

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

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## Abstract

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

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

## Introduction

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

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

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

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

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

## **Methods**

### *Study Population*

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

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

### *Early-life ecological adversity*

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

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

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

#### *Statistical analysis of reproductive metrics*

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

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

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

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

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

## Results

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

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

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

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

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

## Discussion

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

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

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

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

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

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

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

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

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## **Declarations**

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

Competing Interests Statement. We declare no conflict of interest.

Author Contributions section. RHP originally formulated the idea. RHP, LL, and CS design the statistical analyses. LL and RHP performed the analyses. LL and RHP wrote the manuscript and CS provided editorial advise.

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**Tables and Figures**

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

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

“:” stands for factor smooth interaction.

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

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

“:” stands for factor smooth interaction.

## Figure legends

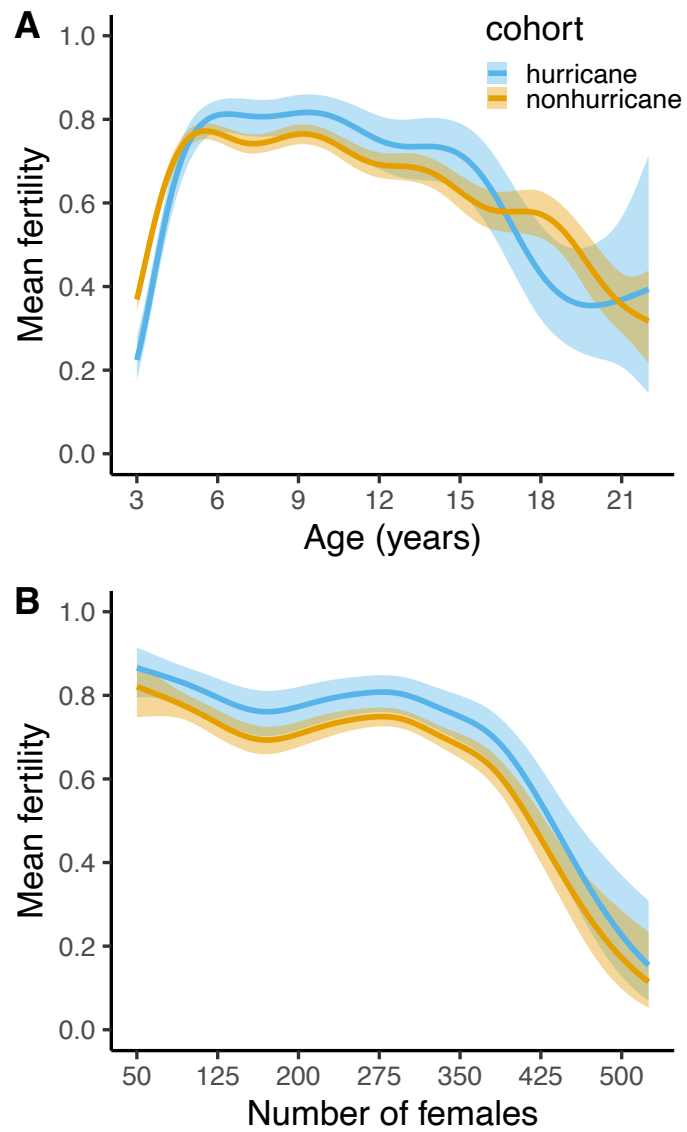
Figure 1. Model predictions for (A) mean age-specific fertility of female rhesus macaques holding the population density at the time series average of 270 adult females, and (B) mean fertility across density at birth holding age at the average age of 8 years. Blue: hurricane cohort; orange: non-hurricane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

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

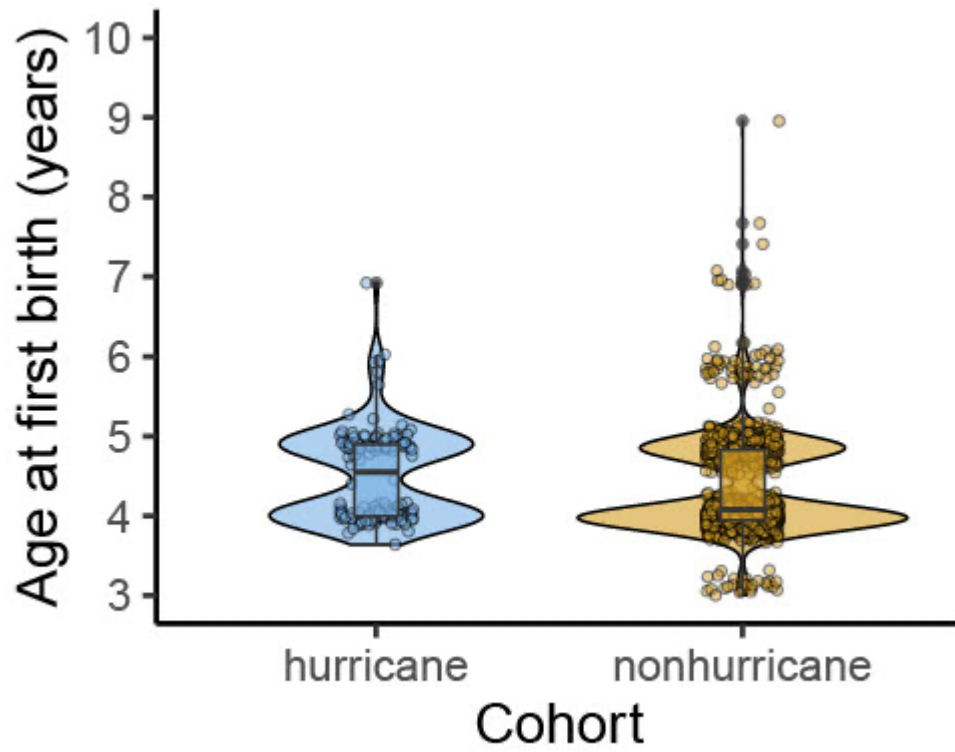
Figure 3. Age-specific inter-birth intervals of female rhesus macaques with surviving offspring. Blue: hurricane cohort; orange: non-hurricane cohort.

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

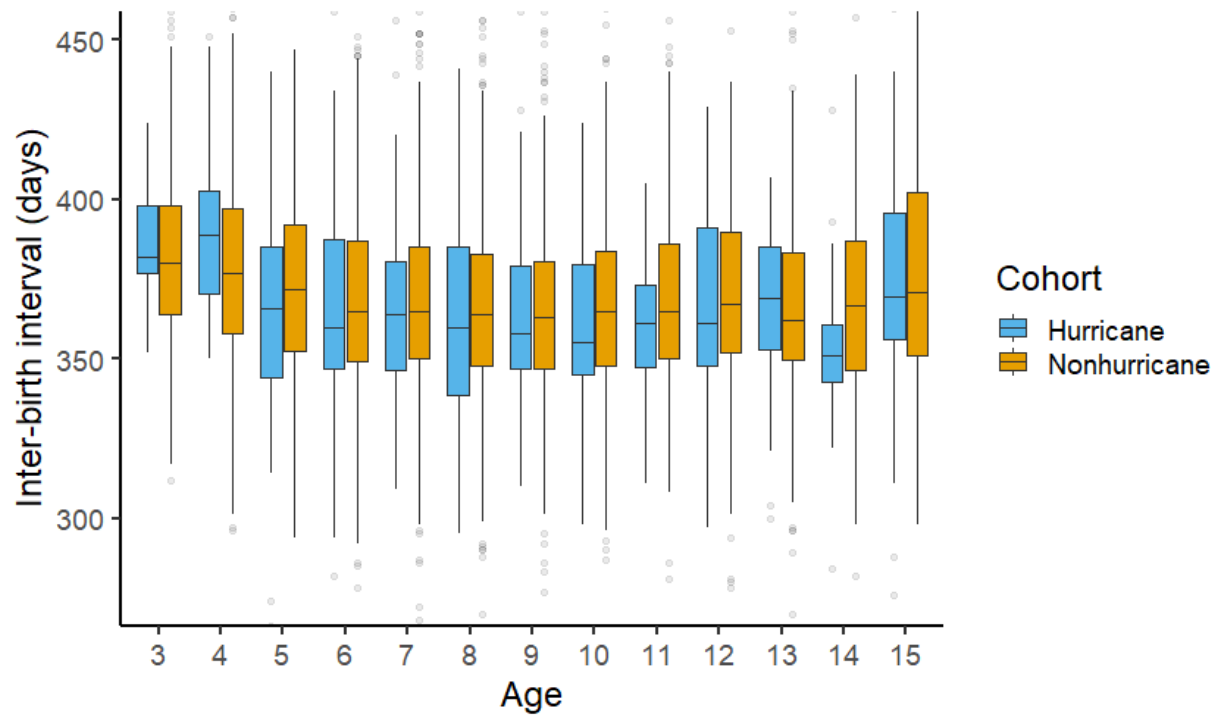
Figure 5. Association between lifespan and lifetime reproductive success of female rhesus macaques. Blue: hurricane cohort; orange: non-hurricane cohort; gray: linear regression with 95% confidence intervals.



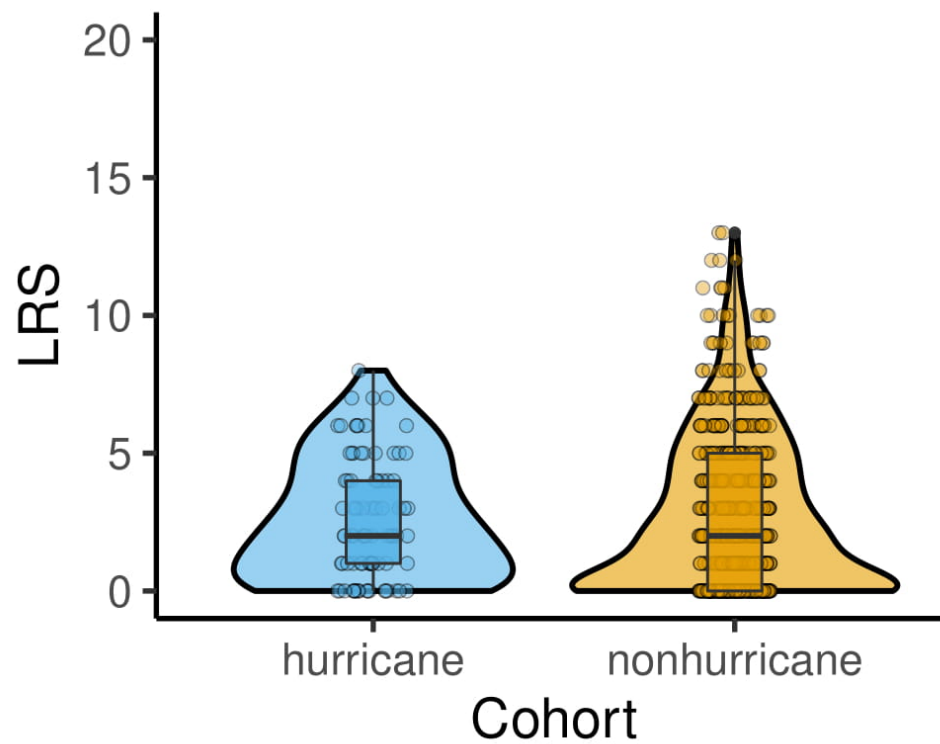
**Figure 1.**



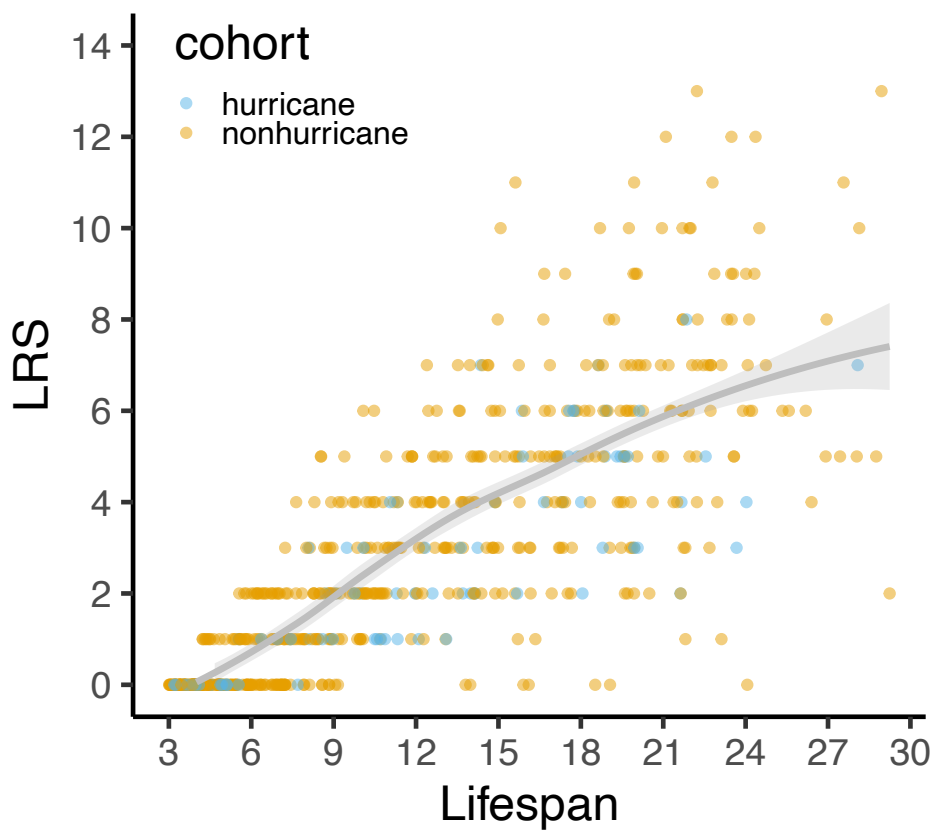
**Figure 2.**



**Figure 3.**



**Figure 4.**



**Figure 5.**