

Des différences, pourquoi? Transmission, maintenance and effects of phenotypic variance

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Supporting information

Appendix S1: Presentation of the model including analytical demonstrations

1 Successive age-dependent mean and variance of a continuous trait for a simple cohort

1.1 definitions

We define the survivorship which is the cumulative survival-and-growth functions, given by

$$L_1(y|x) = \delta_{x,y} \text{ if phenotypes discrete; else Dirac delta,} \quad (1)$$

$$L_2(y|x) = P_1(y|x), \quad (2)$$

$$L_{a+1}(y|x) = \sum_z P_a(y|z) L_a(z|x). \quad (3)$$

The “net” reproduction Φ_a gives the number of offspring produce by a cohort of age a and is equal to

$$\Phi_a = F_a L_a. \quad (4)$$

At equilibrium, let $u_a(x)$ be the normalized phenotype distribution at age a , meaning that $|u_a| = 1$. Then

$$u_{a+1} = \frac{P_a u_a}{|P_a u_a|} = \frac{L_{a+1} u_1}{|L_{a+1} u_1|}. \quad (5)$$

Equilibrium population growth rate r and the vector u_1 together solve the characteristic equation

$$\sum_{a \geq 1} e^{-ra} \Phi_a u_1 = u_1. \quad (6)$$

The average survivorship at age a can be written (from (1 – 3) and (5))

$$l_a = |L_a u_1| = s_{a-1} s_{a-2} \dots s_1. \quad (7)$$

where $s_{a-1}, s_{a-2} \dots s_1$ are the average survival at each age. The average total number of offspring produced by a cohort at age a is

$$\phi_a = m_a l_a. \quad (8)$$

Now take the norm on both sides of (6) to see that the characteristic equation can be written in the deceptively simple form

$$\sum_{a \geq 1} e^{-ra} \phi_a = 1. \quad (9)$$

1.2 Mean demographic rates

We assume that the distribution of the phenotype X_a at each age is approximately normal and can be adequately described by the first 2 moments of the distribution: the mean μ_a and the variance $v_a = \sigma_a^2$. To simplify we assume that the σ_a are small.

For any function representing the survival rate, $S_a(x)$ can be approximated using a Taylor expansion by

$$S_a(x) \approx S(\mu_a) + (x - \mu_a) S'(\mu_a) + \frac{1}{2}(x - \mu_a)^2 S''(\mu_a), \quad (10)$$

where s, S', S'' are respectively S_a and its first and second derivatives. Thus the mean survival rate averaged over X_a is

$$s_a = \mathcal{E}\{s_a\} = S(\mu_a) + \frac{1}{2}v_a S''(\mu_a). \quad (11)$$

This equation shows that the survival at age a can be decomposed into a term dependent on the mean and a term dependent on the variance of the phenotype distribution at this age.

The growth function is defined by $H_a(x)$ whose conditional distribution is the density $G_a(h|x)$. We assume that at each age growth has a systematic part that depends on current phenotype, plus a small variance that is the same for all phenotypes,

$$H_a(x) = \bar{G}_a(x) + K_a, \quad (12)$$

$$\bar{G}_a(x) = \mathcal{E}\{H(x)\}, \text{ averaged over density } G_a(\cdot|x), \quad (13)$$

$$\mathcal{E}\{K_a\} = 0, \text{ averaged over } X_a, \quad (14)$$

$$\text{Var}\{K_a\} = v_G, \text{ for all } x. \quad (15)$$

The systematic part G_a depends on the phenotype distribution at age a . We expand it, similarly to the survival function (10)

$$G_a(x) \approx G(\mu_a) + (x - \mu_a) G'(\mu_a) + \frac{1}{2}(x - \mu_a)^2 G''(\mu_a), \quad (16)$$

where g, G' and G'' are respectively G_a and its first and second derivatives. Thus, average growth of a cohort between age a and $a + 1$ is

$$g_a = G(\mu_a) + \frac{1}{2}v_a G''(\mu_a). \quad (17)$$

1.3 Mean of the phenotype distribution

We have an initial phenotype X with mean μ and we write

$$X = \mu + \delta, \quad \mathcal{E}\{\delta\} = 0, \quad \mathcal{E}\{\delta^2\} = v. \quad (18)$$

Below we ignore terms of order δ^3 and higher, and also terms of order v^2 and higher.

Growth (phenotype change in one time unit) is

$$H = G(X) + K, \quad \mathcal{E}\{K\} = 0, \quad \mathcal{E}\{K^2\} = v_G. \quad (19)$$

The term K is assumed independent of X .

Expand

$$G(X) = G(\mu) + G'(\mu)\delta + \frac{1}{2}G''(\mu)\delta^2, \quad (20)$$

Survival is expanded as (20)

$$\begin{aligned} S(X) &= S(\mu) + S'(\mu)\delta + \frac{1}{2}S''(\mu)\delta^2, \\ s &= \mathcal{E}\{S(X)\}. \end{aligned} \quad (21)$$

An individual starts with phenotype X and after growth, has new phenotype $Y = (X + H)$ if it survives ($S = 1$) and new phenotype $Y = 0$ if it dies ($S = 0$). The first 2 moments of the new phenotype are

$$\mathcal{E}\{Y\} = \frac{\mathcal{E}[(X + H) S]}{\mathcal{E}[S]}, \quad (22)$$

$$\mathcal{E}\{Y^2\} = \frac{\mathcal{E}[(X + H)^2 S]}{\mathcal{E}[S]}. \quad (23)$$

where $\mathcal{E}(\cdot)$ is the expectation taken with respect to the density X .

Remember that we do not consider the terms of order higher than δ^2 and use (18), (20) and (21) to have

$$\mathcal{E}\{Y\} = \frac{\mathcal{E}\{(\mu + \delta)(S(\mu) + S'(\mu)\delta + \frac{1}{2}S''(\mu)\delta^2) + (G(\mu) + G'(\mu)\delta + \frac{1}{2}G''(\mu)\delta^2)(S(\mu) + S'(\mu)\delta + \frac{1}{2}S''(\mu)\delta^2)\}}{s} \quad (24)$$

Simplify (24) to find that the mean phenotype at $a + 1$ is thus the addition of the mean phenotype at age a , the growth of this mean phenotype and a Price covariance that depends on the phenotypic variance.

$$\mu_{a+1} = \mu_a + g_a + \frac{v_a S'(\mu_a) (1 + G'(\mu_a))}{s_a} = \mu_a + g_a + v_a c_a, \quad (25)$$

We can also write a cumulative version of the mean phenotype at any age with respect to μ_1 , the mean birth phenotype of the cohort:

$$\mu_a = \mu_1 + \sum_{k=1}^{a-1} g_k + \sum_{k=1}^{a-1} c_k \quad (26)$$

1.4 Variance of the phenotype distribution

Similarly for the variance, use (20)-(23) to find that

$$v_{a+1} = v_a (1 + G'(\mu_a))^2 + v_G. \quad (27)$$

An amazing consequence of our assumptions is that survival selection does not change the variance of the phenotype distribution. Indeed, exponential selection on a normal variable leaves the variance unchanged and this is also true in more general cases. The exception is truncation selection, which we ignore.

To express the variance of the phenotype distribution at any age with respect to the variance at birth, we define the quantities

$$\gamma_a = (1 + G'(\mu_a))^2, \quad \Gamma_1 = 1, \quad \Gamma_{a+1} = \gamma_a \Gamma_a. \quad (28)$$

A cumulative version of (27) is

$$v_a = \Gamma_a v_1 + k_a v_G, \quad a \geq 2, \quad (29)$$

$$k_2 = \Gamma_1, \quad (30)$$

$$k_a = \Gamma_a \left(\frac{1}{\Gamma_a} + \frac{1}{\Gamma_{a-1}} + \cdots + \frac{1}{\Gamma_2} \right). \quad (31)$$

1.5 Phenotype of mothers

As did for the survival and the growth, the average reproductive rate at age a can be approximated by

$$m_a = \mathcal{E}\{m_a\} = M(\mu_a) + \frac{1}{2}v_a M''(\mu_a). \quad (32)$$

where m and M'' are respectively M_a and its second derivative.

Each year, only a part of the individual of age a will reproduce. The mean phenotype of mothers of age a $\mathcal{E}(X_{Ma})$ must be weighted by reproductive rate and is given by

$$\mathcal{E}(X_{Ma}) = \mu_{Ma} = \frac{\mathcal{E}(X_a M_a)}{\mathcal{E}M_a}, \quad (33)$$

and, by the same kind of reasoning used to derive (25), we have

$$\mu_{Ma} = \mu_a + \frac{v_a M'(\mu_a)}{m_a} \quad (34)$$

where M' is the first derivative of M_a , and $v_{Ma} = v_a$.

Now, to find the mean phenotype of all mothers, independently of the age at which they reproduce, we must weight age dependent mean mother phenotypes by the amount of reproduction at age a , which we call $\bar{\phi}_a$.

For a cohort,

$$\bar{\phi}_a = \phi_a, \text{ and } R_0 = \sum_a \bar{\phi}_a = \sum_a \phi_a, \quad (35)$$

For a stable population,

$$\bar{\phi}_a = e^{-ra} \phi_a, \text{ and } R_0 = \sum_a \bar{\phi}_a = 1. \quad (36)$$

The weighted mean phenotype of mothers is

$$\mathcal{E}(X_M) = \mu_M = \frac{\sum_a \bar{\phi}_a \mu_{Ma}}{R_0}, \quad (37)$$

2 Decomposition of $\mathbf{r}$

We show by recurrence that the parameters describing the population dynamics can be described by three components: a component generated only from the mean of the phenotypic distribution, a component linked to the variance generated from

the growth function that accumulate across ages and a component generated by the transformation of the variance at birth. We ignore the terms of order $v_a v_G$, v_a^2 and v_G^2 or higher.

At age 1, we have μ_1 and v_1 . We take the growth function as a representative case of all demographic rates:

$$\begin{aligned} g_1 &= G(\mu_1) + v_G 0 + v_1 \frac{1}{2} G''(\mu_1) \\ &= \widehat{g}_1 + v_G \widetilde{g}_1 + v_1 \check{g}_1 \end{aligned} \tag{38}$$

At age 2, the mean phenotype distribution became

$$\begin{aligned} \mu_2 &= \mu_1 + \widehat{g}_1 + v_G 0 + v_1 (\check{g}_1 + c_1) \\ &= \widehat{\mu}_2 + v_G \widetilde{\mu}_2 + v_1 \check{\mu}_2 \end{aligned} \tag{39}$$

with

$$c_1 = \frac{S'(\mu_1) (1 + G'(\mu_1))}{\widehat{s}_1} \tag{40}$$

at age 2, the demographic rates can be written as illustrated for the reproductive function:

$$\begin{aligned} m_2 &= M(\widehat{\mu}_2 + v_1 \check{\mu}_2) + v_2 \frac{1}{2} M''(\widehat{\mu}_2 + v_1 \check{\mu}_2) \\ &= M(\widehat{\mu}_2 + v_1 \check{\mu}_2) + (v_G + v_1 (1 + G'(\mu_1))^2) \frac{1}{2} M''(\widehat{\mu}_2 + v_1 \check{\mu}_2) \\ &\approx M(\widehat{\mu}_2) + v_G \frac{1}{2} M''(\widehat{\mu}_2) + v_1 [\check{\mu}_2 M'(\widehat{\mu}_2) + \frac{1}{2} M''(\widehat{\mu}_2) (1 + G'(\mu_1))^2] \\ &\approx \widehat{m}_2 + v_G \widetilde{m}_2 + v_1 \check{m}_2 \end{aligned} \tag{41}$$

So the survivorship is

$$\begin{aligned} \bar{l}_2 &= \widehat{s}_1 + v_G 0 + v_1 \frac{1}{2} S''(\mu_1) \\ &= \widehat{l}_2 + v_G \widetilde{l}_2 + v_1 \check{l}_2 \end{aligned} \tag{42}$$

and the net reproductive rate:

$$\begin{aligned}\bar{\phi}_2 &= \hat{m}_2 \hat{l}_2 + v_G \tilde{m}_2 \hat{l}_2 + v_1 (\check{m}_2 \hat{l}_2 + \hat{m}_2 \check{l}_2) \\ &= \hat{\phi}_2 + v_G \tilde{\phi}_2 + v_1 \check{\phi}_2\end{aligned}\tag{43}$$

Now, we assume that all parameters of age a can be decomposed into three components and show that these parameters at age $a+1$ can also be decomposed into these three components.

The variance at age a can be simplified by $v_a = \Gamma_a v_1 + k_a v_G$ with

$$\begin{aligned}\gamma_a &= (1 + G'(\hat{\mu}_a))^2, \quad \Gamma_1 = 1, \Gamma_{a+1} = \gamma_a \Gamma_a. \\ k_2 &= \Gamma_1, \\ k_a &= \Gamma_a \left(\frac{1}{\Gamma_a} + \frac{1}{\Gamma_{a-1}} + \cdots + \frac{1}{\Gamma_2} \right).\end{aligned}\tag{44}$$

$$\tag{45}$$

At age $a+1$: the mean phenotype is

$$\begin{aligned}\mu_{a+1} &= \mu_a + g_a + v_a c_a \\ &= \hat{\mu}_a + \hat{g}_a + v_G (\tilde{\mu}_a + \tilde{g}_a + k_a c_a) + v_1 (\check{\mu}_a + \check{g}_a + \Gamma_a c_a) \\ &= \hat{\mu}_{a+1} + v_G \tilde{\mu}_{a+1} + v_1 \check{\mu}_{a+1}\end{aligned}\tag{46}$$

Note that we can simplify c_a by

$$c_a = \frac{S'(\hat{\mu}_a) (1 + G'(\hat{\mu}_a))}{\hat{s}_a}\tag{47}$$

The demographic rates at age $a+1$ are illustrated by the case of the reproductive function and can be expanded as:

$$\begin{aligned}m_{a+1} &= M(\hat{\mu}_{a+1} + v_G \tilde{\mu}_{a+1} + v_1 \check{\mu}_{a+1}) + v_a \frac{1}{2} M''(\hat{\mu}_{a+1} + v_G \tilde{\mu}_{a+1} + v_1 \check{\mu}_{a+1}) \\ &\approx M(\hat{\mu}_{a+1}) + v_G (M'(\hat{\mu}_{a+1}) \tilde{\mu}_{a+1} + \frac{1}{2} M''(\hat{\mu}_{a+1}) k_{a+1}) + v_1 (\check{\mu}_{a+1} M'(\hat{\mu}_{a+1}) + \frac{1}{2} M''(\hat{\mu}_{a+1}) \Gamma_{a+1}) \\ &\approx \hat{m}_{a+1} + v_G \tilde{m}_{a+1} + v_1 \check{m}_{a+1}\end{aligned}\tag{48}$$

For the survivorship:

$$\begin{aligned} l_{a+1} &= \widehat{s}_a \widehat{l}_a + v_G (\widetilde{l}_a \widehat{s}_a + \widehat{l}_a \widetilde{s}_a) + v_1 (\check{l}_a \widehat{s}_a + \widehat{l}_a \check{s}_a) \\ &= \widehat{l}_{a+1} + v_G \widetilde{l}_{a+1} + v_1 \check{l}_{a+1} \end{aligned} \quad (49)$$

We can also write the net reproductive rate, ϕ_{a+1} according to v_1 and v_G :

$$\begin{aligned} \phi_{a+1} &= \widehat{m}_{a+1} \widehat{l}_{a+1} + v_G (\widetilde{m}_{a+1} \widehat{l}_{a+1} + \widehat{m}_{a+1} \widetilde{l}_{a+1}) + v_1 (\check{m}_{a+1} \widehat{l}_{a+1} + \widehat{m}_{a+1} \check{l}_{a+1}) \\ &= \widehat{\phi}_{a+1} + v_G \widetilde{\phi}_{a+1} + v_1 \check{\phi}_{a+1} \end{aligned} \quad (50)$$

and so

$$R_0 = \widehat{R}_0 + v_G \widetilde{R}_0 + v_1 \check{R}_0 \quad (51)$$

As a consequence, all these demographic parameters can be decomposed into three components. Now, we consider the net reproductive rate, the generation rate and the population growth rate: r is often estimated using the approximation $\frac{\log(R_0)}{T_c}$ where R_0 is the net reproductive rate and T_c is the generation time.

$$T_c = \frac{1}{K} \sum_a a \phi_a \quad (52)$$

$$(53)$$

The generation rate can be decomposed like that:

$$\begin{aligned} T_c &= \frac{1}{\widehat{R}_0} \sum_a a \widehat{\phi}_a + \frac{v_G}{\widehat{R}_0} \left(\sum_a a \widetilde{\phi}_a - \frac{\widetilde{R}_0}{\widehat{R}_0} \sum_a a \widehat{\phi}_a \right) + \frac{v_1}{\widehat{R}_0} \left(\sum_a a \check{\phi}_a - \frac{\check{R}_0}{\widehat{R}_0} \sum_a a \widehat{\phi}_a \right) \\ &= \widehat{T}_c + v_G \widetilde{T}_c + v_1 \check{T}_c \end{aligned} \quad (54)$$

$$(55)$$

and so the population growth rate can be expanded as

$$\begin{aligned} r &= \frac{\log(\widehat{R}_0 + v_G \widetilde{R}_0 + v_1 \check{R}_0)}{\widehat{T}_c + v_G \widetilde{T}_c + v_1 \check{T}_c} \\ &\approx \frac{\log(\widehat{R}_0)}{\widehat{T}_c} + \frac{v_G}{\widehat{T}_c} \left(\frac{\widetilde{R}_0}{\widehat{R}_0} - \widetilde{T}_c \widehat{r} \right) + \frac{v_1}{\widehat{T}_c} \left(\frac{\check{R}_0}{\widehat{R}_0} - \check{T}_c \widehat{r} \right) \\ &= \widehat{r} + v_G \widetilde{r} + v_1 \check{r} \end{aligned} \quad (56)$$

$$(57)$$

For the purpose of estimation and to avoid the errors accumulated by successive approximations, we solved the characteristic equation to find the different components of r . $\hat{r}$ has been estimated by solving

$$\sum_{a \geq 1} e^{-\hat{r}a} \hat{\phi}_a = 1. \quad (58)$$

$v_G \tilde{r}$ has been estimated by solving

$$\sum_{a \geq 1} e^{-(\hat{r}+v_G \tilde{r})a} (\hat{\phi}_a + v_G \tilde{\phi}_a) = 1. \quad (59)$$

Finally, $v_1 \tilde{r}$ has been estimated by subtracting r and $\hat{r} + v_G \tilde{r}$

3 The variance of offspring

When μ_1 and v_1 are known, we can find the mean and the variance of the phenotype distribution among all individuals and among mothers at each age, using this model. However, in practice, biologists do not know μ_1 and v_1 but model an inheritance function to find the phenotype of offspring according to the phenotype of mothers. Thus, here we use the simple inheritance function described for the base examples where μ_1 is known to find v_1 .

In the base case, the variance of the phenotype of offspring produced by mothers of age a is

$$v_{Oa} = \beta^2 v_a + v_I \quad (60)$$

The variance of all offspring (independently of their mother age) v_1 can be estimated from the sum of the variance intra and inter groups of offspring produced by mothers of different ages:

$$\begin{aligned} v_1 &= \frac{1}{R_0} \sum_a \bar{\phi}_a v_{Oa} + \frac{1}{R_0} \sum_a \bar{\phi}_a (\mu_{Oa} - \mu_1)^2, \\ &= \frac{1}{R_0} \sum_a \bar{\phi}_a v_{Oa} \\ &= \frac{1}{R_0} \sum_a \bar{\phi}_a \beta^2 v_a + v_I \end{aligned} \quad (61)$$

Using (45) and assuming that v_1 and v_G are small, we can use the decomposition of $\bar{\phi}_a$ (50) and R_0 (51) to see that

$$v_1 \approx \frac{\frac{\beta^2}{\widehat{R}_0} \sum_a \widehat{\phi}_a \widehat{k}_a v_G + v_I}{1 - \frac{\beta^2}{\widehat{R}_0} \sum_a \widehat{\phi}_a \widehat{\Gamma}_a} \quad (62)$$

4 Elasticities

Now suppose that we change parameters with a small $0 < \epsilon \ll 1$ so that

$$\phi_a \rightarrow \phi_a + \epsilon \boldsymbol{\delta}_{\phi_a}. \quad (63)$$

Then we have the resulting changes

$$\begin{aligned} r &\rightarrow r + \epsilon \boldsymbol{\delta}_r, \\ \mu_a &\rightarrow \mu_a + \epsilon \boldsymbol{\delta}_{\mu_a}, \end{aligned} \quad (64)$$

$$\begin{aligned} v_a &\rightarrow v_a + \epsilon \boldsymbol{\delta}_{v_a}, \\ v_1 &\rightarrow v_1 + \epsilon \boldsymbol{\delta}_{v_1}. \end{aligned} \quad (65)$$

Note that $\boldsymbol{\delta}$ represents a derivative.

4.1 Elasticity of $\widehat{r}$, $\check{r}$, $\widetilde{r}$, and v_1

We use (55) to find:

$$\begin{aligned} \boldsymbol{\delta}_{\widehat{r}} &= \frac{\boldsymbol{\delta}_{\widehat{R}_0}}{\widehat{R}_0 \widehat{T}_c} - \frac{\boldsymbol{\delta}_{\widehat{T}_c} \widehat{R}_0}{\widehat{T}_c^2} \\ \boldsymbol{\delta}_{\check{r}} &= \frac{\boldsymbol{\delta}_{\widehat{R}_0} \widehat{T}_c \widehat{R}_0 - \check{R}_0 (\boldsymbol{\delta}_{\widehat{R}_0} \widehat{T}_c + \widehat{R}_0 \boldsymbol{\delta}_{\widehat{T}_c})}{\widehat{R}_0^2 \widehat{T}_c^2} - \frac{\widehat{T}_c (\boldsymbol{\delta}_{\widehat{r}} \check{T}_c + \widehat{r} \boldsymbol{\delta}_{\check{T}_c}) - \boldsymbol{\delta}_{\widehat{T}_c} \check{T}_c \widehat{r}}{\widehat{T}_c^2} \\ \boldsymbol{\delta}_{\widetilde{r}} &= \frac{\boldsymbol{\delta}_{\check{R}_0} \widehat{T}_c \widehat{R}_0 - \widetilde{R}_0 (\boldsymbol{\delta}_{\check{R}_0} \widehat{T}_c + \widehat{R}_0 \boldsymbol{\delta}_{\widehat{T}_c})}{\widehat{R}_0^2 \widehat{T}_c^2} - \frac{\widehat{T}_c (\boldsymbol{\delta}_{\widetilde{r}} \check{T}_c + \widetilde{r} \boldsymbol{\delta}_{\check{T}_c}) - \boldsymbol{\delta}_{\widehat{T}_c} \check{T}_c \widetilde{r}}{\widehat{T}_c^2} \end{aligned} \quad (66)$$

with

$$\begin{aligned}
\delta_{\hat{R}_0} &= \sum_a \delta_{\hat{\phi}_a} \\
\delta_{\tilde{R}_0} &= \sum_a \delta_{\tilde{\phi}_a} \\
\delta_{\check{R}_0} &= \sum_a \delta_{\check{\phi}_a} \\
\delta_{\hat{T}_c} &= \frac{1}{\hat{R}_0} \sum_a a \delta_{\hat{\phi}_a} - \frac{\delta_{\hat{R}_0}}{\hat{R}_0^2} \sum_a a \hat{\phi}_a \\
\delta_{\tilde{T}_c} &= \frac{1}{\tilde{R}_0^2} (\hat{R}_0 \sum_a a \delta_{\tilde{\phi}_a} - \delta_{\hat{R}_0} \sum_a a \tilde{\phi}_a) - \frac{1}{\tilde{R}_0^2} (\delta_{\tilde{R}_0} \sum_a a \hat{\phi}_a + \tilde{R}_0 \sum_a a \delta_{\hat{\phi}_a}) + \frac{2\delta_{\hat{R}_0}}{\tilde{R}_0^3} (\tilde{R}_0 \sum_a a \hat{\phi}_a) \\
\delta_{\check{T}_c} &= \frac{1}{\check{R}_0^2} (\hat{R}_0 \sum_a a \delta_{\check{\phi}_a} - \delta_{\hat{R}_0} \sum_a a \check{\phi}_a) - \frac{1}{\check{R}_0^2} (\delta_{\check{R}_0} \sum_a a \hat{\phi}_a + \check{R}_0 \sum_a a \delta_{\hat{\phi}_a}) + \frac{2\delta_{\hat{R}_0}}{\check{R}_0^3} (\check{R}_0 \sum_a a \hat{\phi}_a)
\end{aligned} \tag{67}$$

For v_1 , We simplify (62) with

$$v_1 = \frac{f}{y} \tag{68}$$

so

$$\delta_{v_1} = \frac{\delta_f y - \delta_y f}{y^2} \tag{69}$$

if a vital rate is perturbed,

$$\begin{aligned}
\delta_f &= \frac{\beta^2 v_G}{\hat{R}_0} \sum_a (\delta_{\hat{\phi}_a} k_a + \hat{\phi}_a \delta_{k_a}) - \frac{\delta_{\hat{R}_0} \beta^2 v_G}{\hat{R}_0^2} \sum_a \hat{\phi}_a k_a \\
\delta_g &= \frac{\delta_{\hat{R}_0} \beta^2}{\hat{R}_0^2} \sum_a \hat{\phi}_a \Gamma_a - \frac{\beta^2}{\hat{R}_0} \sum_a (\delta_{\hat{\phi}_a} \Gamma_a + \hat{\phi}_a \delta_{\Gamma_a})
\end{aligned} \tag{70}$$

Perturbation of the reproductive function

- a small perturbation in $M(\mu_a)$ will not change μ_a and v_a but:

$$\begin{aligned}
\delta_{\widehat{\phi}_a} &= \widehat{l}_a. \\
\delta_{\widetilde{\phi}_a} &= \widetilde{l}_a. \\
\delta_{\check{\phi}_a} &= \check{l}_a.
\end{aligned}
\tag{71}$$

- a small perturbation in $M'(\mu_a)$ will not change μ_a, v_a (it can change in some cases μ_1 but not in our simplest case as μ_1 is constant).

$$\begin{aligned}
\delta_{\widehat{\phi}_a} &= 0. \\
\delta_{\widetilde{\phi}_a} &= \widetilde{\mu}_a \widehat{l}_a. \\
\delta_{\check{\phi}_a} &= \check{\mu}_a \widehat{l}_a.
\end{aligned}
\tag{72}$$

- small perturbation in $M''(\mu_a)$ gives:

$$\begin{aligned}
\delta_{\widehat{\phi}_a} &= 0. \\
\delta_{\widetilde{\phi}_a} &= \frac{1}{2} k_a \widehat{l}_a. \\
\delta_{\check{\phi}_a} &= \frac{1}{2} \Gamma_a \widehat{l}_a.
\end{aligned}
\tag{73}$$

Perturbation of the survival and the growth functions

Say we perturb age b . For any $j > b$

$$\begin{aligned}
\delta_{\widehat{\mu}_j} &= \delta_{\widehat{\mu}_{j-1}} + \delta_{\widehat{g}_{j-1}} \\
\delta_{\widetilde{\mu}_j} &= \delta_{\widetilde{\mu}_{j-1}} + \delta_{\widetilde{g}_{j-1}} + \delta_{c_{j-1}} k_{j-1} + c_{j-1} \delta_{k_{j-1}} \\
\delta_{\check{\mu}_j} &= \delta_{\check{\mu}_{j-1}} + \delta_{\check{g}_{j-1}} + \delta_{c_{j-1}} \Gamma_{j-1} + c_{j-1} \delta_{\Gamma_{j-1}}
\end{aligned}
\tag{74}$$

with

$$\begin{aligned}
\delta_{c_j} &= \frac{1}{\widehat{s}_j^2} (\delta_{\widehat{\mu}_j} \widehat{s}_j (S''(\widehat{\mu}_j) (1 + G'(\widehat{\mu}_j)) + S'(\widehat{\mu}_j) G'''(\widehat{\mu}_j)) - S'(\widehat{\mu}_j) (1 + G'(\widehat{\mu}_j)) \delta_{\widehat{s}_j}) \\
\delta_{k_j} &= \delta_{k_{j-1}} (1 + G'(\widehat{\mu}_j))^2 + 2k_{j-1} (1 + G'(\widehat{\mu}_j)) G'''(\widehat{\mu}_j) \delta_{\widehat{\mu}_j} \\
\delta_{\Gamma_j} &= \delta_{\Gamma_{j-1}} (1 + G'(\widehat{\mu}_j))^2 + 2\Gamma_{j-1} (1 + G'(\widehat{\mu}_j)) G'''(\widehat{\mu}_j) \delta_{\widehat{\mu}_j}
\end{aligned} \tag{75}$$

For demographic rates, we show the derivative of the growth function. It is similar for the reproductive and survival functions:

$$\begin{aligned}
\delta_{g_j} &= G'(\widehat{\mu}_j) \delta_{\widehat{\mu}_j} \\
\delta_{\widetilde{g}_j} &= G'(\widehat{\mu}_j) \delta_{\widetilde{\mu}_j} + G''(\widehat{\mu}_j) \delta_{\widehat{\mu}_j} \widetilde{\mu}_j + \frac{1}{2} G'''(\widehat{\mu}_j) \delta_{k_j} + \frac{1}{2} G''''(\widehat{\mu}_j) \delta_{\widehat{\mu}_j} k_j \\
\delta_{\check{g}_j} &= G'(\widehat{\mu}_j) \delta_{\check{\mu}_j} + G''(\widehat{\mu}_j) \delta_{\widehat{\mu}_j} \check{\mu}_j + \frac{1}{2} G'''(\widehat{\mu}_j) \delta_{\Gamma_j} + \frac{1}{2} G''''(\widehat{\mu}_j) \delta_{\widehat{\mu}_j} \Gamma_j
\end{aligned} \tag{76}$$

Then, we use (49) and (50) to find $\delta_{\widehat{\phi}_a}$, $\delta_{\widetilde{\phi}_a}$ and $\delta_{\check{\phi}_a}$

- a small perturbation in $S(\widehat{\mu}_b)$ gives

$$\begin{aligned}
\delta_{\widehat{s}_b} &= 1 \\
\delta_{c_b} &= -\frac{S'(\widehat{\mu}_a) (1 + G'(\widehat{\mu}_a))}{\widehat{s}_a^2}
\end{aligned} \tag{77}$$

- a small perturbation in $S'(\widehat{\mu}_b)$ gives

$$\begin{aligned}
\delta_{\widetilde{s}_b} &= \widetilde{\mu}_b \\
\delta_{\check{s}_b} &= \check{\mu}_b \\
\delta_{c_b} &= \frac{(1 + G'(\widehat{\mu}_a))}{\widehat{s}_a}
\end{aligned} \tag{78}$$

- a small perturbation in $S''(\widehat{\mu}_b)$ gives

$$\begin{aligned}\delta_{\tilde{s}_b} &= \frac{1}{2} k_b \\ \delta_{\check{s}_b} &= \frac{1}{2} \Gamma_b\end{aligned}\tag{79}$$

- a small perturbation in $G(\widehat{\mu}_b)$ gives

$$\delta_{\widehat{g}_b} = 1\tag{80}$$

- a small perturbation in $G'(\widehat{\mu}_b)$ gives

$$\begin{aligned}\delta_{\widetilde{g}_b} &= \widetilde{\mu}_b \\ \delta_{\check{g}_b} &= \check{\mu}_b \\ \delta_{c_b} &= \frac{S'(\widehat{\mu}_b)}{\widehat{s}_b} \\ \delta_{k_b} &= 2k_{b-1} (1 + G'(\widehat{\mu}_b)) \\ \delta_{\Gamma_b} &= 2\Gamma_{b-1} (1 + G'(\widehat{\mu}_b))\end{aligned}\tag{81}$$

- a small perturbation in $G''(\widehat{\mu}_b)$ gives

$$\begin{aligned}\delta_{\widetilde{g}_b} &= \frac{1}{2} k_b \\ \delta_{\check{g}_b} &= \frac{1}{2} \Gamma_b\end{aligned}\tag{82}$$

Perturbation of v_G , v_I and β

These perturbations will change v_1 .

- a perturbation of v_G gives

$$\delta_f = \frac{\beta^2}{\widehat{R}_0} \sum_a \widehat{\phi}_a k_a\tag{83}$$

- a perturbation of β gives

$$\begin{aligned}\delta_f &= \frac{2\beta v_G}{\widehat{R}_0} \sum_a \widehat{\phi}_a k_a \\ \delta_g &= -\frac{2\beta}{\widehat{R}_0} \sum_a \widehat{\phi}_a \Gamma_a\end{aligned}\tag{84}$$

- a perturbation of v_I gives

$$\delta_f = 1\tag{85}$$

4.2 Elasticity of $\mathbf{r}$

We use (9) to find δ_r

$$\delta_r = \frac{\sum_a e^{-ra} \delta_{\phi_a}}{\sum_a a e^{-ra} \phi_a}.\tag{86}$$

We used a similar method as described above to find δ_{ϕ_a} in each perturbation case.

Table S1: Parameters used to build the demographic rates for the short-lived and long-lived life-histories. The reproductive functions have been modeled with a logit and an exponential link for the long- and short-lived life-histories, respectively. The survival function has been modeled with a logit link for both life-histories.

			short	long
Surv.	newb.	a	-3	0
		b	0.3	0.3
		Sm	0.5	1
	juv.	a	-3	-1.5
		b	0.4	0.15
		Sm	0.9	1
	ad.	a	-1000	-2.5
		b	0	0.15
		Sm	0	1
Repro.	juv.	a	1	-2
		b	0.2	0.1
	adult	a	1	-2
		b	0.2	0.2
Growth	newb.	a	4	12
		b	1.2	1.5
	juv.	a	6	10
		b	0.8	0.7
	ad.	a	0	10
		b	0	0.7
Inher.	v_G		4	5
	μ_1		3	2
	β		0.2	0.2
	v_{inh}		1	0.1

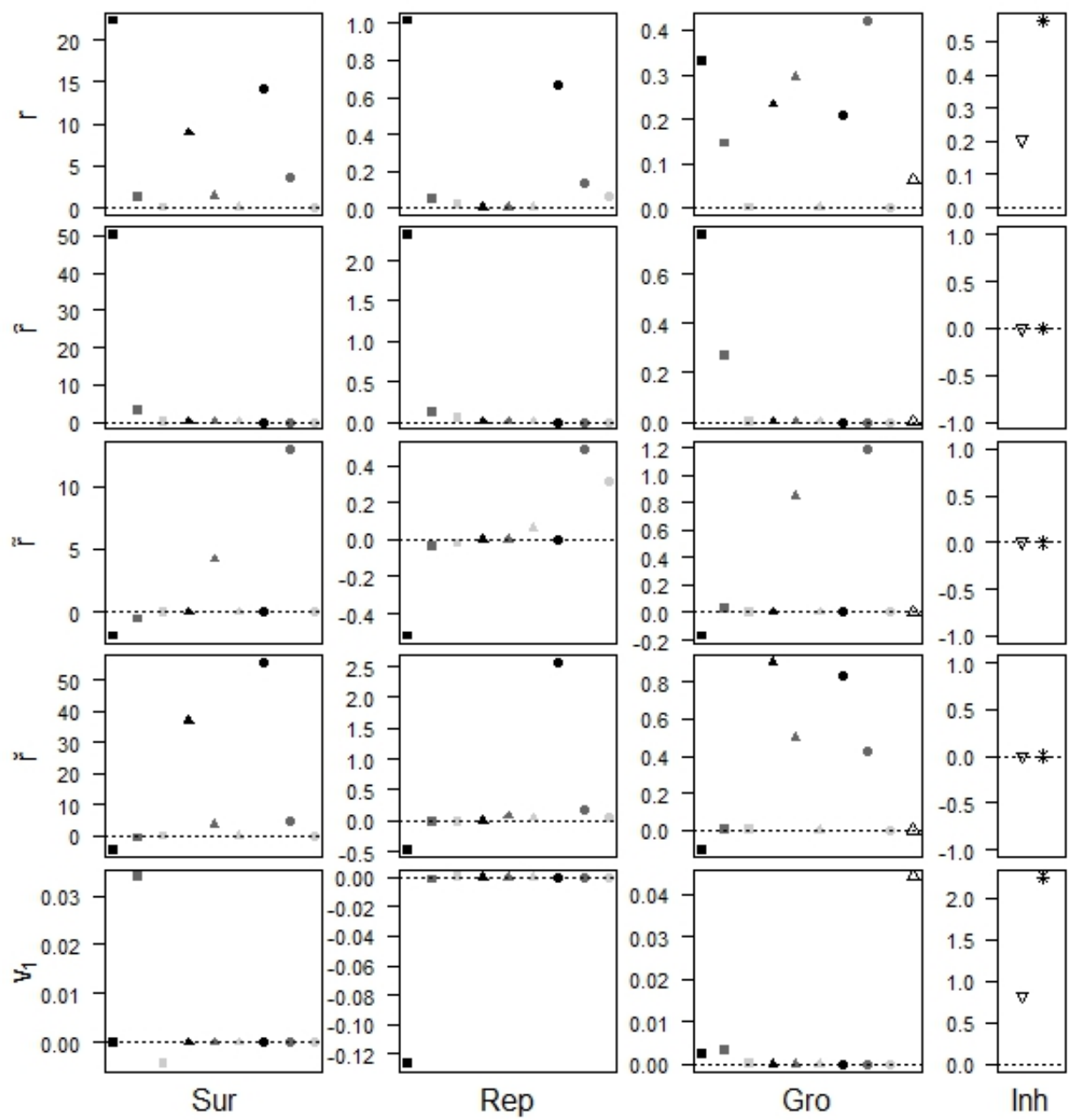


Figure S1: Elasticities of r , $\hat{r}$, $\tilde{r}$, $\check{r}$ and v_1 for the short-lived life-history. The first 3 columns are elasticities to survival, reproduction and growth all computed at the mean phenotype of each age class. Elasticities shown are to values of each quantity (mean of each function at each age, squares), first derivatives (triangles) and second derivative (circles). The column for growth also shows elasticity to the variance of the growth v_G (open triangles). The last column shows elasticities to the inheritance variance v_I (open inverted triangles) and to β (stars). Black and, dark and light grey shades are used to indicate perturbations affecting newborn, juvenile and adult age-class, respectively.

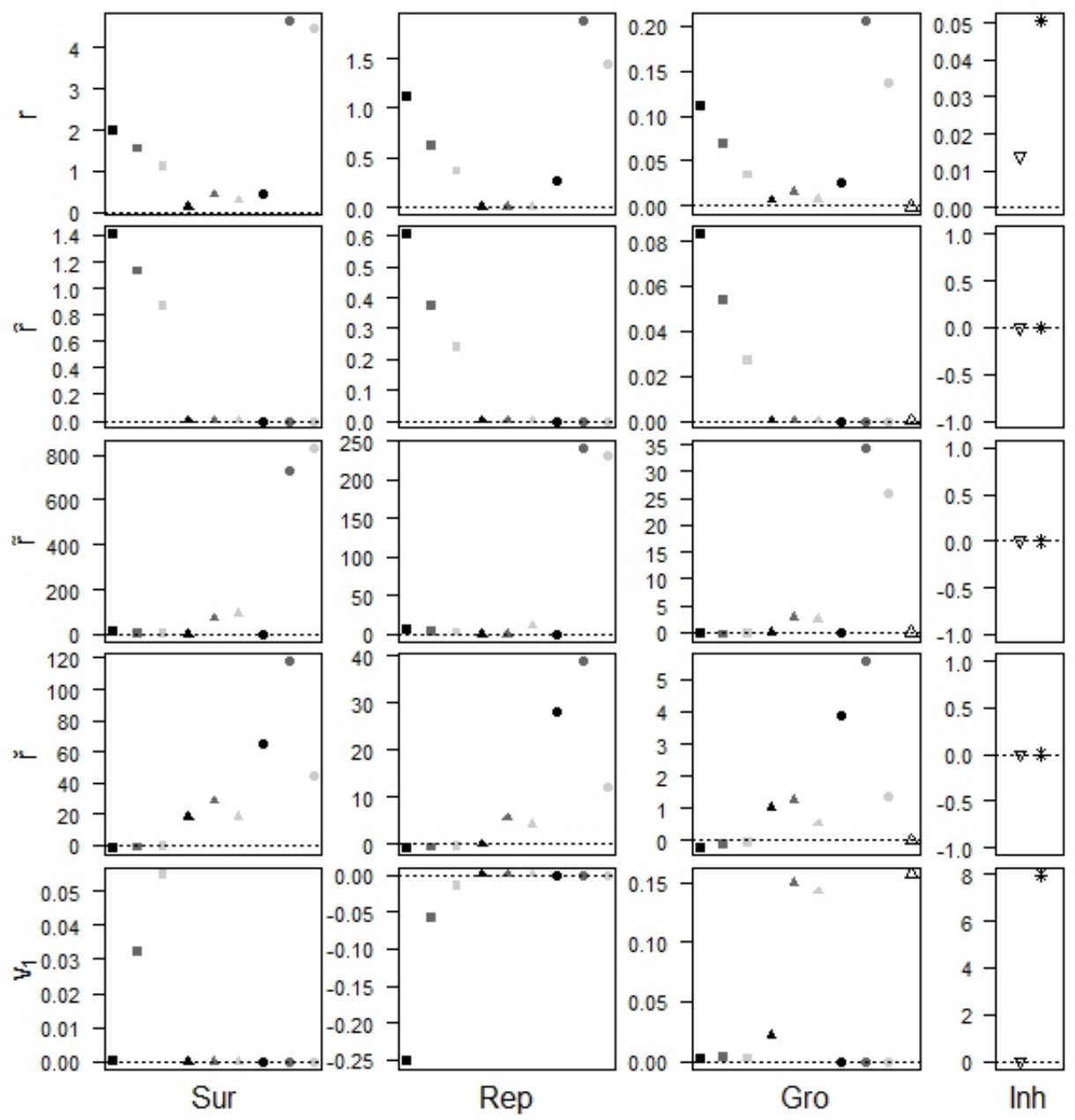


Figure S2: Elasticities of r , $\hat{r}$, $\tilde{r}$, $\check{r}$ and v_1 for the long-lived life-history. The first 3 columns are elasticities to survival, reproduction and growth all computed at the mean phenotype of each age class. Elasticities shown are to values of each quantity (mean of each function at each age, $\square$), first derivatives (triangles) and second derivative (circles). The column for growth also shows elasticity to the variance of the growth v_G (open triangles). The last column shows elasticities to the inheritance variance v_I (open inverted triangles) and to β (stars). Black and, dark and light grey shades are used to indicate perturbations affecting newborn, juvenile and adult age-class, respectively.

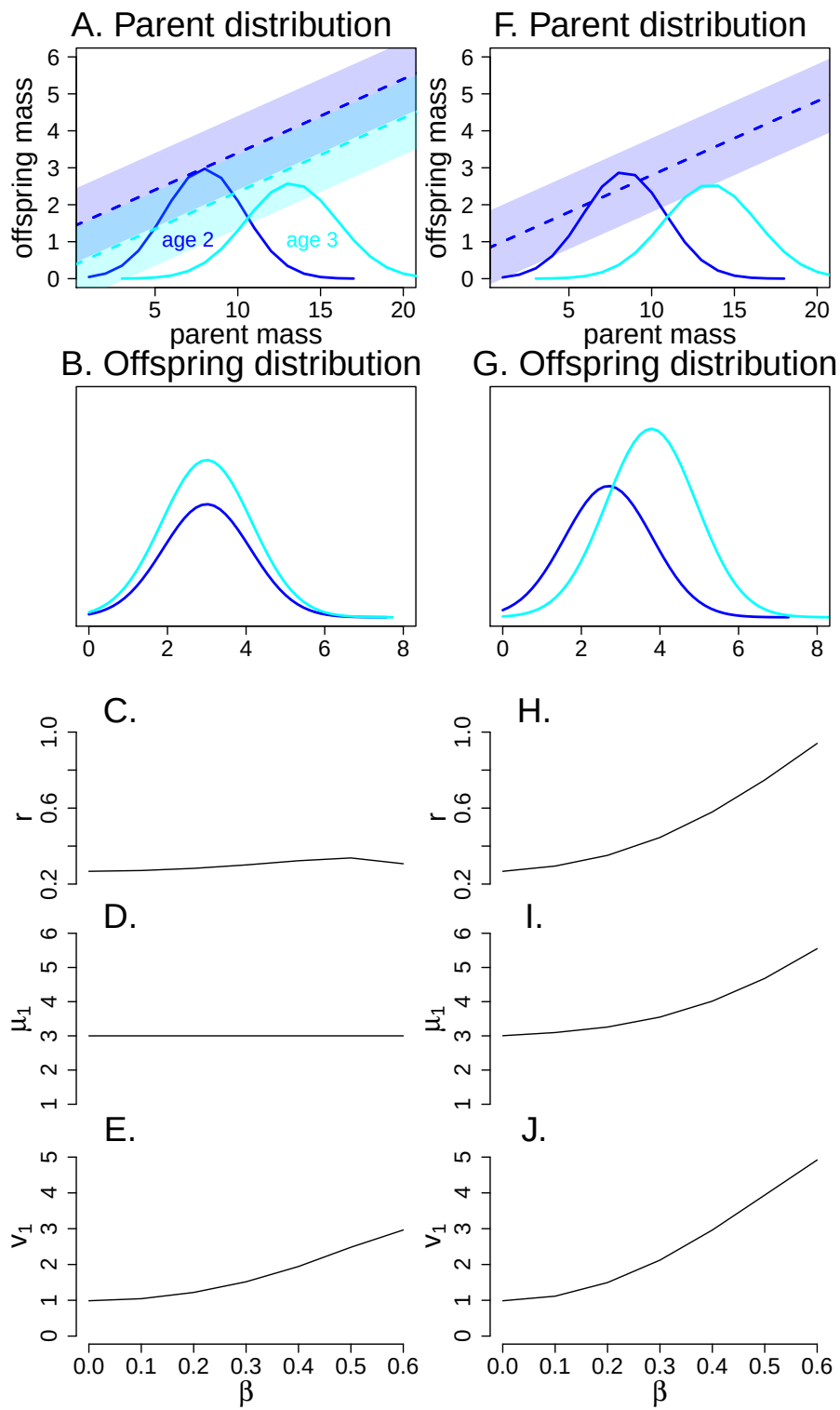


Figure S3: Influence of the inheritance function on the newborn phenotype distribution and on the population growth rate for the short-lived life-history. In the left column (A-E), inheritance follows model A. In the right column (F-J), inheritance follows model B, so that newborns of mothers of different ages have different mean body mass. (A,F) the inheritance function is presented along with parental phenotypic distributions. (B, G) shows the offspring distribution resulting of the parental distribution and the inheritance functions presented in A and G. The others panels show how increasing strength of inheritance affects r (C, H), μ_1 (D, I) and v_1 (E, J).

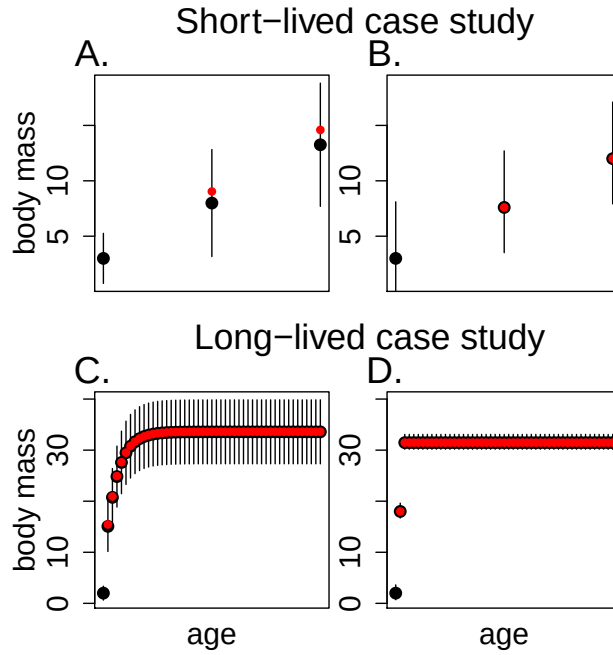


Figure S4: Influence of selection, and stochasticity in growth on the population growth trajectories. The two case studies including selection and stochasticity of growth are presented in the right column (A, C). In the left column (B, D), there is no selection (slopes of survival, growth and reproductive function are null) and no stochasticity in growth. The black and red points show the mean body mass of all individuals and actual mother, respectively at each age.