

Online Supplement:
The contributions of maternal age heterogeneity to variance
in lifetime reproductive output

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S1 Parameterization of the age × maternal age model

The following sections (S1.1 – S1.3) have been modified from [Hernández et al. \(2020\)](#) under the terms of a [Creative Commons Attribution License 4.0 \(CC BY\)](#). Some stylistic elements were adapted to fit with the current paper. Original supplementary figures were not copied.

S1.1 Fertility model: Coale and Trussell

The Coale and Trussell model ([Coale & Trussell, 1974](#)), from human demography, represents differences in the fertility schedules of populations by using a 'natural fertility schedule' ($\tilde{m}(a)$), an age at which the population-specific schedules can diverge from the natural fertility schedule (a_0), and a parameter that controls how rapidly the schedules diverge (θ). The model is

$$m(a) = \tilde{m}(a) \exp[-v(a)], \tag{S1}$$

$$v(a) = \begin{cases} 0 & a \leq a_0 \\ \theta(a - a_0) & a > a_0. \end{cases} \tag{S2}$$

The Coale and Trussell model is typically fit to each population separately by choosing θ and a_0 to satisfy some statistical criterion (e.g., minimizing the sum of squared deviations between the model and the data).

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If we had observed the fertility schedules of individuals in every maternal age class, we could have used model (S1)–(S2) directly. We, however, need to estimate fertility schedules for maternal ages that we did not measure in the laboratory experiment by interpolating among those we did. We therefore amended the Coale and Trussell model to incorporate the effects of maternal age g :

$$m(a, g) = \tilde{m}(a) \exp[-v(a, g)], \quad (\text{S3})$$

$$v(a, g) = \begin{cases} 0 & a \leq a_0 \\ \theta \cdot (g - \tilde{g}) \cdot (a - a_0) & a > a_0. \end{cases} \quad (\text{S4})$$

We now imagine that the "natural fertility schedule" is associated with a "natural maternal age" which, in model (S3)–(S4), is the new parameter \tilde{g} .

To fit model (S3)–(S4), we minimized the sum of squared deviations between the model and the data over all of the possible choices of

$\tilde{m}(a)$. We assumed that natural fertility schedule $\tilde{m}(a)$ was one of five functions: one of the four observed fertility schedules for mothers with maternal age equal to 3, 5, 7 or 9; or the average fertility schedule over all maternal ages.

\tilde{g} . With each of the five candidate natural fertility schedules, we associate exactly one value of \tilde{g} . For the four observed schedules, with maternal ages 3, 5, 7, and 9, we set \tilde{g} equal to the maternal age. For the fifth, average, candidate schedule we set $\tilde{g} = 6$.

a_0 . Based on visual inspection of the observed fertility schedules (Fig. 1B), we assumed that $a_0 \in \{2, 3, 4, 5\}$.

θ . The rate parameter θ was assumed to be a real positive number.

The best fit is achieved by the 'average' fertility schedule for $\tilde{m}(x)$, with $\tilde{g} = 6$, $a_0 = 4$, and $\theta = 0.0192$. The data, model fits, and extrapolated curves are shown in the main text (Fig. 1B).

S1.2 Mortality model: Weibull

The Weibull model is a common representation of the time-to-failure in survival probability estimation for living organisms. It is a continuous probability distribution described by two parameters, and the shape of the probability density function (*pdf*) is very flexible. From the individual culture experiments described in [Bock et al. \(2019\)](#), we have the time-to-death of many individual rotifers—with maternal ages 3, 5, 7, and 9 days—and we used this data to fit the Weibull distribution:

$$f(x|a, b) = \frac{a}{b} \left(\frac{x}{a}\right)^{b-1} e^{-(x/a)^b}. \quad (\text{S5})$$

The failure time, x , of each rotifer in the dataset is the oldest age (days) at which it was observed alive. The Weibull *pdf* (S5) is fit to observed failure times in each maternal age cohort, yielding four Weibull models. Inspection of the parameters from those four models indicates that the parameters a and b vary log-linearly with maternal age group, such that the Weibull parameters are themselves parametric functions of maternal age group, g . Although a linear model would fit equally well to the four points, the log-linear form is necessary so that the Weibull parameters will both be non-negative for maternal age groups up to $g = 16$. With this formulation, the time-to-death description of mortality probabilities is a function of a single variable, g , which varies among groups, and four parameters that are defined for the population as a whole (the slope and intercept of the log-linear functions for a and b). The resulting Weibull *pdfs* are shifted towards earlier and more evenly spread times of death as g increases. The resulting survivorship curves are shown in the main text (Fig. 1C).

S1.3 Birthflow model: fertility and survivorship curves

Birth and death for the lab-cultured rotifers are continuous processes, and by censusing once per day, information on the age of an individual is limited. Neonates were assigned an age of 0 on the day that they were first counted in the census, but their true ages were between 0 and 1. Therefore, estimates of both fecundity and survival probability represent averages over the census interval (1 day), and a birth-flow model ([Caswell, 2001](#)) must be used to build up the

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transition matrix, $\tilde{\mathbf{A}}$.

The survivorship curve (the proportion of neonates that survive to each age) was calculated using $1 - \mathcal{F}(x|a, b)$, where \mathcal{F} is the cumulative distribution function for the Weibull model [S5]. The transition probabilities for the matrix model formulation are given by

$$P_i = \frac{l_i + l_{i+1}}{l_{i-1} + l_i}, \quad (\text{S6})$$

where P_i is the probability of surviving from age class i to age class $i + 1$, and l_i , the probability of surviving to age i , is the survivorship curve derived from the Weibull model (S5).

Likewise, the observed number of offspring produced by an individual in an interval averages over several processes that are unobserved during the interval. Production of neonates by a given age class, F_i ,

$$F_i = \frac{l_0 + l_1}{2} \cdot \frac{m_i + P_i \cdot m_i + 1}{2}, \quad (\text{S7})$$

is determined by the fertility at that age, the fertility at the next age, the probability that individuals survive to that next age, and the probability that the offspring survive long enough to be counted. The average offspring must survive 0.5 days to be counted, and the fertility of the mother is an average, weighted by the probability of surviving to the next age (Caswell, 2001). The values of the m_i in equation (S7) come directly from the fertility model described in Section S1.1.

S2 An extension: Remaining lifetime reproductive output

Lifetime reproductive output, strictly speaking, accounts for the entire life of the individual, so the calculations in Section 2.3 condition on starting in age class 1. However, it may be of interest to compute *remaining* LRO, starting from any age x . Here we show how the calculations of Section 2.3 can be extended to this case.

The vectors containing the group-specific means and variances, in equations (17) – (18) become

$$\mathbf{m}(x) = (\mathbf{e}_x^T \otimes \mathbf{I}_g) \tilde{\boldsymbol{\rho}}_1 \quad g \times 1 \quad (\text{S8})$$

$$\mathbf{v}(x) = (\mathbf{e}_x^T \otimes \mathbf{I}_g) V(\tilde{\boldsymbol{\rho}}) \quad g \times 1, \quad (\text{S9})$$

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where \mathbf{e}_x is a $\omega \times 1$ unit vector with a 1 in the x -th entry.

The mixing distribution $\tilde{\pi}$ now becomes a function of age. At birth

$$\tilde{\pi}(1) = \frac{\tilde{\mathbf{F}} \tilde{\mathbf{w}}}{\mathbf{1}_{g\omega}^T \tilde{\mathbf{F}} \tilde{\mathbf{w}}} \quad g\omega \times 1 \quad (\text{S10})$$

As the cohort ages, its composition changes due to differential mortality of maternal age groups (intra-cohort selection). The mixing distribution for some later age class x is obtained by aging the cohort:

$$\tilde{\pi}(x) = \frac{\tilde{\mathbf{U}}^{(x-1)} \tilde{\pi}(1)}{\mathbf{1}_{g\omega}^T \tilde{\mathbf{U}}^{(x-1)} \tilde{\pi}(1)}. \quad (\text{S11})$$

The mixing distribution among groups at age x is then

$$\boldsymbol{\pi}(x) = (\mathbf{e}_x \otimes \mathbf{I}_g) \tilde{\pi}(x) \quad g \times 1. \quad (\text{S12})$$

The mean of lifetime reproductive output for the set of individuals at age x , distributed according to $\boldsymbol{\pi}(x)$, is

$$\begin{aligned} E(\rho(x)) &= E_{\boldsymbol{\pi}(x)} \left[E(\rho | \text{maternal age group } \gamma) \right] \\ &= \boldsymbol{\pi}^T(x) \mathbf{m}(x). \end{aligned} \quad (\text{S13})$$

The variance in LRO for the set of individuals at age x , distributed among maternal age groups according to $\boldsymbol{\pi}(x)$, has two components, as in equation (S14). The variance within and the variance between maternal age groups now depend on age of the individual. The within-group component of the variance is the weighted mean of the variances within maternal age groups. The between-group component is the weighted variance of the means of maternal age groups.

$$\begin{aligned} V(\rho(x)) &= E_{\boldsymbol{\pi}(x)} \left[V(\rho(x)) \right] + V_{\boldsymbol{\pi}(x)} \left[E(\rho(x)) \right] \\ &= \underbrace{V_w}_{\text{within}} + \underbrace{V_b}_{\text{between}}. \end{aligned} \quad (\text{S14})$$

The expression for the within-group and between-group variance components are

$$V_w(x) = \boldsymbol{\pi}^T(x) \mathbf{v}(x) \quad (\text{S15})$$

$$V_b(x) = \boldsymbol{\pi}^T(x) (\mathbf{m}(x) \circ \mathbf{m}(x)) - (\boldsymbol{\pi}^T(x) \mathbf{m}(x))^2, \quad (\text{S16})$$

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where $\mathbf{m}(x)$ and $\mathbf{v}(x)$ are obtained as in (S8) and (S9). The variance within groups is generated by stochastic outcomes in survival and reproduction among individuals experiencing the same rates in a given maternal age group, whereas the variance between groups reflects the differences in the rates experienced by individuals of different maternal ages.

The fraction of the total variance in remaining LRO at age x due to heterogeneity can be calculated as

$$\mathcal{K}_x = \frac{V_b(x)}{V_b(x) + V_w(x)}. \quad (\text{S17})$$

This fraction tends to diminish with age, as certain cohorts experience higher mortality at older ages than others, leading to the population composition representing fewer maternal age groups.

S3 A note on the role of the mixing distribution

When survival and fertility are reduced in order to mimic different environmental conditions than what rotifers experience in the laboratory, it is no surprise that LRO is affected. The mean LRO is lowered. The within-group, between-group, and total variance in LRO change in ways that are not predictable a priori, but must be calculated. However, the changes in fertility and survival also affect the population composition, and thus the mixing distribution, often in more subtle ways.

In figure S1 we show the mixing distribution that result from the vital rates at three points on the stable population line, as in figure 4. When survival is low but fertility high, the resulting mixing distribution is close to that in the laboratory conditions (left-hand bottom panel in yellow; see Figure 3). When survival is high but fertility low, the population composition results in a flatter mixing distribution (right-hand panel in blue), with a more even distribution of newborn individuals among the maternal age groups.

We can speculate that the increased evenness of the mixing distribution in the bottom right corner helps lead to the higher contribution of heterogeneity under those circumstances. After all, the differences between individuals born to young and to old mothers only matter when those individuals are represented in the population. In the end, however, the variance in LRO

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always results from the combination of the changing mixing distribution, changing fertility, and changing survival. Disentangling these contributions is an interesting open question; the sensitivity analysis presented in van Daalen & Caswell (2020) may provide the key to approaching this problem by LTRE analysis.

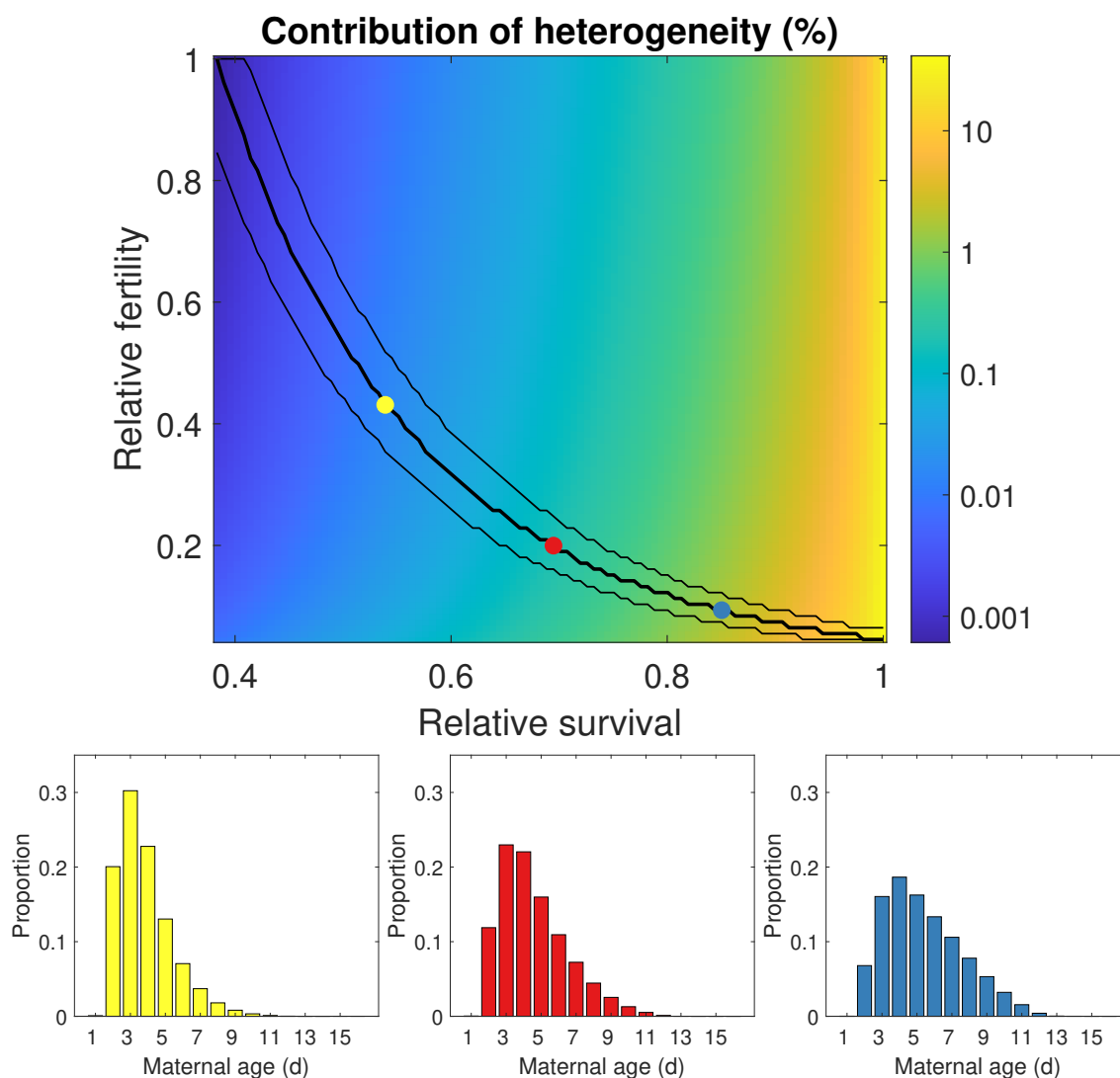


Figure S1: The mixing distributions implied by several combinations of reduced survival and fertility in relation to Figure 4 in the main text, which shows the contribution of heterogeneity to variance in LRO. The thick black line corresponds to combinations of reduced fertility and survival that result in $\lambda \approx 1$.

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