Demographic determinants of the phenotypic mother-offspring correlation

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Running title: Phenotypic mother-offspring correlation

Abstract. Phenotypic traits partly determine expected survival and reproduction and so have been used as the basis for demographic models of population dynamics. Within a population, the distribution of phenotypic traits depends upon their transmission from parents to offspring, yet we still have a limited understanding of the factors shaping phenotypic transmission in wild populations. Phenotypic transmission can be measured using the phenotypic parent-offspring correlation (C), defined as the slope of the regression of offspring phenotypic trait on parental phenotypic trait, both traits measured at the same age, often at birth. This correlation reflects phenotypic variation due to both additive genetic effects and parental effects. Researchers seldom account for the possible influence of selection on estimates of the phenotypic parent-offspring correlation. However, because individuals must grow, survive and reproduce before giving birth to offspring, these demographic processes might influence the phenotypic parent-offspring correlation in addition to the inheritance process, the latter being the direct relationship between parental and offspring phenotypic traits when the parental trait is measured at age of reproduction while the offspring trait is measured at birth. Here we used a female-based population model to study the relative effects of fertility and viability selections, trait ontogeny and inheritance on C. The relative influence of each demographic process is estimated by deriving the exact formulas for the proportional changes in C to changes in the parameters of integral projection models structured by age and phenotypic traits. We illustrate our method for two long-lived species. We find that C can be strongly affected by both viability and fertility selections, mediated by growth and inheritance. Generally, demographic processes that result in mothers reproducing at similar phenotypic traits regardless of their birth traits, such as high fertility selection or converging developmental trajectories, lead to a decreased C. More generally, our models show how the age and phenotypic dependence of fertility and viability selections can influence phenotypic mother-offspring correlation to a much larger extent than ontogeny and inheritance. Our results suggest that accounting for such dependence is needed to reliably model the distribution of offspring phenotypic traits and the eco-evolutionary dynamics of phenotypic traits.

Key words: *heritability, inheritance, integral projection model, IPM, parent-offspring covariance, parent-offspring regression, phenotypic variance, roe deer, Soay sheep, transmission*

INTRODUCTION

The dynamics of phenotypic traits are influenced by ecological and evolutionary processes (Pelletier et al. 2009, Schoener 2011). Ecological studies show that the influence of environmental factors on population dynamics can be mediated by the distribution of individual traits such as body mass or size that influence vital rates (Ozgul et al. 2010, Jenouvrier et al. 2018, Plard et al. 2019). Evolutionary studies seek to understand how traits evolve in natural systems. Models of eco-evolutionary dynamics describe the dynamics of the distribution of continuous traits in populations and require the appropriate modeling of trait transmission between parents and offspring. The aim of this paper is to disentangle the relative influences of selection, ontogeny and inheritance on the parent-offspring correlation.

To evolve in response to selection, a trait needs to vary and to be transmitted to the next generation (Falconer and Mackay 1996). The historical approach to study the evolution of phenotypic traits is based on measuring selection acting on a trait and the trait's heritability. While many phenotypic traits appear to be heritable in wild populations of animals and plants, they do not always evolve as expected under directional selection. In particular, some traits appear to be at evolutionary stasis (Merilä et al. 2001, Kruuk 2004), an observation that challenges our understanding of the dynamics of these traits. While many studies have provided unbiased estimates of heritability (Postma 2006, Morrissey et al. 2010), the difference between expected and observed dynamics of phenotypic traits shows that our understanding of phenotypic transmission from parents to offspring is still limited and does not allow accurate prediction of eco-evolutionary dynamics. A traditional measure of heritability, the phenotypic parent-offspring correlation is usually interpreted as arising from genetic similarity between parents and their offspring. Here for sake of simplicity, we focus on females and use the phenotypic mother-offspring correlation denoted C. The quantity C is the slope of the linear association between maternal and offspring phenotypic traits measured at the same point in the life cycle. This slope has long been interpreted as a fixed measure giving the proportion of phenotypic variation attributable to additive genetic variation—the narrow-sense heritability of a trait (Kempthorne 1957, Falconer and Mackay 1996), once potential confounding factors such as fixed maternal and environmental effects affecting offspring phenotypic traits have been accounted for. But, and contrary to the method presented here, this interpretation of C excluded trait ontogeny (growth, transition to sexual maturity) which determines annual maternal condition and its the variable effect on offspring phenotypic trait (Mousseau and Fox 1998), and also excluded non-genetic inheritance (Bonduriansky and Day 2009, Danchin et al. 2011).

The approach we use here to study the correlation C is to analyse population models at phenotypic equilibrium (Coulson 2020). Population models have been developed to describe the dynamics of a population whose individuals are described by age and/or a continuous phenotypic trait (such as size or mass) (Integral Projection Models, IPM, Easterling et al. 2000 which should not be confounded with Integrated Population Models, Besbeas et al. 2002). Although individuals are under selection and phenotypic traits are heritable, the distribution of phenotypic traits is stable (and constant over time) at equilibrium, as observed in many animals and plants (Merilä et al. 2001, Kruuk 2004). The aim of this paper is to use the phenotypic equilibrium in IPMs structured by both age and phenotypic trait (Coulson et al. 2010), to provide insight into how demographic processes (i.e., viability and fertility selection, growth, and inheritance) lead to positive correlation between mother and offspring phenotypic trait at evolutionary and ecological stasis (e.g. equilibrium). Here, inheritance is defined as the direct relationship between maternal and offspring phenotypic traits when the maternal trait is measured at age of reproduction while the offspring trait is measured at birth. Such IPMs have proven useful to make predictions that match observed phenotypic changes over time (Coulson et al. 2011, Smallegange and Coulson 2012, Vindenes et al. 2014). However, these models do not accord with quantitative genetics theory (Chevin 2015, Janeiro et al. 2016). They rarely follow the genotype (but see Childs et al. 2016, Coulson et al. 2017, Simmonds et al. 2020) and thus do not assume that the phenotypic trait is influenced solely by additive genetic and environmental effects. Nevertheless, IPMs tracking only the phenotype and IPMs tracking the additive genetic and environmental components of the phenotype lead to similar predicted population dynamics under some circumstances (Simmonds et al. 2020). In the present study, we thus use IPMs directly tracking the dynamics of the phenotypic trait to examine how the correlation C is influenced by demographic processes such as ontogeny and selection.

In IPMs, viability and fertility selections are modeled through the dependence of survival and reproduction on the phenotypic trait and age. These models explicitly include ontogeny so that a new-born first inherits a phenotypic trait at birth, then grows to reach a required size or mass at maturity, and lastly reproduces and transmits phenotypic traits to its offspring. Our female-only IPMs do not explicitly model heritability using a genetic model, but instead use the empirical distribution of offspring traits born to a mother of any given trait and age (Janeiro et al. 2016). In this way, IPMs and our approach implicitly capture variable maternal effects on trait transmission through an inheritance function that links the phenotypic trait of the mother at reproduction to the phenotypic trait of the offspring at, or close to, birth. The quantity C calculated here from an IPM implicitly includes both genetic and non-genetic mechanisms of inheritance, assuming both processes are operating in the data used to parameterise the inheritance function.

While it is already known that selection can influence estimates of the mother-offspring phenotypic correlation in quantitative genetics (Hadfield 2008), our approach explicitly quantifies the relative influence of inheritance, ontogeny and selection on C. We analyze the model at eco-evolutionary stasis, meaning that we derive the deterministic equations for C and its proportional changes to the parameters describing the four demographic processes (survival, fertility, growth and inheritance) for a population at equilibrium in a constant environment. We derived proportional changes in C to infinitesimal change in each parameter (i.e. intercept and slope) of the demographic functions that describe an IPM to estimate the relative contribution of each demographic process to C. This approach will allow a better understanding of the mechanisms influencing transmission of phenotypic traits through an explicit estimate of the relative influence of selection, growth and inheritance on C.

We derive and work with proportional changes because it is straightforward to translate these into both standard demographic elasticities and sensitivities (see methods). We apply our general method to two published age and body mass-structured IPMs, one parameterised for Soay Sheep (*Ovis aries*) (Coulson et al. 2010) and one for roe deer (*Capreolus capreolus*) (Plard et al. 2015). In these iteroparous species, body mass is under positive selection, is heritable and develops with age until a plateau corresponding to the asymptotic adult body mass is reached in these determinate growers. We report and compare how the phenotypic mother–offspring correlation for both species depends on selections, ontogeny, and inheritance processes.

MATERIALS AND METHODS

In our models, we consider a population structured by age a and by a continuous phenotypic trait z (note that we also use x for maternal phenotypic trait and y for offspring phenotypic trait), but this method can be extended to populations structured by stages and multiple continuous phenotypic traits (Ellner et al. 2016). The continuous trait can be any trait that influences individual vital rates (survival and/or reproduction) such as body mass, body size, birth date or parasitic load but cannot itself be a vital rate such as the number of offspring produced. We assume that the population faces constant environmental conditions. We assume that the constant environmental conditions have shaped the survival, fertility, growth and inheritance functions of the targeted trait (body mass) over time, and so our results can be used to study the effects of environmentally driven changes in the preceding rates but our study does not explicitly include environmental variation.

We derive the deterministic correlation of the phenotypic trait at birth between mothers and offspring and the deterministic proportional changes in this correlation within the IPM framework. To simplify the model, we only consider females. We begin by introducing IPMs, and then explain how the correlation C is derived. Next we detail the analysis of proportional changes in C to intercepts and slopes of the four functions describing demographic processes. Finally, we apply our general method to two wild populations using age and body mass-structured IPMs.

Integral Projection Models structured by age and a phenotypic trait

Integral Projection Models (IPMs) describe the dynamics of a population according to the dynamics of the age-specific (a) distribution of the continuous phenotypic trait (z) in the population over time (t): $n_{t,a}(z)$ (Ellner et al. 2016). These models project the age-specific trait distribution at each time interval according to survival and growth $P_a(z'|z)$ and fertility $F_a(z'|z)$, i.e. the recruitment of offspring with phenotypic trait z' into the population.

$$n_{t+1,a+1}(z') = \int P_a(z'|z) n_{t,a}(z)\, dz,\ a \geq 1 \tag{1}$$

$$n_{t+1,1}(z') = \int F_a(z'|z) n_{t,a}(z)\, dz \tag{2}$$

Here we use year as an example of the time interval. Viability is defined by a survival function that depends on phenotypic trait and age, so that a female of age a and phenotypic trait z alive in year t has a survival rate $S_a(z)$ to reach year $t+1$. The growth process is defined by changes in female phenotypic trait between t and $t+1$, written as $G_a(z'|z)$. The fertility process includes two functions: the fertility level and the inhertiance function. The level of fertility, also refered as fertility selection is defined by the number of offspring produced by a female of age a and phenotypic trait z, written as $M_a(z)$. The inheritance function gives the phenotypic traits of the offspring at birth z' according to the phenotypic trait z of their mothers at reproductive age a as a distribution $D_a(z'|z)$.

$$\begin{aligned} n_{t+1,a+1}(z') &= \int G_a(z'|z) S_a(z) n_{t,a}(z)\, dz,\ a \geq 1 \\ n_{t+1,1}(z') &= \sum_a \int D_a(z'|z) M_a(z) n_{t,a}(z)\, dz \end{aligned} \tag{3}$$

To build an IPM and to apply our method, one uses long-term individual-based data to model and fit these four functions in relation to the individual phenotypic trait using an appropriate link function (Coulson et al. 2001, Childs et al. 2003, Ellner and Rees 2006, Plard et al. 2018, Vindenes et al. 2014). For instance, in the roe deer and the Soay sheep IPMs (see L7-63 of the DataS1:PMOC_Fcts.R file in the supplementary material), the survival function has been modeled using a generalized linear model of body mass with a logit link and fit to the survival data of individual females monitored from birth to death (Coulson et al. 2010, Plard et al. 2015). Survival data consisted of a binary variable of 0 or 1 corresponding to the annual survival of each individual associated to its annual body mass.

$$logit(S_a(z)) = \alpha(a) + \beta(a)z \tag{4}$$

where $\alpha(a)$ and $\beta(a)$ are age-dependent intercept and slope, respectively. $\beta(a)$ is thus the trait dependent slope of the survival function that is directly linked to the intensity of the viability selection acting on phenotypic trait. For a detailed description of the construction of IPMs see Merow et al. (2014) or Rees et al. (2014). In practice, IPMs are implemented using the midpoints rule as a numerical integration method (Ellner et al. 2016) where phenotypic values are divided into m discrete trait classes that are the elements of the vector $\mathbf{z} = \{z_i\}$. Then, IPMs use extended standard projection matrix that are divided in relation to the artificial trait classes to give the dynamics of a population that can be rewritten using population vectors (bold lower cases) and trait-demography matrices (bold capital cases) as:

$$
\begin{aligned}
\mathbf{n}_{t+1,a+1} &= \mathbf{P}_a \mathbf{n}_{t,a} = \mathbf{G}_a \mathbf{S}_a \mathbf{n}_{t,a}, \; a \geq 1 && (5) \\
\mathbf{n}_{t+1,1} &= \sum_a \mathbf{F}_a \mathbf{n}_{t,a} = \sum_a \mathbf{D}_a \widehat{\mathbf{M}}_a \mathbf{n}_{t,a} && (6)
\end{aligned}
$$

where $\mathbf{n}_{t,a}$ is the vector describing the distribution of the phenotypic trait of all individuals of a given age a. **Survival and growth** together from age a to age $a+1$ are given by a matrix $\mathbf{P}_a$ whose (i,j) element is

$$
\begin{aligned}
P_a(i,z) &\equiv P_a(z_i \mid z_j) && (7) \\
&= \text{Prob.}[\text{Alive at age } a+1 \text{ with trait } z_i \mid \text{Alive at age } a \text{ with } z_j].
\end{aligned}
$$

Fertility of females aged a is a matrix $\mathbf{F}_a = \mathbf{D}_a \widehat{\mathbf{M}}_a$, where $\widehat{\mathbf{M}}_a$ is a diagonal matrix whose (i,i) entry is the total number of offspring that a female of phenotypic trait z_i will produce at age a. The **inheritance** of the phenotypic trait from a mother of phenotypic trait z_i at age a to offspring is captured in the mother-offspring phenotypic transition matrix $\mathbf{D}_a$ whose (i,j) element is

$$
\begin{aligned}
D_a(i,z) &\equiv D_a(z_i \mid z_j) && (8) \\
&= \text{Prob.}[\text{Offspring trait is } z_i \text{ at age of first census} \mid \text{Maternal trait is } z_j \text{ at age } a].
\end{aligned}
$$

Note that $\mathbf{e}^T \mathbf{D}_a = \mathbf{e}^T$, using the vector $\mathbf{e}^T = (1, 1, \ldots, 1)$, so that the probabilities for the transitions out of one maternal phenotypic trait z_j sum to one.

Only the demographic functions and associated trait-demography matrices $(\mathbf{G}_a, \mathbf{S}_a, \mathbf{D}_a, \widehat{\mathbf{M}}_a)$ need to be built to apply the present method (see for instance L101-120 of the DataS1:PMOC.R), but not the population vector.

Phenotypic mother-offspring Correlation

We calculate the phenotypic mother-offspring correlation C of a phenotypic trait z as the ratio of the covariance between offspring and maternal traits at birth to the variance of maternal trait at birth. This ratio is in fact mathematically the slope of the mother-offspring regression, originally used in classical quantitative genetics theory to estimate heritability (Falconer and Mackay 1996). Thus, C corresponds to the slope of the regression of offspring trait values Y_a ("offspring phenotypic trait") at age a on maternal trait values X_a ("mother phenotypic trait") at age a. We estimate C for traits at birth (measured at first census) using phenotypic and life history information from all ages.

The correlation C can be calculated using the formula for the regression slope of the phenotypic traits of offspring born to one female cohort over its lifetime regressed on the phenotypic traits of mothers at their own birth (L166 in DataS1:PMOC.R):

$$\mathrm{C} = \frac{\mathrm{Cov}(Y_0 X_0)}{\mathrm{Var}(X_0)} \tag{9}$$

Coulson et al. (2010) derived a version of the correlation C using IPMs, but they estimated the maternal trait for all females born in a cohort. Here, we analyse only the females that mature (survived to the age at first reproduction, i.e. after viability selection) and then give birth at each age (i.e. after fertility selection) to estimate the phenotypic trait of females at birth. In other words, to assess the influence of the different demographic processes on C, we include only *true* mothers in the mother cohort, excluding their cohort mates that did not produce any offspring.

We analyse the IPM at its equilibrium state. Thus, we derive C when the phenotypic trait distribution has stable, time-invariant proportions in each age and trait class.

Stable distributions of the phenotypic trait at birth

The age and phenotypic trait structure of a population that experiences time-invariant fertility, viability, growth, and inheritance processes converges to a stable age and phenotypic trait distribution with a growth rate r (Keyfitz and Caswell 2005). Stable populations are defined as populations with unchanging trait and age structures.

In these stable populations, we describe three important stable distributions (see Appendix S4: Fig. S1 for a schematic description of these distributions): the **distribution of the phenotypic trait at birth within the stable (female) cohort** ($\mathbf{u}$), the **distribution of maternal phenotypic trait at (its own) birth** (X_0), and the **distribution of offspring phenotypic trait at birth** (Y_0). These offspring have been produced during the lifetime of the stable cohort ($\mathbf{u}$). At its own birth, this stable cohort has therefore stable proportions of newborns in each trait class, here represented by a vector $\mathbf{u} = \{u(i)\} \equiv \{u(z_i)\}$. Note that we set $(\mathbf{e}^T \mathbf{u}) = 1$. Each such cohort contains females who may become mothers if they survive and reproduce. Which of these potential mothers reproduce, and how often, during their lifetime determine the stable distribution of maternal phenotypic trait at (its own) birth. The latter is shifted to higher trait values when compared to the distribution of phenotypic trait at birth within the stable cohort (potential mothers), if viability and fertility selections are positive (i.e. fertility and survival increase with the phenotypic trait).

In stable populations, we can define for any population growth rate r the renewal matrix

$$\mathbf{A}(r) = \sum_a e^{-ra} \, \mathbf{F}_a \, \mathbf{L}_a \, , \tag{10}$$

where **Survivorship** from birth (i.e. at age $a = 0$) to any age a is a matrix $\mathbf{L}_a$ whose (i, j) element is

$$\begin{aligned} L_a(i,j) &\equiv L_a(z_i \mid z_j) \\ &= \text{Prob.[Alive at age } a \text{ with trait } z_i \mid \text{Born at age 0 with } z_j]. \end{aligned} \tag{11}$$

Then the distribution of phenotypic trait at birth within the stable cohort $\mathbf{u}$ and growth rate r are together determined by (L122-148 in DataS1:PMOC.R)

$$\mathbf{A}(r)\,\mathbf{u} = \mathbf{u}. \tag{12}$$

This equation contains two unknowns: r and $\mathbf{u}$. r can be found numerically by noting that the renewal matrix ($\mathbf{A}(r)$) has a dominant eigenvalue of 1. Thus the logarithm of the dominant eigenvalue of $\mathbf{A}(r)$ is 0. Using this, we can find r and $\mathbf{A}(r)$. Then $\mathbf{u}$ is the right eigenvector of $\mathbf{A}(r)$. For other interesting properties of the renewal matrix see Steiner et al. (2014).

Mother-offspring covariance and maternal variance

In the Appendix S1: Section S1 we derive a formula for the covariance between offspring phenotypic trait at birth Y_0 and maternal phenotypic trait at its own birth X_0 that is computable in terms of $\mathbf{F}_{a,}\,\mathbf{L}_a$, and $\mathbf{u}$. As a consequence, this covariance arises out of complex interactions between inheritance, ontogeny and selection.

In a stable age-trait-structured population, the **lifetime number of offspring** produced by females from the stable cohort $\mathbf{u}$ is (L151 in DataS1:PMOC.R)

$$K = \sum_a (\mathbf{e}^T \mathbf{F}_a \mathbf{L}_a\,\mathbf{u}) = \sum_a (\mathbf{e}^T \widehat{\mathbf{M}}_a \mathbf{L}_a\,\mathbf{u}). \tag{13}$$

Using this, the trait-demography matrices $\widehat{\mathbf{M}}_a$, and $\mathbf{L}_a$, and the distribution of phenotypic trait at birth within the stable cohort $\mathbf{u}$ as defined in (12), the **covariance between maternal and**

offspring phenotypic traits at birth is given by (L163 in DataS1:PMOC.R)

$$\begin{aligned}\text{Cov}(Y_0X_0) &= \frac{1}{K}\sum_a \left\{ \mathbf{e}^T \widehat{\mathbf{Z}}\,\mathbf{F}_a\mathbf{L}_a \left(\mathbf{I} - \mathbf{u}\,\mathbf{e}^T \frac{1}{K}\sum_a \widehat{\mathbf{M}}_a\,\mathbf{L}_a\right)\widehat{\mathbf{Z}}\,\mathbf{u}\right\}, &(14)\\ &= \mathbf{e}^T\,\widehat{\mathbf{Z}}\,\mathcal{H}\left(\mathbf{I} - \mathbf{u}\,\mathbf{e}^T \frac{1}{K}\sum_a \widehat{\mathbf{M}}_a\,\mathbf{L}_a\right)\widehat{\mathbf{Z}}\,\mathbf{u}, &(15)\end{aligned}$$

where $\hat{\mathbf{Z}}$ is a diagonal matrix of the phenotypic values $\hat{\mathbf{Z}} = diag(z_i)$, and where we use, for brevity,

$$\mathcal{H} = \frac{1}{K}\sum_a \mathbf{F}_a\mathbf{L}_a. \qquad (16)$$

Details on the derivations are given in the Appendix S1: Section S1.

The **variance in maternal phenotypic trait at birth** is (L156-159 in DataS1:PMOC.R)

$$\text{Var}(X_0) = \frac{1}{K}\sum_a (\mathbf{e}^T\,\widehat{\mathbf{M}}_a\,\mathbf{L}_a\,\widehat{\mathbf{Z}}\,\widehat{\mathbf{Z}}\mathbf{u}) - \frac{1}{K^2}(\sum_a \mathbf{e}^T\,\widehat{\mathbf{M}}_a\,\mathbf{L}_a\,\widehat{\mathbf{Z}}\mathbf{u})^2. \qquad (17)$$

Details on the derivation of the variance are given in the Appendix S1: Section S2.

Computing proportional changes in C

To disentangle the relative influence of fertility and viability selections, trait ontogeny and inheritance on C, we computed $E_{\text{C}} = \frac{\delta\text{C}}{\text{C}}$: the proportional changes in C to infinitesimal changes in any intercept or trait-dependent slope of one of the demographic functions of the IPM describing age-specific demographic rates as a function of the continuous trait. We estimated proportional changes in C because it can easily be used to derive both the standard demographic elasticity and sensitivity of C to any parameter of the IPM. The elasticity of C is the proportional change in C to a proportional change in a parameter and is equal to the multiplication of our measure E_{C} by the target parameter of the IPM that varies. The sensitivity of C is the change in C to an infinitesimal change in the target parameter of the IPM that varies and is directly equal to $\boldsymbol{\delta}$C.

The proportional change in C (E_{C}) caused by an infinitesimal change in a given parameter of a given demographic function, is (L190-207 in DataS1:PMOC.R)

$$E_{\mathrm{C}} = \frac{\boldsymbol{\delta}\mathrm{C}}{\mathrm{C}} = \frac{\boldsymbol{\delta}\mathrm{Cov}(Y_0 X_0)}{\mathrm{Cov}(Y_0 X_0)} - \frac{\boldsymbol{\delta}\mathrm{Var}(X_0)}{\mathrm{Var}(X_0)}. \tag{18}$$

The exact form of E_{C} depends on which model parameter varies. $\boldsymbol{\delta}\mathrm{Cov}(Y_0 X_0)$ and $\boldsymbol{\delta}\mathrm{Var}(X_0)$ are the derivatives of $\mathrm{Cov}(Y_0 X_0)$ and $\mathrm{Var}(X_0)$, respectively, to the target parameter of the IPM that varies. But this parameter is omitted in equations for simplicity.

Any change in an intercept or slope of one of the demographic functions of the IPM will change the viability, fertility, growth or inheritance process. Note that the trait dependent slopes of the fertility and survival functions of the IPMs are directly linked to the fertility and viability selections acting on the phenotypic trait, respectively, in the population. These changes in the demographic processes will then impact $\mathrm{Var}(X_0)$, $\mathrm{Cov}(Y_0 X_0)$, and C as a consequence (Appendix S4: Fig. S1). In the following, we describe how the derivative of $\mathrm{Var}(X_0)$ and $\mathrm{Cov}(Y_0 X_0)$ in relation to the target parameter can be computed. Detailed derivations of the described quantities are given in Appendix S1.

A change in C ($\boldsymbol{\delta}$C) occurs if one model parameter changes by a small amount $\epsilon > 0$. This change was estimated by the derivative of C in relation to the parameter that has changed ($p \to p + \epsilon$). This causes changes in the trait-demography matrices (L168-172 in DataS1:PMOC.R)

$$\mathbf{F}_a \, \mathbf{L}_a \to \mathbf{F}_a \, \mathbf{L}_a + \epsilon \, \boldsymbol{\Delta}_a, \tag{19}$$

where $\boldsymbol{\Delta}_a$ represents the derivative of the matrix $F_a \, \mathbf{L}_a$. More generally in the following, we use $\boldsymbol{\Delta}$, Δ and $\boldsymbol{\delta}$ to represent the derivative of a matrix, a vector, and a number, respectively in relation to the given parameter that varies. The Appendix S1: Sections S4 and S9 give the details on the computation of the changes in the trait-demography matrices with respect to changes in parameters describing viability selection, fertility selection, growth, and inheritance.

The changes included in (19) change the stable population. As a consequence, changes in model parameters can affect C at population equilibrium by affecting the three stable distributions (Appendix S4: Fig. S1): the distribution of phenotypic trait at birth within the stable cohort ($\mathbf{u}$), the distribution of maternal phenotypic trait at (its own) birth (X_0), and the distribution of offspring phenotypic trait at birth (Y_0).

The distribution of phenotypic trait at birth within the stable cohort $\mathbf{u}$ changes by $\epsilon\,\Delta_u$ (see Appendix S1: Sections S3, S6, S7 and S8 for the computation of Δ_u). From here on, we leave off the ϵ (constant proportional factor) since it multiplies every change. In addition, the covariance between maternal and offspring traits at birth Cov(Y_0X_0) changes by $\boldsymbol{\delta}$Cov(Y_0X_0) and the variance in maternal trait at birth Var(X_0) by $\boldsymbol{\delta}$Var(X_0) (see A5 for details on the perturbations of the variance in maternal phenotypic trait at birth).

The perturbation of Cov(Y_0X_0) as given in (15) requires the perturbation of matrix $\mathcal{H}$ (16), which in turn needs the perturbation of K (13). From (16) we see that the change in $\mathcal{H}$ is

$$\boldsymbol{\Delta}_{\mathcal{H}} = -\left(\frac{\boldsymbol{\delta}_K}{K}\right)\mathcal{H} + \frac{\left[\sum_a \boldsymbol{\Delta}_a\right]}{K}. \tag{20}$$

And from (13) we have

$$\boldsymbol{\delta}_K = \sum_a (\mathbf{e}^T \boldsymbol{\Delta}_a \mathbf{u}) + \sum_a (\mathbf{e}^T \mathbf{F}_a\, \mathbf{L}_a)\Delta_u \tag{21}$$

Putting these together, the change in Cov$(Y_0 X_0)$ using (15) and Δ_u (A3) is

$$\begin{aligned}\boldsymbol{\delta}\mathrm{Cov}(Y_0 X_0) = {} & \mathbf{e}^T\,\widehat{\mathbf{Z}}\,[\boldsymbol{\Delta}_{\mathcal{H}}]\left(\mathbf{I}-\mathbf{u}\,\mathbf{e}^T\frac{1}{K}\sum_a \widehat{\mathbf{M}}_a\,\mathbf{L}_a\right)\widehat{\mathbf{Z}}\,\mathbf{u}\\ & +\mathbf{e}^T\,\widehat{\mathbf{Z}}\,\mathcal{H}\left(\mathbf{I}-\mathbf{u}\,\mathbf{e}^T\frac{1}{K}\sum_a \widehat{\mathbf{M}}_a\,\mathbf{L}_a\right)\widehat{\mathbf{Z}}\,\Delta_u\\ & -\mathbf{e}^T\,\widehat{\mathbf{Z}}\,\mathcal{H}\left(\frac{1}{K}\sum_a \mathbf{u}\,\mathbf{e}^T\,\boldsymbol{\Delta}_{\widehat{\mathbf{M}}_a\,\mathbf{L}_a}\right.\\ & \left.+\frac{\Delta_u\,K-\boldsymbol{\delta}_K\,\mathbf{u}}{K^2}\sum_a \mathbf{e}^T\,\widehat{\mathbf{M}}_a\,\mathbf{L}_a\right)\widehat{\mathbf{Z}}\,\mathbf{u}.\end{aligned} \tag{22}$$

Finally, the change in the variance in maternal phenotypic trait at birth (Appendix S1: Section S5) is

$$\begin{aligned}\boldsymbol{\delta}\mathrm{Var}(X_0) = {} & \mathbf{e}^T\sum_a\left\{\frac{\boldsymbol{\Delta}_{\widehat{\mathbf{M}}_a\,\mathbf{L}_a}\,K-\boldsymbol{\delta}_K\,\widehat{\mathbf{M}}_a\,\mathbf{L}_a}{K^2}\,\widehat{\mathbf{Z}}\,\widehat{\mathbf{Z}}\mathbf{u}\right\}\\ & +\frac{1}{K}\sum_a(\mathbf{e}^T\,\widehat{\mathbf{M}}_a\,\mathbf{L}_a\,\widehat{\mathbf{Z}}\,\widehat{\mathbf{Z}}\Delta_u)\\ & -2\,\frac{\mathbf{e}^T}{K}\sum_a\left\{\frac{\boldsymbol{\Delta}_{\widehat{\mathbf{M}}_a\,\mathbf{L}_a}\,K-\boldsymbol{\delta}_K\,\widehat{\mathbf{M}}_a\,\mathbf{L}_a}{K}\,\widehat{\mathbf{Z}}\mathbf{u}+\widehat{\mathbf{M}}_a\,\mathbf{L}_a\,\widehat{\mathbf{Z}}\,\Delta_u\right\}\,\mathbf{z}^T\,\mathbf{u}.\end{aligned} \tag{23}$$

Using (15), (17), (22), and (23), we can now compute C in (9) and its proportional changes in (18).

Application to Soay sheep and roe deer IPMs

We computed C of body mass at age of first census in both Soay sheep and roe deer and E_c (proportional changes in C) to changes in model parameters of the demographic functions for two published IPMs structured by age and body mass (Coulson et al. 2010, Plard et al. 2015). Body mass is a key functional trait in ungulates as it conditions individual survival and reproduction and is directly linked to individual fitness (Traill et al. 2021, Gaillard et al. 2000*a*).

The feral population of Soay sheep lives on the Island of Hirta in the St. Kilda archipelago, Scotland, and fluctuates as a food-limited population between 600 and 2000 individuals, of which about one-third live in the 250ha study area (Clutton-Brock and Pemberton 2004). The population has been studied in detail since 1985. During this time, life-history and body mass data were collected during the yearly captures and year-round censuses. A detailed description of the population and data collection protocols is provided elsewhere (Clutton-Brock and Pemberton 2004). An IPM using the data of this population from 1986 to 1996 has been previously built (Coulson et al. 2010).

The roe deer population of Trois Fontaines lives in an enclosed forest of 1360 ha in North Eastern France. The size of the population has been kept relatively constant around 250 individuals older than one year in March by yearly removals (mainly through exportation of captured individuals) except between 2001-2005 when an experimental manipulation of density was performed and population size peaked at 450 individuals older than one year of age. The population has been monitored by the Office National de la Chasse et de la Faune Sauvage (now Office Français de la Biodiversité) since 1975. Each year, half roe deer of the population are caught between December and March. Each individual is sexed and weighed. All individuals included in this study are of known age. The population and the study site have been described in detail by Gaillard et al. (1993; 2013). An IPM using the data of this population from 1976 to 2008 has been previously built (Plard et al. 2015).

Both published IPMs used data from the female component of the population and are structured by age classes and body mass (see life-cycle graphs in Appendix S2: Fig. S1). The Soay sheep IPM divided individuals into four age-classes: lambs (aged 0 to < 1, census at 4 months old), yearlings (aged 1 to < 2), adults (aged 2 to < 8), and senescent individuals (aged $8+$), while the roe deer IPM distinguished three age-classes: yearlings (aged 0 to < 1, census at 8 months old), adults (aged 1 to < 7), and senescent individuals (aged $7+$). For consistency among the IPMs and the above notation, where age 0 refers to age at birth (i.e. age at first census), we define the roe deer age-classes starting at age 0 to denote the census age of 8 months, instead of age 1 as in Plard et al. (2015). This is purely a question of notation. For both species, we calculate C for their respective census ages of 4 months in Soay sheep and 8 months in roe deer.

The IPM trait-demography matrices were constructed from the relevant demographic functions. The functions were statistically determined using life history and body mass data while controlling for confounding temporal variation in demographic rates using random effects of year (Coulson et al. 2010, Plard et al. 2015). We directly used the published functions inferred, by body mass and age-class in these two published studies to estimate C and its proportional changes in these two populations. As stated in the methods, the survival and growth processes include two functions: depending on their age class and body mass, females alive in year t can survive ($S_a(z)$) and their body mass can grow ($G_a(z'|z)$) to reach year $t+1$. In these two published IPMs, the fertility function, defined as the number of offspring produced by a mother was split into two functions ($M_a(z) = 0.5R_a(z)(1 + T_a(z))$): the probability for a female to recruit at least one offspring (referred as the probability of recruitment $R_a(z)$) and the twinning rate ($T_a(z)$). The twining rate corresponds to the number of recruits each mother produced (1 or 2) each year. Only female offspring are kept in the models assuming a balanced sex-ratio of 0.5. Finally the inheritance function gives the phenotypic trait of the offspring at age of first census according to the phenotypic trait of their mother at reproductive age ($D_a(z'|z)$). The survival, recruitment probability, and twinning rate functions were estimated with a logit transformation. The growth and the inheritance functions were modeled as Gaussian density probabilities. Their mean and variance were modeled with linear functions. Every function has age class-specific intercept and slope values. The total number of model parameters is the total number of coefficients of all functions. The IPMs are described in the Appendix S2.

To check the accuracy of our analytical framework, we also compare the similarities between the values obtain from our analytical results to values obtain from numerical simulation of proportional changes in C with respect to changes in the model parameters. We numerically computed the proportional changes in C from simulations by adding 10^{-5} to each model parameter, one at a time, dividing the resulting change in the perturbed C by the unperturbed C, and then scaling it back up by 10^5. This approach is described in detail in Coulson et al. (2010).

Here, we provided only point estimates of C and its proportional changes without their uncertainty. Uncertainty around derived values estimated at the population level depends on the covariance of all parameters (i.e. slopes and intercepts of all functions) of the model. Because demographic functions were estimated independently in these two published IPMs, from different datasets including different females, covariances among parameters were not available and we could not properly estimate the uncertainty around C and its proportional changes. Nevertheless, a simple way of estimating the uncertainty around the C and its proportional changes would be to run the analysis over the whole parameter probability distributions. For instance, if parameters of the different functions are estimated together in a Bayesian framework (Elderd and Miller 2016), the 95% credible intervals of C and its proportional changes can be obtained by running the analysis using the 95% credible interval of all parameters. Koons et al. (2017) used a similar approach to estimate the uncertainty around elasticities of population growth rate to demographic rates for instance.

RESULTS

The estimated C of body mass at age of first census were 0.20 for Soay sheep and 0.34 for roe deer. While variances in maternal phenotypic trait at birth (denominator used in the estimation of C) were similar (5.59 and 5.39 for roe deer and Soay sheep, respectively), the covariance between offspring and maternal traits at birth (numerator) was smaller in Soay sheep (0.53) than in roe deer (0.94). This is because Soay sheep females can give birth at 1 year of age and so give birth to offspring of different body masses at different ages, whereas roe deer females give birth from 2 years of age onwards (i.e. when they have reached over 90% of their full body mass) to more similar offspring each year. Depending of the model parameter perturbed, the proportional changes in C varied between -6% and 2.5%. A positive and negative proportional change means that a small increase in one of the model parameter leads to increase or decrease in the correlation between maternal and offspring traits (C), respectively. Then, the mechanisms involved in each parameter are described in details in each part of the results. Both the analytically and numerically calculated proportional changes provided equivalent results (Appendix S4: Figs. S1 and S3).

In general, perturbing the mass dependent slopes had larger effects on C than perturbing intercepts (Figs. 1 and 2). In the following, we will present the analytically calculated proportional changes with respect to changes in fertility (i.e. reproductive rate and twinning rate functions) and viability (i.e. survival functions) selections, growth, and inheritance. To understand the proportional changes in C, we also present the underlying proportional changes in the means and variances of the three distributions that contribute to determining C: the distribution of phenotypic trait at birth within the stable cohort ($\mathbf{u}$), the distribution of maternal phenotypic trait at birth (X_0), and the distribution of offspring phenotypic trait at birth (Y_0) (Fig. 5, Appendix S3: Tables S1, and S2).

Proportional changes in C with respect to viability selection

Results are presented for both species together, except when the results differed. For both species and almost all age-classes, increasing the slopes of the survival function and thus altering viability selection resulted in large negative proportional changes in C (Figs. 1 and 2). Changes to the slopes for the adult age-classes had the most pronounced effects. Increasing these slopes increased survival across all trait values but decreased the potential effect of viability selection on the distribution of body mass because these changes increased survival of light adults more than survival of heavy adults. This is because the survival probabilities predicted by the unperturbed survival models were already approaching the boundary of 1 for heavier adults (Figs. 3, 4, also see Appendix S4: Fig. S4 for a graphical display of this effect of the logit scale). In contrast to this, increasing the survival slope for Soay sheep lambs, for example, increased survival and the potential effect of viability selection on the distribution of body mass, meaning that survival increased more for heavier lambs than for lighter lambs (Fig. 3 and Appendix S4: Fig. S4).

Regardless of the direction of the change in viability selection, increasing the adult survival slopes decreased C because more individuals survived and grew to reproduce at heavier masses. This surplus of adult individuals reproducing at large trait values, and producing relatively heavy offspring, increased the mean offspring phenotypic trait and decreased the variance among offspring. This means that potential mothers were heavier and more similar at birth (Fig. 5). As a consequence, the variance in maternal phenotypic trait at birth decreased. The covariance between maternal and offspring traits at birth decreased also substantially. Due to the overall higher survival probabilities and the reduced viability selection, more mothers with light birth mass grew to heavy adult masses where they gave birth to heavy offspring. Defined by the ratio of this covariance and variance in maternal trait at birth, C overall decreased in both species as the survival slope increased (Fig. 5).

Increasing the survival slopes for Soay sheep lambs and yearlings had comparable effects (Fig. 5). However, perturbing the survival slope for roe deer yearlings had little effect because the decrease in the covariance between maternal and offspring traits at birth was relatively weak.

Proportional changes in C with respect to fertility selection

Changing the slopes of the fertility functions and so fertility selection had much larger effects on C for Soay sheep than for roe deer (Figs. 1 and 2). For Soay sheep, fertility selection mostly operated through the probability of recruitment (i.e. probability for a mother to have at least one offspring surviving up to four months of age for Soay sheep and eight months of age for roe deer) because the twinning rates (i.e. number of offspring produced if probability of recruitment is 1) were very low (Fig. 3). Another idiosyncrasy of the Soay sheep was that the probability of recruitment for adults was similar across all phenotypic traits (Fig. 3). Therefore, fertility selection in the adult age-class was low. Introducing fertility selection by increasing the slope of the probability of recruitment function by an infinitesimal change had the largest effect on C of all perturbations for Soay sheep (Fig. 1). It decreased C by approximately 5 %.

Similarly to the effect of increasing the adult survival slope, increasing the slope of the probability of recruitment and positive fertility selection among adult Soay sheep resulted in more adults reproducing at large trait values. This increased the mean of the distribution of phenotypic trait at birth within the stable cohort and decreased its variance (Fig. 5). The increase in fertility selection resulted in an increase in the mean maternal phenotypic trait at birth, but the overall increase in fertility also led to lighter adults having higher fertility and therefore to an increase in the variance in maternal trait at birth. The offspring trait at birth increased due to the increase in fertility selection, and the variance in offspring trait at birth decreased. The covariance between maternal and offspring traits at birth therefore decreased substantially, which resulted in a large decrease in C (Fig. 5). In Soay sheep, lambs have a small probability of recruiting an offspring at one year of age (Fig. 3). Increasing this probability by increasing the slope of the function, increased C (Fig. 1). The increase in the slope of the probability of recruiting an offspring drastically increased the covariance between maternal and offspring traits at birth, because light-born mothers were more likely to remain light at 1 year old when giving birth to light offspring than to become heavy at 1 year old. More lambs reproducing also caused a decrease in the mean and an increase in the variance of all three distributions: potential mothers (stable cohort), mothers, and offspring were on average all lighter and less similar at birth. As a result, C increased (Fig. 5).

For roe deer, altering the probability of recruitment had less pronounced effects (Fig. 2). Increasing the slope of the probability of recruitment and decreasing fertility selection for adults, due to the effect of the logit transformation (Appendix S4: Fig. S4), increased C. The decrease in fertility selection resulted in a decrease in the mean of the distribution of phenotypic trait at birth within the stable cohort because lighter adults had a higher increase in the probability of recruitment than heavier adults. At the same time, the variance in the distribution of phenotypic trait at birth within the stable cohort decreased; potential mothers were lighter and more similar when compared to the unperturbed situation. These smaller mean and variance translated into smaller means and variances for both the maternal and offspring traits at birth. The covariance between offspring and maternal traits at birth increased, because mothers that were born light, and therefore took longer to grow to the asymptotic mass than heavy-born mothers, had a higher probability of recruitment as light adults, resulting in light-born mothers having a higher probability to give birth to light offspring than in the unperturbed situation (Fig. 5).

Proportional changes in C with respect to growth

Changing both intercepts and slopes of the functions that determined the variances in growth had little effect on C for both species (Figs. 1 and 2). These perturbations changed the variances in maternal and offspring phenotypic traits at birth and the covariance between maternal and offspring traits at birth to similar proportions, which then overall had no effect on C (Tables S1 and S2). These findings even held for Soay sheep, where the growth variances have slopes that deviate from 0 (Fig. 3).

Increasing the slope of the mean growth function for adult and senescent Soay sheep had pronounced negative effects on C (Fig. 1). Increasing the slope of the mean growth function in an IPM has generally two consequences. First, all individuals of the targeted age-class attain faster their asymptotic body mass, with this acceleration being even larger for heavy individuals. Second, the mean maximum body mass increases because the mean growth rate function crosses the y = x line at higher trait values.

When the adult mean growth slope for Soay sheep was increased, individuals grew faster to larger trait values at which they had higher survival. This caused an increase in the number of adults reproducing at large trait values and therefore increased the mean mass of potential mothers, but also the variance in mass among them (Fig. 5). The increase in variance of mass among potential mothers (variance of the phenotypic trait at birth within the stable cohort) may have been caused by the increase in the asymptotic mass of adults, which increased the range of trait values over which adults reproduce. This change in the mean and the variance of phenotypic trait at birth within the stable cohort cascaded through and led to similar increases in the mean and variance of maternal and offspring phenotypic traits at birth. The increase in the asymptotic mass of adults, and the increase in how fast females grow to this asymptotic mass, increased the number of females that reproduce at large trait values regardless of their birth phenotypic trait. Consequently, the covariance between maternal and offspring traits at birth decreased, which divided by a much larger variance in maternal phenotypic trait at birth, resulted in lower C (Fig. 5).

To understand how increasing the mean growth slope for senescent Soay sheep influenced C, it is important to notice that the slope for mean inheritance is negative for senescent individuals; the heavier they are, the lighter are their offspring (Fig. 3). As a result, shifting the asymptotic mass for senescent females towards larger trait values, at which females had higher probabilities of recruitment and survival yet gave birth to lighter offspring, decreased the mean and the variance in the phenotypic trait at birth within the stable cohort. This variance further decreased because the variance of the growth function decreases with increasing body mass in the senescent age-class. The decrease in the mean and variance of the phenotypic trait at birth within the stable cohort was again followed by similar developments in the distributions of maternal and offspring phenotypic traits at birth. However, overall C decreased (Fig. 5) because the covariance between maternal and offspring traits at birth decreased even more.

For roe deer, only increasing the growth mean slope for yearlings had a notable effect on C, since most of the growth towards the asymptotic body mass occurs in this age class (i.e. between one and two years of age, Fig. 2). Increasing the slope of yearling growth resulted in individuals growing faster to heavier masses at which they recruited to the adult age-class. They therefore experienced higher probabilities of survival, recruitment, and twinning rates during the first time step as adults. Due to the positive slope of the mean inheritance function (Fig. 4), this increased the mean and decreased the variance in the phenotypic trait at birth within the stable cohort. Since potential mothers were heavier and more similar at birth, plus they grew faster during the yearling stage, both mothers and offspring were also heavier and more similar in birth trait, which increased the covariance between maternal and offspring traits at birth (Fig. 5). Divided by a smaller variance of maternal phenotypic trait at birth, this led to higher C.

Proportional changes in C with respect to inheritance of the phenotypic trait between mother and offspring

The only direct relationship between offspring trait at birth and maternal trait (at birth of their offspring) is modeled by the inheritance function. Nevertheless, perturbing this relationship by increasing the slopes of the mean inheritance function had only moderate effects on C (Figs. 1 and 2). Increasing the slope of the mean inheritance function for Soay sheep yearlings and roe deer adults increased the mean of the phenotypic trait at birth within the stable cohort and decreased its associated variance. It decreased the variance because both age-classes had high probabilities of recruitment for large phenotypic trait values of the respective age-class (Figs. 3 and 4). Offspring produced were therefore heavier and more similar than in the unperturbed situation. Since potential mothers started out heavier and more similar than in the unperturbed situation, the mean birth trait of mothers was also larger and its variance smaller. Since mothers were heavier, they gave birth to heavier and more similar offspring than in the situation when the inheritance function was not perturbed. The covariance between maternal and offspring traits at birth increased, while the variance in maternal trait at birth decreased, resulting in higher C caused by these perturbations.

However, increasing the slope of the mean inheritance function for adult Soay sheep actually decreased C (Fig. 1) because it increased the variance in maternal phenotypic trait at birth. Since both light and heavy adult Soay sheep have about the same number of offspring due to the probability of recruitment being almost constant, increasing the slope of the mean inheritance function shifted the mean of the distribution of phenotypic trait at birth within the stable cohort to heavier masses while spreading out the distribution. Since the stable cohort was heavier and less similar in birth trait, the mean and variance in maternal phenotypic trait at birth also increased. The covariance between maternal and offspring traits at birth also increased, but less than the variance in maternal phenotypic trait at birth, which overall resulted in a lower C.

DISCUSSION

We have demonstrated how the effect of all four demographic processes – viability and fertility selections, growth, and inheritance – on the phenotypic mother-offspring correlation (C) can be quantified and compared. To our knowledge, our work provides the first approach that allows the quantification of the relative influence of the four demographic processes on phenotypic transmission. Heywood (2005) derived a theoretical decomposition of the evolution of a trait, taking selection into account. However, it remains difficult to quantify each component of the decomposition given the data currently available from natural systems. Our method can be applied in populations where the long-term individual-based data, including individual age and phenotypic trait in relation to individual survival, reproduction, growth and inheritance are available, and where environmental conditions can be assumed to be constant. Our expressions for proportional changes in C apply to any IPM of this type, and can be extended to IPMs that describe multivariate traits and to IPMs that are evolutionary explicit (including the genetic and environmental components of the phenotypic trait) (Childs et al. 2016, Coulson et al. 2017).

C has long been considered as a measure of heritability (Falconer and Mackay 1996) which often gives similar measures to animal models (de Villemereuil et al. 2013). Transmission of phenotypic traits is often treated as a fixed value to predict the evolution of traits in wild populations (Kruuk 2004, Wilson et al. 2010). Because viability and fertility selections vary over time within a population (Siepielski et al. 2009), our study reveals that C should also vary in time within wild populations. Indeed, a number of previous studies have reported that C, heritabilities, and additive genetic variances and covariances among traits vary with the strength of selection, and across environmental conditions (Wood and Brodie III 2015; 2016, Wilson et al. 2006, Hadfield 2008, Husby et al. 2011, but see Ramakers et al. 2018). Thus, if C is measured in the same population in two different environments or in two populations within the same species, the two measures are expected to be different (Wilson et al. 2006). Our work demonstrates that measures of transmission of phenotypic traits should not be considered as constant when predicting the dynamics of phenotypic traits over multiple time steps.

Our findings show that viability and fertility selections influence C to a greater extent than growth and, surprisingly, even more than inheritance. Viability and fertility selections will influence phenotypic trait values over generations only when the offspring trait is linked to maternal traits. Inheritance and growth can consequently either dampen or amplify the effects of selection on C. Growth rates can change phenotypic traits within the life of an individual, and be seen as a plastic process (Gianoli and Valladares 2012). Similarly, inheritance may change if the relative influences of environmental, genetic and maternal effects vary with time. Our results show how C proportionally changes in response to changing one parameter in the model. Nonetheless, the observed variation in C will depend on which and how much parameters of the models are impacted by an environmental variation. While our approach measures deterministic proportional changes in C, an exciting extension of our work would be to estimate proportional changes in stochastic environments to account explicitly for environmental variation.

Our method allows understanding how the different demographic processes influence C by influencing the phenotypic covariance between offspring and parental (here mothers) traits, the variance in parental traits, or both. Generally, processes that lead to increase the propensity of individuals to give birth to offspring of different trait values decrease C. For example, a large effect of maternal age on offspring phenotypic trait such as positive effects of maternal experience in early adulthood or negative effect of maternal senescence in late life (Moorad and Nussey 2016, Perez et al. 2017, Kindsvater et al. 2012, Bowen et al. 2006, Saino et al. 2002) will decrease C. Another example of process that lead to increase the propensity of individuals to give birth to offspring of different trait, is an early age of first reproduction before individuals have attained full adult size/mass. Most female mammals do this, giving birth to their first newborn before they have reached asymptotic mass: in ungulates, for example, mass at sexual maturity is 80% of asymptotic mass, but there is substantial variation across species (Servanty et al. 2009). While

Soay sheep can reproduce at markedly different masses in different age classes (about 12kg as lambs, 17kg as yearlings and, 23kg as adults), giving birth to offspring of different masses, roe deer mostly reproduce at masses close to their mean asymptotic body mass (more than 20kg at first reproduction while adult body mass is about 22-24kg), resulting in more similar offspring masses across ages. Within-maternal variation in offspring body mass is 67% and 44% (percent variation explained by within- as opposed to between-individual effect in body mass obtained from a linear mixed model of offspring body mass including maternal identity as a random effect, Van de Pol and Wright 2009) for Soay sheep and roe deer, respectively. Accordingly, we estimated C of body mass at age of first census to be lower in Soay sheep than in roe deer. We next summarize some general insights that provide guidance in distilling these insights from our key findings.

First, perturbing intercepts had smaller effects on C than perturbing slopes, because perturbing intercepts primarily affects the means of phenotypic trait distributions, while perturbing slopes affects the means and the variances of these distributions. Second, perturbations of the same parameter, but for different age classes, do not always impact the processes they capture in the same way. Increasing the slope of the survival function, for example, increased viability selection in Soay sheep lambs, yet decreased it for adults. The reason for this is the slope of the survival function is not a direct measure of the strength of viability selection because we estimated the proportional change in C to the slope of the survival function on the logit scale. The particular effects of perturbing slopes are a function of the logit transformation (see the result part on proportional changes in C with respect to viability selection and Appendix S4: Fig. S4). Third, the different functions can interact to impact the value of C. An increase in viability selection, for example, increases mean offspring mass via the slope of the mean inheritance function. Finally, the more the functions vary among the different age classes, the less predictable are their interactions. This may explain why we see more, and primarily stronger, responses in C to perturbations of model parameters for Soay sheep when compared to roe deer (Figs. 3 and 4). Because selective pressures should vary with age class (e.g. Bonnet et al. 2017), these results show that accounting for different selective pressures in different age-classes should give better prediction of trait transmission, and trait dynamics as a consequence.

Effects of viability and fertility selections

Decreasing the strength of viability selection decreased C, in both Soay sheep and roe deer in the adult and senescent age classes. This is because a greater number of mothers of different birth phenotypic traits survive to grow and give birth to heavy offspring. However, large changes in viability selection on adult Soay sheep and roe deer over time are unlikely to be observed (Gaillard et al. 2000*b*). More realistic is variation in viability selection among young individuals such as Soay sheep lambs, which results in a decrease in C. In both species, viability selection between birth and census age (8 months in roe deer, 4 months in Soay sheep) is included in our models as fertility selection, because the probability of recruitment include the probability of offspring surviving from birth to the first census. Increasing fertility selection had the strongest negative effect on C for Soay sheep. Some studies have found that heritability is generally lower in poor rather than good environmental conditions (Charmantier and Garant 2005, Merilä et al. 2001 but see Husby et al. 2011). Wilson et al. (2006) showed that additive genetic variance decreased with increasing viability selection on offspring phenotypic trait in Soay sheep. In line with their findings, we observed that increasing adult and senescent fertility selection, which includes viability selection on offspring before they are first censused, decreased C.

Effects of growth and inheritance

The effects of viability and fertility selections on C are mediated by ontogeny. If individuals grow slowly, then any effect of selection on C has more time to act via the individuals that are still developing. If, however, individuals grow fast to asymptotic mass or trait value, then selection has less opportunity to influence C. This is why we observed a decrease in C with an increase in the mean growth rate of adult Soay sheep. Furthermore, we found that fertility selection had less effect on C in roe deer than in Soay sheep because roe deer were recruited at 8 months of age when most growth had already taken place ($\sim 70\%$ of the asymptotic mass, Hewison et al. 2011).

Inheritance captures processes that directly relate variation in maternal body condition to offspring phenotypic trait at birth. Despite it being the only direct relationship between maternal and offspring phenotypic traits, the effect of inheritance on C is small. The inheritance will vary if the relative influences of genetic, maternal and environmental effects on offspring trait vary with maternal age, trait or environmental conditions. Maternal effects often vary with maternal age (so-called maternal effects senescence Moorad and Nussey 2016, Saino et al. 2002, Perez et al. 2017) and traits in the wild (Räsänen and Kruuk 2007, Mousseau and Fox 1998, Plard et al. 2021). The mean inheritance function determines variation in offspring phenotypic traits, which then results in variation in mass among mothers via growth and viability and fertility selections. As expected, we found that increasing the slope of the mean inheritance function always increased the covariance between maternal and offspring phenotypic traits at birth. Remarkably though, this did not always result in an increase in C. For Soay sheep adults, the increased variance in the phenotypic trait at birth within the stable cohort also resulted in an increase in the variance in maternal phenotypic trait at birth, which overall decreased C. The variance around the mean inheritance function captures reproductive allocation. Changing this variance has little effect on C because it changes the variance in maternal phenotypic trait at birth and the covariances between maternal and offspring phenotypic traits at birth to similar extents. In some species, such as wild boars and Alpine marmots, individuals allocate resources differently to siblings as a possible evolutionary bet-hedging strategy to minimise the variance in reproductive success (Gamelon et al. 2013, Plard et al. 2021). Our results show that this has no effect on C in roe deer and Soay sheep, but may play a role in species with larger litter sizes.

Evolutionary consequences of demographic effects on C

Because our model includes a growth and an inheritance function that link an offspring's trait at birth to its mother's trait at the age of reproduction (Chevin 2015, Janeiro et al. 2016), it allows us to understand how, and how much, selection and growth can influence the mother-offspring regression of phenotypic trait at birth. C can increase both because the covariance between maternal and offspring phenotypic traits at birth increases, and because the variance in maternal phenotypic trait at birth decreases. Our results show that demography will always influence both the numerator and the denominator of this ratio. As illustrated by our results, the evolution of a continuous phenotypic trait is a complex interaction among transmission, selection and growth. Which of the potential future mothers will actually become mother and be used to estimate C are directly determined by viability and fertility selections (Hadfield 2008). The influence of selections on heritability has already been recognized in quantitative genetics (Hadfield 2008, Nakagawa and Freckleton 2008, Steinsland et al. 2014), but here we managed to quantify how much it will influence the phenotypic correlation between maternal and offspring phenotypic traits. The large negative influence of selection in roe deer and Soay sheep on C may suggest that our measures of heritability are often biased. Interestingly, this negative influence of selection on maternal and offspring resemblance might also partly explain why the evolutionary stasis often occurs in wild populations where many and variable selective pressures can influence a trait (Bonnet et al. 2017).

IPMs help get insights about why evolutionary stasis is so frequently observed while directional evolution is predicted. Thus, they present a powerful approach to study the dynamics of a continuous trait in natural systems, taking into account the interaction among environment, selections and transmission of the trait (Smallegange and Coulson 2012). This suggests that the eco-evolutionary dynamics of phenotypic traits in the wild depend on complex interactions between environment and genetics, which have often been neglected until now. Our study implicitly accounts for these interactions, but does not separate the relative effects of genetic, maternal and environmental effects. An exciting future development would be to estimate the proportional changes in the genetic and environmental components of a phenotypic trait in an IPM (Coulson et al. 2017, Simmonds et al. 2020).

Importantly, our results demonstrate that transmission of phenotypic traits varies with age. Indeed, maternal effects influencing offspring body mass or size (Mousseau and Fox 1998) often change with maternal age, condition, and experience. As a result, offspring phenotypic trait cannot be predicted from additive fixed and independent genetic, maternal and environmental effects only. Models of trait transmission need to account for the varying and dynamic influence of maternal effects. Restraint-Constraint hypotheses (Curio 1983) that explain why young birds reproduce less well, and maternal effect senescence (e.g. Hernández et al. 2020 for a recent analysis) that helps explain why old mothers reproduce less well, which are both increasingly reported in the wild, strongly support our conclusions.

Under the assumption that body mass is determined by a genotype (G) that remains constant throughout life plus some environmental variation (E), a slope of the growth function of 1, where body mass at age $a + 1$ is regressed against body mass at age a, would be expected. Indeed, under this hypothesis: $Z_a = G + E_a$ and $Z_{a+1} = G + E_{a+1}$. Thus, $Z_{a+1} = Z_a + E_{a+1} - E_a$ implying an intercept of 0, a slope of 1 plus some residual environmental variation. However, this is impossible in nature because a slope of 1 in commonly used growth models (such as von Bertalanffy, Gompertz or logistic) would mean either non-growing animals that will not change their body mass or individuals growing forever with the same proportional growth rate. Accordingly, the slope of the growth function has been estimated to be below 1 in published IPMs (Traill et al. 2014, about 0.7 in roe deer and Soay sheep, Coulson et al. 2010, Plard et al. 2015). Thus, body mass cannot only be determined by a genotype that remains constant throughout life plus some environmental variation. A first possibility that would give a slope of less than 1 would be for body mass to be determined by different but correlated genetic effects at different ages (Chevin 2015). Research to date has revealed strong positive genetic covariances across ages (Wilson et al. 2005) suggesting that this large genetic correlation across ages should also generate a slope close to 1 in the growth function and cannot be an explanation for the low regression slopes observed in empirical studies. The second explanation for a slope below 1 involves that the entire growth trajectory is controlled by genetic effects. This suggests that entire development trajectories rather than traits at specific ages should be used in future models of trait dynamics and evolution. Because the same genotype can attain different body masses in different environments, genotype-by-environment interactions are also likely to be influential in size-related traits.

Conclusion

Our deterministic analysis demonstrates that viability and fertility selections influence C more than growth and inheritance in two populations of long-lived mammals in the wild. To better understand the evolution of phenotypic traits, it is necessary to focus on phenotypic trait transmission along individual trajectories across the entire lifetime. Along these trajectories, individuals can be subject to different environments and selective pressures. Thus, variability in both phenotypic transmission and selection should be accounted in future studies predicting eco-evolutionary dynamics of phenotypic traits.

ACKNOWLEDGEMENTS

JAB acknowledges funding from the International Max Planck Research Network on Aging (MaxNetAging). TC acknowledges support from the NERC and an ERC advanced grant. ST was partly supported by US NIA grant R21AG06163901. We thank Jason Matthiopoulos, Ben Sheldon, Michael Morrissey, Tom EX Miller and two anonymous reviewers for helpful comments.

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OPEN RESEARCH

The IPMs for the Soay sheep and roe deer used in this paper used the published functions in Coulson et al. (2010), Plard et al. (2015), and the data used in these two previous analyses can be found at https://www.oikosjournal.org/appendix/oik-00035 (Coulson 2012) and https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.12393 for the Soay sheep and roe deer populations, respectively. The R code used to estimate C (the phenotypic mother-offspring correlation) and the proportional changes in C can be found in the Supporting Information in Data S1.

TABLE 1. Definition of variables used in the text

Variable	Definition
a	age class
z	continuous phenotypic trait (body mass)
$\widehat{\mathbf{Z}}$	Diagonal matrix of the phenotypic values (z_i)
t	time
i, j	indexing elements
p	any parameter (intercept or slope of a given function) of the IPM
$\alpha(a)$ & $\beta(a)$	age-dependent intercept and slope of a function
$n_{t,a}(z), \mathbf{n}_a$	continuous function, vector describing the distribution of the phenotypic trait per age-class in the population at t
$G_a(z'\|z), \mathbf{G}_a$	continuous function, matrix describing the growth function
$S_a(z), \mathbf{S}_a$	continuous function, matrix describing the survival function from age a to age $a+1$
$D_a(z'\|z), \mathbf{D}_a$	continuous function, matrix describing the inheritance function
$M_a(z), \widehat{\mathbf{M}}_a$	continuous function, matrix describing the reproduction function
$P_a(z'\|z), \mathbf{P}_a$	continuous function, matrix describing the survival and growth process
$F_a(z'\|z), \mathbf{F}_a$	continuous function, matrix describing the fertility process
$L_a(z'\|z), \mathbf{L}_a$	continuous function, matrix describing survivorship from phenotypic trait z at age 0 (birth) to trait z' at age a
$\mathbf{A}(r)$	renewal matrix
r	population growth rate
C	phenotypic mother-offspring correlation
Var(X_0)	Variance in maternal phenotypic trait at its own birth
Cov$(Y_0 X_0)$	Covariance between offspring phenotypic trait at birth and maternal phenotypic trait at its own birth
Y_a	offspring phenotypic trait at age a
X_a	maternal phenotypic trait at age a
$u(z_i), \mathbf{u}$	continuous function, vector describing the distribution of the phenotypic trait at birth within the stable cohort
K	lifetime number of offspring produced by the stable cohort $\mathbf{u}$
$\mathcal{H}$	variable used to simplify equations and equal to $\frac{1}{K}\sum_a \mathbf{F}_a \mathbf{L}_a$
E_{C}	proportional change in C
$\boldsymbol{\delta}_{\mathrm{C}}$	derivative of C
$\boldsymbol{\Delta}_a$	derivative of the matrix $\mathbf{F}_a \mathbf{L}_a$
$\boldsymbol{\Delta}$	derivative of a matrix
Δ	derivative of a vector
$\boldsymbol{\delta}$	derivative of a number
e^T	vector of one (1,1,...,1)

FIGURE CAPTIONS

Figure 1: The analytically derived proportional changes in phenotypic mother-offspring correlation with respect to changes in the model parameters of the Soay sheep IPM.

Figure 2: The analytically derived proportional changes in phenotypic mother-offspring correlation with respect to changes in the model parameters of the roe deer IPM.

Figure 3: The phenotypic trait-demography relationships used to parameterize the matrices in the IPM and the predicted stable distributions of phenotypic trait per age-class in the Soay sheep population. The age-class phenotypic trait distributions together sum up to 1. For the phenotypic trait-demography functions, lines represent predictions from regressions and dashed contours distributions around the mean.

Figure 4: The phenotypic trait-demography relationships used to parameterize the matrices in the IPM and the predicted stable distributions of phenotypic trait per age-class in the roe deer population. The age-class phenotypic trait distributions together sum up to 1. For the phenotypic trait-demography functions, lines represent predictions from regressions and dashed contours distributions around the mean. Roe deer yearlings do not reproduce.

Figure 5: roportional changes (in %) in mean and variance of the stable distributions: the distribution of phenotypic trait at birth within the stable cohort (u), the distribution of maternal phenotypic trait at (its own) birth (X_0), the distribution of offspring phenotypic trait at birth (Y_0), the covariance between offspring and maternal phenotypic traits at birth (Cov(Y_0X_0)), and C when selected slopes of the IPM are perturbed. We did not show all slopes but only the ones with large influence on C. See Appendix S3: Tables S1 and S2 for proportional changes in mean and variance of the stable distributions due to the perturbations of all intercepts and slopes of the IPM. Note that shown values were calculated numerically by adding 10^{-5} to model parameters.

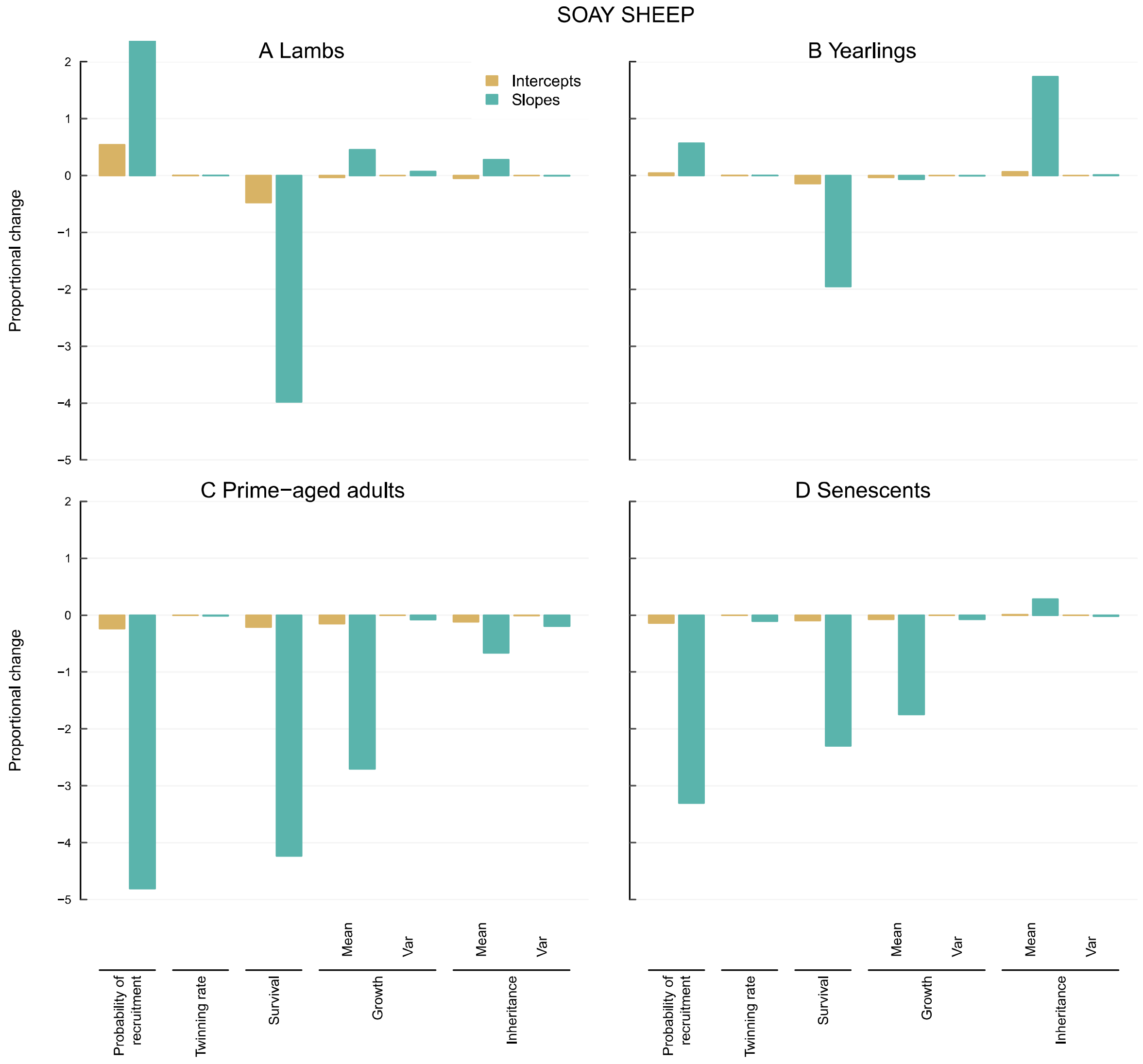

FIGURE 1. The analytically derived proportional changes in phenotypic mother-offspring correlation with respect to changes in the model parameters of the Soay sheep IPM.

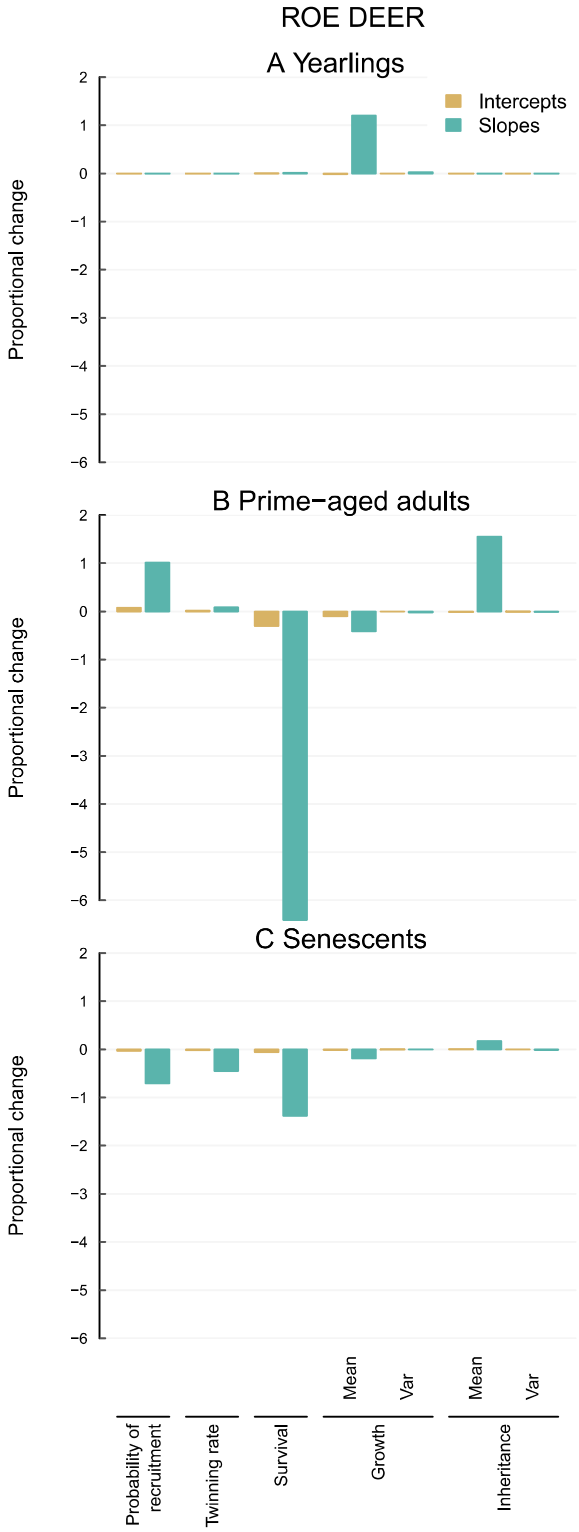

FIGURE 2. The analytically derived proportional changes in phenotypic mother-offspring correlation with respect to changes in the model parameters of the roe deer IPM.

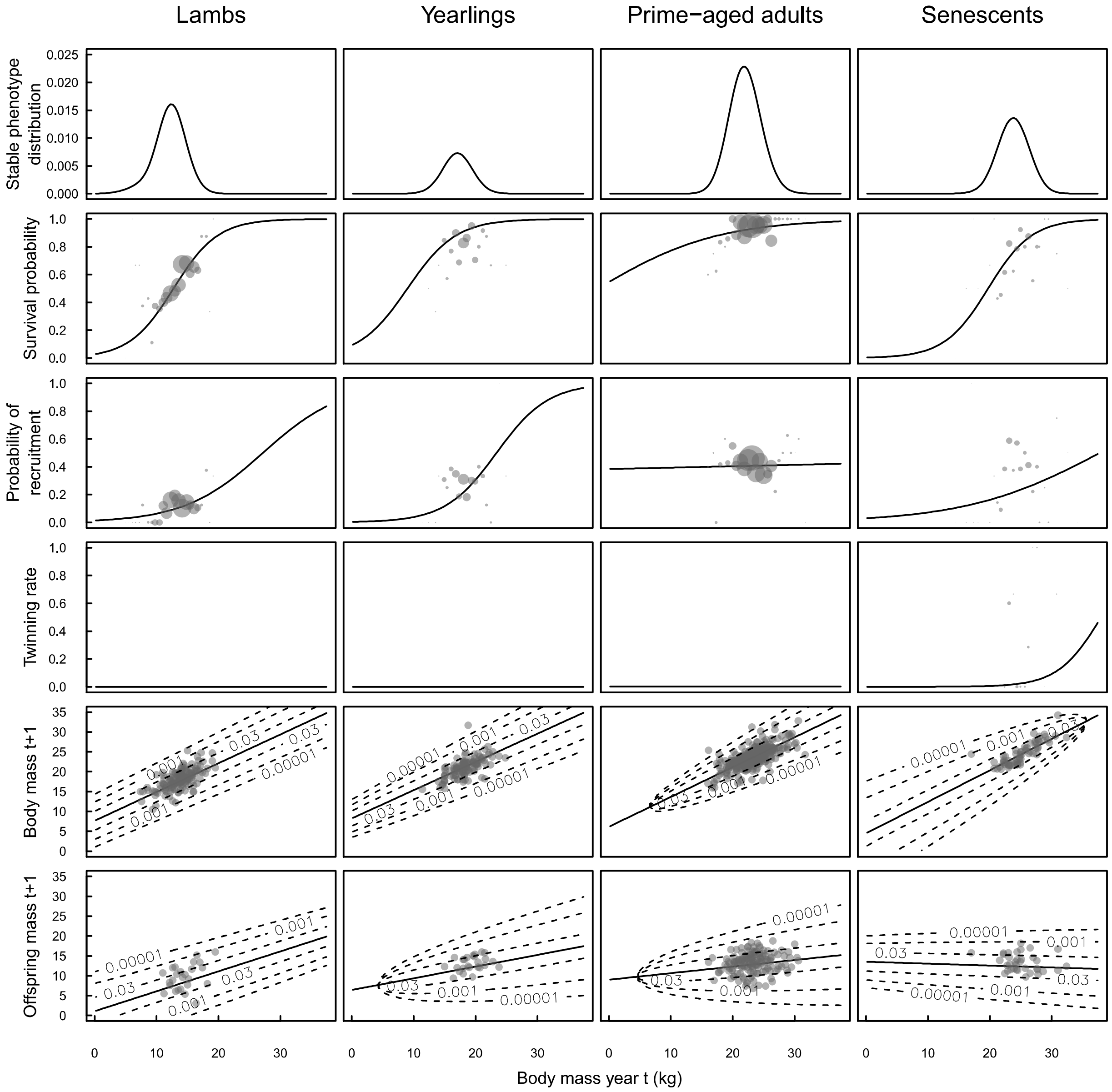

FIGURE 3. The phenotypic trait-demography relationships used to parameterize the matrices in the IPM and the predicted stable distributions of phenotypic trait per age-class in the Soay sheep population. The age-class phenotypic trait distributions together sum up to 1. For the phenotypic trait-demography functions, lines represent predictions from regressions and dashed contours distributions around the mean.

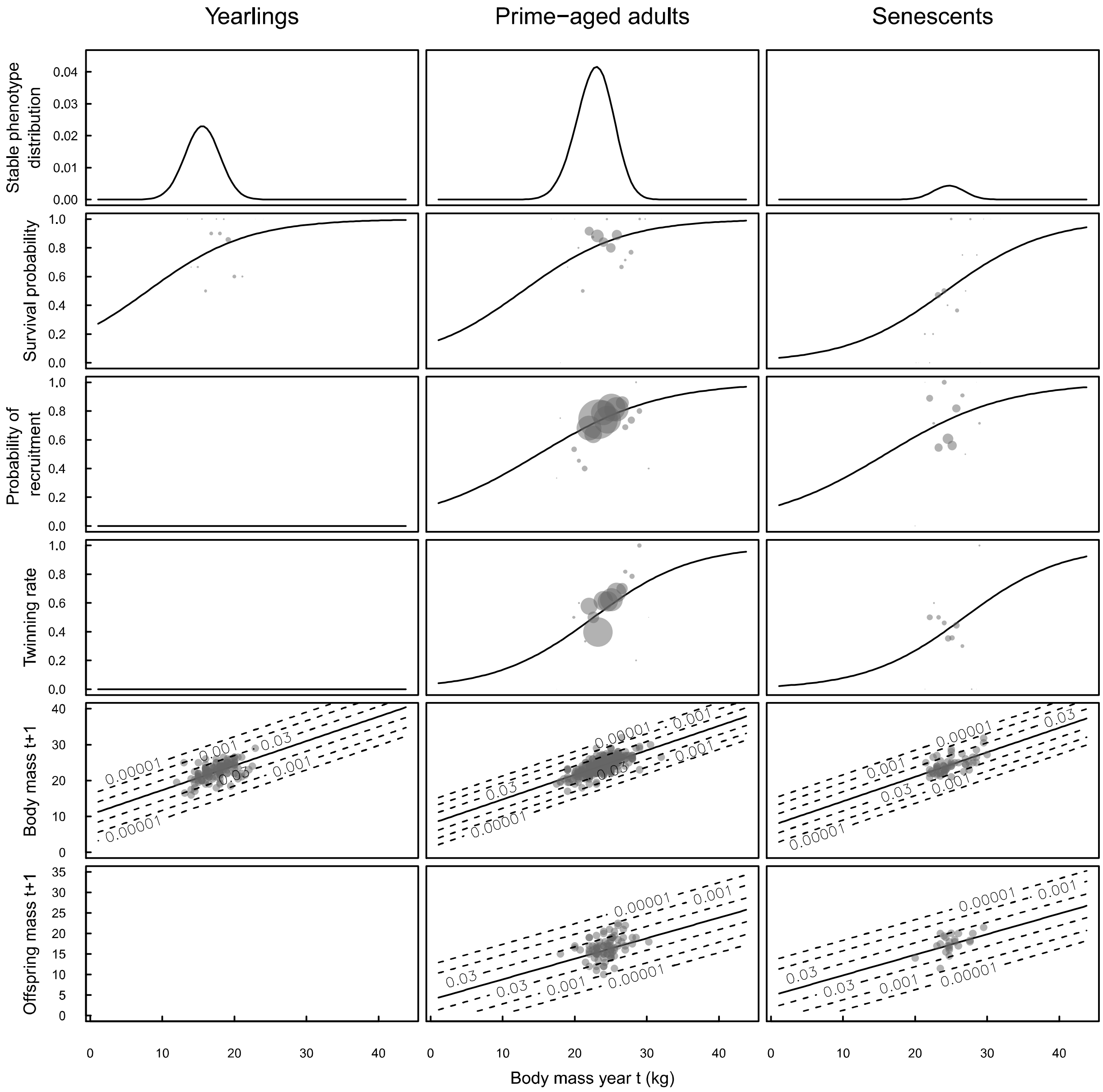

FIGURE 4. The phenotypic trait-demography relationships used to parameterize the matrices in the IPM and the predicted stable distributions of phenotypic trait per age-class in the roe deer population. The age-class phenotypic trait distributions together sum up to 1. For the phenotypic trait-demography functions, lines represent predictions from regressions and dashed contours distributions around the mean. Roe deer yearlings do not reproduce.

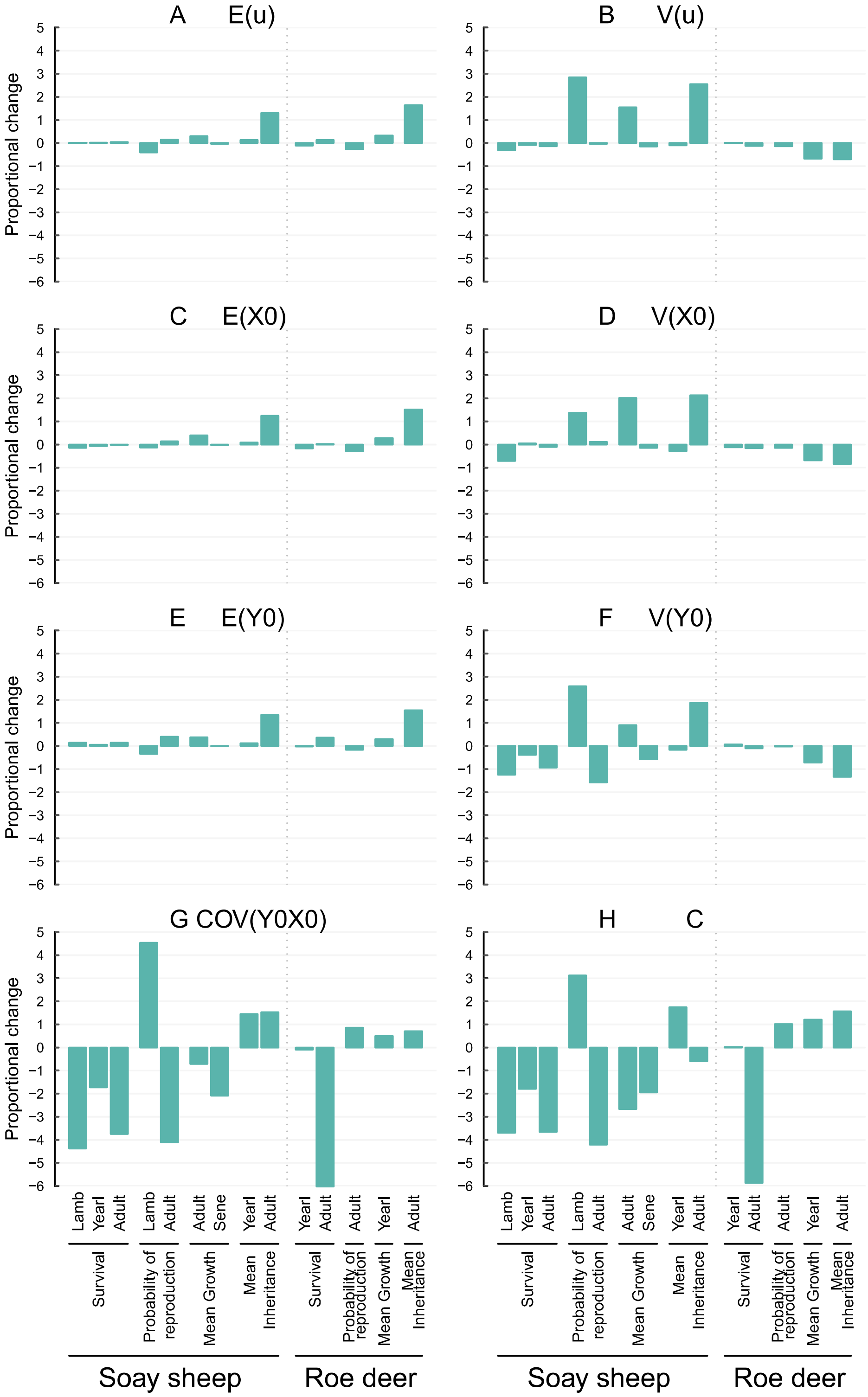

FIGURE 5. Proportional changes (in %) in mean and variance of the stable distributions: the distribution of phenotypic trait at birth within the stable cohort (u), the distribution of maternal phenotypic trait at (its own) birth (X_0), the distribution of offspring phenotypic trait at birth (Y_0), the covariance between offspring and maternal phenotypic traits at birth ($\mathrm{Cov}(Y_0 X_0)$), and C when selected slopes of the IPM are perturbed. We did not show all slopes but only the ones with large influence on C. See Appendix S3: Tables S1 and S2 for proportional changes in mean and variance of the stable distributions due to the perturbations of all intercepts and slopes of the IPM. Note that shown values were calculated numerically by adding 10^{-5} to model parameters.