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Appendix from A. J. Lea et al., “Developmental Constraints in a Wild Primate”
(Am. Nat., vol. 185, no. 6, p. 000)

Additional Results for Developmental Constraints in a Wild Primate

Effects of Rainfall during the Periparturitional Period on Adult Fertility

We initially focused on rainfall during the first year of life, because resource access during this period influences adult reproduction and longevity in our population (Altmann 1991). However, it may be the case that experiences during other periods of early life, such as gestation, have important consequences as well. For example, previous studies suggest that maternal nutrition during gestation influences physiology and health in both animals (Dantzer et al. 2013) and humans (Roseboom et al. 2006). We therefore repeated our main analyses using cumulative rainfall over the 365 days following conception, which includes 6 months of gestation and 6 months after birth, to define the early environment. We report the results of these analyses in the main text but describe them in more detail here.

We summed cumulative rainfall over 365 days following conception (rather than birth) for all females that had reached maturity in our population. We defined early-life rainfall environments as previously described (low quality = lowest 30% of years, high quality = middle 40% of years) and repeated our analyses of conception and resumption of cycling using these redefined sets of females born in low-quality versus high-quality environments ($N = 51$). We did not detect a significant interaction effect between early-life and adult environmental conditions on conception or resumption of cycling probabilities (tables A1, A2). Taken together, it appears that baboons in Amboseli are particularly sensitive to ecological conditions and resource access during the year after birth; this finding is consistent with previous work in the Amboseli population (Altmann 1991).

Translating Model Parameter Estimates into Percentages

In the main text, we report some of our model results as percentages (e.g., conception probabilities decreased by a mean of 24% during the 2009 drought). To translate our fitted generalized linear mixed-effects model into these reported percentages, we substituted the estimated coefficients for each fixed effect, as well as the model intercept (as reported in table 2), into the logistic function

$$P = 1/\left(1 + \exp\left\{-\beta_0 + \sum_{k=1}^{7} -\beta_k x_k\right\}\right). \tag{A1}$$

Here, we used the estimated model intercept (β_0) and the estimated coefficient (β_k) for each of the seven fixed effects (k) to calculate the probability of conception (P) for a given individual. To isolate how ecological effects influenced this probability, we modeled an “average” female in the population by using the average value (x_k) for each nonecological predictor of fertility (k) in our data set (average values were age = 11.36 years, rank = 10, group size = 70 individuals, and time since last live birth = 278.73 days; individuals were not pregnant and had not experienced a recent infant death). We then calculated how changes in an ecological predictor (e.g., low-quality vs. high-quality early environment) altered the probability of conception for this “average” female. We multiplied these probabilities by 100 to obtain the percentages reported in the main text.

We used a similar approach to estimate how, for females born in low-quality environments, the probability of resumption of cycling and conception changed as a function of maternal dominance rank. Below, we describe this approach for conception probabilities alone; however, an identical procedure was used to estimate the effect of maternal rank on resumption of cycling probabilities.

Current dominance rank and maternal dominance were collinear ($r^2 = 0.67$) and thus could not be included in a single model. As described elsewhere, we therefore used the residual variation from a generalized linear model (logit link) that included all nonecological predictors (age, a_i; group size, s_i; dominance rank, r_i; infant death, d_i; pregnant, p_i; time since last live birth, t_i) to predict conception probability. Here, females are indexed by i, β_0 is the intercept, and ε_i denotes variation that is not explained by the predictor variables:

$$P(y_i = 1|a_i, s_i, d_i, t_i, p_i, r_i) = \text{logit}(\beta_a a_i + \beta_{a2} a_i^2 + \beta_s s_i + \beta_d d_i + \beta_r r_i + \beta_t t_i + \beta_p p_i + \beta_0 + \varepsilon_i). \tag{A2}$$

We then fit a linear model predicting residual variation in conception during the 2009 drought (ε_i) as a function of maternal dominance rank (r_i) for females born in low-quality environments ($N = 14$):

$$\varepsilon_i = \beta_r \text{r}_i + \beta_0 + \varepsilon_{i2}. \tag{A3}$$

Using the parameter estimates from this linear model (β_r, β_0), we determined the predicted values of $\hat{\varepsilon}_i$ given maternal dominance rank values from 1 (alpha/high) to 15 (low ranking). These predicted values represent the additional effect (before logit link transformation) of maternal dominance rank on a female's probability of conception during the 2009 drought. To estimate the impact of a change in dominance rank on conception probability for females born in low-quality environments, we added these values to the predicted probability of conception for an "average" female (calculated from the generalized linear model for nonecological predictors described above). This procedure allowed us to calculate that the probability of conception for females born in low-quality environments increased by 1.34% ± 0.14% (mean ± SD) for each improvement of one rank position in maternal social status. In other words, 1.34% is the average difference in conception probabilities for two females born to adjacently ranked mothers multiplied by 100. For resumption of cycling, each improvement of one rank position in maternal social status translated to a 1.84% ± 0.48% gain in cycle resumption probability.

Between-Condition Analyses: Comparison between the Two Groups of Study Females (Those Born in Low-Quality Environments and Those Born in High-Quality Environments) within a Given Adult Environment

The primary analysis we presented in the main text focused on within-individual responses to the 2009 drought versus normal years. We found that females born in high-quality environments were less affected by the 2009 drought than females born in low-quality environments for both of the fertility outcomes that we examined (see first section of "Results"). We also tested for aggregate differences in reproductive performance during adulthood, comparing females born in low-quality environments with females born in high-quality environments, in either 2009 or high-quality years (i.e., we tested whether females born in low-quality environments experienced reduced fertility overall compared with females born in high-quality years). The corresponding methods for those analyses are described in greater detail here.

First, we examined resumption of cycling and conception during the 2009 drought. This data set consisted of the same females included in the within-individual analyses (i.e., females who were multiparous and potentially reproductive in 2009). One additional female who was multiparous in 2009 (but did not live through an average rainfall year as a multiparous adult) was also included in the analysis (total $N = 51$ females). Using this data set, we predicted resumption of cycling and conception, in separate analyses, using the following generalized linear model:

$$P(y_i = 1|a_i, s_i, d_i, t_i, p_i, r_i) = \text{logit}(\beta_a a_i + \beta_{a2} a_i^2 + \beta_s s_i + \beta_d d_i + \beta_r r_i + \beta_t t_i + \beta_p p_i + \beta_0 + \varepsilon_i). \tag{A4}$$

We controlled for the effects of age (a_i), group size (s_i), dominance rank (r_i), and all reproductive readiness measures (recent infant death: d_i; time since last live birth: t_i; pregnancy status at the beginning of the year for the conception model or cycling status at the beginning of the year for the resumption of cycling model: p_i) on each reproductive outcome (y_i). Here, β_0 represents the intercept and ε_i denotes model error. We extracted residuals from each drought-specific model (one for resumption of cycling and one for conception) and compared these residuals between females born in poor-quality environments and females born in high-quality environments (Welch two-sample t-test). This approach allowed us to test for differences in cycling resumption and conception during the 2009 drought that were not explained by other predictors of fertility. As reported in the main text, we observed a trend toward reduced conception probabilities among females born in low-quality environments relative to females born in high-quality environments ($t = -1.646$, $P = .107$) but no detectable pattern for resumption of cycling ($t = -1.139$, $P = .263$).

Next, we conducted parallel analyses to compare reproductive performance between the two groups of females in high-quality years. For these comparisons, we focused on females born in low-quality and high-quality early environments that experienced at least one high-quality year as a multiparous adult. However, in this case, we did not constrain the data set to females who had also experienced the 2009 drought as a multiparous adult, resulting in a larger sample size of females ($N = 105$ females). Because most of these females were adult in multiple high-quality years, we tested for aggregate differences between females born in low-quality versus high-quality environments by randomly selecting one observation (i.e., resumption of cycling or conception event measured during one high-quality year) per female. We then modeled each reproductive outcome separately, using the generalized linear models described above. Again, we extracted residuals from these models and compared resumption of cycling and conception probabilities for females born in low- and high-quality environments (Welch two-sample *t*-test) after controlling for age, group size, and all reproductive readiness measures. We repeated this procedure 100 times, each time extracting the *P* value corresponding to the *t* statistic. This approach allowed us to ask whether, for any subset of female observations, the early rainfall environment significantly influenced conception or resumption of cycling during high-quality years. As reported in the main text, we found no evidence that this was the case (resumption of cycling: $P > .10$ for 97% of tests; conception: $P > .10$ for 100% of tests).

In total, these results suggest that females born in low-quality environments tended to be less fertile than females born in high-quality environments during the 2009 drought. However, during high-quality years, it appears that reproductive performance was similar between these two groups of females. These results highlight the variation that existed within as well as between the groups of females that we studied (i.e., within females born in high-quality or low-quality environments). We observed a stronger signal of early-life adversity on adult fertility when contrasting fertility in high- versus low-quality adult environments within females than in a cross-sectional analysis between conditions. Notably, this result is consistent with our finding that maternal dominance rank also influenced the severity of the effects of early-life ecological adversity (thus creating heterogeneity in the set of females born in low-quality years and stressing the multidimensional nature of the early environment).

Testing for an Interaction between Early-Life Group Size and Current Group Size

Cumulative annual rainfall influences resource competition through its effects on the abundance and distribution of food. However, group size can also influence the level of resource competition experienced by an individual in a social group. Therefore, we performed additional analyses to test whether early-life group size or adult group size influenced female fertility. In addition, we asked whether these variables interacted in ways that were consistent with the predictions of a PAR or developmental constraints model. To do so, we constructed models similar to those described in the main text but included an additional continuous fixed-effect variable denoting the size of the social group at the time the focal female was born. We also included an interaction term between group size at birth and group size at the start of the focal adult period. Using this approach, we found no evidence for a main effect of early-life group size on conception or resumption of cycling (main effect of early-life group size on conception: $\beta \pm \mathrm{SE} = -1.973 \times 10^{-3} \pm 0.056$, $P = .972$; resumption of cycling: $\beta \pm \mathrm{SE} = 0.016 \pm 0.034$, $P = .642$). In addition, we found no evidence for an interaction effect on either fertility outcome (interaction effect on conception: $\beta \pm \mathrm{SE} = -1.907 \times 10^{-4} \pm 7.794 \times 10^{-4}$, $P = .807$; resumption of cycling: $\beta \pm \mathrm{SE} = -3.594 \times 10^{-4} \pm 5.000 \times 10^{-4}$, $P = .460$).

Relatedness Does Not Confound the Effects of Early-Life Conditions on Adult Fertility

Earlier studies have suggested that phenotypic plasticity is heritable (e.g., Nussey et al. 2005; Pelletier et al. 2007). Consequently, genetic relatedness could confound our results if females born in low- versus high-quality environments were more related to each other than expected by chance (i.e., compared to background levels of relatedness in our data set). To investigate this possibility, we calculated pedigree-based pairwise genetic relatedness for all females in our data set (theoretically ranging from 0 for unrelated to 1 for genetically identical) using the R package pedantics (Morrissey and Wilson 2010). We then compared the distribution of pairwise relatedness values among females born in low-quality environments and among females born in high-quality environments to the distribution of relatedness coefficients in our data set as a whole (using two-tailed Kolmogorov-Smirnov tests). These relatedness values were based on an extended pedigree compiled from known maternal and paternal assignments for individuals in Amboseli. Maternity in our population was assigned through direct observation of mother-offspring pairs, and paternity was assigned through microsatellite genotyping of blood-derived or fecal-derived DNA (Buchan et al. 2003; Alberts et al. 2006).

Using these pedigree data, we found no evidence that the sets of females born in low-quality environments or high-quality environments contained more close relatives than expected by chance (Kolmogorov-Smirnov two-sided tests: $D = 0.044$, $P = .842$ for low-quality environments; $D = 0.010$, $P = .999$ for high-quality environments). Additionally, females born in low-quality environments and females born in high-quality environments were similarly represented across social groups ($\chi^2 = 10.010$, $P = .265$ by χ^2 test), which serve to some degree as proxies for maternal relatedness (females in this species are philopatric). Thus, early environment–dependent differences in the responses of females to low- and high-quality environments in adulthood cannot be explained by higher degrees of relatedness within either group.

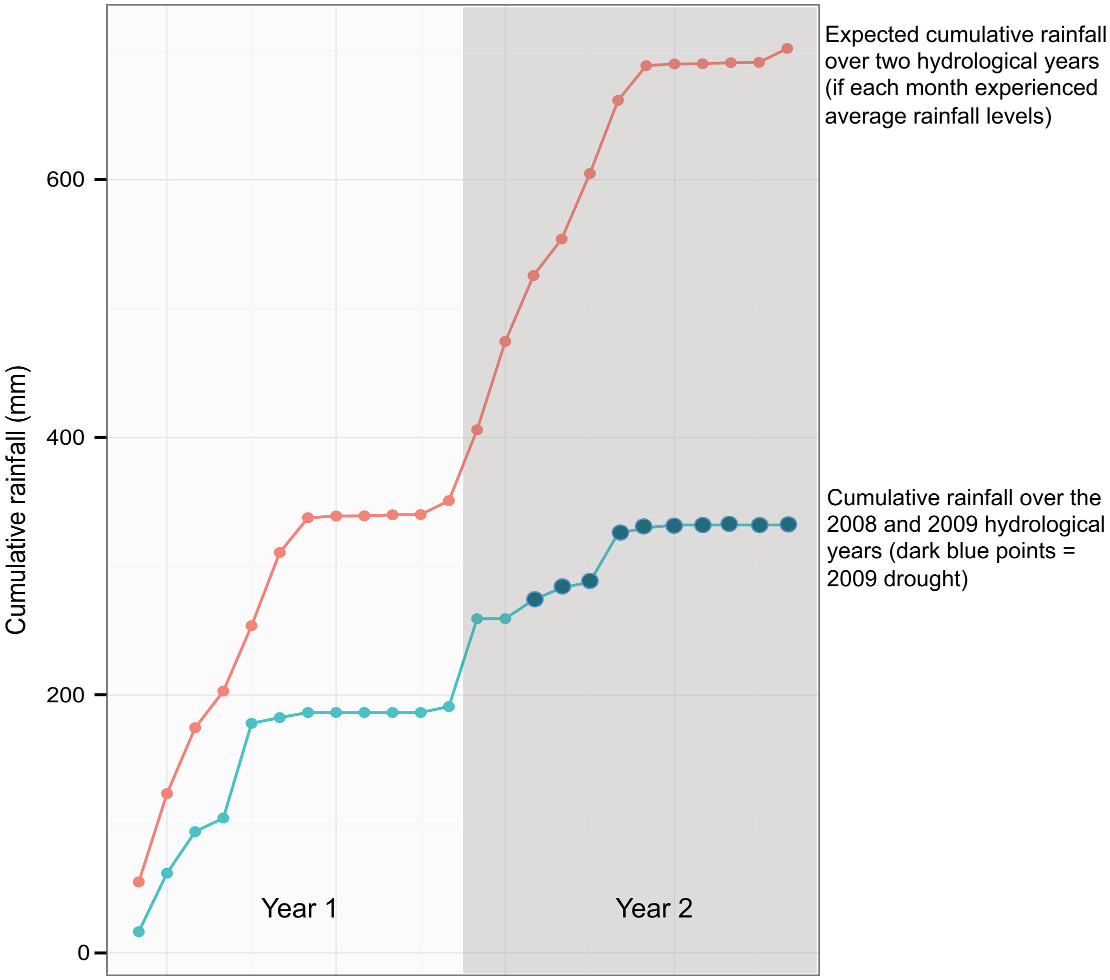

Figure A1: Cumulative rainfall during the 2008 and 2009 hydrological years was abnormally low. Blue dots and line show cumulative rainfall (mm) over the 2008 and 2009 hydrological years (year 1: November 1, 2007, to October 31, 2008; year 2: November 1, 2008, to October 31, 2009). Months included in the 2009 drought (January 1, 2009, to October 31, 2009) are denoted as dark blue points. For comparison, the pink line shows the expected level of cumulative rainfall across consecutive hydrological years if each month experienced average rainfall levels for Amboseli; these monthly averages were calculated using data from 1977–2011, excluding months in the 2008 and 2009 hydrological years. Cumulative rainfall during the 2008 hydrological year (year 1) was already lower than average, making the lack of rainfall in 2009 particularly severe.

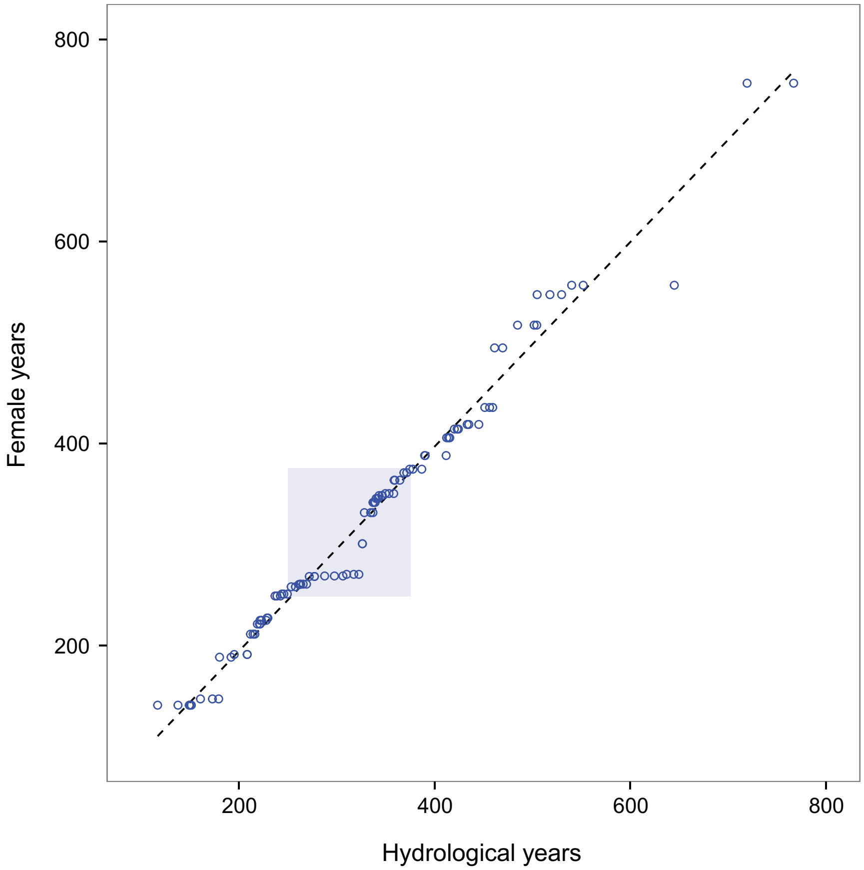

Figure A2: High-quality early years and high-quality adult years were statistically indistinguishable. Quantile-quantile plot comparing the distribution of cumulative rainfall during the first year of life for all females in the study population versus the distribution of cumulative rainfall over all hydrological years on record (1977–2011). Years that fell within the middle 40% of these distributions were defined as high-quality early and adult environments, respectively (highlighted in blue shaded square). Cutoffs used to classify high-quality early-life environments (i.e., rainfall over the first year of life) and high-quality adult environments (i.e., rainfall over a given hydrological year) are essentially identical (within ± 1 mm).

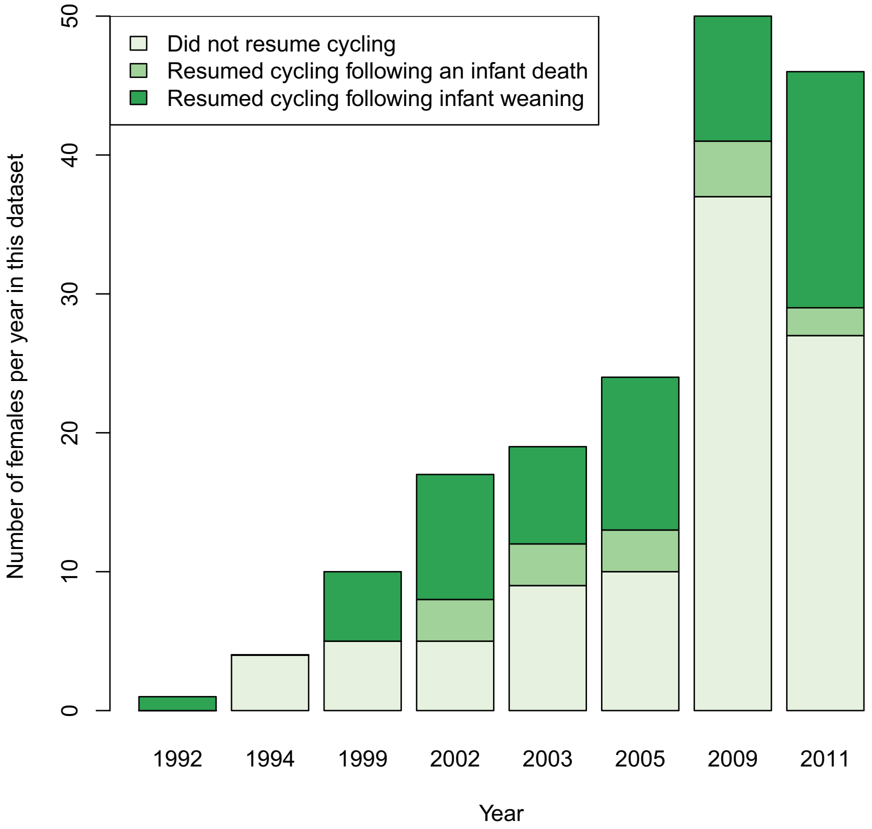

Figure A3: Variation in resumption of cycling during the 2009 drought and during high-quality years. Years represented on the *X*-axis comprise all the high-quality years in our data set as well as the year encompassing the 2009 drought (2009). Our data set was restricted to females born in a low- or high-quality environment that experienced both the 2009 drought and at least one high-quality year as a multiparous adult ($N = 50$ unique females, 172 female-years). Thus, the numbers of females are low in some high-quality years because relatively few females that lived in those years survived until the 2009 drought. Bars depict the numbers of females that (i) did not resume cycling, (ii) resumed cycling after the death of a dependent offspring, or (iii) resumed cycling after the successful weaning of a dependent offspring.

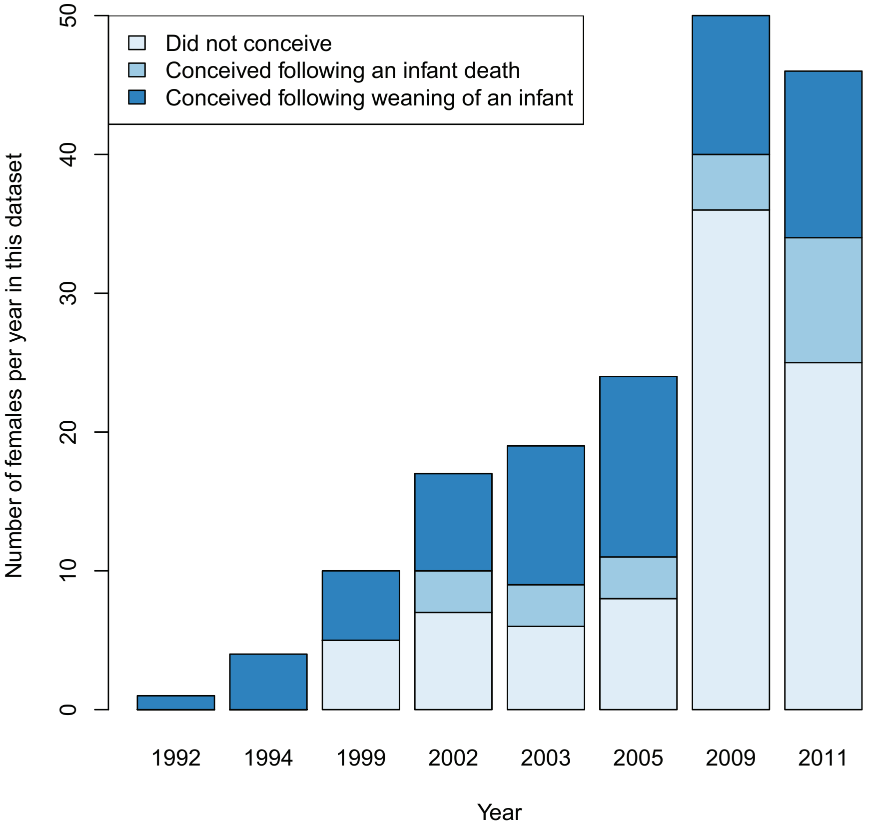

Figure A4: Variation in conception during the 2009 drought and during high-quality years. Years represented on the *X*-axis comprise all the high-quality years in our data set as well as the year encompassing the 2009 drought (2009). Our data set was restricted to females born in a low- or high-quality environment that experienced both the 2009 drought and at least one high-quality year as a multiparous adult ($N = 50$ unique females, 172 female-years). Thus, the numbers of females are low in some high-quality years because relatively few females that lived in those years survived until the 2009 drought. Bars depicts the numbers of females that (i) did not conceive, (ii) conceived after the death of a dependent offspring and cycle resumption, or (iii) conceived following the successful weaning of an offspring and cycle resumption.

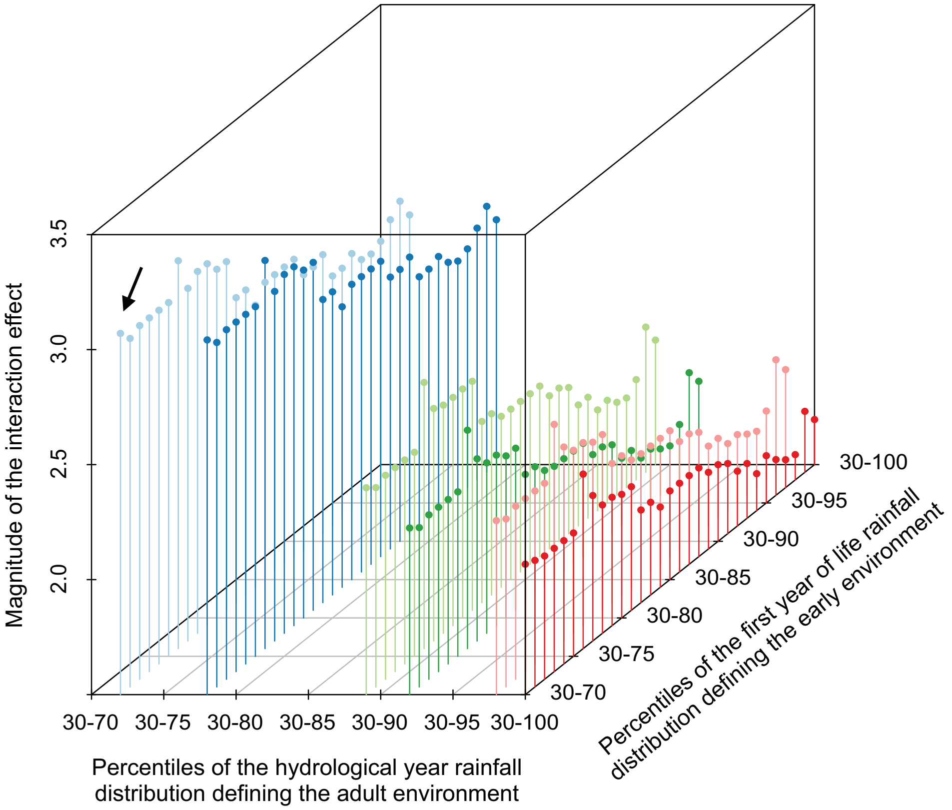

Figure A5: Interactions between adult and early-life environments under alternative definitions of high-quality environment. The magnitude (i.e., the absolute value) of the interaction effect between adult and early environments on female conception are plotted on the *Z*-axis as a function of different definitions of a high-quality environment. Percentiles used as cutoffs for high-quality environments (i.e., where all years above the 30th percentile and below the cutoff are considered high-quality years) are plotted on the *X*-axis (adult environment) and *Y*-axis (early environment), respectively. For cases in which model estimates did not change as a result of changes in the definition of the adult environment (because no new data were included in the analysis), points are not plotted. For the two most restrictive definitions of high-quality adult years (light blue and dark blue points), the interaction effect was significant across all definitions of high-quality early years ($P < .05$). The black arrow points to the estimate reported in the main text (i.e., where high-quality adult years and high-quality early-life years are defined as years falling between the 30th and 70th percentiles of the cumulative rainfall distribution). For all analyses reported here, we used the definitions of low-quality early years and low-quality adult years described in the main text.

Table A1: Results from a generalized linear mixed-effects model predicting resumption of cycling, with early life defined as the periparturitional period

	Variable type	Estimate	SE	Z	P	Explanation of effects ($P < .10$)
(Intercept)		2.359	1.779	1.326	.184	…
Age	Continuous	−.305	.253	−1.206	.228	…
Age^2	Continuous	.012	.010	1.231	.218	…
Current rainfall environment	Binary (0 = drought/1 = high quality)	.375	.638	.589	.556	…
Early rainfall environment[a]	Binary (0 = low quality/1 = high quality)	−.755	.655	−1.15	.248	…
Current × early rainfall environment	Interaction between two binary variables	.167	.782	.215	.830	…
Cycling	Binary (N = 0/Y = 1)	−1.668	.507	−3.287	.001	Females cycling on January 1 were less likely to resume cycling over the following 10 months
Time since live birth	Continuous	.003	.001	2.955	.003	Females that had recently given birth were less likely to resume cycling
Infant death	Binary (N = 0/Y = 1)	.694	.608	1.140	.254	…
Dominance rank	Continuous	.031	.297	1.042	.297	…
Group size	Continuous	<.001	.008	−.071	.943	…

Note: All variables were fit as fixed effects. Female identity was fit as a random effect (random effect variance ± SD = 0.114 ± 0.206).

[a] For this analysis, the early rainfall environment is defined from a distribution of cumulative rainfall over the 365 days following the focal female's conception (i.e., gestation and the first 6 months of life) rather than the first year of life.

Table A2: Results from a generalized linear mixed-effects model predicting conception, with early life defined as the periparturitional period

	Variable type	Estimate	SE	Z	P	Explanation of effects ($P < .10$)
(Intercept)		−6.848	2.638	−2.59	.009	…
Age	Continuous	1.486	.407	3.644	<.001	…
Age^2	Continuous	−.066	.017	−3.815	<.001	Very young and old females were less likely to conceive
Current rainfall environment	Binary (0 = drought/1 = high-quality)	.823	.826	.997	.319	…
Early rainfall environment[a]	Binary (0 = low quality/1 = high quality)	−.177	.888	−.200	.841	…
Current × early rainfall environment	Interaction between two binary variables	.195	.993	.196	.844	…
Pregnant	Binary (N = 0/Y = 1)	−5.778	1.129	−5.120	<.001	Females that were pregnant at the start of the time period were less likely to conceive over the following 10 months
Time since live birth	Continuous	.005	.001	4.226	<.001	Females that had recently given birth were less likely to conceive over the following 10 months
Infant death	Binary (N = 0/Y = 1)	4.242	1.188	3.570	<.001	Following a recent infant death, females were more likely to conceive
Dominance rank	Continuous	−.035	.041	−.86	.388	…
Group size	Continuous	−.024	.011	2.139	.032	In larger groups, females were less likely to conceive

Note: All variables described in table A1 were fit as fixed effects. Female identity was fit as a random effect (random effect variance ± SD = 0.960 ± 0.980).

[a] For this analysis, the early rainfall environment is defined from a distribution of cumulative rainfall over the 365 days following the focal female's conception (i.e., gestation and the first 6 months of life) rather than the first year of life.

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