<u>SUPPLEMENTARY MATERIAL</u>

Lifetime fitness in wild female baboons: individual heterogeneity in quality drives relationships among life history traits, By Emily M. McLean, Elizabeth A. Archie, Susan C. Alberts

Supplementary Methods

Selection on reproductive lifespan and birth rate. We calculated selection differentials and selection gradients for the phenotypes considered in our quality indices (age at first reproduction, proportion offspring surviving, surviving interbirth interval and reproductive lifespan). We report selection gradients and differentials that reflect the phenotypic relationships between traits and fitness. In this approach, we are unable to estimate how traits will respond to selection (to do so would require measuring the genetic correlation between a given trait and fitness); instead, the analysis produces estimates of how traits and correlations between traits influence phenotypic natural selection (described in Lande and Arnold 1983; see Langeloh et al. 2016; Kooyers et al. 2017; Tanner et al. 2017 for recent applications).

Selection differentials measure total predicted change in a trait resulting from selection on that trait, but do not distinguish between changes that result from *direct* selection on that trait and changes that result from *correlations* between that trait and other traits (*indirect* selection). Selection differentials were calculated from univariate regressions between the trait in question and individual fitness (LRS or λ_{ind}). Selection gradients, in contrast, measure the association between a given trait and fitness that is independent of the other correlated traits included in the model. Selection gradients are represented by partial regression coefficients from a multiple regression between fitness and multiple correlated traits (Lande and Arnold 1983; see Tanner et al. 2017 for an example of this approach).

We calculated linear selection differentials and gradients. Linear selection differentials and gradients can be interpreted as changes that will alter the mean of the trait distribution (evidence of directional selection). For all the regression models in the selection analyses, we standardized the predictor variable(s) (zero mean, unit variance). We also standardized our fitness measures relative to the population mean.

Determining the relationship between quality and the multivariate selection gradient

In order to determine if the heterogeneity we observed in our multivariate index of quality was a salient feature with respect to selective pressures acting on our population, we compared the axes of variation in our quality indices to the vector, β, representing the partial regression coefficients of our traits of interest on LRS (table S6). β is the vector of selection and is integral to quantitative genetic theory (Lande Arnold 1983, Wilson Nussey 2009). To measure how well our quality indices corresponded to the vector of selection, we calculated Θ, the angle between the vector represented by variation in quality and β, the vector of selection, in multivariate space.

Because we were concerned that the close association between reproductive lifespan and lifetime reproductive success could be solely responsible for the association between our quality index and fitness, we also constructed an alternative quality index based only on AFLB, OS and IBI_S. We tested the relationship between our alternative index and fitness and found very similar results using this index, so we present only the results from our complete index.

Permutation test of the tradeoff models. We designed a permutation test to examine the possibility that covariation between our response variables (RL or OS) and our predictor variable (IBI_S) may have influenced our quality metric in such a way as to bias our tradeoff models in favor of detecting tradeoffs. We conducted two separate permutation tests, one for each tradeoff model. To conduct each test, we constructed 10,000 simulated datasets. Each dataset preserved the observed pattern of covariation between the response trait (RL in tradeoff model 1 and OS in tradeoff model 2) and the predictor trait (IBI_S in both tradeoff models) by retaining the observed values for these traits. For each individual in the simulated dataset, her values for the other life history traits (AFLB and OS for tradeoff model 1, AFLB and RL for tradeoff model 2) were drawn at random from our observed values. We expected this procedure to retain evidence of tradeoffs only if the tradeoff was an inevitable artifact of the observed relationship in the principal components analysis between IBI_S and RL or between IBI_S and OS, which were the only relationships that were preserved in the randomizations. For each dataset, we then recalculated our quality index (as PC1 of a PCA using all 4 life history variables) and reconstructed our tradeoff model. To calculate p-values for our tradeoff models, we compared our observed tradeoff (the partial regression coefficient for IBI_S in each tradeoff model, using the non-randomized observed data) to the distribution of partial regression coefficients for IBI_S from tradeoff models using the 10,000 randomized datasets.

Supplementary Tables

Table S1. Outlying individuals removed from all analyses

Individual	Phenotypic outlier[1]:	Influential datapoint[2] for:	Known or suspected pathology:
K05	Age at first birth (late)	Fitness ~ Reproductive Lifespan (low fitness given lifespan)	Congenital reproductive system pathology
J00	Age at first birth (late)		Broken leg shortly after reaching sexual maturity, followed by cessation of reproductive cycling for nearly a year
D38		Fitness ~ Reproductive Lifespan (low fitness given lifespan)	None observed
L47		Fitness ~ Reproductive Lifespan (low fitness-given-lifespan)	None observed
A05	Live interbirth interval (long)	Reproductive Lifespan ~ IBI_L (short lifespan given interbirth interval)	“Disabled”; legs weak with permanently impaired locomotion
H82	Live interbirth interval (long)	Reproductive Lifespan ~ IBI_L (short lifespan given interbirth interval)	None observed

[1]Phenotypic outliers had a phenotype > 3 standard deviations from the mean
[2]Influential outliers had a disproportionate influence on the results of the given regression model, as indicated by a Cook’s distance > 0.5.

Table S2. Definition and summary statistics of all phenotypes measured.

Trait	Definition	Mean ± SD in study population	Median in study population
Age at first live birth (AFLB)	Age at which female first gives birth to a live offspring.	6.01 ± 0.60 (years)	5.9 (years)
Age at death (AD)	Age at observed death or permanent disappearance.	7.91 ± 7.69 (years - complete dataset) 14.71 ± 5.44 (years - breeders only)	5.41 (years – complete dataset) 14.31 (years – breeders only)
Reproductive Lifespan (RL)	Span between age at first live birth and age at death.	8.74 ± 5.45 (years)	8.27 (years)
Offspring Survival (OS)	Proportion of a female's live born offspring that survived to 70 weeks of age.	0.66 ± 0.29	0.75
Live interbirth interval (IBI_L)	The time between two successive live births.	1.67 ± 0.29 (years) 613 ± 106 (days)	1.67 (years) 608.6 (days)
Surviving interbirth interval (IBI_S)	The time between the birth of an infant that survived to 70 weeks of age and the next live born infant.	1.80 ± 0.33 (years) 659 ± 119 (days)	1.75 (years) 638.5 (days)

Table S3. Detailed results from path analysis (Figure 3 in main text).

	Analysis in main text (n=87)		Analysis with outliers (n=93)		Analysis with alternate definition of reproductive lifespan (n=87)	
Path	Estimate	p value	Estimate	p value	Estimate	p value
Offspring survival -> Reproductive Lifespan	0.271	0.006	0.263	0.012	0.220	0.039
Offspring survival -> LRS	0*	0.998*	-0.001*	0.978*	-0.01*	0.551*
Offspring survival -> Live interbirth interval	0.46	0.006	0.44	<0.0001	0.31	0.003
Reproductive Lifespan -> LRS	0.97	<0.0001	0.90	<0.0001	0.92	<0.0001
Live interbirth interval -> LRS	-0.21	<0.0001	-0.28	<0.0001	-0.33	<0.0001
Live interbirth interval -> Reproductive lifespan	-0.05*	0.693*	-0.10*	0.411*	-0.12*	0.253*

*Not included in best model, these results are from the full model

Table S4. Detailed results from models of offspring survival (the 'OS model') and live interbirth interval (the 'IBI_L model'); Figure 3 in main text.

		Analysis in main text (Offspring survival: n=539 offspring, n=96 females; Live birth interval: n=443 intervals, n=87 females; Surviving birth intervals, n=337 intervals, n=82 females)		Analysis with outliers (Offspring survival: n=567 offspring, n=102 females; live birth interval: n=465 intervals, n=93 females)		Analysis with alternate definition of reproductive lifespan (Offspring survival: n=539 offspring, n=96 females; live birth interval: n=443 intervals, n=87 females)	
Response variable	Predictor	Estimate	p value	Estimate	p value	Estimate	p value
Offspring survival probability (OS)	Mother's age at birth	-0.367	0.018	-0.327	0.0274	-0.347	0.0246
	Mother nulliparous (Y)	-0.616	0.056	-0.654	0.0381	-0.6117	0.0572
	Mother's death in weaning period (Y)	-1.42	<0.0001	-1.52	<0.0001	-1.478	<0.0001
	Mother's reproductive lifespan	0.353	0.017	0.301	0.322	0.3154	0.0302
	Mother's ID (random)	Variance: 0.1248	0.381*	Variance: 0.12614	0.373*	Variance: 0.1387	0.3338*
	Offspring Birth year (random)	Variance: 0.0455	0.6347*	Variance: 0.07808	0.4247*	Variance: 0.04567	0.6356*
Live interbirth interval (IBI_L)	Mother's age at birth	1.352	0.885	0.7222	0.9398	1.911	0.839
	Mother nulliparous (Y)	-15.588	0.397	-32.479	0.0849	-15.821	0.390
	Offspring death in weaning period (Y)	-170.71	<0.0001	-175.849	<0.0001	-170.354	<0.0001
	Mother's reproductive lifespan	-5.705	0.590	-20.164	0.0865	-7.88	0.456
	Mother's ID (random)	Variance: 4132	<0.0001*	Variance: 6859	<0.0001*	Variance: 4105	<0.0001*
	Offspring Birth year (random)	Variance: 1733	0.0002*	Variance: 1893	0.0001*	Variance: 1737	0.0002*

*significance values determined by likelihood ratio test between models with and without the indicated random effect

Table S5. Results from our four tradeoff models of the relationships between surviving interbirth interval (IBI_S) and RL, and between IBI_S and OS, controlling for individual quality. Here we present the results if we include outliers, and the results if we use our alternative definition of reproductive lifespan (see main text and Table 2 for results excluding outliers)

			Analysis with outliers (n=86)		Analysis with alternate definition of reproductive lifespan (n=82)	
Response variable	Model description	Predictor	Effect Size (se)	p value	Effect size (se)	p value
1. Reproductive Lifespan	RL~IBI_S not controlling for quality	Surviving interbirth interval	0.005 (0.004)	0.30	0.001 (0.004)	0.757
2. Reproductive Lifespan	RL~IBI_S controlling for quality	Surviving interbirth interval	-0.007 (0.009)	0.45	0.02 (0.007)	0.003
		Quality	1.34 (0.94)	0.16	2.35 (0.67)	0.0006
3. Proportion offspring surviving	OS~IBI_S not controlling for quality	Surviving interbirth interval	0.0001 (0.0002)	0.57	4.4e-05 (1.89e-04)	0.82
4. Proportion offspring surviving	OS~IBI_S controlling for quality	Surviving interbirth interval	0.0006 (0.0004)	0.093	0.001 (0.0003)	0.0003
		Quality	-0.06 (0.04)	0.11	0.12 (0.027)	1.96e-05

*Higher values of surviving interbirth interval represent longer birth intervals and slower birth rates. Therefore, a positive regression coefficient is indicative of a tradeoff (slower birth rates associated with longer lives)

Table S6. Selection differentials (univariate regression coefficients) and selection gradients (partial regression coefficients) for the four components of the quality metrics: age at first live birth, offspring survival, surviving birth interval and reproductive lifespan, with significant relationships in bold.

Fitness Measure	Trait*	Linear Selection Differential – Univariate Selection (p)	Linear Selection Gradient ** – Multivariate Selection (p)
LRS	Age at first live birth, AFLB	**-0.11 (0.02)**	**-0.07 (0.002)**
LRS	Offspring surviving, OS	-0.02 (0.63)	**-0.07 (0.001)**
LRS	Surviving interbirth interval, IBI_S	**-0.12 (0.01)**	**-0.08 (0.0009)**
LRS	Reproductive Lifespan, RL	**0.42 (<0.0001)**	**0.42 (<0.0001)**
λ_{IND}	Age at first live birth, AFLB	**-0.02 (0.0003)**	**-0.01 (<0.0001)**
λ_{IND}	Offspring survival, OS	**-0.01 (0.046)**	**-0.01 (<0.0001)**
λ_{IND}	Surviving interbirth interval, IBI_S	**-0.02 (<0.0001)**	**-0.01 (0.002)**
λ_{IND}	Reproductive Lifespan, RL	**0.03 (<0.0001)**	**0.03 (<0.0001)**

*See table S1 for definitions

** The selection gradients represent the multivariate vectors of selection that were then used to determine Θ, the angle between the vector of multivariate selection and PC1 shown in table S7.

Table S7. Relationships between PC1 and PC2 of our multivariate quality index and the vectors of multivariate selection for LRS and λ_{IND}.

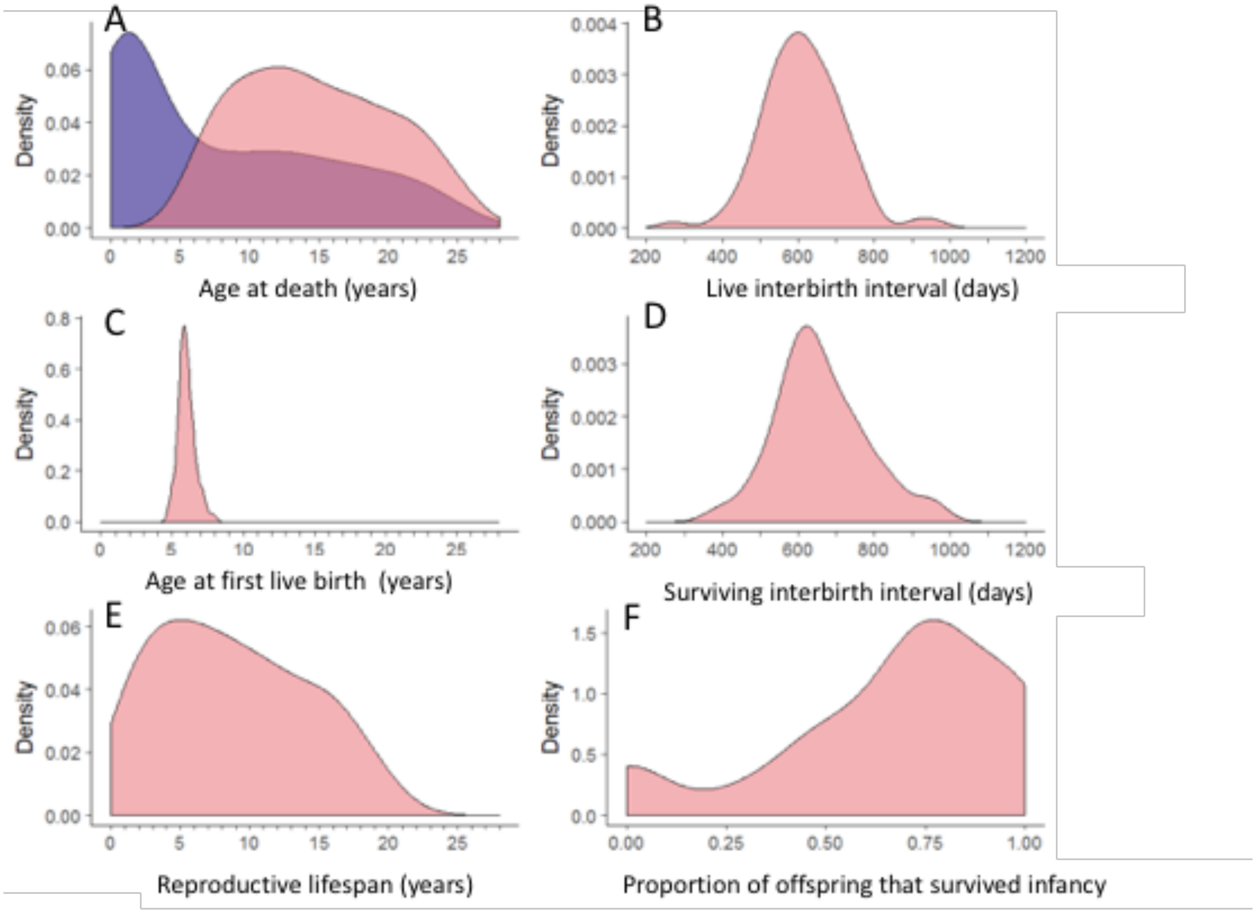
Measures contributing to the quality Index	**Principle Component**	Θ_{LRS}	$\Theta_{\lambda ind}$
AFLB, OS, IBI_S, RL*	PC1	75°	70°
	PC2	59°	70°

*See table S1 for definitions of acronyms

Table S8. Proportion of variance explained by each principal component

	PC1	PC2	PC3	PC4
Proportion of variance	0.3756	0.2825	0.2203	0.1216
Cumulative Proportion	0.3756	0.6581	0.8783	1.00

107 **Supplementary Figures**



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109 **Figure S1.** Kernel density plots showing the distributions of life history variables for breeders (pink) and
110 entire population (purple). Only age at death could be measured for females who failed to reproduce.

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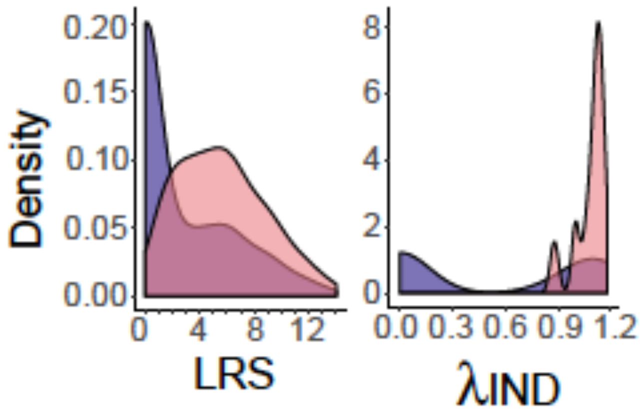

Figure S2. Kernel density plots showing the distribution of **(A)** values of LRS and **(B)** values of λ_{IND}, for the entire sample (dark purple) and for breeders only (light orange).

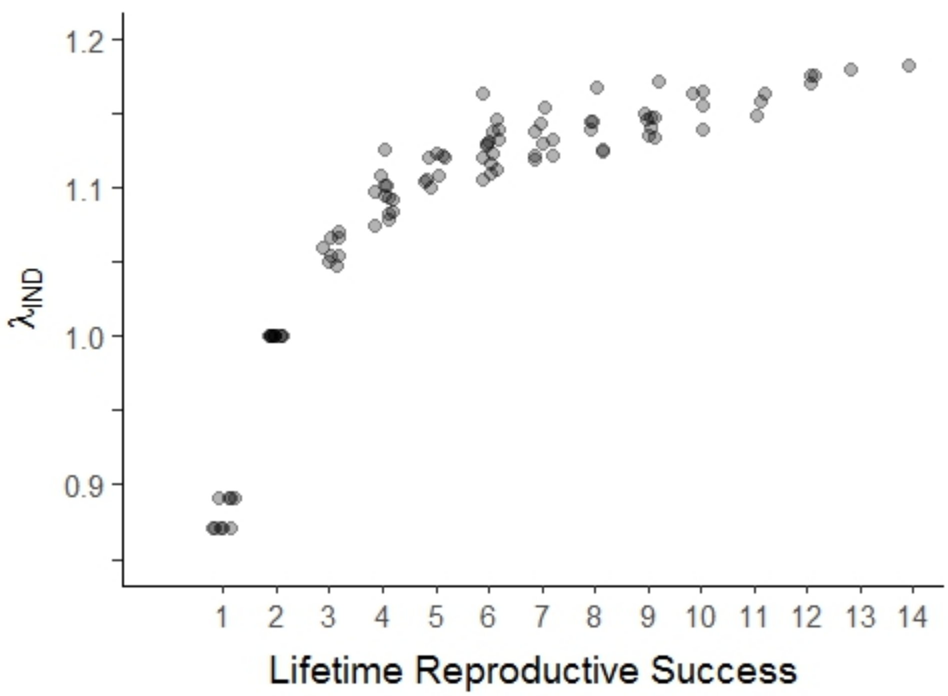

Figure S3. Curvilinear relationship between LRS and λ_{IND}.

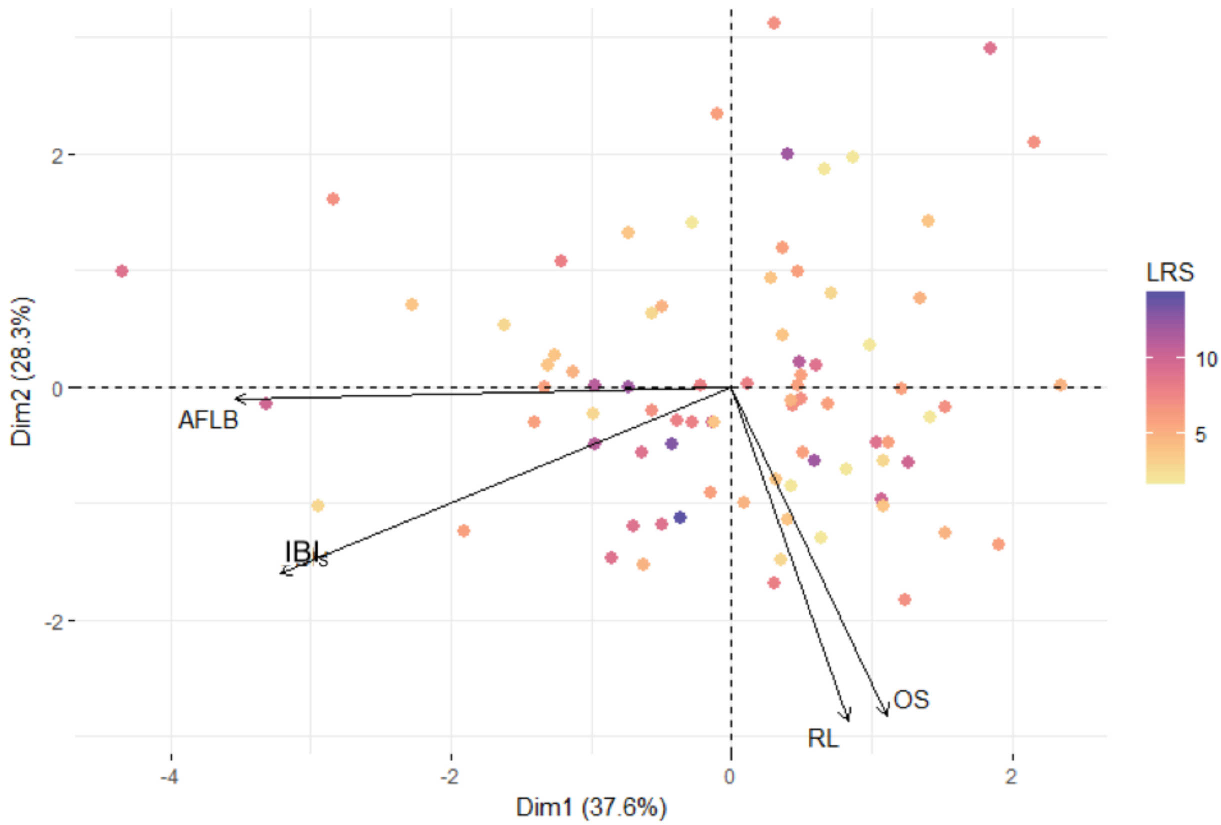

Figure S4. Visualization of principal components analysis. Points represent individual baboons and are colored to reflect their lifetime reproductive success. Arrows represent the variables included in the analysis. The direction and magnitude of the arrows reflects how well the variables correspond to PC1 (x-axis) and PC2 (y-axis). Dim1 (x-axis) is our quality metric, individuals on the left side of the plot have early ages at first live birth (AFLB) and short birth intervals (IBI_S).

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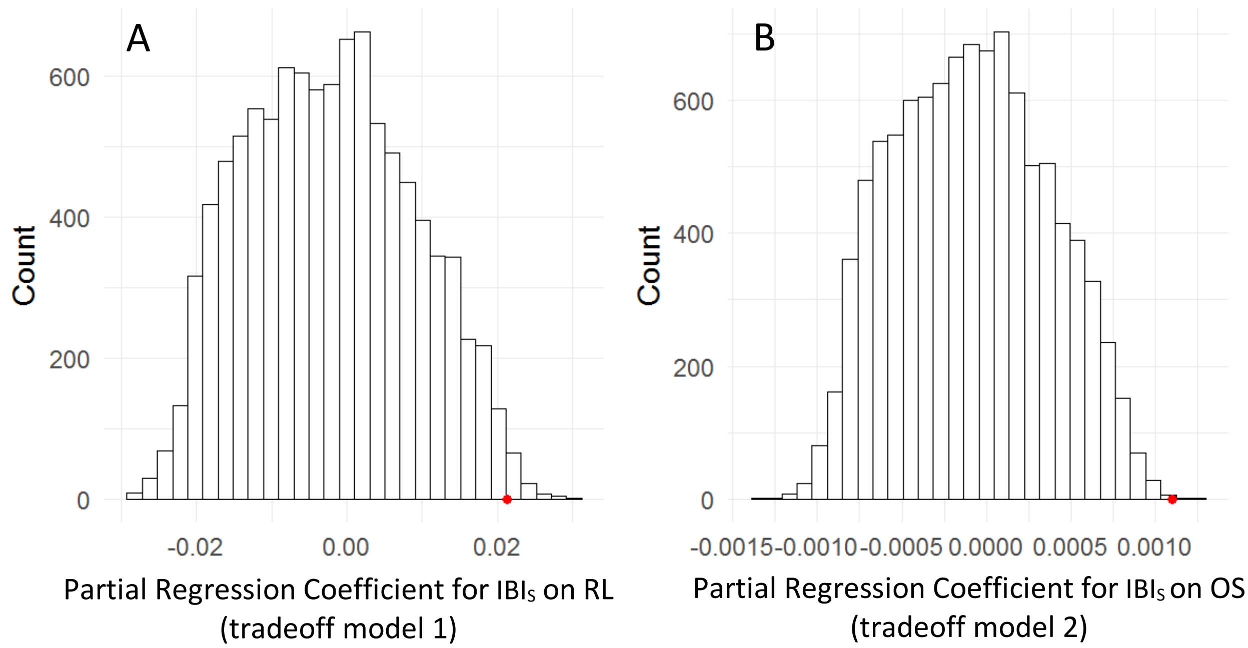

Figure S5. Distribution of tradeoff values from permutation tests. Panel A shows the distribution of partial regression coefficients for IBI_S from our permutation test for tradeoff model 1 (RL~IBI_S+Quality). Panel B shows the distribution of partial regression coefficients for IBI_S from our permutation test for tradeoff model 2 (OS~IBI_S+Quality). The values of partial regression coefficients for IBI_S from our actual, non-randomized dataset are indicated by a red dot along the x-axis in each panel. Our observed tradeoff in model 1 (A) was greater than 99.05% of the tradeoff values reported from randomized datasets (p=0.0095). Our observed tradeoff in model 2 (B) was greater than 99.95% of the tradeoff values reported from randomized datasets (p=0.0005). Note: positive values of the partial regression coefficient for IBI_S indicate a tradeoff, because high values of IBI_S indicate long intervals between births, i.e., slow birth rates.