

1 Rhesus macaques compensate for reproductive delay following ecological adversity early in life

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24 **Abstract**

25 Adversity early in life can shape the reproductive potential of individuals through negative
26 effects on health and lifespan. However, long-lived populations with multiple reproductive
27 events may present alternative life history strategies to optimize reproductive schedules and
28 compensate for shorter lifespans when experiencing adversities early in life. Here, we quantify
29 the effects of major hurricanes and density-dependence as sources of early-life ecological
30 adversity on the mean age-specific fertility, reproductive pace, and lifetime reproductive success
31 (LRS) of Cayo Santiago rhesus macaque females, and explored demographic mechanisms for
32 reproductive schedule optimization later in life. Females experiencing major hurricanes early in
33 life exhibit a delayed reproductive debut, but maintain inter-birth intervals and show a higher
34 mean fertility during prime reproductive ages relative to females experiencing no hurricanes.
35 Increasing density at birth is associated to a decrease in mean fertility and LRS. When combined,
36 our study reveals that early-life ecological adversities predict a delay-overshoot pattern in mean
37 age-specific fertility that supports the maintenance of LRS. In contrast to predictive adaptive
38 response models of accelerated reproduction, the long-lived Cayo Santiago population presents a
39 novel reproductive strategy where females who experience major natural disasters early in life
40 ultimately overcome their initial reproductive penalty with no overall negative fitness outcomes.
41 Such strategy suggests that investing more energy into development and maintenance at younger
42 ages allows long-lived females experiencing early-life ecological adversity to reproduce at a
43 mean rate equivalent to that of a typical female cohort later in life.

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45 **Keywords:** Cayo Santiago; Density-dependence; Fitness; Hurricanes; PAR

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47 **Introduction**

48 Adversity early in life can have negative effects on the reproductive performance of
49 individuals, and thus influences life history evolution and population fitness (Lindström 1999;
50 Nussey et al. 2007; Douhard et al. 2014; Lu et al. 2019). Under the predictive adaptive response
51 model (PAR), this exposure to adverse conditions is hypothesized to “program” individuals onto
52 distinct life history tracks in preparation for either the forecasted future internal somatic state of
53 the organism (iPAR; Nettle et al. 2013) or the forecasted future external environment which the
54 organism will eventually inhabit (ePAR; Gluckman et al. 2005; Nettle et al. 2013; Bateson et al.
55 2014). For example, nutritional adversity early in life (e.g., competing siblings, maternal dietary
56 restrictions) is associated with shorter lifespans in rats (Desai and Hales 1997), birds (Lindström
57 1999), and primates (Tung et al. 2016; Campos et al. 2021), as well as a delay in reproductive
58 debut (Nussey et al. 2007) and consequent lower reproductive success in ungulates (Rose et al.
59 1998; Douhard 2014). Similarly, psychosocial adversity during the first year of life (e.g.,
60 maternal loss, low social rank) predicts both lower survival (Tung et al. 2016; Stanton et al.
61 2020; Campos et al. 2021) and lower fitness (Zippel et al. 2021) in primates. Such predisposition
62 to hardship later in life can be explained through cohort effects in which observed differences in
63 health and consequent fitness components are shared among individuals subjected to the same
64 environmental conditions during developmental stages, such as adversities experienced in utero
65 and exposure to environmental hazards during infancy (O’Rand 1996; Lindström 1999;
66 Lindström and Kokko 2002; Gaillard et. al 2003; Garrott et al. 2012; Payo-Payo et al. 2016). As
67 evidence supporting early-life adversity and cohort effects frameworks continue emerging, it is
68 crucial to understand demographic mechanisms for life history optimization following adverse
69 conditions early in life.

70 A potential iPAR strategy for individuals exposed to early-life adversity involves changes
71 in the pace of reproduction due to predicted shorter lifespans (Gluckman et al. 2005; Nettle et al.
72 2013). In such a scenario, selection is hypothesized to optimize the reproductive schedule of
73 individuals who experience adversity during developmental stages by accelerating reproduction
74 to maintain a higher lifetime reproductive success (LRS; Draper and Harpending 1982; Belsky et
75 al. 1991). Consistent with this, adversity early in life has been associated with younger ages of
76 reproductive debut among many mammals (Sloboda et al. 2009; Douhard et al. 2014; Mumby et
77 al. 2015), including humans (Nettle et al. 2011; Rickard et al. 2014; Belsky 2019). However,
78 recent evidence suggests that accelerated reproduction may not be an adaptive response to early-
79 life adversity in nonhuman primates as early-life adversity in female baboons did not accelerate
80 their reproduction, and thus was not associated with high LRS maintenance (Weibel et al. 2020).
81 These findings open questions regarding other potential evolutionary strategies that long-lived
82 populations develop to cope with early-life adversity and compensate for shorter lifespans.

83 In this study, we quantify the effects of early-life ecological adversity in a long-living
84 nonhuman primate and evaluate potential demographic mechanisms for optimal reproductive
85 success later in life. We focus on major hurricanes and density-dependence as main sources of
86 ecological adversity on the rhesus macaque population at Cayo Santiago. Cayo Santiago, located
87 in the Caribbean region, is subjected to major hurricane events which suppress annual mean
88 fertility (Morcillo et al. 2020) and change the social structure of the population (Testard et al.
89 2021). Moreover, this population is known to be regulated by density through negative density-
90 dependence in fertility (Hernández-Pacheco et al. 2013; 2016a). Rather than a strong nutritional
91 adversity, density-dependence at Cayo Santiago is likely associated with increased prevalence of
92 aggressive interactions resulting in the suppression of female fertility (Judge and De Waal 1997;

93 Sterck et al. 1997; Dettmer et al. 2014). Thus, major hurricane events and increased population
94 density early in the life of Cayo Santiago rhesus macaque females may represent sources of both
95 nutritional, as well as psychosocial adversities.

96 In contrast to the iPAR hypothesis of accelerated reproduction, we hypothesize that early-
97 life adversity suppresses reproduction at younger adult ages and evaluate alternative
98 demographic mechanisms for the evolution and maintenance of LRS. First, to test whether
99 adversity early in life reduces mean fertility in particular age groups, we investigate variation in
100 mean age-specific fertility. In such a scenario, a life history strategy for optimal reproductive
101 schedules may involve the increased reproductive performance of females during prime
102 reproductive ages. Second, we quantify the effects of early-life ecological adversity on
103 reproductive pace (i.e., reproductive debut and inter-birth intervals). Adversity may decrease the
104 reproductive pace of females by delaying reproductive debut. Here, optimizing reproductive
105 success later in life may involve accelerating inter-birth intervals (IBIs) at older ages. Finally, we
106 quantify whether females experiencing harsh environments early in life attain a different LRS
107 relative to females not experiencing adversities. No reduction in LRS among females who
108 experience adversity would suggest the evolution of demographic mechanisms for optimal
109 reproductive success later in life.

110 **Methods**

111 *Study Population*

112 The Cayo Santiago Field Station (CSFS) is a 15.2 ha island that serves as a research
113 facility managed by the Caribbean Primate Research Center of the University of Puerto Rico for
114 behavioral and non-invasive research. Located 1km off the southeastern coast of Puerto Rico
115 (18°09'N, 65°44'W), the CSFS is inhabited by a population of free-ranging rhesus macaques

116 (*Macaca mulatta*), all of which descended from a group of 409 individuals released onto Cayo
117 Santiago in 1938. Since establishment, the population has been maintained under semi-natural
118 conditions allowing for the natural formation of social groups, social rank, and mating seasons
119 (Rawlins and Kessler 1986). Monkeys forage on vegetation, spending 50% of their time on
120 average eating vegetation found on the island (Marriott et al. 1989). The population is also
121 provisioned with ad-libitum, high-protein monkey chow rationed at approximately 0.23
122 kg/monkey/day and ad libitum drinking water via automatic drinkers located throughout the
123 island. Veterinary intervention is restricted to the annual trapping season in which yearlings are
124 trapped, marked for identification using ear notches and a unique ID tattoo, physical samples are
125 collected, and tetanus inoculation at 1 year of age and booster at 2 years of age are administered.
126 During trapping, some individuals are also permanently removed from the island to control for
127 population size (Hernández-Pacheco et al. 2016a). Since 1956, the population has been
128 monitored through visual censuses resulting in a demographic database which includes the date
129 of birth, sex, matrilineage, and date of death or permanent removal of the population for all
130 individuals. Births, deaths, and removals are reported within 2 days of occurrence (Ruiz-
131 Lambides et al. 2017). During data collection, all applicable institutional and/or national
132 guidelines for the care and use of animals were followed.

133 *Early-life ecological adversity*

134 We addressed the effects of two ecological sources of early-life adversity on
135 reproduction: major hurricanes and population density. We defined early-life as the period from
136 gestation (i.e., in utero) to infancy (< 1 year of age). The gestation period was estimated by
137 subtracting 165 days from the date of birth for each individual (Rawlins and Kessler, 1985).
138 Since the establishment of census records, the CSFS has experienced the direct effect of three

139 major hurricanes (Category ≥ 3); Hugo (18-Sep-1989), Georges (21-Sep-1998), and Maria (20-
140 Sep-2017; Morcillo et al. 2020). We focused only on hurricanes Hugo and Georges as
141 individuals experiencing Maria did not have complete reproductive life histories at the moment
142 of our study. Hurricanes Hugo and Georges were category 3 hurricanes when their centers were
143 closest to the CSFS (~ 23 km and ~ 8.4 km from CSFS, respectively). These hurricanes exhibited
144 sustained windspeeds of approximately 201 km h^{-1} and 185 km h^{-1} , respectively, with hurricane-
145 force winds extending over the entire field station (Morcillo et al. 2020). Both hurricanes
146 produced severe damage to Cayo Santiago's vegetation, with 60-90% canopy loss following
147 each hurricane (Morcillo et al. 2020). Major hurricanes have also been observed to cause
148 changes in behavior involving an increase in the proximity of social networks (Testard et al.
149 2021). Food provisioning and census taking resumed after 1 (Hugo) and 2 (Georges) days
150 (Morcillo et al. 2020). Given negative density-dependence in reproduction driven by the annual
151 number of adult females alive in the population (Hernández-Pacheco et al. 2013; Hernández-
152 Pacheco and Steiner 2017), we also considered the experienced female adult density at birth as a
153 second source of early-life ecological adversity. For this, we defined population density as the
154 total number of adult females (≥ 3 years of age) alive at the onset of each birth season. Cayo
155 Santiago monkeys exhibit reproductive synchrony with 73% of births occurring in a 3-month
156 period (Hernández-Pacheco et al. 2016b). Density at the onset of the birth season represents
157 more accurately the experienced density early in life as opposed to the density at birth for a
158 particular female due to the potential variation in density caused by culling events, especially late
159 in the birth season. With this information, all females were classified into two birth cohorts; a
160 hurricane cohort and a non-hurricane cohort, each with a corresponding experienced female adult
161 density at the onset of the birth season. The hurricane cohort included all female adults that

162 experienced hurricanes Hugo or Georges, either in utero or as infants, and the non-hurricane
163 cohort included all females born during the study period that did not experience these hurricanes
164 early in life.

165 *Statistical analysis of reproductive metrics*

166 To quantify the effects of early-life adversity on reproductive output we used four
167 different metrics that characterize fertility, pace of reproduction, and individual fitness. We
168 addressed fertility across the lifespan by measuring mean age-specific fertility, the pace of
169 reproduction by measuring age at reproductive debut and IBIs, and individual fitness by
170 measuring lifetime reproductive success. Our analysis included 2,108 life histories of adult
171 females born in the 44-year period between 1973 and 2017 ($n_{\text{hurricane}}=212$ females;
172 $n_{\text{nonhurricane}}=1,896$ females).

173 To address the effects of early-life adversity on mean age-specific fertility rate, we
174 tracked each adult female over time and recorded whether she produced an offspring or not at
175 each age. We censored data from the last reproductive age class (23 years of age) because 22
176 years of age was the last age represented in the hurricane cohort (a total of 58 censored
177 observations). We analyzed these data using generalized additive mixed models (GAMM). These
178 models are non-parametric extensions of generalized linear models that allow the evaluation of
179 nonlinear relationships, and thus are appropriate to model age-specific fertility in primates. For
180 this, we used a logit link function for the binary outcome of whether a female reproduced in a
181 given year. We considered cohort (born in a hurricane or non-hurricane year) as a fixed effect,
182 and age and density at birth as smooth terms. We fitted a series of competing models that
183 included cohort as both an additive effect, i.e., intercepts vary but varying slopes are consistent
184 across cohorts, and as an interactive effect, i.e., intercepts and the smooth terms vary by cohort.

185 We also included a random intercept of individual ID to account for unobserved maternal traits
186 and repeated measurements. Considering all factor combinations resulted in a total of 9
187 competing models that were evaluated using the Akaike's Information Criterion (AIC; Burnham
188 and Anderson 2002).

189 To address the effects of early-life adversity on reproductive pace, we estimated the age
190 at reproductive debut and IBIs across the reproductive lifespan. We measured reproductive debut
191 as the age at which females gave birth to their first offspring. Given the reproductive synchrony
192 of the population, age at delivery exhibits a distribution described by pulses within age classes.
193 Because of this, we tested differences in age at reproductive debut between cohorts using a
194 Wilcoxon rank-sum test and whether or not density predicted reproductive debut using a series of
195 simple linear regressions evaluated with AIC. We measured IBI as the number of days between
196 two offspring births produced in consecutive birth seasons. We restricted our analyses to
197 consecutive births only to examine the distribution of IBIs uninterrupted by annual birth
198 skipping, which can affect future reproductive success by advancing the timing of estrus
199 contributing to shorter IBIs (Lee et al. 2019). As infant mortality is also predicted to advance the
200 timing of estrus and thus contribute to shorter IBIs in this population (Johnson et al. 1993, 1998),
201 we only considered consecutive births for which the first offspring survived past weaning. To
202 model IBI, we employed a GAMM with a Gaussian error distribution evaluated for cohort type
203 as grouping factor, and age and density at birth as the smooth terms. We fitted 9 competing
204 models that included a linear fixed effect for each level of cohort, a factor smooth interaction for
205 age, individual ID as random intercepts and evaluated them using AIC. To avoid low
206 representation at old ages, in this analysis we grouped all individuals age 15 and above into a
207 single age class.

208 To address the effects of early-life adversity on individual fitness, we estimated lifetime
209 reproductive success (LRS) as the total number of offspring born to each female and who
210 survived until adulthood (≥ 3 years of age). With this, we assigned offspring fitness components
211 (i.e., early survival) to maternal traits and thus assumed that early offspring viability is controlled
212 largely by the mother (Wolf and Wade 2001), an assumption that holds in rhesus macaques
213 (Hinde and Spencer-Booth 1967; Maestripieri 2018). This analysis used data from adult females
214 living their entire life in Cayo Santiago (i.e., never removed; $n_{\text{(hurricane)}} = 84$, $n_{\text{(nonhurricane)}} = 579$).
215 We also performed a second analysis by defining LRS as the total number of offspring born to
216 each female, independently of whether the offspring survived to maturity. We present this
217 analysis as a direct comparison with other primate studies (Weibel et. al 2020). Given the
218 significantly skewed distribution of LRS, as observed in other organisms (Tuljapurkar et al.
219 2020), we tested differences in LRS between cohorts using a Wilcoxon rank-sum test and
220 whether density predicted LRS using a series of simple linear regressions evaluated with AIC.
221 As lifespan is known to be critical factor in determining LRS for long-lived primates (Blomquist
222 2013; Weibel et al. 2020), a final set of linear regression models was performed and compared
223 using AIC to determine the relationship between LRS and lifespan of females.

224 **Results**

225 Mean age-specific fertility was found to be driven by both major hurricanes and density
226 at birth ($n = 13,968$, $adjR^2 = 0.12$; cumulative model weight = 0.70; Figure 1A; Table 1; Table
227 ESM1). Females in the hurricane cohort exhibited a lower probability of successfully
228 reproducing during early ages (3-5 years; 0.490 ± 0.282 , mean \pm SD), relative to the non-
229 hurricane cohort females (0.526 ± 0.210 ; Figure 1A). However, females in the hurricane cohort
230 had a higher probability of successfully reproducing during reproductive prime ages (6-14 years;

231 0.765 ± 0.055), relative to females in the non-hurricane cohort (0.713 ± 0.037; Figure 1A).
232 Increased density at birth had a negative effect on fertility in both cohorts (Figure 1B; Table 1;
233 Figure ESM1; Table ESM1).

234 Age at reproductive debut varied from 3.00 to 8.95 years of age. Females experiencing a
235 major hurricane early in life showed a delayed sexual maturity debuting at a median age of 4.55
236 years (95% CI: 3.86, 5.89) in contrast to females from the non-hurricane cohort who debuted at a
237 median age of 4.08 years (95% CI: 3.73, 5.79; $n=1,620$, $W=120075$, $P = 0.000076$; Figure 2).
238 Density at birth was nonlinearly associated to age at reproductive debut where increasing
239 densities delayed maturity until an intermediate density value (~350 adult females) in which the
240 age at reproductive debut decreased with increasing density ($y=-9.4e^{-6}+0.006x+3.50$, cumulative
241 model weight = 1.0; ESM4). Inter-birth intervals were similar between both cohorts (hurricane =
242 367.0±33.0 days [mean±SD], non-hurricane = 371.2±33.3 days), and thus we found no cohort-
243 effects on IBI (Figure 3). However, our analysis suggests age-specific differences and density
244 effects on IBI ($adjR^2=0.023$, $n=4,941$, cumulative model weight = 1.0; Table 2; ESM2). Age-
245 specific effects were nonlinear with very young and very old females exhibiting the highest IBIs,
246 while density effects were mostly negative and stronger at intermediate population sizes (Figure
247 ESM2; Table ESM2). When including all offspring regardless of survival, the density and age
248 effects remain as significant predictors (Figure ESM3; Table ESM3).

249 Despite the age-specific differences documented above, we found no differences in LRS
250 between cohorts. Females in the hurricane cohort had a median LRS of 2 offspring (95% CI: 0,
251 7). Similarly, females in the non-hurricane cohort had a median LRS of 2 offspring (95% CI: 0,
252 10; $W = 25076$, $n = 663$, $P = 0.64$; Figure 4). When considering all offspring independently of
253 whether they survived to maturity, we still found no evidence of differences in LRS among

254 cohorts (hurricane cohort: 7 offspring, 95% CI: 0, 15; non-hurricane cohort: 5 offspring, 95% CI:
255 0, 17; $W = 27078$, $n = 663$, $P = 0.09$). In contrast, LRS had a nonlinear relationship with density
256 in which increased density initially increased LRS at smaller density values, but decreased LRS
257 at higher ones ($y = -0.00002x^2 + 0.0026x + 3.91$, cumulative model weight = 0.65, Table ESM5). A
258 similar trend was found when considering all offspring independently of whether they survived
259 to maturity ($y = -0.0001x^2 + 0.05x + 1.44$, cumulative model weight = 1, Table ESM6). LRS also had
260 a nonlinear relationship with lifespan with longer lifespan corresponding to higher LRS until
261 reaching an asymptote at post-reproductive ages (> 23 years of age; $y = -0.005x^2 + 0.475x - 1.85$,
262 cumulative model weight = 0.99; Figure 5; Table ESM7).

263 **Discussion**

264 In this study, we show that Cayo Santiago rhesus macaque females exposed to early-life
265 ecological adversity maintain LRS by compensating for a delayed reproductive debut later in
266 life. Females who experience adversities early in life also exhibit a higher mean fertility during
267 prime reproductive ages (i.e., 5-14 years of age) that results in no difference in LRS relative to
268 females experiencing no adversities. Our study reveals an alternative life history strategy in this
269 long-lived species to that proposed by the iPAR of accelerated reproduction following early-life
270 adversities.

271 Females display a similar trend in mean age-specific fertility. Mean fertility rates were
272 low during reproductive debut, peaked at 5-6 years of age, and remained high until age 14.
273 Increased density at birth reduced the fertility of all females, however two different reproductive
274 life history strategies were observed between the hurricane cohort (i.e., adversity-affected
275 strategy) and the non-hurricane cohort (i.e., typical strategy). The adversity-affected strategy
276 involved delaying reproductive debut. Harsh conditions early in life, especially those involving

277 psychosocial and nutritional adversities, may delay reproductive debut by imposing constraints
278 on development (e.g., low body fat storage, low nutrient intake; Monaghan 2008) due to
279 associations between birth weight and behavioral and physical performance later in life
280 (Zablocki-Thomas et al. 2017). Density-dependent delays in reproductive maturation have been
281 observed in Cayo Santiago females (Bercovitch and Berard 1993) and major hurricanes are
282 known to suppress their annual mean fertility (Morcillo et al. 2020). Here we show that both
283 ecological adversities, when experienced early in life, also predict a reproductive life history
284 strategy that involves reductions in mean fertility. Yet, females maintained LRS. Delaying early
285 reproduction and compensating for it later may support LRS maintenance among Cayo Santiago
286 females because of their high mean survival, long lifespan, and multiple reproductive events in
287 life. As increased reproduction during early stages (i.e., typical strategy) can impose constraints
288 on energy usage by females through a conflict in the need for growth and development between
289 the mother and offspring (Pittet et al. 2017), the delay-overshoot pattern in mean age-specific
290 fertility displayed by females may be a trade-off-induced adaptive life history decision
291 (McNamara and Houston 1996). Such strategy suggests that investing in reproduction at later
292 ages allows females that experience early-life adversity allocate more energy to development and
293 maintenance at younger ages in order to reproduce at an overall mean rate equivalent to that of
294 the typical cohort.

295 Exposure to major hurricane events early in life decreased the pace of reproduction in
296 females by delaying reproductive debut but did not affect IBIs. Cayo Santiago rhesus macaques
297 are seasonal breeders but the timing of birth during the season (i.e., early vs late), and the
298 spacing between annual breeding seasons, allows a proportion of females to go into estrus
299 annually and reproduce in consecutive seasons (Hernández-Pacheco et al. 2016b). Rhesus

300 macaques that are born during the peak of the birth season also possess higher survivorship than
301 those born outside of it, making consistent crest-to-crest intervals an advantaged reproductive
302 strategy (Small and Smith 1986; Bercovitch 1997). Additionally, later reproductive debut may be
303 associated with faster postpartum recuperation (Mas-Rivera and Bercovitch 2008), potentially
304 allowing early-life adversity affected females to maintain their IBIs.

305 The mean reproductive schedule exhibited by females experiencing early-life adversity
306 allowed them to maintain a LRS similar to that of unaffected females. Rather than being
307 associated to early-life ecological adversities, LRS was associated with lifespan. For long-lived
308 primates, lifespan is an important predictor of LRS (Blomquist 2013; Weibel et al. 2020).
309 Previous studies at Cayo Santiago also found that differences in reproductive timing are not
310 associated with significant differences in LRS (Bercovitch and Berard 1993). Thus, accelerated
311 reproduction is not supported as an adaptive response to early-life adversity in Cayo Santiago
312 rhesus macaque females. Instead, our study suggests potential trade-offs between survival and
313 reproduction in which adversity-affected females allocate more energy to growth or maintenance
314 processes at younger adult ages, in order to ensure future reproductive potential (Thompson
315 2017; Morcillo et al. 2020).

316 The Cayo Santiago population presents a novel reproductive strategy where females
317 experiencing major natural disasters and high competition at birth ultimately overcome their
318 initial reproductive penalty and exhibit no overall negative fitness outcomes. Our study reflects
319 previous findings in other long lived nonhuman primate populations in which accelerated
320 reproduction does not result in a favored strategy among females experiencing nutritional and
321 psychosocial sources of early-life adversity (PAR; Weibel et al. 2020). In the event that early-life
322 adversity is triggering a PAR response involving delayed reproduction, differential gene

323 expression through epigenetics may play some role in activating the alternative reproductive
324 strategies utilized by female cohorts (Szyf 2013; Szyf and Bick 2013; Kinnally 2014; Mitchell et
325 al. 2016; Bar-Sadeh et al. 2020;), but this remains to be explored. Our analysis also provides new
326 information on potential adaptive mechanisms following harsh conditions early in life, including
327 natural disasters. Research on how extreme climactic events act as a source of early-life
328 ecological adversity is increasingly relevant as climate change is expected to increase both the
329 prevalence and severity of major hurricane events (Knutson et al. 2020) with detrimental
330 consequences on primate population viability (Ameca Y Juárez et al. 2015). As data from long-
331 term studies accumulates, new opportunities to contribute to the early-life adversity and cohort
332 effects frameworks becomes possible. If the adversity-affected strategy exhibited by females in
333 our study is indeed adaptive, this cohort may also exhibit reproductive success during other years
334 of ecological adversity (e.g., hurricane years), outperforming those born under favorable
335 conditions (Douhard et al. 2014). Finally, our study provides further insight into factors that
336 shape the reproductive life history of individuals within populations exposed to major natural
337 disasters and reduced resources during developmental stages highlighting the need for studies
338 addressing the demographic mechanisms for life history optimization following adverse
339 conditions early in life.

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349 **Declarations**

350 Data Accessibility. Data and R codes are provided as supplementary material.

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352 Author Contributions section. RHP originally formulated the idea. RHP, LL, and CS design the
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354 CS provided editorial advise.

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525 **Tables and Figures**

526 **Table 1.** Coefficients of the top model describing mean age-specific fertility of Cayo Santiago
527 rhesus macaque females as a function of cohort type and population density at birth.

Parameter	Estimate	SE
$\beta_{(intercept)}$	0.499	0.022
Smooth terms	Estimated degree of freedom	
s(age):hurricane	6.804	
s(age):non-hurricane	8.320	
s(density)	6.045	

528 “:” stands for factor smooth interaction.

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539 **Table 2.** Coefficients of the top model describing the variability in inter-birth intervals in Cayo
 540 Santiago rhesus macaque females as a function of population density, age of the mother when
 541 giving birth, and individual monkey ID as a random effect.

Parameter	Estimate	SE
$\beta_{(intercept)}$	370.769	0.468
Smooth terms	Estimated degree of freedom	
s(age)	3.747	
s(density)	3.546	

542 “:” stands for factor smooth interaction.

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559 **Figure legends**

560 Figure 1. Model predictions for (A) mean age-specific fertility of female rhesus macaques
561 holding the population density at the time series average of 270 adult females, and (B) mean
562 fertility across density at birth holding age at the average age of 8 years. Blue: hurricane cohort;
563 orange: non-hurricane cohort. Ribbons represent 95% confidence intervals.

564 Figure 2. Age at reproductive debut of female rhesus macaques. Blue: hurricane cohort; orange:
565 non-hurricane cohort.

566 Figure 3. Age-specific inter-birth intervals of female rhesus macaques with surviving offspring.
567 Blue: hurricane cohort; orange: non-hurricane cohort.

568 Figure 4. Lifetime reproductive success for female rhesus macaques. Blue: hurricane cohort;
569 orange: non-hurricane cohort.

570 Figure 5. Association between lifespan and lifetime reproductive success of female rhesus
571 macaques. Blue: hurricane cohort; orange: non-hurricane cohort; gray: linear regression with
572 95% confidence intervals.

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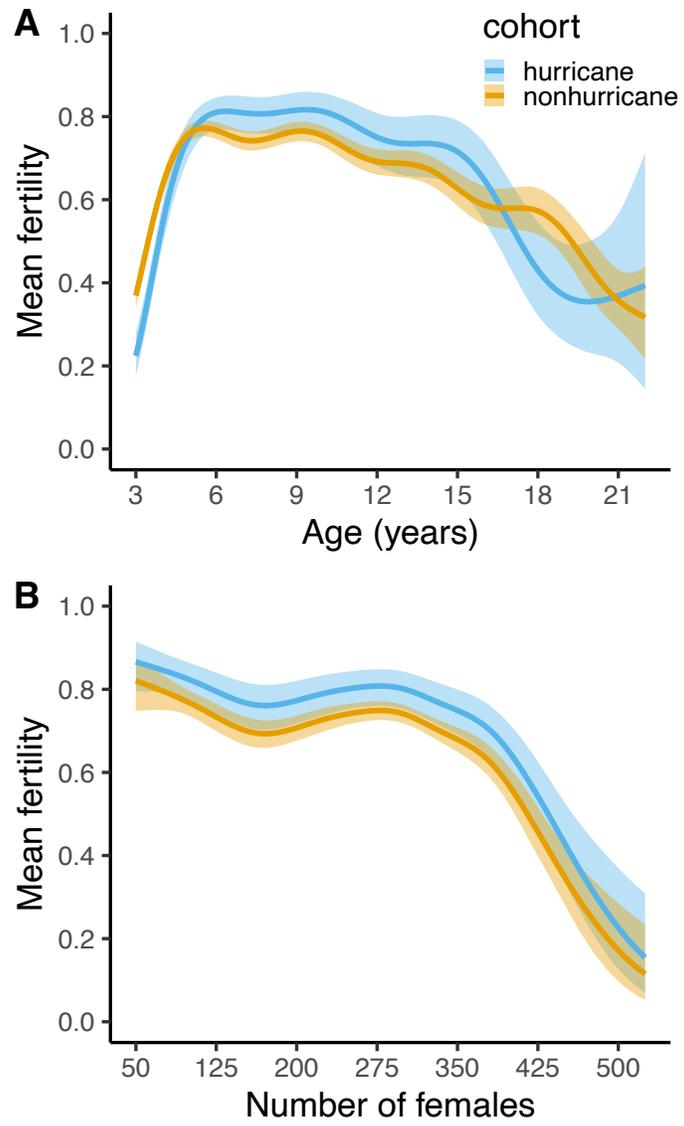
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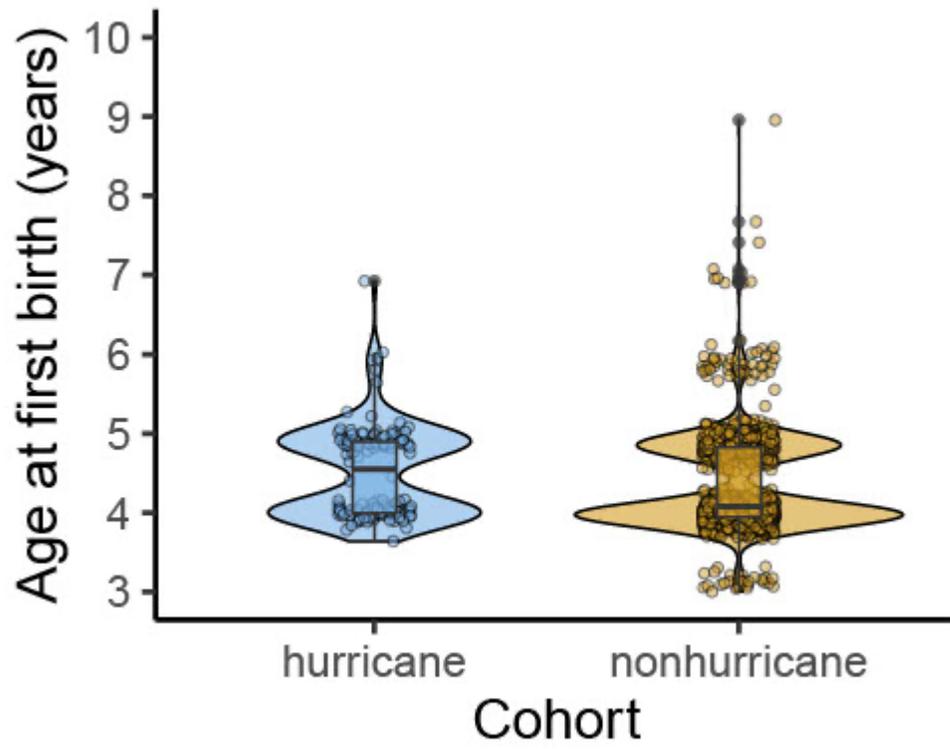
580 **Figure 1.**

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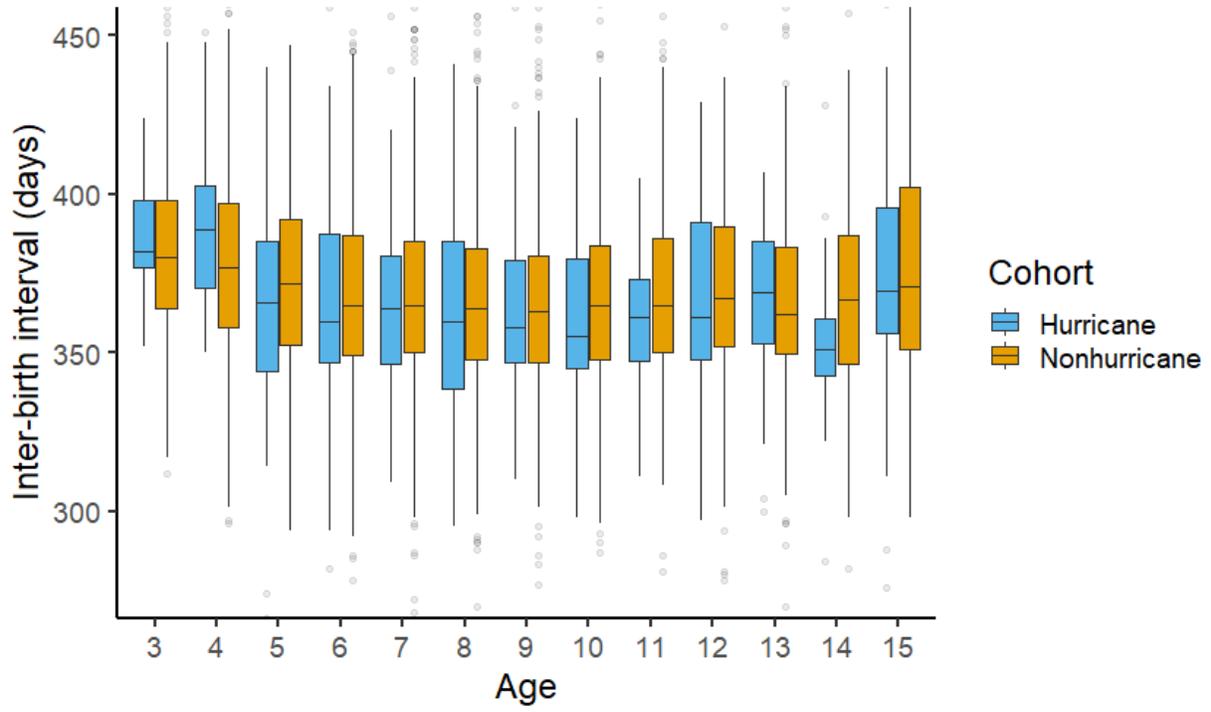


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586 **Figure 2.**

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590 **Figure 3.**

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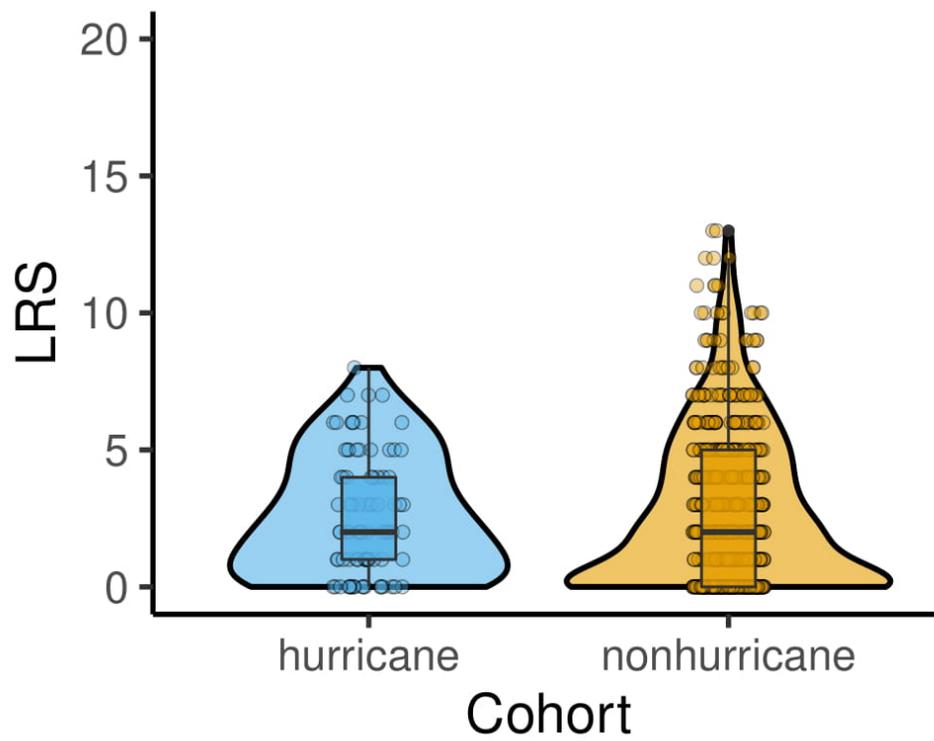
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602 **Figure 4.**

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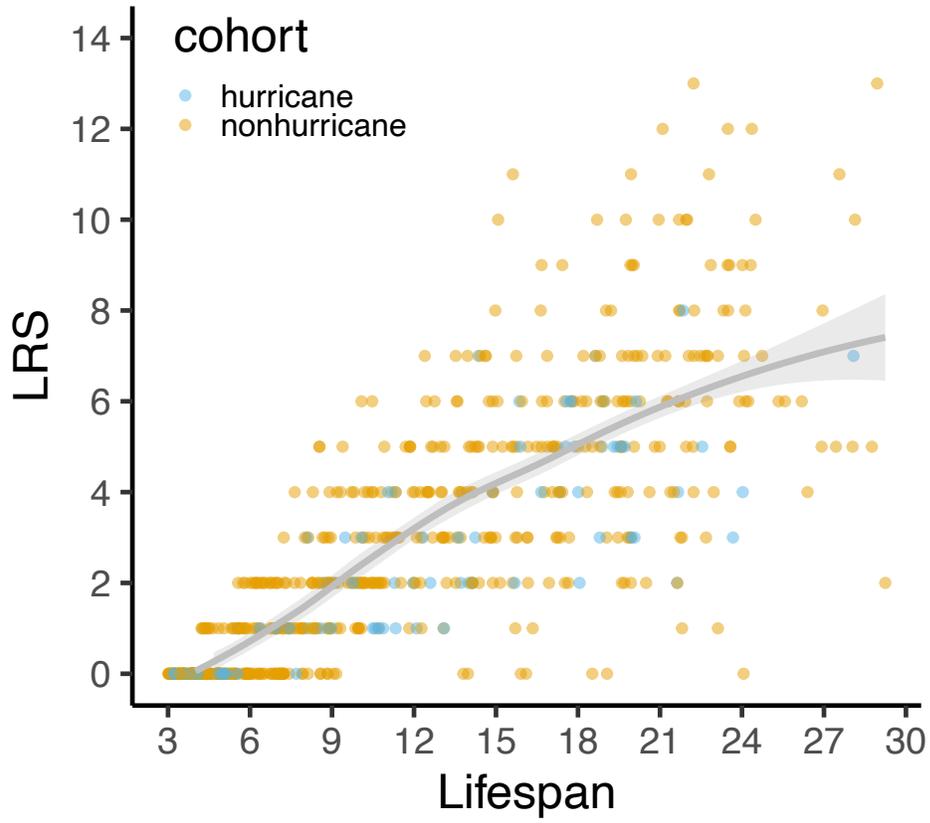
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611 **Figure 5.**

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