample size for these models was 194 females because adult social
286 connectedness information was missing for 22 females.
287
288 *Objective 3: Testing the predictors of father-daughter grooming and co-residency*
289 To test why some fathers are more likely to groom their daughters than others, we ran a
290 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 of
292 co-residency in that year. The fixed effects were: (i-iii) the ages of the juvenile, father, and mother at

293 the start of the year; (iv) the father's average ordinal dominance rank in that year; (v) the average
294 number of fertile (i.e., peri-ovulatory) females in the group each day in that year; (vi) the proportion
295 of observed consort time the male had with the focal female's mother during the 5-day period when
296 she was conceived; (vii) the number of other adult males (i.e., potential fathers) in the group at the
297 daughter's conception; (viii and ix) whether the father sired a prior or future offspring with the
298 daughter's mother; (x) the number of juvenile paternal offspring the father had in the group in that
299 year ("co-resident offspring years"); (xi) the daughter's cumulative early-life adversity score; and (xii)
300 observer effort. Paternal identity was a random effect (N=495 father-years years involving 81 fathers
301 and 169 juvenile females). Because these models used imputed paternity assignments for some of
302 the prior/future offspring, we present the median of the model estimates, test statistics, and p-values
303 across 1000 imputed data sets. In the supplement, we also present a "complete cases" version of this
304 model without imputation (N=379 father-years years involving 70 fathers and 130 juvenile females).
305 We also performed a parallel analysis for all co-resident males (i.e., not just father-daughter pairs),
306 which included a binary fixed effect for if the adult male was the father (N=8,078 male-years years,
307 involving 297 males and 185 juvenile females). This analysis used imputed paternity assignments for
308 some of the prior/future offspring. We present the median of the model estimates, test statistics,
309 and p-values across 1000 imputed data sets.

310 To test why some fathers have longer co-residency with their daughters, we ran a LMM
311 where the response variable was the number of days the father resided in the same group as his
312 daughter in the first four years of her life. The fixed effects were: (i-ii) the father's and mother's ages
313 in the month that father-daughter co-residency ended (juvenile age was excluded because it was
314 colinear with the duration of co-residency); (iii) the father's dominance rank in the month co-
315 residency ended; (iv) the daily rate of fertile females in the group in the month co-residency ended;
316 (v) the proportion of consort time the male had with the focal female's mother during the 5-day
317 period when the daughter was conceived; (vi) the number of other adult males (i.e., potential fathers)
318 in the group at the daughter's conception; (vii) whether the father sired a prior offspring with the
319 daughter's mother (future offspring was excluded because only males with relatively long co-
320 residencies would be able to sire this future offspring); (viii) the number of juvenile paternal
321 offspring the father had in the group in the year the co-residency ended (co-resident offspring years);
322 and (ix) the daughter's cumulative early-life adversity score. Paternal identity was included as a
323 random effect (N=166 co-residencies involving 86 fathers and 166 juvenile females).

Before performing our analyses, we checked for multicollinearity using variance inflation factor (VIF) analysis adapted for lmer models [75]. No variables had VIF > 2.5.

3. RESULTS

(a) Objective 1: Patterns of co-residency and grooming between juvenile females and their fathers

The median co-residency between the 216 daughters and their fathers was 33 months (**Fig. 1A**; range=0-48 months). More than a third of these females (n=80; 37%) lived in the same group with their father for ≥ 3 of their juvenile years, while for the remaining 63% of females (n=136), their fathers either left the group or died sometime between their conception and 3 years of age (**Fig. 1A**). Thirteen females (6%) never co-resided with their fathers because the male dispersed or died between the focal female's conception and birth (**Fig. 1A**).

Grooming between juvenile females, their fathers, and other adult males changed in frequency and directionality across females' juvenile years. From birth to 4 years of age, females groomed with an increasing number of adult males (β=0.35; p=<0.001) and were more likely to initiate grooming with adult males (**Fig. 1B**: binomial LMM: β=1.00; p<0.001). Among females in the first year of life, 18.2% of the observed grooming interactions with adult males were initiated by the females (**Fig. 1B**), and each female groomed on average with 1.15 adult males (range=1-3 males). However, by the 4th year of life, females had, on average, 1.54 male grooming partners (range=1-6 males), and 83% of these interactions were initiated by the female (**Fig. 1B**).

Consistent with prior evidence that males and their offspring have differentiated relationships [31-36], daughters' DSI_{all} values were significantly stronger with their fathers than with other co-resident adult males (**Table 1;** β=0.117; p=0.0047). However, the effect size was weak: DSI_{all} values between juvenile females and their fathers were just 4.29% stronger than DSI_{all} between juvenile females and non-paternal males, reflecting the fact that juvenile females also groom adult males who are not their fathers, and these bonds are sometimes as strong (**Fig. S1**).

Table 1. LMM explaining dyadic bond strength between juvenile females and all co-resident adult males in a given year (N=4,968 DSI_{all} values between 216 females and 298 males, including 91 fathers).

Term	*β (SE)*	t	df	p-value	Interpretation
Age of juvenile female	0.134 (0.010)	13.103	10578.7	<0.001	↑juvenile age ↑bond strength
Male is the father	0.117 (0.042)	2.827	10527.1	0.0047	male is father ↑bond strength

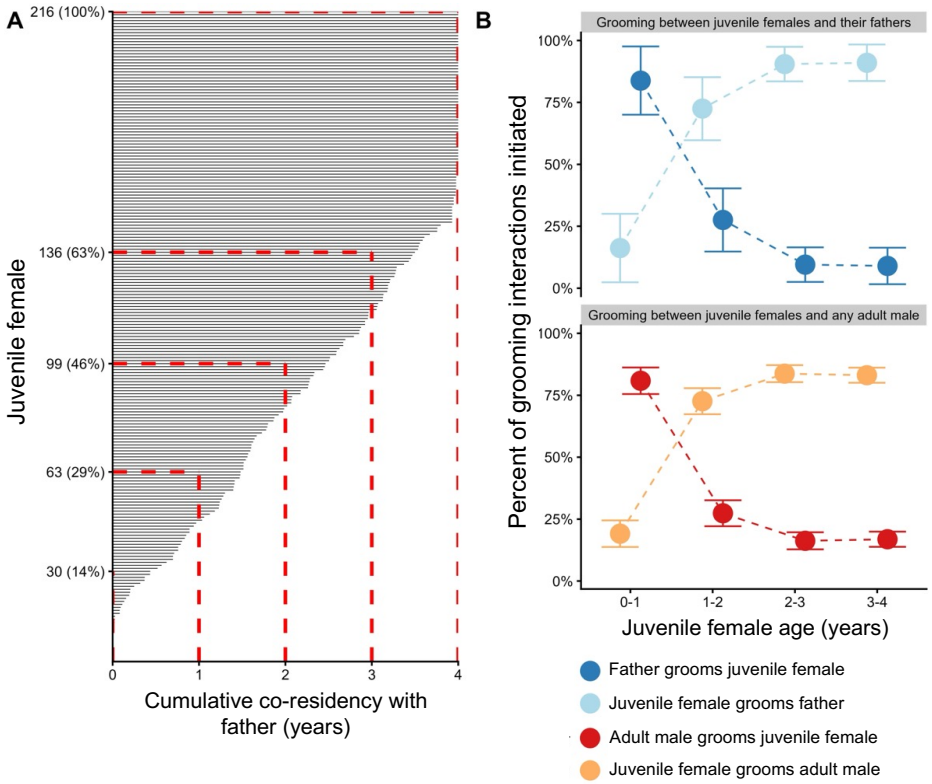

Figure 1. Patterns of co-residency and grooming directionality between juvenile females, their fathers, and other adult males. **(A)** Cumulative paternal co-residency (x-axis) for the 216 juvenile females (y-axis). Each black bar represents the cumulative duration of time one female lived in the same 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 relatively strong $DSI_{paternal}$ scores with their fathers, or who had relatively 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

372 predicting adult female survival included either the female's average $DSI_{paternal}$ score in the first four
373 years of life, the duration of co-residency with her father, or both variables (**Fig. 2**; **Table 2 rows A-**
374 **C**). $DSI_{paternal}$ and co-residency were positively correlated with each other (**Fig. S2**; Pearson's
375 r=0.274, p=0.001), consistent with the idea that father-daughter pairs who co-reside for longer will
376 also have stronger grooming relationships. Models that included either one or both variables were
377 interchangeable in their ability to explain adult female mortality (**Fig. 2**; **Table 2 rows A-C;** range in
378 ΔAICc=0.31-1.28). This effect was specific to $DSI_{paternal}$: strong social relationships during the
379 juvenile period with adult males in general (DSI_{all}), or with non-fathers ($DSI_{non\text{-}paternal}$), did not predict
380 adult survival (**Table 2 rows A-C** versus **rows D, F, and G**).
381 Early-life adversity also predicted adult female mortality (**Table 2 all models,** [7, 51]), but
382 the models that included $DSI_{paternal}$ and/or co-residency were a better fit to the data than a model
383 that only included early-life adversity (**Table 2 rows A-C vs row E**; range in ΔAICc=3.228-4.56).
384 We therefore asked whether relationships with fathers predicted adult female survival more so for
385 females who experienced harsh early-life circumstances. However, adding an interaction effect
386 between female early-life adversity and either $DSI_{paternal}$ or paternal co-residency did not improve
387 model fit (range in ΔAICc=1.66-3.57; **Table S1**). Hence, the effects of paternal relationships and
388 early-life adversity appear to be mostly independent. For the "median" female who experienced one
389 major source of early-life adversity, having a mean $DSI_{paternal}$ score in the top quartile for the
390 population predicted a median difference in survival of 1.8 years compared to females in the bottom
391 quartile of mean $DSI_{paternal}$ scores (**Fig. 2B**). Adult females who experienced one source of adversity
392 and lived with their fathers for all 4 years were predicted to live 2.6 years longer than females who
393 only lived with their father for 1 year (**Fig. 2C**). Females who experienced 3 or more sources of
394 early-life adversity were predicted to live 4.3 to 4.6 years longer if they co-resided with their father
395 for 4 years versus 1 year or had grooming relationships with their fathers in the top versus bottom
396 quartile (**Figs. 2B and 2C**).
397 Finally, we wondered whether some of the survival effects we observed could be explained
398 by adult females' social bonds with either sex in adulthood, both of which predict adult female
399 survival [51, 60, 74, 76]. This effect might arise if, for instance, juvenile females who have strong
400 $DSI_{paternal}$ scores tend to be more social overall, or if strong paternal bonds directly promote adult
401 social connectedness (e.g., a mediation effect that operates via social effects on health in adulthood).
402 We found that females who had stronger average $DSI_{paternal}$ scores across the first 4 years of life also
403 tended to have strong social bonds with both adult males (SCI_M; **Table S2**; β=0.16; p<0.001) and

404 adult females (SCI_F; **Table S2**; β=0.11; p=0.035) in adulthood. In support of the idea that $DSI_{paternal}$,
405 SCI_F, and SCI_M all contribute to adult mortality risk, four of the seven best models in **Table S3**
406 (those with ΔAICc <2 from the best model) included a metric of adult social connectedness (SCI_F,
407 SCI_M, or both; **Table S3 rows 3, 4, 6 and 7**), while six of the best seven models included $DSI_{paternal}$,
408 paternal co-residency, or both variables (**Table S3 rows 1-6**).
409
410 **Table 2.** Results from seven alternative Cox proportional hazards models (n=216 females with 124 censored
411 values) showing predictors of adult female survival. Each cell shows the variable's hazard ratio (and 95%
412 confidence interval). Models are ordered by AICc. No model violated the proportional hazards assumption
413 (p-values ranged from 0.34 to 0.77).

Model	Cumulative early-life adversity	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

414
415

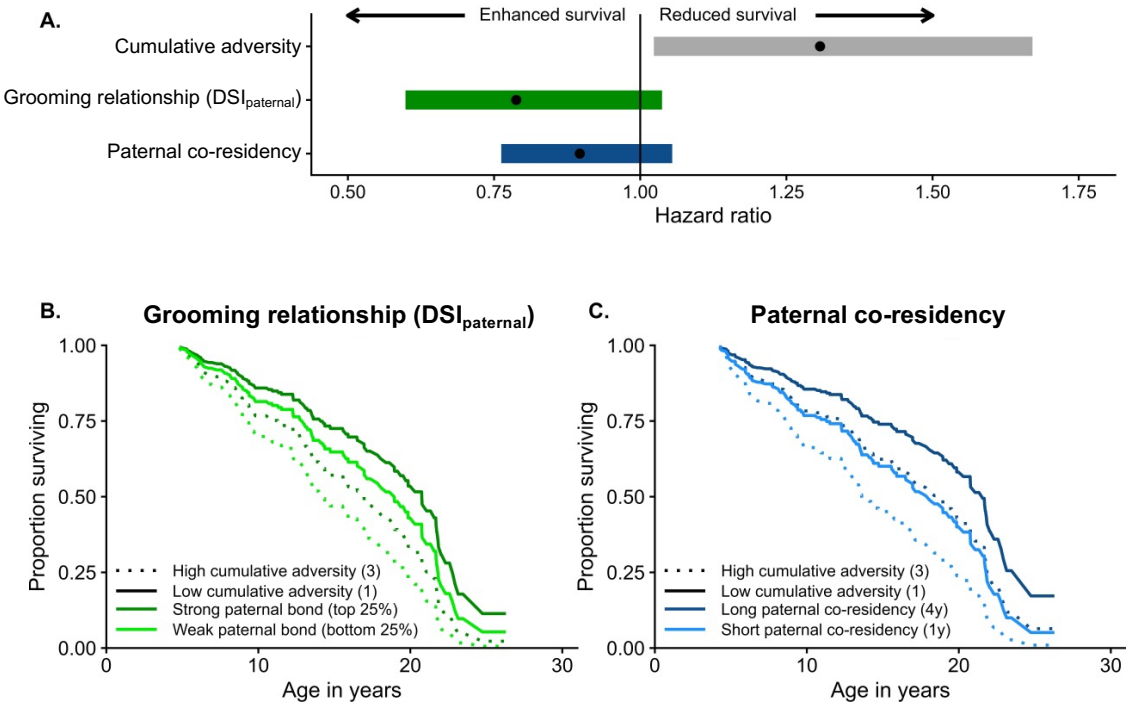

Figure 2. Juvenile females' paternal grooming relationships and co-residency predict their adult survival. (A) Estimates from the time-to-event effects on the hazard of death in adult female baboons. Effects and 95% CI are from **row A in Table 2**, the model that had the lowest AICc and that includes mean $DSI_{paternal}$ (green), paternal co-residency (blue) and early-life adversity (grey). **(B)** Predicted survival curves showing the effects of juvenile females' mean $DSI_{paternal}$ and early-life adversity on adult female survival (Wald test P= 0.006, N= 216; predictions from model B in Table 2). Dark green lines are females in the top quartile of $DSI_{paternal}$ scores; light green lines show females in the bottom quartile of $DSI_{paternal}$. Solid lines show females who experienced one source of early-life adversity; dashed lines show females who experienced 3 sources of adversity. **(C)** Predicted survival curves showing the effects of juvenile females' duration of co-residency with their fathers and early-life adversity on adult female survival (Wald test P= 0.007, N= 216; predictions from model C in **Table 2**). Dark blue lines show females who lived with their father for 1 year; light blue lines show females who lived with their fathers for all 4 juvenile years. Solid lines show females who experienced one source of adversity; dashed lines show females who experienced three sources of adversity.

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

Father-daughter relationships should be stronger when males have greater paternity certainty and fewer reproductive opportunities. In support, males were most likely to groom their daughters in a given year if the male was low-ranking, there were relatively few cycling females in the group that year, the male had a higher proportion of consort time with the female's mother during the cycle the daughter was conceived, and if the male had more offspring in the group (**Table 3; Table S4**). Consistent with prior studies that suggest that male "primary associate" behavior is better explained by parenting than mating effort [33, 35, 36], males who groomed their daughters were not more likely to sire the mother's previous or next infant (**Table 3; Table S4**). A similar subset of these variables also explained whether adult males had a grooming interaction with a juvenile female, regardless of whether the male was the father (**Table S5**), suggesting that a male's rank and mating behavior at the time of an infant's conception may influence his behavior towards that infant, regardless of whether he is the father.

A slightly different set of variables predicted the duration of co-residency between fathers and their daughters (**Table 4**). Adult males had longer co-residencies with their daughters if the males were older, the mother was older, if there were more cycling females in the group that year of the juvenile's life, and if they had more offspring in the group (**Table 4**). Longer co-residencies also tended to occur if the male had a prior offspring with the female's mother, but this effect was not significant (**Table 4**).

Table 3. Binomial GLMM of whether a male did (1) or did not groom (0) his juvenile daughter in a year of her life (N=495 years; 81 fathers and 169 juvenile females with at least 30 days of co-residency >1 year).

Term	*β (SE)*	t-value	p-value	interpretation
Juvenile age	0.869 (0.209)	4.162	<0.001	↑juvenile age ↑grooming
Paternal age	0.201 (0.191)	1.057	0.291	
Maternal age	0.061 (0.085)	0.703	0.481	
Father's average ordinal rank	0.175 (0.058)	3.036	0.002	higher ordinal rank ↓grooming
Daily rate of fertile females	-9.342 (2.034)	-4.609	<0.001	↑fertile females ↓grooming
Proportion of consort time	2.334 (0.816)	2.881	0.004	↑consort time ↑grooming
Number of potential fathers at conception	0.030 (0.078)	0.381	0.704	
Father had future offspring with the mother	-0.470 (0.572)	-0.796	0.085	trend: will have offspring ↑grooming
Father had previous offspring with the mother	-0.835 (0.802)	-0.892	0.284	
Father's co-resident offspring-years	0.237 (0.045)	5.227	<0.001	↑co-resident offspring ↑grooming

Daughter's cumulative adversity	-0.059 (0.353)	-0.171	0.861	
Observer effort	1.711 (0.239)	7.168	<0.001	↑effort ↑grooming

Table 4. LMM of the duration of father-daughter co-residency during the daughter's 4-year juvenile period (N=166 co-residencies between 166 juvenile females and 86 fathers).

Term	*β (SE)*	t-value	p-value	interpretation
Maternal age	0.068 (0.021)	3.180	0.002	↑maternal age ↑co-residency
Paternal age	0.153 (0.051)	2.985	0.004	↑male age ↑co-residency
Father's ordinal rank	0.01 (0.040)	0.256	0.799	
Daily rate of fertile females	2.00 (0.994)	2.013	0.046	↑fertile females ↑co-residency
Proportion of consort time	0.009 (0.209)	0.045	0.9638	
Number of potential fathers at conception	-0.011 (0.022)	-0.523	0.602	
Father had previous offspring with the mother	-0.421 (0.238)	-1.769	0.080	trend: had offspring ↑co-residency
Father's co-resident offspring-years	0.102 (0.037)	2.795	0.006	↑offspring ↑ co-residency
Daughter's cumulative adversity score	-0.027 (0.097)	-0.284	0.777	

4. DISCUSSION

In many group-living mammals, males selectively interact with and provide low-cost forms of care to offspring [14, 23]. The selective pressures shaping these behaviors, and their importance to offspring health and survival, have received considerable attention in baboons [28, 31-42]. Here we report that the strength of early-life paternal social relationships predicts meaningful differences in adult survival for female baboons in Amboseli, Kenya. These differences are on the order of 2 to 4 years for adult females in the top versus bottom quartile for paternal grooming or co-residency time—effect sizes that are comparable to those for other major predictors of adult survival in Amboseli baboons, such as social isolation and early-life adversity [7, 60, 77]. This result joins prior evidence for early-life paternal effects in baboons, including the observations that paternal presence predicts earlier sexual maturity in daughters [31] and stronger social bonds between paternal half-siblings [44]. Other mammal species also have subtle or indirect forms of paternal care [14, 18, 24-30]; hence, early-life paternal social relationships may have long-term consequences for offspring in a greater number of species than is currently appreciated.

(a) What mechanisms explain early-life paternal social effects on female survival?

479 The two measures of father-offspring relationships we focused on—co-residency and
480 grooming—are not themselves parental care, raising the question: how do these measures lead to
481 early-life paternal effects on offspring? One possibility is that father-daughter grooming and co-
482 residency may be correlated with other male care behaviors, which in turn, directly benefit their
483 daughter's health and longevity. Prior studies show that male care in baboons includes intervening
484 on behalf of offspring in conflicts and providing a zone of safety that protects daughters and their
485 mothers from negative interactions with other group members, including threats from potentially
486 infanticidal males [78-80]. These forms of protection may reduce injury risk and improve offspring
487 and maternal health and survival [7, 61]. If strong early-life paternal relationships promote social
488 development [43], then fathers' presence may promote the development of adult female social
489 relationships. Grooming with fathers may also be one way that females learn to identify their
490 paternal sisters, who can themselves be important sources of social support in adulthood [81, 82].
491 However, early-life relationships with fathers do not necessarily have direct, causal effects on
492 offspring health and survival. Another possibility is that the strength of father-offspring
493 relationships reflects daughters' own phenotypic quality, which in turn, partly or completely explains
494 the relationship between these traits and female survival. Under this scenario, strong, healthy
495 juvenile females may build and maintain strong relationships with their fathers in early life, and also
496 lead long, healthy adult lives. In support, father-daughter grooming relationships are largely
497 maintained by daughters, not their fathers. Paternal effects may also be mediated by male health if
498 paternal health affects offspring health, even in the absence of a direct relationship between fathers
499 and offspring (through, for instance, epigenetic marks, semen quality, or other processes [19]). For
500 instance, in commercial pig farms, fathers kept in enriched conditions produced more live-born and
501 weaned piglets than those kept in pens—even though fathers had no contact with their offspring
502 [83]. Under this scenario, if fathers who are healthy and in good physical condition produce healthy
503 offspring, are less likely to disperse from groups in which they fathered offspring, and are more
504 socially engaged, including with their daughters, then these effects could create a correlation between
505 father-offspring social relationships and offspring health and survival that is not directly causal. In
506 support, the females in our data sometimes formed strong grooming relationships with males who
507 were not their fathers, but these relationships did not predict adult female survival.
508
509 **(b) Do male baboons experience selection to provide parental care?**

510 If male care behaviors have direct effects on their daughters' lifespans and fitness, then our
511 results help illuminate the selective pressures male baboons might experience with respect to
512 parenting effort. In Amboseli, adult female longevity is the largest contributor to female fitness for
513 baboons, explaining ~80-90% of individual variation in adult female lifetime reproductive success
514 [7, 45, 46]. Because female baboons typically produce one offspring every two years [84], the
515 increased years of survival predicted by paternal co-residency or grooming could translate to one to
516 two additional offspring over these females' lifespans. These results suggest that fathers and their
517 juvenile daughters experience selection to stay close and socially engage with each other.
518 Paternal care in baboons also lends context to the evolution of male parental behavior in
519 other primates, including humans [24]. Mating systems in early hominins are unknown, but the
520 presence of paternal care in modern humans has led many researchers to suggest that early hominins
521 lived in pair-bonded systems where males had limited alternative mating opportunities and high
522 paternity certainty [85-89]. However, our results, together with those from Assamese macaques and
523 mountain gorillas, which also provide evidence for subtle forms of paternal care in non-pair-bonded
524 systems [29, 90-92]—raise the possibility that male parental care could have emerged in early
525 hominins in the absence of strong pair-bonding [24].
526 While pair-bonds may not be a pre-requisite for male care in primates, male baboons are
527 more likely to invest in social bonds with offspring when the reproductive tradeoffs are favorable
528 [93-95]. In support, the males in our population were more likely to groom their daughters when
529 they had cues of paternity certainty (e.g., they consorted her mother near the time of her conception)
530 and few current mating opportunities (e.g., there were few fertile females in the group at the time of
531 her conception). Favorable reproductive tradeoffs may also explain why male "primary associates"
532 are more likely to be older than younger males, if the benefits males derive from mating effort may
533 decline as males age and their competitive abilities decline [34].
534 These observations, together with the survival patterns we observed, suggest that baboon
535 mothers may experience selection to increase males' paternity certainty. Doing so would be
536 advantageous to females if a prospective male sire meets other criteria for being a caring male (e.g.,
537 he sired a cohort of paternal siblings in the group). Selection for paternity certainty may also
538 contribute to the evolution of sexual swellings in female baboons, which provide obvious and
539 reliable signals of female ovulation and conception [35, 36, 65, 96, 97].
540
541 **(c) How do early-life paternal relationships interact with other early-life conditions?**

Paternal relationships did not seem to moderate the effects of early-life adversity on adult female survival. If early-life adversity and paternal relationships during the juvenile period have independent effects on adult female survival, then weak paternal relationships neither exacerbate the effects of other forms of early-life adversity, nor do paternal relationships have strong mitigating effects. However, the fact that they are independent means that, if a high adversity female has a strong early-life paternal relationship, she may be buffered against the effects of early-life adversity on adult survival. These results parallel those for the effects of adult social connectedness and fecal glucocorticoid hormones in our population, which also have effects on adult survival that are strong and appear to be mostly independent of early-life adversity [51, 77]. Hence, our data support the existence of multiple paths for mitigating early-life effects, including paternal relationships.

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DATA STATEMENT

572 Our data are publicly available on Zenodo at https://doi.org/10.5281/zenodo.14590285. Our code
573 are available on GitHub at https://github.com/david-awam-
574 jansen/BaboonPaternalRelationshipsSurvival
575

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