

1 **Title: Intergenerational effects of early adversity on survival in wild baboons**

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12 **Abstract:** Early life adversity can affect an individual's health, survival, and fertility for many
13 years after the adverse experience. Whether early life adversity also imposes intergenerational
14 effects on the exposed individual's offspring is not well understood. We fill this gap by
15 leveraging prospective, longitudinal data on a wild, long-lived primate. We find that juveniles
16 whose mothers experienced early life adversity exhibit high mortality before age 4, independent
17 of the juvenile's own experience of early adversity. These juveniles often preceded their mothers
18 in death by 1 to 2 years, indicating that high adversity females decline in their ability to raise
19 offspring near the end of life. While we cannot exclude direct effects of a parent's environment
20 on offspring quality (e.g., inherited epigenetic changes), our results are completely consistent
21 with a classic parental effect, in which the environment experienced by a parent affects its future
22 phenotype and therefore its offspring's phenotype.

23

24 **Introduction**

25 An individual's health, survival, and fertility can be profoundly shaped by its early life
26 environment (1). For example, in humans, low early life socioeconomic status predicts increased
27 risk of mortality and many measures of poor health (2–10) in adulthood. Similarly, several
28 studies of wild mammals (11–14) and birds (15–17) find that adult fecundity is reduced in
29 animals that experienced adverse early life environments, and some have also found an effect of
30 early life adversity on adult survival (13–15, 18).

31 If the effects of early adversity extend to the descendants of exposed individuals, the
32 epidemiological and evolutionary impact of these effects would be further amplified. However,
33 in humans, evidence that intergenerational effects stem directly from parental experience is
34 mixed, as studies have produced somewhat contradictory results (19–22). For example, a study

35 of the historical Överkalix population in Sweden identified strong, contrasting effects of
36 grandparents' exposure to early-life food scarcity on grand-offspring survival, depending on
37 small differences in the age at which the grandparent was exposed to scarcity (22). Similarly,
38 two studies of a population that was exposed *in utero* to the Dutch hunger winter (a famine that
39 resulted from a German blockade of the Netherlands during the winter of 1944-1945) found
40 contradictory, sex-specific intergenerational effects, in one case suggesting an intergenerational
41 effect that depended only upon the mother's early experience (20), and in the other case an effect
42 that depended only upon the father's early experience (19).

43 Compelling evidence for intergenerational effects of early adversity faced only in the
44 parental generation comes from numerous laboratory studies of short-lived animals, which find
45 strong relationships between a female's early life environment and the body size of her offspring
46 [(23–32), reviewed in (33), but see (34) for a rare example in the wild on house wrens]. These
47 findings provide important evidence that intergenerational effects of early adversity can occur.
48 However, these studies do not address whether intergenerational effects of early adversity,
49 independent of parent-offspring environmental correlations, occur in natural populations of long-
50 lived animals. And while a few studies of short-lived captive animals have demonstrated a
51 relationship between a female's early environment and her offspring's survival or reproduction
52 (35–37), the ecological validity of these findings has yet to be verified by studying
53 intergenerational fitness effects in a population of wild and/or long-lived animals. In wild
54 populations, animals are exposed only to natural, unmanipulated levels of early adversity, and
55 are also subject to any social factors which might mitigate or aggravate the influence of those
56 early adverse events.

57 Addressing whether the effects of early adversity in one generation affect reproduction or
58 survival in the next is challenging because of the difficulties of linking high-quality data on early
59 adversity in one generation to health and survival outcomes in the next. Here, we overcome these
60 challenges by taking advantage of a prospective longitudinal dataset from a natural primate
61 population: the baboons of the Amboseli ecosystem in southern Kenya (38). This dataset
62 includes 45 years of individual-based data on early adversity, and real-time observations of later-
63 life survival outcomes for hundreds of subjects with known maternities and grand maternities.
64 Moreover, unlike many human populations, we do not observe inter-generational transmission of
65 adverse conditions; that is, offspring of females who experienced early life adversity are not
66 more likely to experience early life adversity themselves (except in the case of inheritance of low
67 social rank, see below), allowing us to avoid this common confound in human societies.

68 To test for intergenerational effects of early adversity, we focused on early adversity
69 experienced by female baboons who later became mothers, and whose offspring were also in our
70 dataset. We asked whether the early adversity experienced by these females (“maternal early
71 adversity”) predicted the survival of their juvenile offspring in the next generation, after
72 controlling for the early adversity directly experienced by the offspring themselves.

73 We considered five types of early adverse conditions (Table 1), based on previous work
74 in our study population that demonstrated effects of these conditions on a female baboon’s own
75 adult survival (18). These included: (i) maternal death during development (0-4 years of age),
76 which indicates the loss of an important source of social support, physical protection, and
77 nutrition (39, 40), (ii) being born to a low-ranking mother, which influences growth rates and age
78 at maturation (41–43) (iii) being born into a large social group (and thus experiencing high
79 density conditions and high levels of within-group competition) (11, 41, 44) (iv) being born

80 during a drought, which reduces fertility in adulthood (11, 45), and (v) experiencing the birth of
81 a close-in-age younger sibling, which may reduce maternal investment received during
82 development (46). Importantly—and in contrast to research on humans (47)—sources of early
83 adversity are not strongly correlated in our population, which allows us to measure the
84 independent effects of different sources of adversity (Table S1).

85 **Results**

86 We built a mixed effects Cox proportional hazards model of offspring survival during the
87 juvenile period that included early adversity measures present in the mother's and the offspring's
88 early life as binary fixed effects. We defined the juvenile period based on survival until age 4,
89 near the age of menarche for females and earliest dispersal for males in this population (48). We
90 included data on maternal early adversity for all five adverse early life conditions, and we
91 included data on offspring early adversity for four of the five conditions. We excluded the birth
92 of a close-in-age younger sibling for the offspring generation to avoid including a potential
93 reverse-causal factor in our model. Specifically, the closest-in-age siblings in our dataset tend to
94 occur *as a result of* the focal offspring's death, because female baboons (who are not seasonal
95 reproducers) who lose a dependent offspring will often quickly conceive again. In these cases,
96 early mortality would be correlated with short interbirth intervals, but only because the
97 offspring's death predicts subsequent production of another infant, not because short interbirth
98 intervals constitute a form of adversity. We included maternal and grandmaternal ID as random
99 effects. In total, we used data collected from 1976-2017 to analyze the survival of 687 offspring
100 (46.5% males) born to 169 females (mean 4.1 offspring per female, range 1-12) for whom we
101 had data on all five adverse conditions in the mother's early life, and all four adverse conditions
102 in the offspring's early life.

103 Each adverse condition was scored as present or absent for each subject, and each one
104 affected a minority of our study subjects (range 6%-34%). Mothers and offspring had similar
105 chances of experiencing adverse conditions, except for social density: offspring were more likely
106 than mothers to be born into large social groups because of population growth over the 5-decade
107 study period (Table 1). Unlike typical patterns of early adversity in human populations (47),
108 different sources of early life adversity in our population were not strongly correlated with each
109 other: no adverse condition explained more than 4% of the variance in any other condition, either
110 within or between generations, with the exception of maternal rank in the mother and offsprng's
111 generation ($p<0.0001$, $r^2 = 0.16$) (Table S1).

112 *Maternal Early Life Adversity and Offspring Survival:* Our full multivariate Cox
113 proportional hazards model for offspring survival (Table S2) included all 9 early adverse
114 conditions (five for mothers and four for offspring). We found strong negative effects of two
115 characteristics of the *mother's* early life environment on their offspring's survival during the first
116 4 years of life: maternal loss (hazard ratio = 1.48, $p=0.006$) and presence of a close-in-age
117 younger sibling ($HR = 1.39$, $p=0.03$). Following backwards model selection (performed by
118 removing the parameters with the highest p values until only predictors with a p-value < 0.05
119 remained), these two characteristics remained the only significant maternal early life predictors
120 of offspring survival (Table 2, Figure 1, along with two conditions in the offspring's early life
121 environment: see below). Adding maternal age, offspring sex or interactions between maternal
122 age or offspring sex and sources of maternal adversity did not improve the fit of the model
123 (Tables S3-S5).

124 In sum, offspring whose mothers experienced early maternal loss experienced a 48%
125 higher probability of dying throughout the first four years of life than unaffected offspring, and

126 offspring whose mothers had a close-in-age sibling experienced a 39% higher probability of
127 dying than unaffected offspring. This effect is striking especially considering that a median of
128 7.0 and 8.0 years separated the offspring's own birth from the mother's experience of maternal
129 loss or birth of a close-in-age sibling, respectively. A similar pattern holds if mothers, rather than
130 offspring, are treated as the unit of analysis: mothers who experienced early adversity have lower
131 average offspring survival than mothers who did not (see Fig 1c).

132 Notably, previous work in our population found that these two sources of adversity—
133 maternal loss and the presence of a close-in-age younger sibling during early life—are also
134 sources of mortality risk once females reach adulthood, and in fact are the two strongest
135 predictors of adult survival among six different early-life conditions considered (18). Hence,
136 early-life conditions that are especially adverse for females when they reach adulthood also
137 negatively affect the survival of their offspring.

138 Both the full and reduced models of offspring survival also included two conditions in the
139 offspring's early life environment as significant predictors of juvenile survival. Specifically,
140 maternal loss experienced by the offspring and low maternal rank during the offspring's juvenile
141 period had strong negative effects on offspring survival (Tables 2 and S2, maternal death:
142 Hazard Ratio = 1.95 [1.51-2.54], $p = 5 \times 10^{-7}$, low maternal rank: Hazard Ratio = 1.43 [1.05-
143 1.94], $p = 0.025$). Thus, maternal loss in the offspring's generation had a stronger effect on
144 offspring survival (nearly doubling offspring mortality risk) than maternal loss in the mother's
145 generation. In contrast, the effect of having a low-ranking mother, which was associated with a
146 43% increase in offspring mortality risk, was comparable in its effect size to the two significant
147 predictors from the maternal generation (maternal loss and close-in-age sibling for the mother,
148 48% and 39% increase in offspring mortality, respectively). Thus, two adverse conditions in a

149 mother's early life had as large or larger of an impact on her offspring's survival than all but one
150 adverse condition experienced by the offspring directly.

151 *Maternal Viability and Offspring Survival:* The strong effect of the mother's death on
152 offspring survival prior to four years (Table 2) is unsurprising at first consideration: the most
153 obvious explanation for this effect is that offspring depend upon their mothers, so that if the
154 mother dies the offspring is also likely to die at the same time or die subsequently. Indeed, this
155 sequence of events does occur in our population: of the 32 offspring that were alive and less than
156 eight months old when their mother died, 31 (97%) died before reaching one year of age.

157 However, offspring death could also precede maternal death if it acts as a *harbinger* of
158 the mother's death, as opposed to a *consequence* of it. In this scenario, offspring mortality risk is
159 increased because their mothers are in poor condition and hence unable to provide adequate care
160 or resources to the offspring. This hypothesis therefore proposes an alternative causal chain from
161 poor maternal health to offspring death, which would occur while the mother is still alive.

162 To examine whether this phenomenon occurs in our study population, we modeled
163 offspring survival to age 2 years (halfway through the juvenile period) as a function of maternal
164 death during years 2-4 after an offspring's birth (i.e., the two years that *followed* the offspring
165 survival period modeled in the response variable). In this analysis, we considered only the subset
166 of offspring in our dataset whose mothers survived the entire first two years of the offspring's
167 life, and for whom we were able to evaluate the four significant predictors of offspring survival
168 identified above and in Table 2 (N=671). Our results were striking: offspring were less likely to
169 survive during the first two years of life if their mothers died 2-4 years after their birth. In other
170 words, these offspring were more likely to die even when their mother was still present (hazard
171 ratio=1.50 [1.01-2.23], p=0.045).

172 To test for a role of maternal early adversity in this effect, we next partitioned our
173 analysis of offspring survival to age 2 based on whether the mother experienced either maternal
174 loss or a close-in-age younger sibling (i.e., either or both of the two maternal early life conditions
175 that significantly predicted their offspring's survival; Table 2). We found that, among offspring
176 whose mothers experienced either or both of these two adverse events (N=247), maternal death
177 in years 2-4 after the offspring's birth significantly predicted reduced offspring survival to age 2
178 years (Figure 2a, hazards ratio=1.78, 95% CI = [1.05-3.01], p=0.034). Maternal death in the
179 same period did not, however, predict reduced offspring survival when mothers had not
180 experienced maternal loss or a close-in-age younger sibling (N=424; Figure 2b, hazard
181 ratio=1.21, 95% CI = [0.7-2.2], p=0.53). Hence, the pattern we observed when analyzing the full
182 data set of offspring that survived to age 2 (N=671) is completely driven by the offspring of
183 mothers who experienced substantial early adversity. This finding is consistent with the
184 hypothesis that maternal early life adversity results in compromised maternal condition in
185 adulthood, which in turn results in both earlier death for adult females and a reduction in their
186 ability to successfully raise offspring towards the end of their lives (i.e., a maternal effect on the
187 offspring generation).

188

189 **Discussion**

190 We have demonstrated that adverse environmental conditions during the early life of a
191 female baboon, which are already known to negatively affect both her survival (18) and her
192 reproduction (11) in adulthood, also reduce the survival of her offspring. Importantly, this effect
193 is independent of the environment experienced by those offspring themselves (Figure 1). The
194 reduction in offspring survival is likely linked to reductions in maternal viability: mothers that

195 experienced early life adversity are significantly less able to successfully raise offspring born
196 near the ends of their lives, while the same is not true for mothers that did not experience early
197 life adversity (Figure 2). Together, these findings support the hypothesis that early life adversity
198 produces constraints during development that lead not only to reduced adult survival and lifetime
199 reproductive success (18) but also to a reduced ability to successfully raise those offspring that
200 are produced (Fig 2a). We did not identify any sex-specific intergenerational effects of maternal
201 early adversity.

202 The results reported here help to fill a key gap in the literature concerning the
203 intergenerational effects of early life adversity on survival. Human studies have yielded
204 inconsistent results on this topic thus far when maternal and offspring environments are not
205 correlated: different studies on the same populations have reported contradictory sex-specific
206 effects on health (19, 20) or have found that small differences in the age at which subjects'
207 parents or grandparents were exposed to adversity can lead to a reversal in the direction of these
208 effects (21, 22). Among studies in non-human animals, several studies in fish (49, 50), reptiles
209 (51), birds (52, 53), and ungulates (54–58) have found that parental body condition at the time of
210 offspring birth influences offspring survival, but none have linked parents' early adverse
211 experiences to offspring survival. Additionally, while previous studies have identified effects of
212 parental early adversity on offspring traits in a limited number of captive, short-lived systems
213 (33, 35, 36), ours is the first to link parental early adversity to an important component of
214 offspring fitness in a wild, long-lived animal.

215 Our findings help to explain the persistence of health deficits across generations (59–61),
216 by revealing that in long-lived primates, the early life experiences of mothers have important
217 implications for offspring health and survival. Recent studies in humans have demonstrated that

218 conditions experienced by mothers during pregnancy (e.g., low SES, psychosocial stress, mood
219 dysregulation, prenatal smoking) can affect HPA axis regulation (62, 63) and birthweight (59,
220 60) in her offspring. These and other maternal characteristics present during pregnancy are
221 influenced not only by mothers' experiences in adulthood, but also by the long-term effects of
222 environmental conditions experienced in mothers' early lives (60, 64). Our findings therefore
223 motivate future work to test for comparable intergenerational fitness effects of early adversity in
224 humans and other non-human animals.

225 Our findings are consistent with the hypothesis that early adversity results in
226 intergenerational developmental constraints (11, 65–67) and are not consistent with an
227 intergenerational predictive adaptive response hypothesis (66, 68, 69). Rather than being
228 buffered against the effects of maternal loss, those offspring that experienced maternal loss and
229 whose mothers had also experienced maternal loss were more likely, not less likely, to die, as
230 compared to offspring that experienced maternal loss but whose mothers did not. Thus,
231 individuals in the offspring generation experience constraints not only as a result of their own
232 early environment, but also as a result of their mothers' developmental histories, including
233 events that occurred years before their own conception. Our results are consistent with the
234 hypothesis that a female's condition at the time of her offspring's conception and/or birth reflects
235 her previous experiences, and that her condition thereby influences the development and survival
236 of her offspring (64, 70, 71).

237 Our study is unable to definitively identify the mechanism by which effects of early
238 adversity may be transmitted from parent to offspring. However, our finding that reduced
239 offspring survival appears to be partially mediated by reduced maternal viability suggests that
240 the mode of transmission is most readily explained as a classic parental effect, in which early life

241 adversity affects the phenotypic quality of the mother during adulthood, and in turn affects her
242 offspring's development (72–75). Recently, intergenerational transmission of adversity has been
243 discussed as a potential consequence of inherited epigenetic changes (76). While we cannot
244 exclude this possibility, our results are a reminder that simpler mechanisms—in this case, a
245 classic maternal effect—may be a more parsimonious (albeit non-mutually exclusive)
246 explanation.

247 Notably, the importance of both maternal death and a close-in-age younger sibling
248 suggest that maternal investment may be key to understanding the intergenerational
249 developmental constraints we observed. Both maternal death and the presence of a close-in-age
250 sibling suggest a possible reduction in the amount of maternal investment that the mothers in our
251 analysis received during their early life. Maternal loss, even after weaning, may affect a
252 developing primate's ability to learn to forage, to avoid social harassment, and to receive social
253 benefits, such as grooming, that are linked to health (77–82). Having a close-in-age sibling likely
254 predicts a relatively early weaning event, which may reflect less maternal provisioning than
255 would occur with more delayed weaning and a longer birth interval (83–85). Thus, we
256 hypothesize that mothers who lost their own mothers or had a close-in-age sibling suffered
257 reduced energetic and social input from their mothers, which subsequently led to lifelong
258 developmental constraints. Additionally, these females may not have had adequate time to learn
259 from their mothers how to provide high quality maternal care later in life. While we do not
260 routinely collect detailed data on maternal care as part of long-term monitoring, the results
261 reported here motivate targeted analyses of how maternal adversity relates to differences in
262 maternal care and style in future work.

263

264 **Methods**

265 *Study system:* The Amboseli Baboon Research Project is a long-term longitudinal study of
266 wild baboons living in and around Amboseli National Park, Kenya. A detailed description of the
267 study system can be found elsewhere (38). Researchers have continuously collected behavioral,
268 environmental, and demographic data from the population since 1971. All subjects are visually
269 recognized, and near-daily censuses allow us to precisely document the timing of demographic
270 events, including the birth and death of study individuals. Critical to this study, we have
271 continuously collected near-daily measures of group size, daily rainfall levels (beginning in
272 1976), and monthly calculations of social dominance rank (86).

273 *Study Subjects:* In our analyses of offspring survival, we included all individuals who met
274 two criteria: (i) they lived in social groups that fed exclusively on wild foods rather than having
275 their diet supplemented with human-sourced refuse; and (ii) we were able to evaluate each of the
276 five sources of maternal early life adversity and four sources of offspring early life adversity
277 outlined below. Although transmission of paternal early adversity may also occur in our
278 population, we did not consider it here because we knew paternal identities for only a subset of
279 our study subjects and had early life data on only a subset number of fathers. Our analysis
280 ultimately relied on data spanning more than four decades, from 1976 to 2017.

281 *Measuring Early Life Adversity:* Previous work in the Amboseli population defined six
282 binary indicators of early life adversity and considered a single index of cumulative adversity
283 based on the sum of these indicators (18). This cumulative adversity index is a strong predictor
284 of adult lifespan: females that experienced high levels of early life adversity (i.e., a greater
285 number of adverse early life conditions) but still survived to adulthood lived dramatically shorter
286 lives compared to females that did not experience early adversity (18). In addition to the five

287 sources of early adversity discussed above, this previous analysis also considered early social
288 connectedness (social integration versus social isolation) as a sixth source of adversity (18).
289 Social connectedness data are missing for some mothers who were born relatively early in the
290 long-term study. To maximize our sample size, we therefore did not include measures of social
291 connectedness in this analysis.

292 Our operational definitions for each source of adversity mirrored those used by Tung *et al*
293 (18) for the remaining five conditions, except that here we employed measures of proportional
294 rather than ordinal dominance rank (i.e., rank measured as a proportion of females that the focal
295 individual dominates, rather than her ordinal rank number). We also built an index of cumulative
296 maternal adversity, but because that model did not fit the data better than our reduced
297 multivariate model (in contrast to the results for adult female survival (18)) we report the
298 multivariate model in the main text. The alternative model based on cumulative maternal
299 adversity is presented in Table S6.

300 *Statistical Analysis:* We built a mixed effects Cox proportional hazards model of offspring
301 survival during the first four years of life using the R package coxme (87, 88). The response
302 variable in our model was the age at which offspring death occurred (if at all) during the first 4
303 years of life. We considered offspring survival to age 4 as the key survival period of interest
304 because it roughly corresponds to the end of the juvenile period for baboons (48). Offspring that
305 survived beyond age 4 were treated as censored individuals who survived until at least age 4. In
306 our models of offspring survival as a function of maternal viability (Figure 2), we altered the first
307 model to predict survival during the first two years of life as a function of maternal survival
308 during years 2-4 after offspring birth (see Table S7 for model syntax).

309

310 **Data Availability:** Datasets presented in this article can be downloaded from Dryad using the
311 following Digital object identifier (DOI): 10.5061/dryad.4hc8k1r (90).

312

313

314 **Table 1. Early adverse conditions and the frequencies with which they occur in maternal**
 315 **and offspring generations of our dataset.**

Adverse Condition ^a	Criterion	Frequency	
		Maternal Generation	Offspring Generation
Drought	During the first year of life, the focal individual experienced less than 200 mm of rainfall (i.e., drought conditions (45)).	0.09	0.15
High Social Density	The individual was born into a group with a high social density (>35 adults), indicating high levels of within-group competition.	0.06	0.32
Maternal Loss	The mother of the focal individual died within four years of the individual's birth.	0.21	0.25
Low Maternal Rank ^b	The focal individual was born to a mother with a low social rank (mother's rank fell in the bottom quartile of the group's dominance hierarchy, rank < 0.25).	0.17	0.23
Close-In-Age Younger Sibling ^c	The focal individual had a younger sibling born to its mother within 18 months of the focal's birth.	0.20	--

316 ^aThese criteria were used in a previous analysis in our population (18), with the exception of
 317 maternal rank, which is evaluated here as a proportional measure rather than an ordinal one as in
 318 the previous analysis.

319 ^bProportional rank is the proportion of other adult females in a group that an individual's mother
 320 outranks. The reduced frequency with which low maternal rank appears in the maternal
 321 generation is a likely a result of offspring of low-ranking mothers surviving less well (89), and
 322 therefore not surviving to appear as mothers in our dataset.

323 ^cWe excluded the birth of a close-in-age younger sibling for the offspring generation to avoid
 324 including a potential reverse-causal factor in our model: the closest-in-age siblings in our dataset
 325 occur as a result of the focal offspring's death, because female baboons (who are not seasonal
 326 reproducers) accelerate their next conception after the death of a dependent offspring.

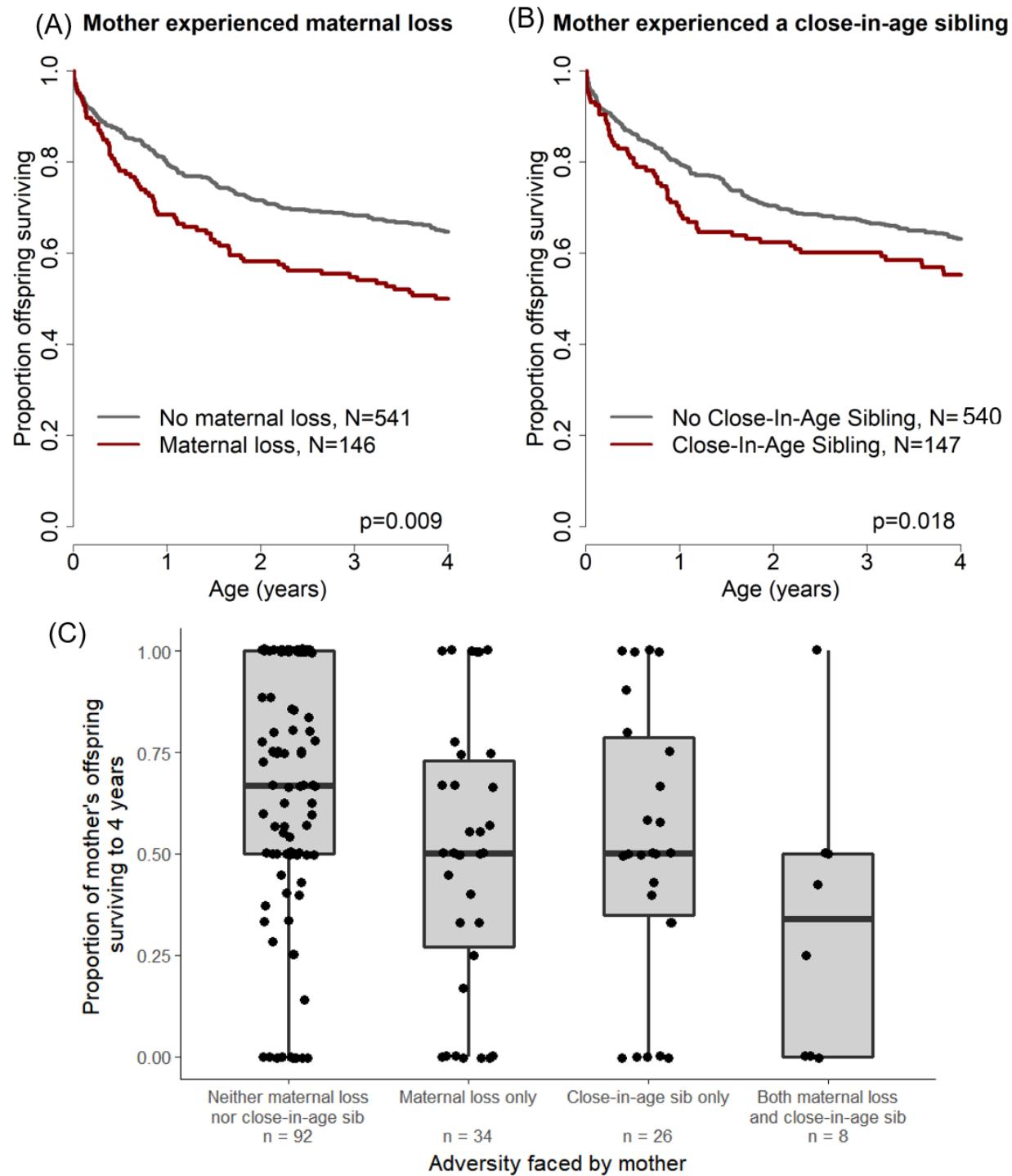
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329 **Table 2.** Reduced model of the effects of maternal and offspring early adversity on offspring
 330 survival during early life ($R^2=0.07$).

Generation	Parameter ^a	Coefficient	Hazard Ratio (95% CI)	p value	Interpretation
<i>Maternal</i>	Maternal Loss	0.37	1.44 (1.10-1.90)	0.009	Offspring survive less well if their mother experienced maternal loss during her early life.
	Close-in-age Younger Sibling	0.35	1.42 (1.06-1.90)	0.018	Offspring survive less well if their mother had a close-in-age younger sibling during her early life.
<i>Offspring</i>	Maternal Loss	0.68	1.98 (1.53-2.56)	3x10⁻⁷	Offspring survive less well if they experienced maternal loss within four years of their birth.
	Low Maternal Rank	0.43	1.54 (1.17-2.01)	0.002	Offspring survive less well if they were born to a low-ranking mother.

331 ^aAn alternative model that considered cumulative maternal adversity was not a better or worse fit
 332 than the reduced multivariate maternal adversity model (see Table S6. For both the model
 333 presented here and that in Table S6, $R^2=0.07$, log likelihood = -1598).

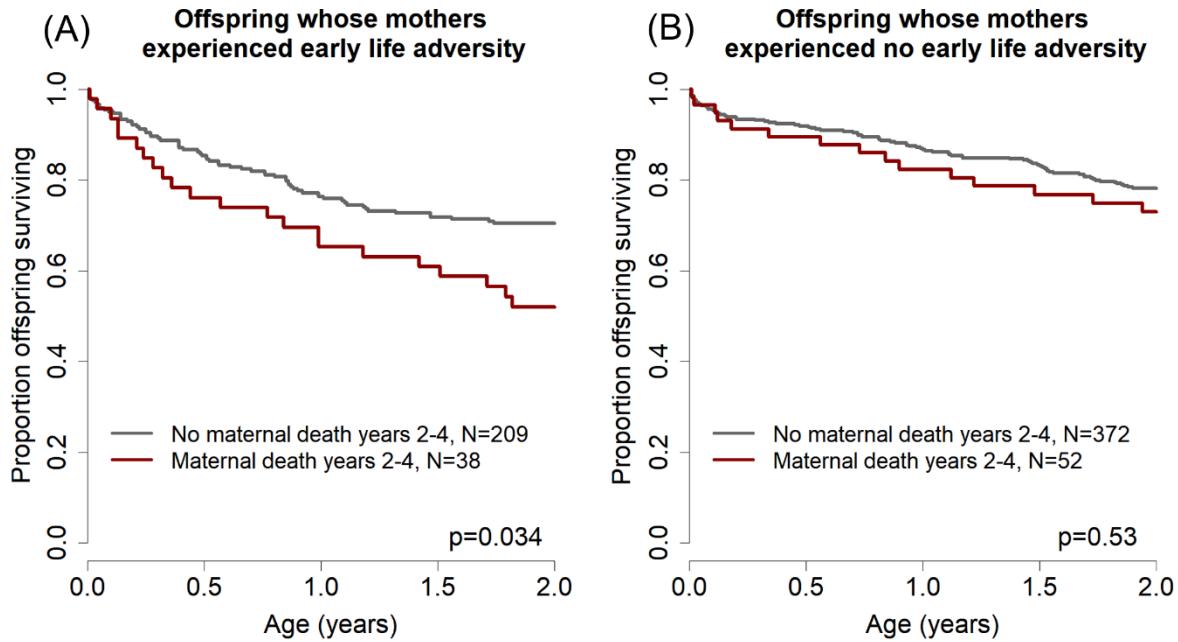
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335

336 **Figure 1. Offspring survival was influenced by characteristics of their mothers' early-life**
 337 **environments.** Offspring survived relatively less well during the juvenile period if (A) their
 338 mother lost her own mother during her early life and/or (B) their mother experienced a close-in-
 339 age younger sibling. An alternative visualization of the data (C) shows an equivalent pattern
 340 when mothers, rather than offspring, are treated as the unit of analysis.

341



342

343 **Figure 2. Effects of maternal adversity on offspring survival are explained by reduced**
 344 **maternal viability.** (A) Among those offspring whose mothers experienced significant early life
 345 adversity (maternal loss and/or a competing younger sibling), poor offspring survival from ages 0-
 346 2 (while the mother was still alive) was predicted by maternal death in years 2-4 after the
 347 offspring's birth. (B) In contrast, there was no relationship between offspring survival in the first
 348 two years of life and maternal death in years 2 - 4 for the offspring of mothers who did not
 349 experience early life adversity.

350

351 Supplementary File 1: Tables S1-S7.

352

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