

1 Early life adversity has sex-dependent effects on 2 survival across the lifespan in rhesus macaques

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35 Abstract

36 Exposure to early life adversity is linked to detrimental fitness outcomes across taxa.

37 However, due to the challenges of collecting longitudinal data, direct evidence for long-

38 term fitness effects of early life adversity from long-lived species remains relatively

39 scarce. Here we test the effects of early life adversity on male and female longevity in a

40 free-ranging population of rhesus macaques (*Macaca mulatta*) on Cayo Santiago,

41 Puerto Rico. We leveraged six decades of data to quantify the relative importance of ten

42 forms of early life adversity for 6,599 macaques. Individuals who experienced more

43 early life adversity died earlier than those who experienced less adversity. Mortality risk

44 was highest during early life, defined as birth to four years old, but heightened mortality

45 risk was also present in macaques who survived to adulthood. Females and males were

46 affected differently by some forms of adversity, and these differences might be driven by

47 varying energetic demands and dispersal patterns. Our results show that the fitness

48 consequences of early life adversity are not uniform across individuals but vary as a

49 function of the type of adversity, timing, and social context, and thus contribute to our

50 limited but growing understanding of the evolution of early life sensitivities.

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57 Introduction

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59 Adversity such as food shortages and social isolation experienced prior to adulthood
60 can result in long-term health and evolutionary fitness consequences in a wide range of
61 insects, birds, fish, reptiles, and mammals (1–4). These detrimental outcomes in
62 adulthood are hypothesized to arise from organisms adjusting their developmental
63 trajectories in response to adversity in order to improve immediate survival (3,5,6). To
64 date, research on non-human animals has borrowed hypotheses and methodologies
65 from the extensive literature on early life adversity in humans. Early life adversity in
66 humans is associated with poorer health and reduced longevity (7–9). A common and
67 growing approach in the study of humans is to use cumulative indices which measure
68 the total amount of adversities experienced by an individual in their early life, rather than
69 focus on different forms of adversity separately (10–13). Empirical evidence suggests
70 that the accumulation of multiple adversities is a better predictor of adult outcomes than
71 any particular form of adversity, but there is also evidence that specific forms of
72 adversity lead to different outcomes (11,14,15). A small but growing number of studies
73 have tested the long-term impacts of early life adversity, but further research on how
74 cumulative early life adversity and different forms of adversity shape the timing of fitness
75 consequences in a variety of species, populations, and contexts is needed to better
76 understand the evolution of early life sensitivities to adversity.

77

78 In long-lived species, females who live longer have a longer reproductive span and are
79 able to produce more offspring, such that longevity or survival can be used as proxies of
80 fitness (16–21). Long-term studies of female yellow baboons (*Papio cynocephalus*) and

81 spotted hyenas (*Crocuta crocuta*) have shown that exposure to greater amounts of
82 cumulative early life adversity is associated with reduced survival in adulthood
83 (14,15,22,23). In addition to the adverse effects experienced in adulthood, mortality
84 prior to reproductive maturity results in a fitness of zero as organisms fail to reproduce.
85 Accordingly, in populations characterized by high mortality rates prior to reproductive
86 maturity, the total number of offspring *reaching reproductive maturity* is the best proxy
87 for fitness (24). Male and female mountain gorillas (*Gorilla beringei beringei*) exposed to
88 more cumulative early life adversity experience reduced survival prior to reproductive
89 maturity, but do not experience survival costs after maturity (25). As such, adult survival
90 patterns as a function of cumulative early life adversity in gorillas differ from those in
91 yellow baboons and spotted hyenas, but pre-reproductive survival patterns are not yet
92 available across species for comparison. More studies across different species are thus
93 needed to draw comparisons and better understand the evolutionary pressures which
94 shape early life sensitivities to cumulative adversity and different forms of putative
95 adversity, and to test the relationships between developmental responses to adversity,
96 the timing of fitness consequences across the lifespan, and detrimental adult outcomes.
97

98 The fitness consequences of early life adversity might vary in a sex-dependent manner
99 due to differences in life history strategies. During adverse early life conditions, the sex
100 with more energetically demanding traits is predicted to be more susceptible to
101 nutritional constraints (26,27). In many species, male life histories are considered more
102 energetically costly given faster growth and larger body size compared to females.
103 When male fitness is largely determined by access to mates via competitive ability,

104 males should also invest in costly developmental processes like play and motor skill
105 development (28). Support for these predicted differences come from a study focusing
106 on one form of adversity: maternal death prior to weaning in red deer (*Cervus elaphus*)
107 was linked to higher mortality risk among male compared to female offspring (29). Sex-
108 dependent effects of early life adversity are challenging to study because many species
109 are characterized by sex-biased dispersal such that pre- or post-dispersal data are
110 typically missing for individuals of the dispersing sex (e.g., (15)). More studies are thus
111 needed that can follow both males and females from birth till death to investigate how
112 life history strategies shape sex-specific fitness consequences and developmental
113 responses to early life adversity.

114

115 Here we study the free-ranging rhesus macaques (*Macaca mulatta*) of Cayo Santiago to
116 advance our understanding of the magnitude, form, timing, and sex-dependence of
117 early life adversity effects. To date, direct evidence of the lifelong effects of early life
118 adversity is relatively scarce in long-lived species due to the difficulties of collecting data
119 from early life till death. In this study, we leveraged complete demographic records that
120 extend back to the late 1950s for thousands of male and female macaques at the Cayo
121 Santiago field site. We add to the growing body of early life adversity research in long-
122 lived species (14,15,23,25,30,31). Following these previous studies, we examined both
123 the effects of cumulative early life adversity and the effects of specific forms of early life
124 adversity to identify which forms best predict survival. We build upon this previous work
125 by incorporating more forms of adversity and leveraging an exceptionally large sample
126 size. Further, this analysis incorporates data from females and males from birth till

127 death, which has only been previously examined in one study of wild mountain gorillas
128 (25). Specifically, we examined the effects of ten forms of potential early life adversity
129 on sex-specific mortality risk across early life, and separately, across adulthood. By
130 examining mortality across the lifespan, we can identify the full extent of variation in the
131 fitness consequences of early life adversity, including how survivorship biases in early
132 life may influence survival patterns observed in adulthood.

133

134 Previous research has demonstrated that some forms of early life adversity can shape
135 the behavior and health of macaques. In captivity, infant macaques experimentally
136 exposed to abusive mothers or reared with peers show decreased immune function,
137 more self-injury, more impulsivity, differential DNA methylation in brain cells, and a suite
138 of physical health anomalies in adulthood (32). Such experimental studies are
139 complemented by targeted observational studies that have examined the effects of one
140 or two forms of naturally occurring adversity. In the Cayo Santiago population, abusive
141 maternal care behavior is linked to differences in HPA function in juveniles, the
142 presence of a competing younger sibling is linked to reduced survival during juvenility,
143 and exposure to hurricanes and high population density during early life are linked to life
144 history trade-offs in adulthood (33–35).

145

146 As for wild rhesus macaques, the Cayo Santiago monkeys live in naturally forming
147 multi-male, multi-female social groups characterized by dominance hierarchies and
148 male dispersal. This species is sexually dimorphic, with males exhibiting larger body
149 mass and canine length than females (36,37). Males queue for dominance rank, have

150 large testes, and experience strong indirect male-male competition, including sperm
151 competition (38–40). We predicted that rhesus macaques exposed to greater amounts
152 of early life adversity would have increased mortality risk. We predicted mortality risks
153 would be more severe during the first four years of life when individuals are still growing
154 and adversity is more recent. However, we also predicted heightened mortality risk
155 would persist into adulthood among those who survive past four years of age. Given
156 that male life history strategies in this species (41) prioritize costly traits like faster
157 growth, larger body size, and motor skill development (36,37,42), we predicted that
158 early life adversity would exert larger effects on males than females. We also predicted
159 that some forms of early life adversity, such as maternal loss, would have larger effects
160 on mortality risk than others.

161

162 Methods

163 Study site and population

164 We studied a free-ranging population of rhesus macaques living on Cayo Santiago, a
165 15.2-ha island off the southeastern coast of Puerto Rico. The current population of
166 ~1,700 individually recognized rhesus macaques living in 12 social groups are the
167 descendants of 409 monkeys that were transported from India to the island in 1938.
168 This population is managed by the Caribbean Primate Research Center (CPRC) of the
169 University of Puerto Rico. Monkeys are fed monkey chow daily and water catchments
170 provide *ad libitum* access to drinking water.

171

172 During the study period (1960-2021), observers monitored and recorded demographic
173 events daily. These records included births, deaths, sex, matriline, matriline rank,
174 maternal identification, sires when genetic data were available, and group emigration
175 and immigration events. The island is free of predators and, as approved by IACUC,
176 there is no regular veterinary intervention, such that the primary causes of death are
177 injury and illness (43). Injured individuals are three times more likely to die than
178 uninjured individuals in the population (43). We have had few obvious outbreaks of
179 infectious diseases, an exception being the 1940 and 2010 outbreaks of *Shigella*
180 (44,45). If a carcass is found then animals are confirmed as dead and removed as per
181 the date the carcass is retrieved. The daily census notes when animals were last seen.
182 If animals have not been seen by anyone for 6 months, then they are assumed dead
183 with death date recorded as the last date of observation plus one day. A genetic
184 pedigree is available for much of the population (46). Daily total rainfall and mean
185 maximum temperature data were obtained from the NOAA station in Rio Piedras,
186 Puerto Rico. Over a 61-year period (1959-2020), data were not recorded by this NOAA
187 station for 21% of days. Rather than removing a large portion of data, we imputed
188 missing rainfall and temperature data using the 'mice' package (v 3.14.0) in R (47). This
189 study included 6,599 individuals for which there were complete data available, including
190 data covering the entire lifespan—birth to death—for 2,513 macaques. The remaining
191 4,086 macaques were either alive (N= 173) at the time of this study or were removed
192 (N=3,914) from the island prior to natural death as a result of population management
193 (i.e., constituted right-censored samples). Over the course of the study, three forms of
194 selection criteria for animal removal have been used: removal of entire social groups,

195 removal based on sex (e.g., removal of adult males to maintain appropriate sex ratios),
196 and removal based on age (e.g., removal of immature individuals) (48). Note that these
197 selection criteria are independent of the early life adversity variables used in our
198 analysis.

199

200

201 Early life adversities

202

203 We used historical demographic records to assess individual exposure to early life
204 adversity. We considered ten forms of potential early life adversity. Here, we aim to
205 select experiences or inputs that limit resources available to an individual or otherwise
206 lead an individual to allocate their resources across life history traits in a suboptimal
207 manner. In other words, early life adversity is an experience that sets an individual off
208 their optimal developmental trajectory. Eight of these forms of adversity have been used
209 in previous studies of primates (15,34,49), while two additional forms of adversity were
210 chosen based on the natural history of the present study system (Hurricanes and high
211 temperatures). Each form of adversity is further justified below, with previous research
212 demonstrating its deleterious consequences (see Table S1 for further details regarding
213 empirical support). In choosing time periods of exposure for each form of adversity, we
214 followed the methods presented by Tung and colleagues 2016 in regards to wild
215 baboons, which wean and reach reproductive maturity at similar ages as rhesus
216 macaques. Each of these ten adversities could be considered an early life advantage
217 from the flipped perspective because the measures can be considered on an axis that

218 ranges from “adversity” to “advantage” (50). For example, monkeys born into small
219 maternal social networks are predicted to experience adversity, while monkeys born into
220 large maternal networks are predicted to experience advantage. For consistency with
221 previous work, we recorded when individuals experienced the “adversity” end of the axis
222 for each variable.

223

224 **Maternal loss:** Maternal death increases offspring mortality in humans and other
225 mammals (15,29,51–54). We considered an individual to experience maternal loss if their
226 mother died (including natural death due to causes such as disease or injury (N=1,165),
227 and permanent removal from the population (N=299)) before the individual reached 4
228 years of age (15,55). This four year window includes the period during which young
229 macaques are nutritionally dependent on their mothers, and the period during which
230 young macaques are weaned but still socially dependent on their mothers. While a
231 mother’s removal from the population had to occur while the offspring was alive (i.e.,
232 prior to offspring death if they have died) to be considered an adversity, this was not a
233 requirement for natural maternal death because an impending maternal death is linked
234 to offspring mortality risk—an association likely explained by poor maternal condition
235 (55). We do not know the cause of death in most cases, but most deaths on the island
236 are due to illness, injury, and old age, and we would consider all or most natural deaths
237 to be condition dependent. Our decision to include cases in which the mother died
238 within 4 years after the offspring’s birth was based on previously established
239 methodology used by Zippel and colleagues (55). In their study of several primate
240 species (chimpanzees (*Pan troglodytes*), northern muriquis (*Brachyteles hypoxanthus*),

241 blue monkeys (*Cercopithecus mitis*), mountain gorillas, yellow baboons, capuchins
242 (*Cebus capucinus*), and Verreaux's sifakas (*Propithecus verreauxi*), offspring death
243 was significantly associated with an impending maternal death, even if the mother's
244 death did not occur until 3 to 4 years after the offspring's birth (55). Further, offspring did
245 not have a higher mortality risk if their mother's death was more imminent (within 1 year
246 of birth) versus more delayed (3.5 to 4 years after birth) (55). In our study, there were
247 220 maternal death cases in which the focal individual died before their mother died.
248 The delay in death was as short as 2 days and as long as 3.8 years (median = 358.5
249 days; mean = 470 days). About 73% of the delayed maternal deaths occurred within 2
250 years of the infant death. Maternal loss was measured as a binary variable:
251 experienced maternal loss or did not experience loss.

252 **Competing sibling:** The presence of a close in age younger sibling represents a
253 source of competition over maternal resources and is associated with higher mortality
254 risk (15,33). We considered a sibling to be a competitor if the sibling was born within
255 355 days of a subject, which represented the bottom quartile of interbirth intervals (IBI)
256 in our sample. While short IBIs have been linked to high juvenile mortality risk in the
257 study population (33), in other primates, short IBIs can also be an indicator of high
258 maternal quality (49,56), complicating the interpretation of results. The presence of a
259 close in age older sibling could also constitute a cost for the younger sibling, although
260 there are further complexities for this metric. In this study population, a short or long
261 preceding IBI is predictive of higher infant mortality (33), and the presence of older
262 siblings could represent an important source of social support (57). Here, we followed
263 previous work that focused on the presence of close in age younger siblings (e.g.,

264 (15,25)). Last born offspring and individuals that died before their sibling was born could
265 not experience this adversity. The presence of competing siblings was measured as a
266 binary variable.

267 **Group size:** High group size and high population density are indicative of more
268 competition and are associated with reductions in fecundity (17,34,58,59). We used
269 group size as a proxy for within-group competition. Demographic records were used to
270 construct group composition over the study period. Group size was defined as the
271 number of adults (≥ 4 years of age) of both sexes in an individual's social group on the
272 day that individual was born (15), and was included in our models as a continuous
273 variable. Group size varied across the study period (range: 2-222 individuals), but was
274 fairly consistent across individuals' early lives (group size at birth and 4 years of age:
275 pearson's $r = 0.75$, $p\text{-value} < 0.0005$).

276 **Primiparity:** The high energetic demands on first time mothers can result in negative
277 outcomes for offspring such as increased mortality risk (51,60–64). First time mothers
278 might struggle to provide care, social support, and energetic resources for their
279 offspring. Being born to a first time mother might limit the energetic resources available
280 for the developing individual and how those resources are allocated, which meets our
281 definition of adversity. We used a binary measurement for primiparity: first born or not
282 first born.

283 **Matriline rank:** Dominance rank mediates access to food and is linked to survival,
284 fecundity, and offspring growth in primates (65–69). Matrilineal dominance hierarchies
285 for a given social group and year are recorded by the CPRC as categorical – high,
286 middle, low – based on dyadic agonistic interactions recorded over the course of each

287 observation year (e.g., threats, displacements, submissive behaviors) (33,70). As such,
288 this measure represents the matrilineal rank for an individual's birth year. We follow
289 previously established methods for characterizing rank (66,71). Female macaques
290 acquire the rank adjacent to their mothers so individuals who are members of the same
291 matriline (i.e., descendants of a shared crown female ancestor) tend to be adjacent in
292 rank. The rank of a matriline can thus serve as a proxy for individual rank. Because
293 matriline ranks are stable over time (72), if the rank of a matriline is not measured in
294 some years, it can be extrapolated back or forward in time based on known ranks. As a
295 point of methodological comparison, we also treated matrilineal rank as an ordinal
296 variable (i.e., "0, 1, 2" rather than "high, middle, low"). Since females inherit rank from
297 their mothers, matriline rank might be considered a measure of experiences across the
298 lifespan for females and a measure of early life experience for males. However, given
299 previous research treating maternal rank as a form of early life adversity in females and
300 males in similar social systems, we included it here for comparative purposes.

301 **Kin network:** Among prime aged adult females at Cayo Santiago, the presence of more
302 maternal kin is linked to better survival in any given year (71). We measured an
303 individual's maternal kin network size at birth as the number of living females over 4
304 years of age with a relatedness coefficient of at least 0.063. This relatedness coefficient
305 was chosen because it represents the threshold at which macaques in this population
306 can recognize kin via vocalizations (73), and this threshold was used in previous work
307 showing a positive association between the number of relatives present and adult
308 survival (71). Kin network size was included as a continuous variable (range: 1-21

309 individuals). The size of kin networks was fairly stable across individuals' early lives
310 (size at birth and four years: pearson's $r = 0.75$, p -value < 0.0005).

311 **Maternal social isolation:** Greater social connectedness is associated with longer
312 adult lifespans, lower age-specific mortality risks, the production of a greater number of
313 offspring, and greater offspring survival (74–79). We used behavioral data collected
314 during 10-min focal animal samples on adults in several social groups from 2010-2017
315 (details provided in the supplementary online materials (SOM)). To measure maternal
316 social isolation, we calculated a composite sociality index (CSI) using the affiliative
317 social behaviors, approaches and grooming. For each mother in each year, we
318 tabulated the rate of approaches (approaches to and from other adult females / hours
319 observed) and the rate of grooming bouts (number of grooming bouts given and
320 received / hours observed). A mother's approach and grooming rates were divided by
321 the mean rate for all adult females in each social group in each year. These
322 standardized approach and grooming rates were added together and divided by 2 (the
323 number of behaviors) to create the CSI for each mother. Here, we followed Tung and
324 colleagues (2016): for each offspring in our analyses, we averaged their mother's
325 composite sociality index for the first two years of life.

326 **Rainfall:** More rainfall is indicative of greater food and water availability, and is linked to
327 greater fecundity and better survival in primates (80–82). Because food and water are
328 provisioned, low rainfall might not be as impactful in this population compared to wild
329 primate populations in marginal environments, but we still predict low rainfall to be
330 predictive of higher mortality risk. We also predict that negative outcomes could be
331 associated with high rainfall, given the association between high rainfall and tropical

332 storms. Here, we used total rainfall across the first year of life (range: 1,021.4-3,157.1
333 mm).

334 **Temperature:** Higher temperatures are linked to reduced cognitive performance in
335 Western Australian magpies (*Cracticus tibicen doralis*), poorer health and welfare in dairy
336 cattle (*Bos taurus*), and higher mortality risk in southern pied babblers (*Turdoides*
337 *bicolor*) and geladas (*Theropithecus gelada*) (but also increased fecundity in geladas)
338 (81–84), thus we predicted negative outcomes associated with high temperatures. Here,
339 we averaged mean maximum daily temperatures across the first year of life (range:
340 85.12-89.89 F).

341 **Hurricanes:** In this population, exposure to major hurricanes is associated with
342 accelerated age-related immune changes. Among females on Cayo Santiago, hurricane
343 exposure during early life is associated with delayed reproductive maturation, but higher
344 fertility during reproductive prime, and during hurricane years, adult females are less
345 likely to produce offspring that survive to one year old (34,86,87). We recorded
346 individual exposure to any of the 3 major hurricanes that had major impacts on Cayo
347 Santiago (Hugo on September 18, 1989, Georges on September 21, 1998, and Maria
348 on September 20, 2017) during the first year of life. We treated this as a categorical
349 variable to assess the effects of each major storm. Hurricane exposure was not
350 included in previous studies of early life adversity, so we chose the first year of life as
351 our window of exposure to align with our other weather variables, rainfall and
352 temperature. If individuals were exposed to hurricanes when they were over one year
353 old, we did not consider them to have experienced this adversity as *early life* adversity.
354

355 Here, following previous theoretical and empirical work (11,13–15), we examined
356 cumulative adversity measures and individual forms of adversity separately. To
357 construct a cumulative early life adversity index, we summed individuals' exposure to
358 different forms of adversity. Previous studies typically relied on binary scores for each
359 form of adversity. Following Patterson et al 2021, to avoid arbitrary categorization and to
360 consider the severity of exposure, we used continuous measures of adversity when
361 feasible. For purposes of the cumulative index, continuous measures (i.e., group size,
362 kin network size, temperature, and rainfall) were normalized so values ranged from zero
363 to one. Variables for which lower values indicate greater adversity, such as kin network
364 size and rainfall, the normalized variables were reversed so that values closer to one
365 (i.e., higher values) always indicate greater adversity. For binary and categorical
366 measures (i.e., maternal loss, being a first born, presence of a competing sibling,
367 matriline rank, and hurricane exposure), individuals were assigned a value of one if they
368 experienced a given form of adversity and a value of zero if they did not experience it.
369 Those born into high ranking matriline were assigned a zero, mid ranking matriline
370 were assigned 0.5, and low ranking matriline were assigned a value of one. Those
371 exposed to any of the three major hurricanes during the first year of life were assigned a
372 one, and those who were not exposed to any of these major hurricanes during the first
373 year of life were assigned a zero. As such, each variable ranged from zero to one and
374 for each individual the variables were summed together into a cumulative index to
375 represent the total exposure to early life adversity. Our main cumulative early life
376 adversity index could range from 0-9 because it included nine variables: maternal loss,
377 presence of a competing younger sibling, high group size, primiparity, low matrilineal

378 dominance rank, small kin network, hurricane exposure, high temperature, and low
379 rainfall. Maternal social isolation was not included in the cumulative adversity index
380 because it relied on behavioral observations of individuals and was thus derived only for
381 a subset of our data (N=299 early life survival; N=101 adult survival).

382

383 Data analysis

384 To determine if early life adversity predicts survival, we used survival models. The
385 outcome variable was age at death. Individuals who were either still alive at the end of
386 the study or removed from the island for population control were right-censored. We ran
387 models on the full sample of all ages (N=6,599) but right-censored to four years old to
388 examine early life mortality, and we ran models on a subsample of individuals who
389 survived beyond four years of age (N=2,866) to examine mortality across adulthood.
390 Early life adversity predictor variables were modeled two ways: 1) cumulative index
391 model which included all forms of adversity summed together into one variable; and 2)
392 multivariate model which included all nine forms of adversity (maternal social isolation is
393 run separately) modeled as separate predictor variables in the same model. We
394 assessed the efficacy of these two approaches by comparing the fit of the cumulative
395 index models versus the multivariate models using information on the difference in the
396 expected predictive accuracy. Models included early life adversity index or all individual
397 adversity variables, sex, and an interaction term between sex and early life adversity.
398 Models also included a varying intercept for birth year and maternal identification. The
399 different forms of adversity we examined were not correlated, but temperatures in the
400 first year of life were highly correlated with birth year (Table S2).

401
402 Analyses were run in R (v 4.1.2) and RStudio (v 1.4.1106) (88,89). We first used Cox
403 survival models, but the proportional hazards assumption in the Cox model was violated
404 (cox.zph function in R package, “survival” (v 3.2.13): $p < 0.05$; see SOM for specifics).
405 Instead, we fit Accelerated Failure Time (AFT) survival models with a Weibull
406 distribution. The presence of a competing younger sibling is time-dependent since
407 individuals cannot experience this exposure unless they survive till a given age, i.e.,
408 until it’s biologically possible for the mother to give birth again. To include this variable,
409 we would need to include it as a time-varying variable in a Cox proportional hazard
410 model. Alternatively, one could subset the data to examine survival during periods in
411 which it is biologically possible for a younger sibling to be born (e.g., 2-4 years),
412 however, this could create biases in the dataset since this involves removing individuals
413 based on their age at death. As such, we were unable to test how the presence of a
414 competing younger sibling affects survival in early life and we excluded this variable
415 from the cumulative index for the early life survival model. We could, however, examine
416 this in adulthood since all individuals in the sample survived to adulthood and the
417 presence of a competing younger sibling is not time-varying.

418
419 Genetics can contribute to the effects of early life adversity. For example, individuals
420 experiencing maternal loss might have shorter lifespans due to genes shared by both
421 the mother and offspring. To estimate to what extent variance in survival is explained by
422 genetics, we accounted for pedigree in a subsample of the data for which we had
423 complete pedigree information (N=923 individuals during early life; N=307 adults). To do

424 so, we used the animal model (90) and incorporated the genetic relationship covariance
425 matrix as a random effect. The effects of pedigree on survival were substantial, but
426 accounting for genetic relatedness in the model did not diminish the effects of early life
427 adversity on survival in early life (with pedigree: $\beta=-0.33\pm0.12$; without pedigree: $\beta=-$
428 0.31 ± 0.11 ; Table S3) or adulthood (with pedigree: $\beta=-0.12\pm0.04$; without pedigree: $\beta=-$
429 0.12 ± 0.04 ; Table S3). Some forms of adversity are likely dependent on genetics (i.e.,
430 maternal loss, competing sibling, matriline rank, kin network) whereas other forms of
431 adversity are genetics-independent (i.e., rainfall, hurricanes, temperature, primarity, group
432 size), though there is likely a genetic basis to how one responds to adversity in all cases.
433 Because pedigree might differentially impact the effect of these genetics-dependent and
434 genetics-independent adversities, we ran our pedigree models with cumulative adversity
435 indices based only on genetics-dependent and genetics-independent adversities. The effects
436 of pedigree on survival remained substantial, but including genetic relatedness in these
437 models did not reduce the effects of adversity on survival during early life (genetics-
438 independent: with pedigree $\beta=-0.19\pm0.08$; without pedigree $\beta=-0.11\pm0.07$; genetics-
439 dependent with pedigree $\beta=-0.40\pm0.09$; without pedigree $\beta=-0.35\pm0.08$; Table S3) or
440 adulthood (genetics-independent: with pedigree $\beta=0.03\pm0.03$; without pedigree
441 $\beta=0.01\pm0.02$; genetics-dependent with pedigree $\beta=-0.07\pm0.03$; without pedigree $\beta=-$
442 0.08 ± 0.02 ; Table S3). Because the effects of early life adversity were unaffected by pedigree
443 inclusion and because the sample size for pedigree inclusion was much smaller (paternity is

444 unknown for many animals earlier in the study), we have presented the larger set of data
445 without pedigree in the main text.

446

447 Models were run with the brms package (v 2.16.3) (91). All continuous predictor
448 variables were standardized to a mean of 0 and a standard deviation of 1 (note that this
449 differs from how we normalized the continuous adversities to range from 0 to 1 for
450 addition into the cumulative early life adversity index). We ran our analyses with
451 continuous variables modeled linearly and quadratically, and compared the fit of each
452 modeling approach using the “loo” criterion in the brms package in R (90). The
453 nonlinear models provided no more explanatory power compared to the linear models
454 (see SOM for results of model comparisons). These results suggest that the linear
455 models with fewer parameters should be used, so we reported the linear results here.
456 All models were Bayesian, and we used weakly informative priors for fixed effects,
457 setting the mean to zero and the standard deviation to one. To produce more accurate
458 predictions for age at death, we used more regularizing priors for the intercept (a mean
459 of 1 and standard deviation of 0.1 for the early life survival models, and a mean of 12
460 and standard deviation of 0.4 for the adult survival models). Specifically, our analyses
461 contained a high proportion of right-censored cases, which can lead to model
462 predictions that overestimate life expectancy (92). We used credible intervals to
463 determine whether the effect of a variable was substantial or not. If the 85% credible
464 interval for an effect did not overlap with zero, the effect was considered substantial.
465 When the vast majority of the 85% credible interval did not span zero, but there was
466 some overlap, we described the model as being ‘uncertain’ about the effect. To

467 compare how the cumulative index and multivariate models fit the data, we used the
468 “loo” model fit criterion in the brms package (90). The code and data used can be found
469 here: https://github.com/skpatter/ELA_Survival_Macaques

470

471 Results

472 *Cumulative early life adversity is associated with reduced survival during early life and*
473 *during adulthood*

474

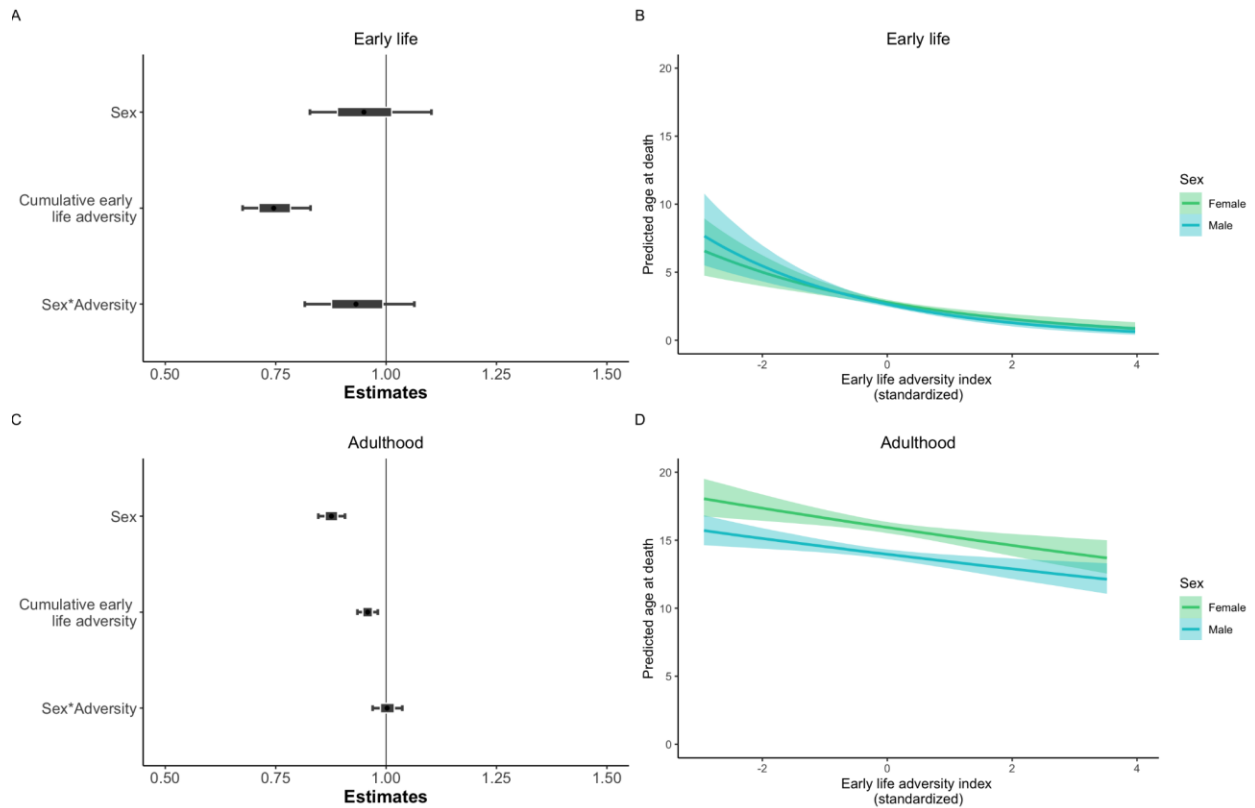
475 Individuals who experienced more cumulative early life adversity had higher mortality
476 during early life ($\beta=-0.29\pm0.07$; Figure 1, Table S4). There were no clear differences in
477 mortality for males versus females during early life ($\beta=-0.05\pm0.10$), and there was no
478 evidence that early life adversity differentially affected mortality risk as a function of sex
479 during early life ($\beta=-0.07\pm0.09$; Figure 1, Table S4). Adults who experienced more
480 cumulative early life adversity had shorter lives than adults who experienced less early
481 life adversity ($\beta=-0.04\pm0.02$; Figure 1, Table S4). Among adults, females lived longer
482 than males ($\beta=-0.13\pm0.02$), and there was no evidence that cumulative early life
483 adversity affected mortality risk differentially between males and females ($\beta=0.00\pm0.02$;
484 Figure 1; Table S3). Between those who experienced the least and the most amount of
485 cumulative early life adversity in our sample, these effects translate to a 4.78-year
486 difference in average life expectancy among adult females and a 3.94-year difference in
487 average life expectancy among adult males. The maximum age observed was 31 for
488 females and 29 for males on Cayo, and the average lifespan for those who survived to
489 adulthood was approximately 18 and 15 years for females and males respectively (70;

490 CPRC data). Given that we defined adulthood as beginning at four years of age, this
491 indicates an average adult lifespan of 14 years for females and 11 years for males. The
492 average difference in life expectancy (4.78 and 3.94 years) represents a substantial
493 portion of the adult lifespan: approximately 34% of the lifespan for females and 36% for
494 males.

495

496

497 **Fig 1.** Model effects of cumulative early life adversity and sex on survival during early
498 life (A) and adulthood (C). The outer bars show the 85% credible intervals, the inner box
499 shows the 50% credible intervals, and the black circle in the middle shows the median
500 of the posterior distribution. Model predictions are shown for the effect of cumulative
501 early life adversity on lifespan in early life (B) and adulthood (D). Cumulative early life
502 adversity on the x-axis is standardized such that an adversity value of zero represents
503 the mean amount of adversity experienced in the sample. Green predictions represent
504 females and blue predictions represent males. The solid lines show the median
505 estimates and the shaded region shows the 85% credible intervals.



506

507

508 *Several forms of early life adversity are associated with reduced survival, and some*
 509 *effects are sex-dependent*

510

511 Individuals who **lost their mother** during the first four years of life had a higher mortality
 512 risk during early life ($\beta=-0.33\pm0.14$) and adulthood ($\beta=-0.06\pm0.04$) than those who did
 513 not lose their mother (Figure 2, Table S5). Maternal loss had a larger negative effect on
 514 sons than daughters in both early life ($\beta=-0.32\pm0.20$) and adulthood ($\beta=-0.05\pm0.06$;
 515 Figure 3, Table S5). **First-born** offspring had elevated mortality risk during early life ($\beta=-$
 516 0.36 ± 0.16). In contrast, individuals born to primiparous mothers had better survival in
 517 adulthood than those born to multiparous mothers, although the model was uncertain
 518 about this effect ($\beta=0.06\pm0.05$). Effects of maternal primiparity were not moderated by

519 sex (early life: $\beta=0.09\pm0.22$; adulthood: $\beta=-0.04\pm0.07$). Macaques born into **low ranking**
520 **matrilines** had a higher mortality risk during early life ($\beta=-0.44\pm0.17$) and adulthood ($\beta=-$
521 0.16 ± 0.05) than those born into high ranking matriline. Matrilineal rank was more
522 strongly associated with female survival than male survival during both periods of life
523 (early life: $\beta=0.47\pm0.22$; adulthood: $\beta=0.04\pm0.06$; Figure 3; Table S5). We also treated
524 matrilineal rank as an ordinal variable and found similar results (Table S5). **Smaller**
525 **maternal kin networks** at birth were associated with higher early life mortality risk,
526 especially for males ($\beta=0.05\pm0.07$; sex interaction: $\beta=0.14\pm0.10$). Smaller maternal kin
527 networks at birth were associated with better survival for adult males, but reduced
528 survival for adult females ($\beta=0.01\pm0.02$; sex interaction: $\beta=-0.05\pm0.03$; Figure 3; Table
529 S5). The presence of **competing younger siblings** was associated with higher
530 mortality risk in adulthood, but the model was uncertain about this effect ($\beta=-0.03\pm0.04$).
531 Although the model was uncertain, a competing sibling had a slightly larger effect on
532 females ($\beta=0.06\pm0.06$). We were unable to examine survival effects during early life given
533 time-varying issues. The model was uncertain about the effects of maternal social isolation;
534 individuals born to socially isolated mothers seemed to have higher mortality during early
535 life than those born to more socially connected mothers ($\beta=0.15\pm0.17$; Table S6), and males
536 were more affected by this than females ($\beta=0.29\pm0.25$). No effect of maternal social isolation
537 was observed among adults ($\beta=-0.04\pm0.02$; Table S6).

538

539 Higher temperatures during the first year of life were associated with higher mortality risks
540 in early life ($\beta=-0.06\pm0.24$) and adulthood ($\beta=-0.02\pm0.02$), but the models were uncertain

541 about these effects (Figure 2, Table S5). The effect of high temperatures on survival was
542 moderated by sex (Figure 3; Table S5). Higher temperatures during the first year of life were
543 more strongly associated with reduced survival among males than females during early life
544 ($\beta=-0.23\pm0.09$), but in adulthood, only females experienced this survival cost ($\beta=0.02\pm0.03$).
545 Low **rainfall** was associated with reduced survival during early life, but the model was
546 uncertain about this estimate ($\beta=0.23\pm0.18$). No effect of rainfall was found during
547 adulthood ($\beta=-0.01\pm0.02$; Figure 2; Table S5). No effect of **group size** was observed
548 during early life ($\beta=0.01\pm0.07$), and while the model was uncertain, it seems adults born
549 into larger groups exhibited reduced survival ($\beta=-0.02\pm0.02$; Figure 2; Table S5). No
550 effect of major **hurricanes** was observed during early life (Georges: $\beta=-0.04\pm0.50$;
551 Hugo: $\beta=-0.08\pm0.50$; Maria: $\beta=0.08\pm0.44$) or adulthood (Georges: $\beta=-0.02\pm0.10$; Hugo:
552 $\beta=-0.04\pm0.10$; Figure 2; Table S5).

553

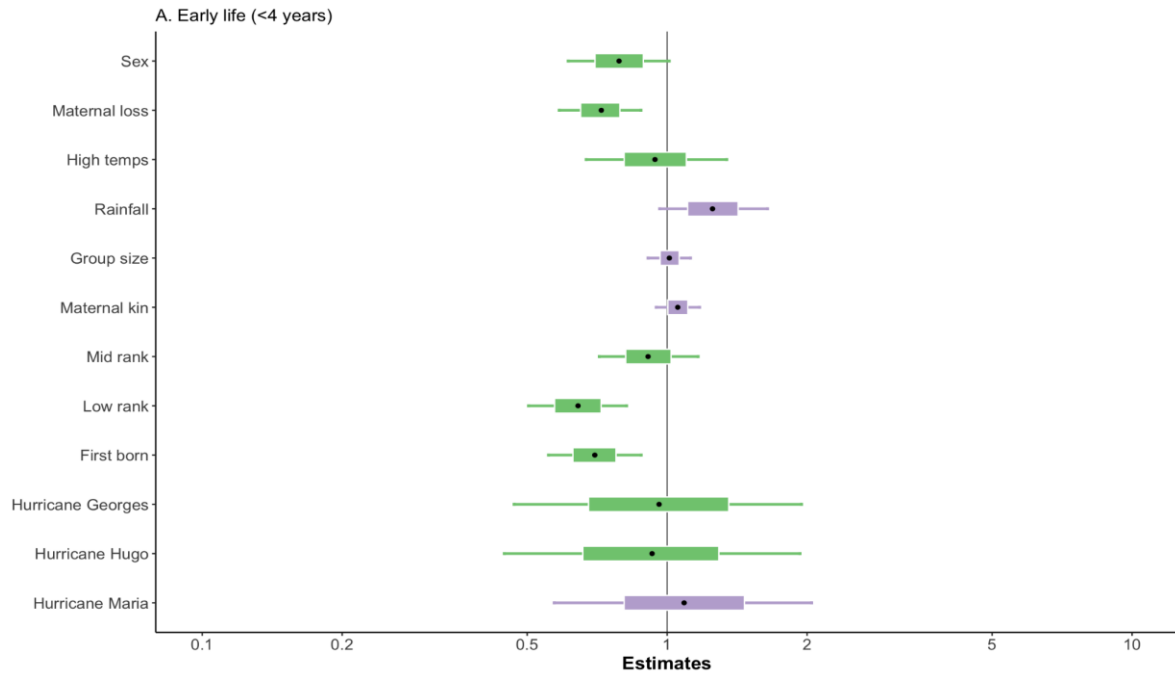
554 Model comparisons revealed no substantial difference between models constructed with the
555 cumulative early life adversity index versus those constructed with each form of early life
556 adversity separately (Table S7). We ran additional models with a cumulative adversity index
557 that excluded maternal loss and matriline rank, the two strongest predictors of mortality, to
558 see if the accumulation of adversities with smaller effect sizes impacted mortality (Table S8).
559 Individuals who experienced more adversity, as measured by the reduced index, had a higher
560 mortality risk during early life, but the effect size was smaller than in the model with the full
561 cumulative index ($\beta=-0.13\pm0.08$). In the reduced index model, an interaction with sex arose

562 such that male survival was more negatively affected by cumulative adversity than female
563 survival during early life ($\beta=-0.12\pm0.09$). The effect of cumulative early life adversity on
564 adult survival disappears with the reduced adversity index ($\beta=0.00\pm0.02$), however, this is at
565 least partially explained by an interaction with sex: more cumulative adversity, as measured
566 with the reduced index, was associated with poorer adult female survival but better adult
567 male survival ($\beta=0.02\pm0.02$). The sex-dependent multivariate results above provide more
568 nuanced, informative findings than the cumulative and reduced cumulative index models.

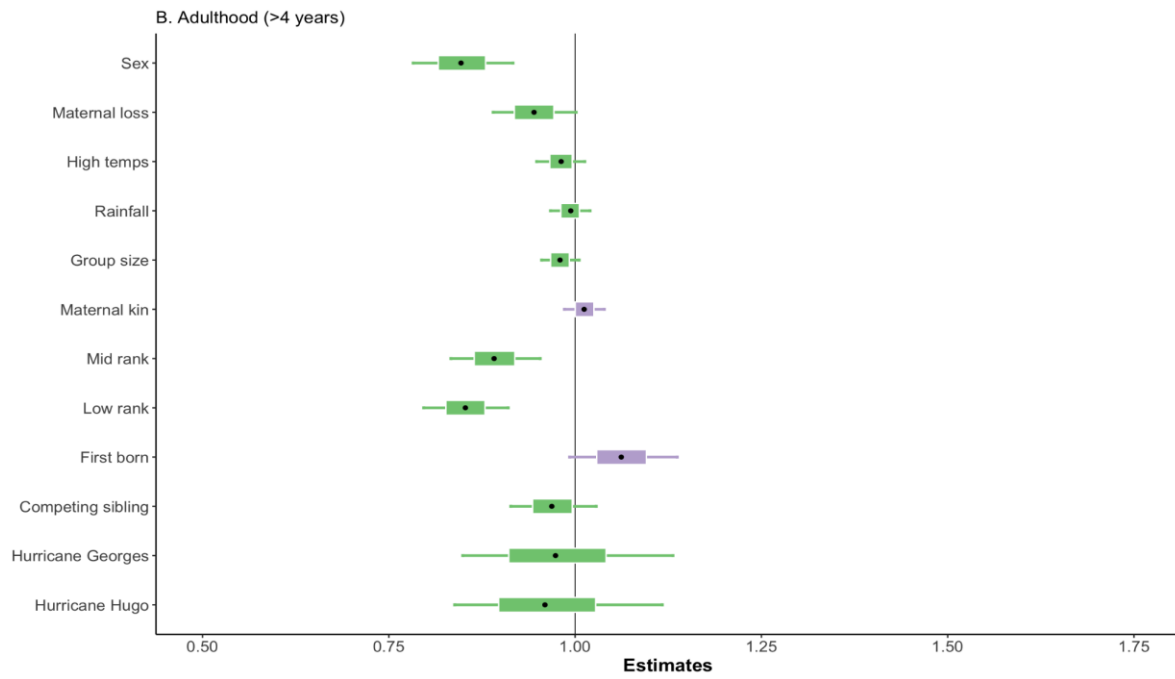
569

570 **Fig2.** Model effects of sex and the forms of early life adversity on survival during early
571 life (A) and adulthood (B). The outer bars show the 85% credible intervals, the inner
572 boxes show the 50% credible intervals, and the black circles in the middle show the
573 medians of the posterior distributions. Green shading represents negative effect sizes,
574 meaning that the variable is associated with shorter lifespans, and purple shading
575 represents positive effect sizes, meaning that the variable is associated with longer
576 lifespans. Note that we do not include the interaction effects between sex and early life
577 adversity in this figure. Because interaction effects influence the interpretation of the sex
578 and adversity effects, this figure should be interpreted with caution as it does not
579 illustrate the complete picture. The full model results, including interaction effects, are

580 presented in Figure S1.



581

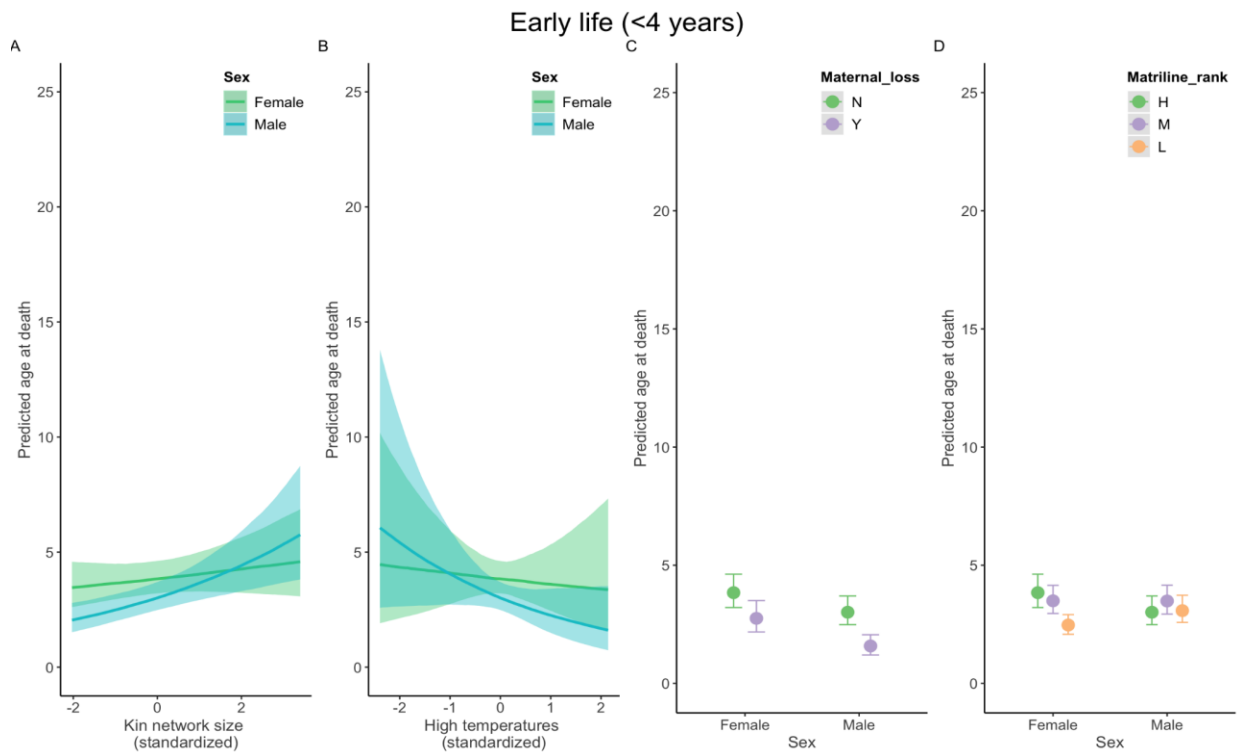


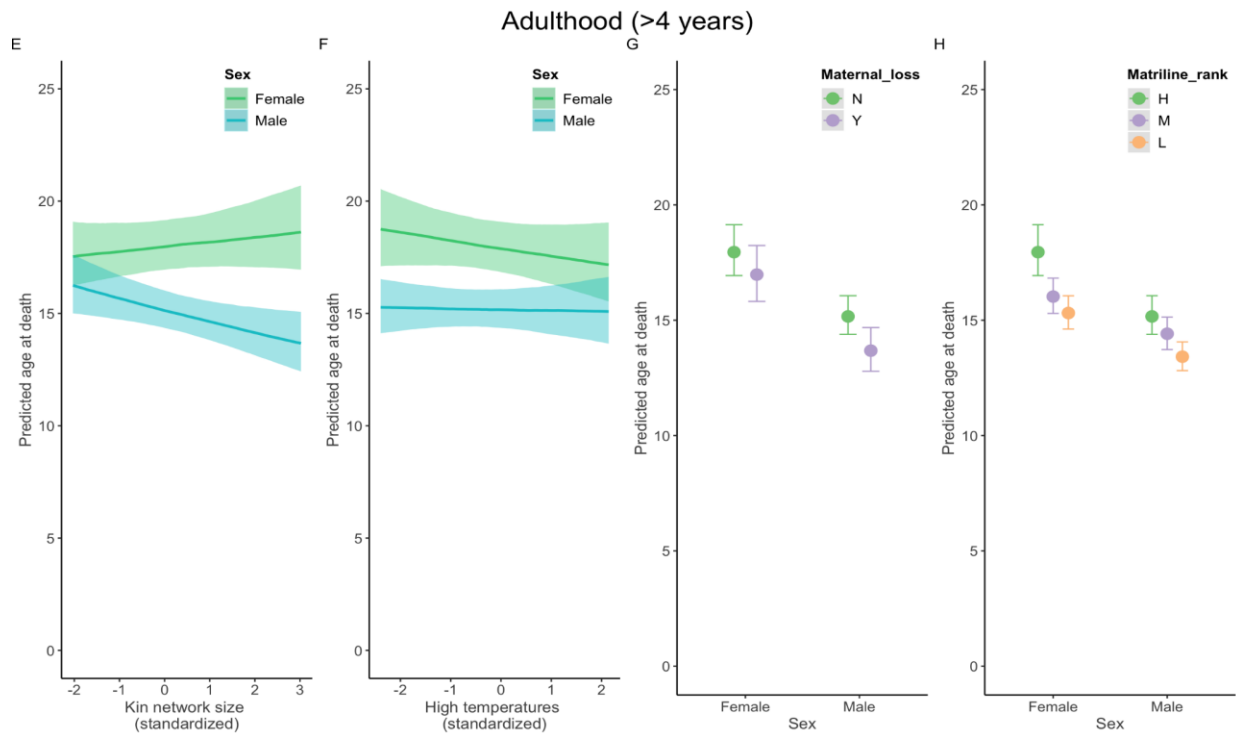
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583

584 **Fig 3.** Interactions between sex and three forms of early life adversity on adult survival.

585 (A) and (E) Predicted relationship between maternal kin network size at birth and
 586 survival for females (green) and males (blue). (B) and (F) Predicted relationship
 587 between high temperatures during the first year of life and survival for females (green)
 588 and males (blue). (C) and (G) Predicted relationship between maternal loss during the
 589 first four years of life and survival for males versus females. The circles show the
 590 median estimate, and the bars show the 85% credible intervals. (D) and (H) Predicted
 591 relationship between matrilineal rank and survival for males versus females. The circles
 592 show the median estimate, and the bars show the 85% credible intervals.





594

595

596 Discussion

597 Our findings indicate that early life adversity shapes both early life survival and adult
 598 survival in free-ranging rhesus macaques. Individuals that experienced more cumulative
 599 early life adversity lived shorter lives than those that experienced less adversity. The
 600 effect size of early life adversity on mortality risk was larger in the first four years of life
 601 than adulthood, but risks were also elevated in adulthood. Strong effects on early life
 602 mortality risk are consistent with the notion of an overall greater vulnerability during
 603 development (93,94). Given the fitness costs of dying prior to reproduction, our results
 604 demonstrate that the effects of early life adversity prior to maturity have major fitness
 605 ramifications and the full consequences of early life adversity are likely to be larger than
 606 predicted in previous studies focused on adult fitness.

607

608 The accumulation of multiple adversities did not predict mortality risk better than
609 individual forms of adversity, and assessing the various forms of potential adversity
610 revealed that maternal-related adversities exhibited the largest effects on survival.
611 Maternal death and low matrilineal rank were associated with higher mortality risk in
612 early life and adulthood. The lasting effects of these maternal-related adversities are
613 unsurprising given similar consequences in other mammalian species (23,54,55), as
614 well as consequences of parental-related hardships in humans (95–99). Survival
615 advantages were also observed among offspring born to more socially connected
616 mothers, but there was considerable variation in this effect and it did not persist into
617 adulthood. From previous analyses, we know the presence of a competing younger
618 sibling increases mortality risk during early life (33), and these effects appear to persist
619 into adulthood, at least for females. We found that first born offspring were more likely to
620 die during early life than those who were not the first born. However, while our model
621 estimates were uncertain, among those who survived into adulthood, survival odds were
622 better for those born to primiparous than multiparous mothers. Given the strong
623 negative effects of primiparity on offspring survival in the first four years of life, the
624 higher survival odds of adults who were first borns could reflect survivorship bias.
625 Alternatively, because primiparous mothers are young, first-born daughters might have
626 more older kin present (e.g., grandmother, older aunts, older cousins) across a larger
627 span of their life than daughters born to older, multiparous mothers. This can create
628 trade-offs such that first-borns face elevated infant mortality risks due to constraints on

629 maternal care and investment, but if they survive, they might experience reduced
630 mortality risks stemming from support provided by older maternal kin.

631

632 Consistent with previous analyses in this population (34,100), we did not find substantial
633 impacts of early life hurricane exposure on survival. This is surprising given that
634 macaques in this population exposed to Hurricane Maria showed divergent immune cell
635 gene regulation, suggestive of accelerated aging (87). Exposure to major hurricanes
636 also led to greater heterogeneity in reproductive strategies and longevity, and
637 macaques might reduce fertility as a strategy to prioritize survival odds (86,100). Given
638 our results showing heat effects on mortality and the fact that temperatures increase
639 following hurricanes on Cayo Santiago (44,87), hurricanes might affect macaques
640 indirectly via factors such as deforestation, shade scarcity, and heat. Further, given the
641 recency of Hurricane Maria and our small sample of individuals exposed to Maria in this
642 study's dataset, we are currently limited in our ability to analyze survival outcomes for
643 this most recent hurricane event. Potential impacts of Hurricane Maria may also have
644 been buffered socially - macaques on Cayo Santiago adjusted their social networks
645 after Hurricane Maria (44) and built new social connections, which may buffer negative
646 impacts.

647

648 The survival effects of some forms of early life adversity were sex-dependent. During
649 early life, male survival was more negatively affected by three forms of adversity: small
650 maternal kin networks, high temperatures, and maternal loss. In adulthood, males
651 continued to suffer greater costs of early maternal loss, perhaps reflecting the long-term

652 costs of severe energetic constraints during early life. Males might be more affected by
653 these adversities than females prior to reproductive maturity due to their energetically
654 costly developmental trajectories and/or due to maternal decisions to reduce investment
655 in energetically costly offspring during harsh environments (26,27,101). In adulthood,
656 females were more affected by several forms of early life adversity than males: matriline
657 rank, maternal kin network, and temperature. Adult females were more affected by
658 matriline rank than adult males, likely because males disperse (69), female dominance
659 hierarchies are fairly stable across time (66), and females typically inherit dominance
660 rank via their matriline. Being born into large maternal kin networks had a positive effect
661 on adult female survival but a negative effect on adult male survival. Given dispersal,
662 males might not receive any immediate benefits of kin support in adulthood and thus
663 only experience the long-term costs associated with earlier competition, consistent with
664 the idea that individuals face tradeoffs between benefits of kin support and costs of
665 competition with kin (102). Males were more susceptible than females to high
666 temperatures during early life, but females were more susceptible in adulthood. In
667 humans, findings have suggested both greater and lesser susceptibility to heat stroke in
668 women versus men (103) females but not males exhibited delayed myocardial
669 dysfunction following exertional heat stroke (104). Future work is needed to explore
670 these temperature effects and potential underlying or mediating factors such as how
671 body size, physiology, cardiovascular health, and energetic expense patterns are linked
672 to temperature fluctuations, hurricane exposures, and mortality across ages in this
673 population.
674

675 We faced several limitations in this study. Our results could be shaped by the nature,
676 structure, and characteristics of the data. Specifically, the data contain a large
677 proportion of right-censored observations, which could affect the accuracy of lifespan
678 estimates. We were also unable to use time-varying variables because the data violated
679 the Cox model assumptions. This led to the exclusion of the competing sibling variable
680 from our early life survival model, and led us to treat maternal loss as a binary variable
681 rather than a continuous variable (i.e., age at maternal loss). Some forms of potential
682 early life adversity had minimal to no effect on mortality risk, which is not entirely
683 unexpected given similar null findings for variables such as drought, group size, and
684 maternal social isolation in other primate species (15,25). However, it is also plausible
685 that some variables like rainfall and group size might have limited effects on survival
686 because drinking water and food are provisioned in the study population. While the
687 macaques still compete over access to food and water resources, competition is likely
688 reduced compared to wild populations. The consequences of adversity might further be
689 hampered in this population because the macaques are not exposed to predators. Our
690 study population might navigate an environment in which the consequences of early life
691 adversity are relaxed, but this represents natural variation which exists across species
692 and populations.

693

694 The results of this study open the door for future lines of inquiry. Our results illustrate
695 clear fitness consequences of early life adversity in the form of increased mortality risk,
696 but further research into the biological mechanisms underlying these survival patterns is
697 needed to better understand how early life adversity impacts fitness and health. It was

698 beyond the scope of this analysis to investigate how the timing and length of the
699 windows of exposure to adversity might impact mortality risk. Sensitive windows are
700 periods during which individuals are especially sensitive to inputs and exhibit
701 heightened plasticity (105). The timing of these windows are hypothesized to vary
702 across forms of adversity, biological systems, individuals, and populations (93).
703 Additional analyses are also needed to investigate more nuanced aspects of early life
704 adversity such as the severity, duration, frequency, and predictability of exposure to
705 different forms of adversity (6). Another angle to investigate, especially given the sex-
706 dependent mortality patterns, is how effects of early life adversity might be moderated
707 or mediated by developmental trajectories and parental investment strategies. Analyses
708 are also needed that examine whether individuals adjust other aspects of their life
709 history strategies (e.g., pace of reproduction, age at maturity) to compensate for
710 reduced life expectancy (34,86,106). Importantly, variation in model estimates and
711 predictions convey that while early life adversity can have negative consequences, such
712 effects are not definitive. Social connections and behavioral adjustments (44,107)
713 should be investigated as potential contributors to resilience.

714

715 In sum, our study demonstrates that exposure to early life adversity increases mortality
716 risk in male and female rhesus macaques. Lower odds of surviving to reproductive age
717 indicates that early life adversity can have major fitness ramifications for both an
718 organism and their parents. Reduced life expectancy among those who survive to
719 adulthood, suggests that early life adversity can have persisting fitness costs and long-
720 term health consequences. Adversities related to the maternal, social, and nutritional

721 environment generally had the largest impacts on offspring survival. Sex-dependent
722 effects of early life adversity in rhesus macaques are likely driven by social system
723 characteristics (i.e., female philopatry) and sex-based variation in energetic demands.
724 We were able to show that the form of adversity, socio-sexual context, and other
725 biological factors interact to shape the timing and severity of consequences. Natural
726 populations of non-human animals can prove valuable not only for improving our
727 understanding of the evolutionary pressures that shape developmental plasticity, life
728 history strategies, and early life sensitivities, but also for better contextualizing findings
729 in humans and informing future research in humans.

730

731

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741

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