
**Eco-evolutionary dynamics in the
bighorn sheep: linking population
growth, trait variation and heritability of
body mass**

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Abstract

Environmental change can simultaneously cause responses in population dynamics, life history, gene frequencies and phenotypic traits in a number of species. Because ecological and evolutionary dynamics are intimately linked and affected by the environment, a major challenge is to disentangle their relative roles in maintaining individual variability within a population. Here I implemented an integral projection model on the bighorn ewes and investigated the interaction between demography, life-history trait dynamics, quantitative genetics and an individual trait. By following individual fates and body size at different life-history stages, I investigated how body size influenced demographic rates. Moreover I analyzed cohort dynamics by following the fate of newborns in the population through their life and estimating heritability of body mass. By implementing a prospective perturbation analysis, I mimicked the effect of environmental changes and addressed which stage-specific demographic or trait-transition rate had the greatest influence on population dynamics, phenotypic plasticity, character heritability, additive variance and phenotypic variance among parents. Different age classes responded differently to environmental changes, highlighting the importance of accounting for different life-history stages in the analyses of population and evolutionary biology. Population growth rate, character mean, and the quantitative genetics quantities estimated responded differently to environmental changes, suggesting that environmental change can generate a very wide range of eco-evolutionary dynamics. Finally, I showed that fertility rates and ontogenetic development of body mass mostly affected body mass heritability and additive variance estimates in the bighorn sheep.

Key-words: integral-projection models; body mass; bighorn sheep; *Ovis canadensis*; eco-evolutionary dynamics; life-history theory; heritability

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Introduction

Body size is frequently a central consideration in study of evolutionary biology, life-history theory and population dynamic (review in Peters 1983). This is because body size is considered to be a fitness-related trait in many taxa, where bigger individuals are more likely to survive or successfully reproduce (Roff 2002). Body size is a phenotypic trait that varies among populations and within populations. This variation is shaped by the genetic composition of the population, as well as a range of environmental variables, such as resource availability and weather (e.g. through costs of thermoregulation Steinheim et al. 2004). Importantly, the environment may influence an individual's phenotype directly (phenotypic plasticity, Gause 1947), it may change the genotype-phenotype map (genotype-environment interactions, Via and Lande 1985), and finally it may shape how phenotypic variation is related to variation in fitness (environment-dependent selection, Siepielski et al. 2009).

Evolutionary biology, life-history theory and population dynamics deal with different aspects of the distribution of fitness-related phenotypes in a population and have traditionally studied different aspects of the distribution of body size. For example, evolutionary biology is interested in the presence of heritable variation in body size to study evolutionary responses to selection. The heritability (h^2) expresses the potential for a trait to evolve and is defined as the ratio of additive genetic variance to total phenotypic variance (V_A/V_P) (Falconer and Mackay 1996). Fitness related traits, such as body size, are expected to be under strong directional selection, and therefore should exhibit little additive genetic variance (Fisher 1930). However empirical studies have both corroborated (e.g. Mousseau and Roff 1987, Kruuk 2004) and disproved this hypothesis (e.g. Mousseau and Roff 1987). Since body size is not a static trait of phenotype and the selective pressure acting on individuals changes over their lifetime (e.g. juvenile vs. adult viability), the covariance between size and fitness may differ at particular ages or ontogenetic stages. Life-

history theory primarily focuses on size at birth, growth pattern, size of offspring, and age- and size- reproductive investments (Stearns 1992). Finally, population ecology concentrates on population size fluctuations by analyzing the means and variances of the distribution of body size in the population (Coulson et al. 2010). Despite the fact that population ecology, life history and evolutionary biology were developed as separate disciplines, recently there has been growing interest in the effects that ecological and evolutionary processes have on each other (review in Pelletier et al. 2009). For example life-histories emerge from transitions between life stages and can therefore influence population dynamics (Saether and Bakke 2000, Oli and Dobson 2003); and phenotypic change can influence population growth and dynamics (Ozgul et al. 2009). Given that ecological and evolutionary processes are intertwined, studying these linkages and the relative role of ecological and evolutionary dynamics would allow a deeper understanding of the relationships between phenotype, genotype, fitness and environment.

From an evolutionary perspective, phenotypic changes of continuous traits over time depend mainly on the intensity of the selection and the heritable fraction of the trait (Falconer and Mackay 1996). Selection on quantitative traits is generally estimated by relating individual measurements to individual relative fitness (Lande and Arnold 1983), but, even in presence of selection, an essential requirement for evolutionary change is the amount of genetic variability expressed for the trait under selection (Charmantier and Garant 2005). Early investigations of trait heritability ($h^2 = V_A/V_P$) showed that the magnitude of genetic and environmental components in total phenotypic variation for specific traits can change with environmental conditions (Hoffmann and Parsons 1991). This implies that the amount of additive genetic variation on which evolution could act varies according to the environment. Understanding the amplitude and direction of this change depending on environmental conditions would greatly improve the extent to which one could predict evolutionary change (Charmantier and Garant 2005). However, there has been discussion about whether unfavorable versus favorable environments should increase or decrease heritable variation (Hoffmann and Merila 1999). Several empirical studies found an increase of heritability under favorable conditions (e.g. Charmantier and Garant 2005), or lower heritability in unfavorable conditions (e.g. Merila and Sheldon 2001); while others found higher heritable variation in unfavorable conditions (e.g. Hoffmann and Parsons 1991). Finally, some studies found complex and unpredictable responses to

changing environmental conditions (e.g. Ebert et al. 1993). These results suggest that the relationship between environment, phenotype and potential evolutionary change are extremely complex. Given that environment influences also population dynamics (see above), understanding the feedback between environment, ecology and evolution is important in predicting dynamics and evolutionary potentials of populations under environmental change (Billington and Pelham 1991, Charmantier and Garant 2005).

Unfortunately simply tracking the dynamics of a character distribution, such as body size, is not sufficient to link the fields of population ecology, life history and character evolution: it is necessary to derive a model that incorporates different key processes that interest each field (Coulson et al. 2010). Integral projection models (IPMs) are powerful models for studying population with complex structure. They are discrete time structured population model and allow population structure to be defined by a mix of continuous and discrete individual attributes such as size, age, or any other attribute that affect demographic rates (Easterling et al. 2000, Ellner and Rees 2006). IPMs can be deterministic or stochastic, and provide predictions for population growth and life time reproduction success under density dependent and independent conditions. The ease, with which these models can be parameterized, means that both simple and more complex models can be constructed using data routinely collected by biologists (Coulson 2012). Coulson and Tuljapurkar (2008) and Coulson et al. (2010) developed general theory linking IPMs, the Price equation (Price 1970), generation length and biometric heritabilities estimates (Jacquard 1983) from mother-daughter regression. By analyzing the relationships between body size, age and survival, fertility, ontogenetic development and inheritance of the character, this new modeling approach allows the simultaneous calculation of fundamental quantities that underpin population ecology, evolutionary biology and life history. For example, from this structured model one can calculate: (i) the distribution of modeled character; (ii) the covariance between parent and offspring character that is often interpreted as an estimate of additive genetic variance; (iii) the biometric heritability of the character calculated from the parent-offspring phenotypic covariance; (iv) descriptors of the life history including generation length; and (v) the strength of selection on characters via lifetime reproductive success. Because a range of quantities can be calculated from a single model one can gain insight into how the different quantities are associated. Furthermore, perturbation analysis can elucidate the relative importance of the different demographic and trait transition functions constituting the model in shaping the size and

shape of the phenotype distribution and in contributing to processes such as ontogeny and genetics (Coulson et al. 2010). However, despite their great promise, the applications of these techniques to link population dynamics and quantitative genetics remain scarce (but see e.g. Ozgul et al. 2009, Ozgul et al. 2010).

In this paper I analyze body mass and life-history data from a long-term individual based study of the bighorn sheep (*Ovis canadensis*) inhabiting Ram Mountain, Alberta, Canada. I implement the modeling approach developed by Coulson et al. (2010) to calculate population biology, life-history theory and quantitative genetics quantities. The objective is to evaluate the relative importance of demographic and trait transition in shaping the population dynamics and in determining life-history descriptors at different ages. Since cohort variations in early development mass can affect life-history traits and population-dynamics (Clutton-Brock et al. 1987, Post et al. 1997, Rose et al. 1998), I am particularly interested in the role of each part of the life cycle in influencing heritability of body mass and additive genetic variance in the population. To do so, I investigate and compare the effect of perturbations to the parameter estimates constituting the IPM on different life-history and population descriptors. At the best of my knowledge, it is the first time that a study implementing an IPM simultaneously analyzes the sensitivities of heritability of body mass, parent-offspring phenotypic covariance and phenotypic variance among parents to perturbations to model parameters. Finally, this approach allows making predictions of the population consequences of environmental change.

Materials and methods

(i) The integral projection model

IPMs provide a powerful framework to simultaneously investigate population dynamics and quantitative genetics and their relation with environmental change (e.g. Coulson et al. 2011). I developed, applied, and analyzed an IPM to explore how population dynamics and heritability of body mass in the bighorn ewes may respond to changes in the vital rates.

The IPM describes the temporal dynamics of the distribution of body weight at different ages. The model consists of functions describing associations between individual body mass and: (i) annual survival (the survival function $S(\mathbf{a}, t, \mathbf{z}')$) being the probability of

an individual of age a weighting z' to survive from time t to $t + 1$; (ii) the probability of a surviving individual growing from weight z' at time t to weight z at time $t + 1$ (the growth function $G(z|z', a, t)$); (iii) the probability of producing a female lamb between t and $t + 1$ that survives to $t + 1$ (the recruitment function $R(a, t, z')$); and (iv) the probability that a parent of body weight z' at time t produces an offspring with body weight z at time $t + 1$ when the offspring recruits to the population (the inheritance function $D(z|z', a, t)$). These functions constituting the IPM describe how the body weight distribution is transformed by the fundamental biological processes of reproduction, inheritance, survival and development (Easterling et al. 2000). The IPM is extended to include age- dependent demography, to account for age- related differences in survival, body growth, recruitment, and inheritance probabilities. The term $n(a, t, z)$ denotes the number of density of individuals at age a and character value z . The dynamics of this distribution from time t to $t + 1$ can be written:

$$n(1, t + 1, z) = \sum_a \int dz' D(z|a, t, z') R(a, t, z') n(a, t, z') \quad \text{eqn 1}$$

$$n(a + 1, t + 1, z) = \int dz' G(z|a, t, z') S(a, t, z') n(a, t, z'); \quad a \geq 1 \quad \text{eqn 2}$$

Definitions of variables are provided in Table 1. Eqn (1) gives the number density distribution of character values among recruits to be added to the population at time $t + 1$ as a function of parental character values at time t in all the fertile ages. The recruitment function $R(a, t, z')$ produces a number density distribution of parental character values that is then multiplied by the probability density function $D(z|a, t, z')$ to give the number density distribution of offspring character values. The integral is taken over all character values. The population level number density distribution of newborns corresponds to the sum of the age-specific number density distributions of offspring character across all fertile ages. Eqn (2) describes how the survival function $S(a, t, z')$ lowers the number density from $n(a, t, z')$ and how the character values distribution changes among survivors via ontogenetic development $G(z|a, t, z')$.

It is convenient to write the age- structured IPM in matrix form (matrices are denoted with bold-face uppercase, letters and vectors with bold lowercase letters), which is given by:

$$\mathbf{n}(t + 1) = \mathbf{K} \mathbf{n}(t) \quad \text{eqn 3}$$

where a terms from 1 to m and \mathbf{K} is the matrix:

$$\mathbf{K} = \begin{pmatrix} \mathbf{D}(1, t)\mathbf{R}(1, t) & \mathbf{D}(2, t)\mathbf{R}(2, t) & \dots & \mathbf{D}(m - 1, t)\mathbf{R}(m - 1, t) & \mathbf{D}(m, t)\mathbf{R}(m, t) \\ \mathbf{G}(1, t)\mathbf{S}(1, t) & 0 & & 0 & 0 \\ 0 & \mathbf{G}(2, t)\mathbf{S}(2, t) & & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & & \mathbf{G}(m - 1, t)\mathbf{S}(m - 1, t) & \mathbf{G}(m, t)\mathbf{S}(m, t) \end{pmatrix} \quad \text{eqn 4}$$

and $\mathbf{n}(t) = (n(1, t, z'), n(2, t, z'), n(3, t, z'), \dots, n(m, t, z'))^T$. In other words, the associations of the demographic rates with body mass, functions $S(a, t, z')$ and $R(a, t, z')$, are described by diagonal matrices $\mathbf{S}(a, t)$ and $\mathbf{R}(a, t)$ respectively. The trait transitions kernels, $G(z|a, t, z')$ and $D(z|a, t, z')$ are described by square matrices $\mathbf{G}(a, t)$ and $\mathbf{D}(a, t)$ respectively, with columns summing to unity to fulfill the normalization requirements $\int dz G(z|a, t, z') = 1$ and $\int dz D(z|a, t, z') = 1$. These matrices are all incorporated into one big matrix \mathbf{K} . To solve the model it is necessary to use numerical integration methods (Easterling et al. 2000): each component function is evaluated at q equally spaced quadrature meshpoints, z_j . Details of the numerical approximation of eqn (3) are explained in the appendix A2.

Childs et al. 2003 proved that the \mathbf{K} matrix of an age-size structure IPM, under biologically reasonable conditions, has a dominant eigenvalue λ , that is positive and strictly exceeds all others. A population growing at a constant rate λ , settles to a stable size-age distribution, which is given by the right dominant eigenvector of \mathbf{K} . The left eigenvector associated with λ is the reproductive value. The mean character value in the population \bar{z} , is given by $\bar{z} = \sum \mathbf{z}\mathbf{n}(t) / \sum \mathbf{n}(t)$; where \mathbf{z} is a vector of body mass midpoints across ages and $\mathbf{n}(t)$ is a vector of number of individuals at time t .

(ii) Calculating quantitative genetic quantities

As shown by Coulson and Tuljapurkar (2008) and Coulson et al. (2010), IPMs can be used to calculate life history descriptors, as well as quantitative genetics quantities, such as the estimate of character heritability and selection on the character via lifetime reproductive success. I now define the main quantities that I use to describe life history and quantitative genetic; other mathematical details and formulas are in the appendix A1. Theory has been formulated by Fisher (1930), and Lande (1982). Coulson and Tuljapurkar (2008) and Coulson et al. (2010) implemented IPM to combine evolutionary and ecological dynamics.

The performance of cohorts is tracked in terms of survivorship and fertility. Given a cohort of newborns in the population, survivorship describes the fraction of the individual of the cohort alive through time and their body mass distribution. In other words, it is the probability of living to age at least a , and is derived from the survival $S(a, t, z')$ and ontogenetic development $G(z|a, t, z')$ functions. Survivorship is denoted by $L(z|1, t, x)$ for a cohort of individuals that have born with character value x ; and by $L(z|a + 1, t + 1, x)$ in the other ages, where x is the body mass at age 1.

The expected distribution of offspring with character value z produced at age a by a parent born at time t with a character value x is denoted by $M(z|a, t + a - 1, x)$ and is calculated from the inheritance $D(z|a, t, z')$ and fertility $R(a, t, z')$ functions and the survivorship function above defined.

The lifetime reproduction $M_L(z|a, t, x)$ of a parent born at time t with character value x is calculated adding all the offspring produced at all ages. Ages are extended to a large maximum age A , which has to be higher than the average life-span and is different from the maximum age m used in the IPM.

The equations that calculate survivorship, expected distribution of offspring, and lifetime reproductive success are used to calculate a number of life history quantities. In the formulation developed by Coulson et al. (2010) such calculations are implemented in a constant, density-independent environment, when rates are time-independent. Generation length $T_c(a, t, z')$, is the average age of reproduction in a population in stable age distribution. In species reproducing at several ages, the extent of iteroparity is described by

the dispersion of reproduction with respect to age. The parameter measuring the dispersion of reproduction events across age is called demographic dispersion σ_a^2 . In other words, the demographic dispersion measures the age dispersion of reproduction, the extent of iteroparity, and whether individuals often skip breeding years (Tuljapurkar et al. 2009).

One can also adapt the IPM approach to address quantitative genetic analysis. The breeder's equation has been widely used to understand phenotypic change of heritable characters (Bulmer 1980, Lande and Arnold 1983). Specifically it describes the response to selection defined as the per generation change in the mean of the breeding value distribution. A breeding value of a character describes the additive genetic worth of a parent for that character (Coulson et al. 2010).

The breeder's equation, in the form implemented by Coulson et al. (2010) contains two terms: (i) a selection differential between the character z and lifetime reproductive success (M_L) and (ii) a character heritability h^2 . The heritability is the ratio of the additive genetic variance to the phenotypic variance: V_A/V_P . Heritabilities and additive genetic variance are estimated through a regression of daughter body mass at age a against maternal body mass at age a . Twice the slope of the regression line is the character heritability (Falconer and Mackay 1996). To estimate the biometric heritability of body mass measured at age 1, it is necessary to start with a cohort of newborns who progress through the life cycle and become parents. This cohort of newborns is described by a number density over character values $n(\mathbf{1}, t, z)$, which is iterated to track the number density distribution of offspring produced at each age in the life course. From the iteration one can calculate the number density distribution of the stage classes of offspring born to parents with a certain body mass at age 1 through their life course (Coulson et al. 2010). Considering a one sex model, the regression of offspring trait value Z^0 on parental trait value Z^p has a slope that equals half the heritability,

$$\frac{h^2}{2} = \frac{Cov(Z^0, Z^p)}{Var Z^p} \quad \text{eqn 5}$$

Equations to estimate $Cov(Z^0, Z^p)$ and $Var Z^p$ can be found in the appendix A1. Here I need to note only that these equations yield the mean character values of parents and offspring, and the variance among parents and can be used to explore several aspects of biometric heritability. First, it is possible to analyze the effects of changes in the mean

environment and in the vital rates on life history transitions. To do so, I compare the equilibrium heritability obtained by starting with a stable character density distribution of newborns with time-dependent values for cohorts who are observed over their reproductive lives (Coulson et al. 2010). Second, it is possible to examine the effects of age on heritability of body mass. This is done by considering only offspring produced at age a and estimating biometric heritabilities at each age a .

All the quantities here presented are integral functions of body size. They are approximated by a discrete matrix, in a similar way that eqns (1) and (2) are approximated by eqn (3). Details on numerical calculation can be found in the appendix A2.

(iii) Study species and data collection

The bighorn sheep has been studied at Ram Mountain, in Alberta, Canada, about 30km east of the main range of the Canadian Rockies (52°N, 115°W, elevation 1082-2173 m). Potential predators include wolves (*Canis lupus*), cougars (*Felis concolor*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), and golden eagles (*Aquila chrysaetos*). Rams are hunted during the summer.

Individuals were captured in a corral trap baited with salt from late May to early October, and marked with colored plastic ear tags or collars for individual identification since 1973. At each capture, sheep were weighted to the nearest 125 g with a Detecto spring scale. Data collection methods are described in details elsewhere (e.g. Jorgenson et al. 1993b, FestaBianchet et al. 1997). The capture efficiency rate was extremely high: more than 98% of the sheep were individually recognizable; all ewes were marked from 1976 onward; and in most years, more than 80% of the lambs were captured (e.g. Festa-Bianchet and Jorgenson 1998). I used data on life history and body masses collected from the female component of the population between 1973 and 2011. Females that died during trapping ($n = 2$) or were culled ($n = 36$; (Jorgenson et al. 1993a) were not considered in the analysis. Ewes live a long life, with the oldest female ever trapped at age 19. However, ewes aged 14+ were pooled to ensure reasonable sample sizes. Females start to reproduce at age 2. Ewes always produced singleton lambs. Because they are highly philopatric, do not preferentially associate with adult kin, and all ewes in the population use the same home range, common environmental effects on heritability estimates should be very limited (Reale et al. 1999). The mean birthdate of bighorn sheep lambs in Alberta corresponds to

May 25 (Festa-Bianchet 1988). Lamb-ewe matches were established through repeated observations of suckling. Yearly individual reproductive success was measured by lamb survival till September 15, the approximate time of weaning (Festa-Bianchet 1988).

Ewes of all ages were typically caught between four and six times each summer. Body mass of individual sheep was adjusted to September 15 by fitting mass as a function of date using linear mixed models (Martin and Pelletier 2011). I chose to analyze autumn mass because by mid-September adult ewes were near their peak yearly mass. Mortality tended to occur during the winter months, and body mass in September has been related to individual survival over winter (e.g. FestaBianchet et al. 1997). I used the number of adult females (≥ 2 years old) in June each year as an index of density. From 1973 to 1981, the population was maintained at low density (average of 34 ewes) through yearly removals of 12-24% of ewes (Jorgenson et al. 1993b). After 1981, the population increased, peaking at 104 ewes in 1992 and declining to 24 ewes in 2011. This observed decline has been related with an apparent deterioration of environmental conditions (Pelletier et al. 2007b).

(iv) Model parameterization

The probabilities that an individual, given its body weight at time t (i) survives from time t to time $t + 1$; (ii) reproduces between time t and $t + 1$; (iii) grows to a certain body mass at $t + 1$; and (iv) produces a lamb of a certain body mass at time $t + 1$ were estimated using individual data collected from 1973 to 2011.

All the statistical analyses were run in R version 2.15.1 (R Development Core Team 2011) using the lme4 package (Bates et al. 2011). All associations were tested using general linear mixed model (glmm) under the appropriate error structure (binomial for survival and recruitment, Gaussian for ontogenetic development and inheritance functions). Body mass and population size were held as fixed effects. Year was added as a random effect to correct for temporal variation in demographic rates. Age was treated as a factor. To increase the fit of each glmm to the data and to apply the principle of parsimony, ages were grouped in age classes. Competing models characterized by different age classes were then compared using their Akaike information criterion values (AIC, e.g. Burnham and Anderson 2004). The model with lower AIC value was preferred. In the same way the slopes of body mass were allowed to differ between age classes only after comparing models by their AIC score. It follows that the survival, recruitment, ontogenetic

development and inheritance functions in the IPM were parameterized according to different age classes' classification. For example, if lambs and yearlings are characterized by the same probability to survive from time t to $t + 1$, the parameter estimates α and β (see below for definition of parameter values) for the survival functions in the IPM in the ages 0 and 1 will be set to the same parameter value. However, if the ontogenetic development probabilities were found statistically different between lambs and yearlings, the parameter estimates α and β for the growth functions in the IPM in the ages 0 and 1 will have different parameter values. The process of increasing model fit to the data is essential because an IPM will only accurately capture the dynamics of a population and character distributions if the statistical functions used to construct the model accurately capture observation (Coulson et al. 2010). I tested all the functions for nonlinearity using generalized mixed additive models (mgcv package, Wood 2012), but found no compelling evidence for nonlinearity.

The character-survival functions $S(\mathbf{a}, t, \mathbf{z}')$ are of the form $\exp(\alpha + \beta z + \gamma N + \Phi(0, \sigma_s)) / (1 + \exp(\alpha + \beta z + \gamma N + \Phi(0, \sigma_s)))$ where α , β , γ , and σ_s are obtained from logistic regressions for survival. The fertility functions assume a similar form. The body weight development functions $G(\mathbf{z}|\mathbf{a}, t, \mathbf{z}')$ describe how body mass changes among survivors from time t to $t + 1$. Of course, some individuals will have identical masses, some will lose weight, some others will gain mass between a time step. Therefore, to estimate the growth kernel it is necessary to evaluate a function describing mean body size at time $t + 1$ given body size at time t , and also a function describing the variance around these associations. These functions are combined and then scaled so that all transition rates out of an age-stage class sum to unity. To estimate the variance function I regressed the squared residuals around the mean body mass function against the fixed and random factors defining the glmm as above mentioned (Easterling et al. 2000). Define α_μ ; β_μ ; γ_μ ; and σ_μ respectively the intercept, slope for body mass, slope for density and variance for year effect of the linear regression of ontogenetic development. Then define α_σ ; β_σ ; γ_σ and σ_g respectively the intercept, slope for body mass, slope for population size and variance for year effect of the variance function. It follows that $\sigma(\mathbf{z})$ and $\mu(\mathbf{z})$ are $\sigma(\mathbf{z}) = \sqrt{\alpha_\sigma + \beta_\sigma z + \gamma_\sigma N + \Phi(0, \sigma_g)}$ and $\mu(\mathbf{z}) = \alpha_\mu + \beta_\mu z + \gamma_\mu N + \Phi(0, \sigma_\mu)$. In the

age- structured IPM the probability density functions describing transition rates between z and z' in each age are:

$$G(z|a, t, z') = \frac{1}{\sqrt{2\pi\sigma(z)}} \exp\left(-\frac{(z' - \mu(z))^2}{2\sigma(z)^2}\right) \quad \text{eqn 6}$$

The $D(z|a, t, z')$ functions for each age are similarly defined and assume analogous form.

(v) Implementation of the IPM and perturbation analysis

Given the parameter values estimated I construct and analyze the age-structured IPM in R 2.15.1 (R Development Core Team 2011). Code for constructing IPMs is provided by Easterling et al. (2000) and Ellner and Rees (2006). The integration limit in eqns (1) and (2) was from 10.44 kg below the smallest value of z observed (11.6 kg) and to 97.9 kg above the largest value (89.0 kg). I discretized the continuous component of the IPM into 150 bins, which provided sufficient resolution for convergence of model output. I constructed a deterministic IPM (Easterling et al. 2000) by fixing the random effects and population size at constant values (Coulson 2012). In particular the year random effect was fixed at 0, while the population size (N) was fixed at the average of 60 females. I firstly calculate key quantities from the age-size structure IPM at equilibrium. Secondly, to estimate quantitative genetics quantities I iterated the last age-class to a larger maximum age chosen to be 50, in order to let the functions stabilize to a stable distribution. Finally, I perturbed individual parameter values in the character-demography functions and examined how each perturbation altered the following quantities: λ , \bar{z} , h^2 , V_A , V_P and σ_d^2 . The direction of each perturbation was chosen so as to increase λ . The proportional change of a quantity, p , from the equilibrium value due to a small perturbation of 0.1% to a specific parameter value a_s is given by a partial derivative $\partial p / \partial a_s$ and is approximated by $(\ln(p') - \ln(p)) / (a'_s - a_s)$; where p' is the new estimate of the quantity p , and a'_s is the value of the parameter value a_s after a perturbation of 0.1%. This is a form of sensitivity analysis (Caswell 2001) and it is commonly implemented in the analysis of IPM (e.g. Coulson et al. 2010, Coulson et al. 2011). Altering the intercepts and slope distributions mimics environmental variation and changes in the vital rates. For example, increasing the value of the intercept for the survival function mimics the effect of environmental change that improves average annual survival rates (Coulson et al. 2011). Instead, increasing the value of the slope mimics the effect of change that improves average annual survival rates

for all individuals, but by imposing stronger trait dependence, bigger weight individuals have bigger increased survival rates than smaller individuals. Perturbation analysis can be also used to analyze the action of natural selection. In fact, selection deals with perturbations: it favors changes in the phenotype that increase fitness. Fitness is a demographic concept (the rate at which a genotype propagates itself), so an essential part of the theory of natural selection is devoted to understand how changes in the phenotype affect λ (Keyfitz and Caswell 2005). For example, by separately perturbing the parameter estimates in the IPM it is possible to predict the rates that mostly impact λ . Similarly perturbation of parameter values can be implemented to examine how each perturbation alters any of the quantities calculated from the IPM.

Results

(i) Model parameterization

The relationship between body mass and survival, fertility, growth among survivors and inheritance of body mass in different age classes are displayed in fig. 1. The statistical analysis demonstrates that the probabilities to survive, reproduce, grow to a different body mass and produce an offspring of a certain body mass at time $t + 1$ differ in respect to age at time t . In fact ages are grouped in different age classes in each function and kernel. Parameter values for all functions and details on the age classification are in the appendix A3. In general, the generalized linear mixed models predict that females with bigger body weight are more likely to survive, reproduce, gain weight next year and produce bigger offspring in all the age classes (fig.1). It makes an exception the survival function in the age class from 2 to 8 years, where the probability of survival is almost 1 in all the body mass range. The slope for body mass in the function is near to 0 indicating that the relation between survival and body mass between 2 and 8 years of age is random. Population size negatively affects population growth, suggesting a decrease in the population density distribution at time $t + 1$ for large population sizes at time t . The year effect variance is quite large in most functions, which suggests that yearly variations play an important role on shaping population density distribution.

Parameter	Definition
a	Age
m	Maximum age
t	Time
z, z'	Character value
x	Character value at age 1
\bar{y}	the population mean of variable y
σ_y^2	population variance of y
λ	predicted mean fitness at equilibrium population structure
$n(a, t, z), \mathbf{n}(a, t)$	continuous, discrete distribution of character values in age class a at time t
$S(a, t, z'), \mathbf{S}(a, t)$	continuous function, matrix describing expected survival in age class a at time t
$R(a, t, z'), \mathbf{R}(a, t)$	continuous function, matrix describing expected recruitment in age class a at time t
$G(z a, t, z'), \mathbf{G}(a, t)$	continuous function, matrix describing expected development kernel in age class a at time t
$D(z a, t, z'), \mathbf{D}(a, t)$	continuous function, matrix describing expected reproductive allocation kernel in age class a at time t
T_c	generation time
h^2	character heritability
V_A	additive genetic variance of the character
V_P	variance of the character among parents
M_L	lifetime reproductive success
N	female population size
σ_d^2	dispersion of reproduction

Tab. 1 Definitions of variables used in the text.

(ii) Descriptive properties of the model

The IPM was evaluated in a deterministic framework, at an average population size of 60 females, and fixing the year random effect at 0. The descriptive properties of the

parameterized model can be assessed by calculating the stable size-age distribution numerically and comparing this with the data. The observed and predicted values for mean body mass in the population are compared in fig. 2. The stable mass distribution predicted by the IPM captures the bimodal distribution of body mass in the population: the smaller peak represents the juveniles, while the second peak represents the adults.

The values predicted by the model and those calculated from the observed data are displayed in tab. 2. Many estimates made from approximating the IPM as a matrix model are reasonably close to the observed values, whilst others correspond less well. In general the model overestimates values. The predicted estimate for mean body mass is in excellent agreement with the field data (tab. 2). However, a large mismatch occurs between observed and predicted population growth rate. This mismatch probably occurs because the model is density independent and does not include environmental stochasticity. Population size greatly fluctuated between 1973 and 2011, with a maximum value of 103 females in 1992. As the number of ewes increased, the population showed clear evidence of resource limitation, including delayed age of primiparity (Jorgenson et al. 1993a), lower survival of lambs and of yearlings (FestaBianchet et al. 1997, Jorgenson et al. 1997), and reduced mass gain and horn growth for young sheep (Festa-Bianchet et al. 1998). After 1992, lamb survival was low and variable and the population started to decline, reaching a minimum of 16 females in 2007. Moreover, variable weather conditions have been asserted affecting survival and fertility rates (e.g. FestaBianchet et al. 1997).

A large disparity between observation and prediction from the IPM was also in the generation time. A better estimate is given for the mean lifetime reproductive success (tab. 2). The estimate of character heritability is consistent to the one estimated from the animal model (Coltman et al. 2005). However it is important to note that the h^2 calculated from the animal model includes male offspring and corrects for maternal effect.

(iii) Perturbation analysis

I now describe how model predictions change as model parameters are altered. I focused my attention to six quantities: the population growth rate, the character mean, the heritability of body mass, the additive variance, the parent's character variance, and the dispersion of reproduction. Fig. 3 shows how perturbations of 0.1% impact these quantities. In general, perturbations to the slopes for body mass in most of the functions

had greater effects than perturbations to the intercepts. Increasing the intercept of the function of survival, for example, mimics the effects of environmental changes that improves average annual survival rates; whereas increasing the slope for body mass in the same function mimics the effect of changes that favor especially bigger individuals (bigger individuals have bigger increased demographic rates than smaller individuals). The latter might be related to asymmetrical intra-specific competition which leads some individuals of better quality to survive, grow and reproduce well, while others are suppressed in growth (contest competition, Nicholson 1954).

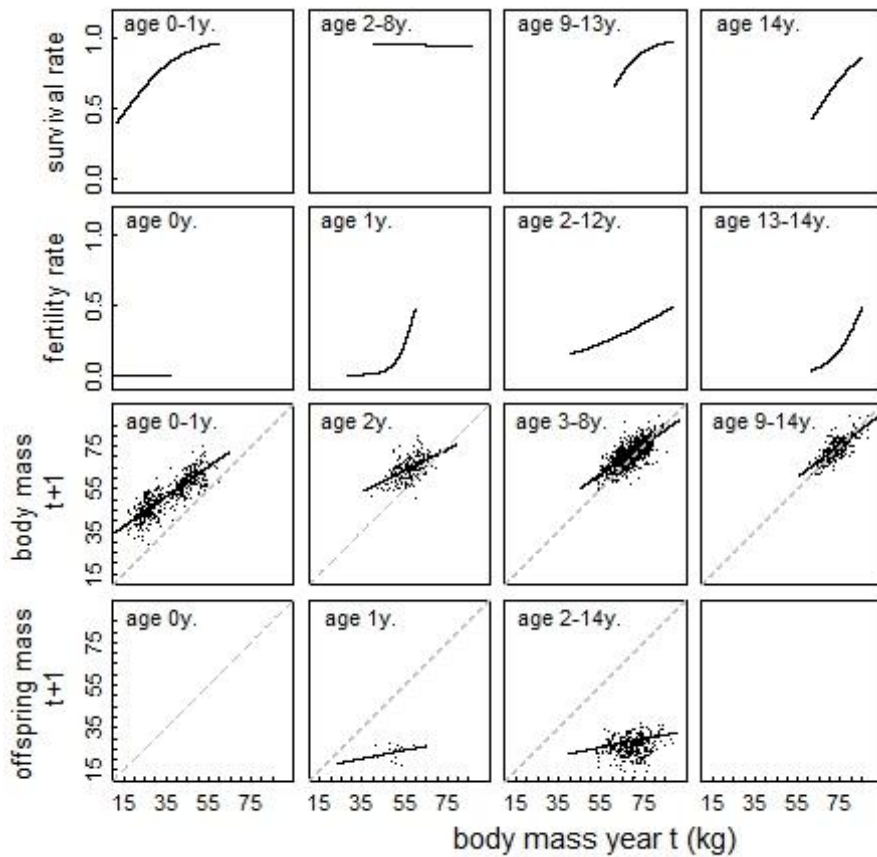


Fig 1. Shapes of the statistical functions between body mass and survival, fertility, mean growth rate, and mean reproductive allocation within the age classes (see also Appendix A3 for age class classification) used to parameterize the IPM. Body-mass variance functions are not displayed. Points represent the raw data, lines the predictions from the statistical model. In the third and fourth rows of the plot the grey dotted lines represent the function $y = x$. In the time transition from age 0 to age 1, ewes are infertile and therefore their probability of reproduce is 0 and there is no heritability estimate.

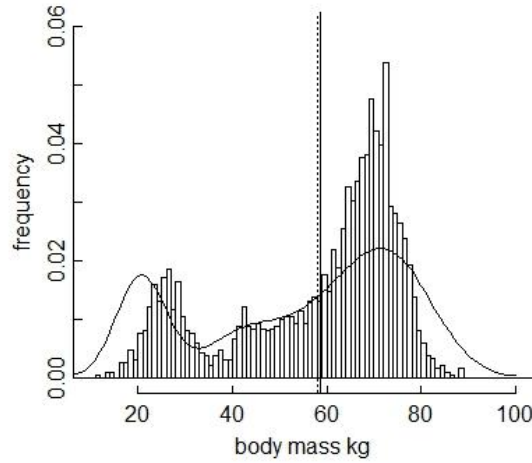


Fig. 2. Stable September body mass distribution (line) for the bighorn ewes. Bars indicate the observed distribution of body mass in the population between 1973 and 2011. Vertical lines show the observed (dotted line) and predicted (continuous line) mean body masses.

Quantity	Observed	Predicted
λ	1.03	1.16
\bar{z}	58.01	58.58
M_L	0.25	0.23
T_c	6.54	8.73
h^2	0.25 ± 0.04	0.26
V_A		29.66
V_P		113.46
σ_d^2		53.22

Tab. 2. Observed values from the data and predicted quantities from the model assuming equilibrium age-character structure. The estimated λ is calculated as the asymptotic ratio between population size in subsequent time steps ($N(t+1)/N(t)$). Weights are measured in kg.

The population growth rate lambda strongly increased with increasing slopes of survival and fertility rates, and also with increasing the slope of mean body growth. This is no surprise. In fact the population growth rate in deterministic environment is a measure

of fitness (Caswell 2001). By increasing survival and fertility rates individuals move more quickly to the fertile ages, and produce a higher number of offspring that survive to weaning. This means an increase in population size. The mean body mass in the population responded differently. Unsurprisingly, increasing the slopes for the mean body growth caused an increase in the mean body mass of the population. Furthermore, increasing the slopes for the recruitment functions produced a decrease in the mean body mass. With increasing the fertility functions more young individuals are added to the population, which in turn implies that the averaged body mass in the population decreases. Similarly increasing the slope for survival in lambs and yearlings causes a decrease in the character mean, while increasing the slope for body mass in the survival functions for older individuals causes an increase in the mean body mass. Demographic dispersion of reproduction decreased with increasing slopes for body mass in the survival functions, and the slope for body mass in the adults (2-12 years old). At the opposite it increased with increasing slope for body mass in the mean ontogenetic development in senescent individuals (9-14 years old), and the slope in the fertility function for mothers at least 13 years of age. These changes can be understood in terms of the changing age-stage distribution of the population. For example, when the slopes in the growth rates increase, the population shifts to include mostly larger but also smaller individuals. This might cause an increase in the dispersion of reproduction if the reproductive output becomes dispersed over a wide range of sizes.

I now focus on the overall heritability. Since heritability of body mass equals the ratio between overall parent-offspring covariance and phenotypic variance among parents, the three quantities are correlated. Estimates of heritability were strongly influenced by changes in the fertility rates, and in the mean ontogenetic development, although the direction of change was often different. The fertility function is characterized by 3 age classes: (i) yearlings; (ii) females from 2 to 12 years of age; and (iii) females older than 13 years. Increasing (iii) later fertility in the age class 13-14+ tends to strongly decrease the additive variance, and thus reduce heritability. On the other side increasing (ii) fertility rates in the adults (2-12 years of age) slightly reduces character heritability. This is because both additive variance and variance among mothers are negatively affected, thus changing the ratio between those two quantities. Increasing (i) the fertility rate in the yearling strongly increases additive variance, variance among parents and slightly increases character heritability. Furthermore, it is noteworthy that increasing the slopes for mean ontogenetic

development strongly affects character heritability, additive variance and variance among mothers. The growth function is characterized by 4 age classes: (i) lambs and yearlings; (ii) 2 years old females; (iii) females between 3 to 8 years of age; and (iv) individuals older than 9 years. Character heritability decreases after perturbations to the slopes of mean body mass development (i) in the young of 0 to 1 year of age, and (ii) in the prime aged adults (2 years of age). This is due to a decrease in the overall parent-offspring covariance and also a smaller decrease in the variance among parents. Perturbing (iii) the slope for mean ontogenetic development in females from 3 to 8 years of age causes a decrease in the character heritability. Between 3 to 8 years of age females body mass increases exponentially to reach a maximum mean weight. Increasing the slope of this function implies that bigger females grow faster than smaller females and that the phenotypic variance among parents increases. The overall parent-offspring covariance also increases with a smaller proportional change. Finally, perturbing (iv) the slope for mean ontogenetic development in adults aged at least 9 years causes an increase in the heritability of body mass. This is because the additive variance increases in a bigger proportion than the variance among parents. Perturbing parameter values of survival also impacts additive variance and phenotypic variance among mothers. However the heritability of body mass was only slightly affected by the same perturbations.

The dispersion of reproduction was mostly affected by perturbations (i) to the slopes for body mass in the mean ontogenetic development functions for ewes of 9 years of age or older; (ii) the slopes for body mass in the recruitment functions for females from 2 to 12 years of age and for older females; and (iii) the slope for body mass in the survival function of females of 14+ years of age.

Perturbing parameters in the inheritance function had no relevant effects on all quantities. Perturbing parameters in the variance functions used to construct the transition kernels $G(\mathbf{z}|\mathbf{a}, t, \mathbf{z}')$ had also small effects in almost all the quantities. Exceptions to this are the heritability of body mass, additive variance and phenotypic variance among mothers, which are slightly affected by perturbations to the slopes for body mass in the $G(\mathbf{z}|\mathbf{a}, t, \mathbf{z}')$ function. Increasing the variance around the mean ontogenetic development implies that the variability between individuals increases. The result is to slightly increase both the additive variance and the variance among mothers. It follows that character heritability slightly decreases.

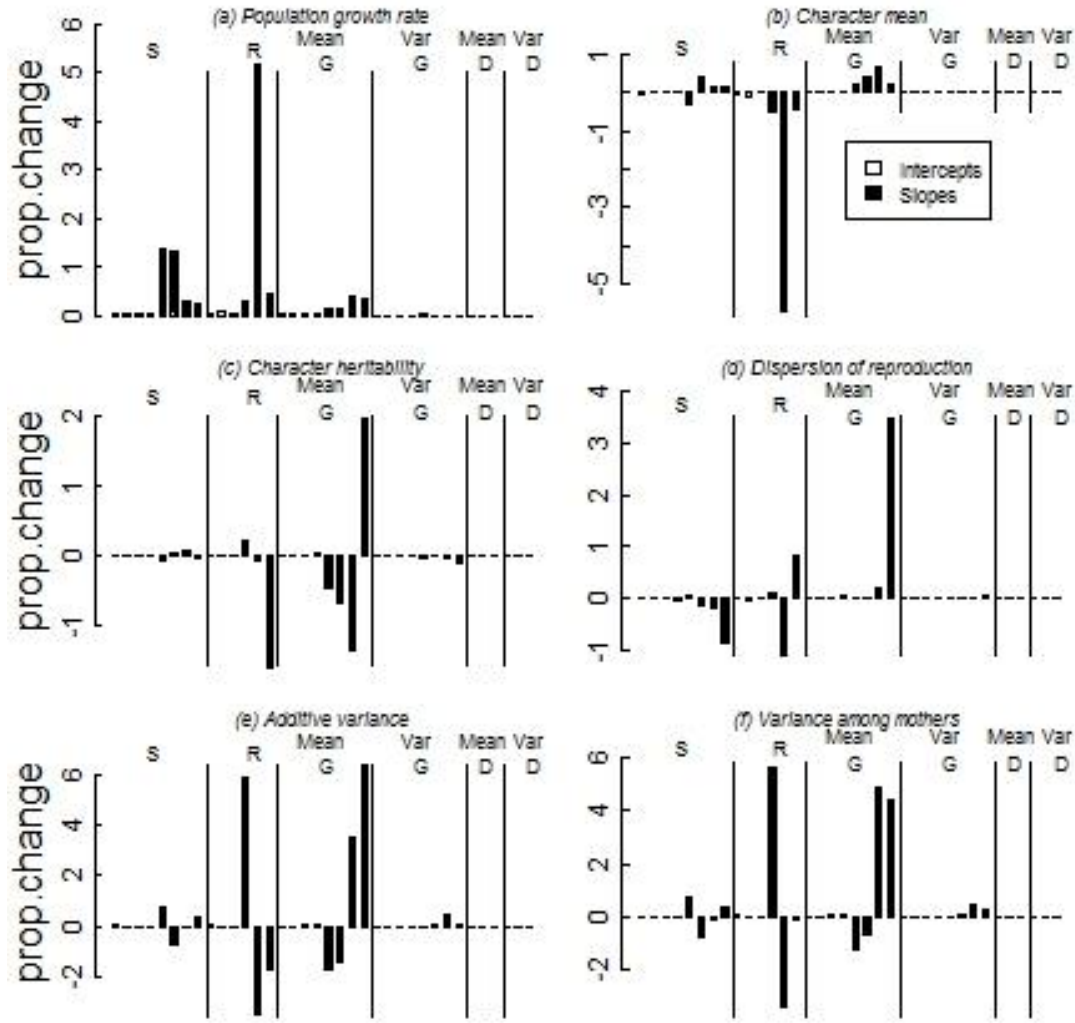


Fig. 3. The proportional consequences of 0.1% perturbation to intercepts (white bars) and slopes (black bars) for body mass in the functions of survival, fertility, mean growth rate, variance around the mean growth rate, mean reproductive allocation, and variance around the mean reproductive allocation for 6 quantities: (a) population growth rate λ ; (b) the mean of body mass in the population \bar{z} ; (c) the character's heritability h^2 ; (d) the dispersion of reproduction σ_a^2 ; (e) the additive variance V_A ; and (f) the variance among parents V_P . Vertical lines separate intercepts and slopes of different functions. The number of intercepts and slopes for body mass varies between functions because ages are grouped in different age classes in the four functions. In the survival function there are 4 age classes: 0-1 years, 2-8 years, 9-13 years, and 14 years of age. In the recruitment function there are 3 age-classes: 1 year, 2-12 years and 13-14 years of age. In the ontogenetic development ewes are grouped as follow: 0-1 years, 2 years, 3-8 years and 9-14 years of age. Finally in the inheritance function there are 2 age classes: 1 year, and 2-14 years of age.

(iv) **Biometric heritabilities at different ages**

I analyzed if heritability of body mass at age 1 varies with mother age. These heritability estimates are calculated from the covariance between parent and offspring (eqn (18) in appendix A1) considering only offspring produced at age a . Fig. 4 shows how character heritability varies in respect to age. The heritability of body mass in the lambs is estimated at 0 because sheep do not reproduce in the time transition between lamb and yearling. The character heritability fluctuates in mothers aged 2 to 4 years. In mothers between 5 and 10 years of age the heritabilities of body mass progressively decrease. In mothers aged 11 to 13 years the heritabilities increase. After 14 years of age the heritabilities estimates stabilize to a constant. I also conducted a perturbation analysis on the biometric heritabilities at different ages. The results are not shown here for space-limits. The results confirm those from the perturbation analysis of the overall character heritability: age-specific heritabilities are mostly affected by perturbations to the slopes in the recruitment and mean ontogenetic development functions.

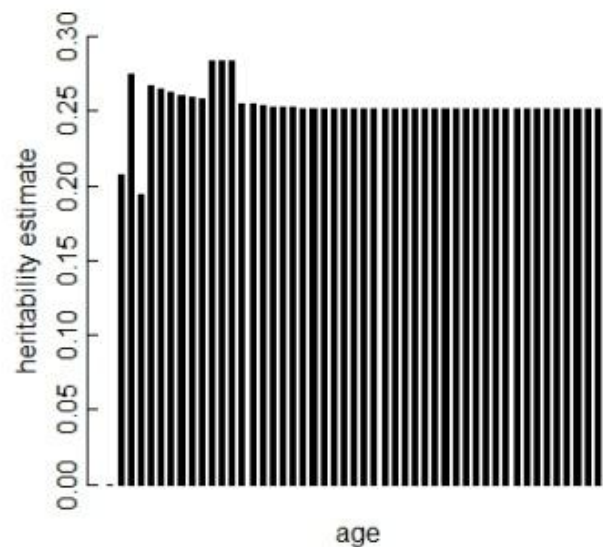


Fig. 4. Age specific heritabilities of body mass. Heritabilities are calculated to a maximum age of 50 years.

Discussion

A growing number of studies are devoted to understand how evolutionary dynamics are shaped by ecological processes (e.g. Coulson et al. 2006, Pelletier et al. 2007a). This study contributes to this research network by implementing an IPM to analyze links between environmental change, population dynamics and life history traits. The model provides specific insight to the bighorn sheep system. By implementing an IPM, I show how changes in the vital rates simultaneously impact population dynamics and quantitative genetics descriptors. According to previous studies (Coulson et al. 2010, Ozgul et al. 2012), changes to attributes of the functions describing the association between body mass, age and demography transitions generate a wide range of eco-evolutionary dynamics. Furthermore, I show how feedback between environment and population descriptors can affect heritability of body mass, parent-offspring phenotypic covariance and phenotypic covariance among parents. These findings help understanding how environmental change might affect the genetic variability expressed for a fitness- related character and highlight the importance of accounting for different life- history stages in quantitative genetics analysis.

(i) Model performance

IPMs simultaneously describe the association between the values of a continuous phenotypic trait and the probability of an individual surviving, reproducing, but also how the character distribution changes among surviving individuals and newborns in the population (Easterling et al. 2000). As in the IPM herein implemented, IPMs can be extended to include discrete character such as age and account for age-related heterogeneities in the associations between body mass and demographic rates. Immigration and emigration are not comprised in the analysis. However emigration from the study areas has been observed only in a few individuals in the population. In fact Jorgenson et al. (1997) report only 3 females and 13 males emigrating from the population between 1973 and 1996. These facts suggest that immigration and emigration rates are probably negligible in the ewes of Ram Mountain.

The parameterized model provides an accurate description of the average size in the population, mean lifetime reproductive success and heritability of body mass. Despite this the predictions differ from the observed population growth rate (which corresponds to

population fitness in constant environments, Keyfitz and Caswell 2005) and generation length. These discrepancies indicate that important aspects of the selection pressure acting on the bighorn ewes are not included in the model, because the model is evaluated at the average population size of 60 individuals and the year effect is kept to 0. However, it is straightforward to include density dependence and environmental stochasticity in the framework I have developed. Previous studies on the sheep have proved that high density negatively affect survival (Jorgenson et al. 1997), recruitment (e.g. Portier et al. 1998), body mass gain (Festa-Bianchet and Jorgenson 1998), and heritability of body mass (Reale et al. 1999). Annual survival, fertility rate and mass changes are also positively correlated with yearly weather conditions (FestaBianchet et al. 1996, Portier et al. 1998). Furthermore, Festa-Bianchet et al. (2006) demonstrated that stochastic predation events have dramatic impacts on bighorn population dynamics. Cougar predation on bighorn sheep occurs unpredictably, but, when predation occurs, cougars concentrate on the same bighorn population causing its drastic decline. For example, the mean annual growth rate for the bighorn sheep population in Ram Mountain declined from 1.017 to 0.789 in presence of cougar predation. Correcting for density-dependence, year variability and possibly stochastic predation would have provided a richer understanding of the dynamics of the study population. However, in this study I choose to analyze the model in a deterministic framework to categorize life history traits and to predict their eco-evolutionary dynamics at the stable stage distribution. This approach falls under the traditional theoretical research on life-history evolution that assumes constant environmental conditions (e.g. Fisher 1930, Stearns 1992). Recently Tuljapurkar et al. (2009) have argued that environmental stochasticity plays an important role in life-history evolution and that a stable environment may be an unrealistic assumption. In fact ‘optimal phenotypes’ in fluctuating environment are likely to differ from those in constant environments. The IPM for the bighorn sheep can be extended to include environmental stochasticity and density-dependence (e.g. Ellner and Rees 2006, 2007), and life-history descriptors could be calculated in a stochastic environment. Another option to test for the effect of density-dependence and environmental stochasticity is to examine how the quantities estimated vary as density and year effect are altered in the deterministic model (Coulson 2012). I will leave these for future work.

(ii) Perturbation analysis and population dynamics descriptors

I next examined how perturbing model parameters influenced population biology and quantitative genetics quantities. Changes to most of the parameter in the model simultaneously influenced estimates of all the examined quantities. The impact of changes in the fundamental functions constituting the IPM vary among different age-classes, suggesting that each life-history stage responds differently to environmental changes and has a different impact on population dynamics. For example, increasing the survival in the age classes 0 to 1 year of age and 2 to 8 years of age had a greater impact on the population growth rate than increasing the survival rate in older ages. This confirms previous findings. In ungulates juvenile survival is typically more sensitive to degradation of environmental conditions while adult survival is high and shows low variability (Gaillard et al. 2000b). More specifically, Festa-Bianchet et al. (1997) showed that survival at the younger ages in the bighorn sheep is high but variable between years and strongly affected by weather conditions and population density. Therefore, increasing young survival has a stronger effect in terms of population dynamics. The survival rate in relation with body mass between ages 2 to 8 is almost random, because most ewes survive despite their body size. Increasing the slope for body mass mimics an increase especially in the survival of bigger individuals (while the survival in smaller individuals increases at a slower rate), which implies an increased survival of individuals of better quality. This in turn positively affects population growth if bigger individuals produce more and better quality offspring. Not surprisingly increasing fertility rates, and thus the number of new born, causes an increase in the population growth rate. Increasing the mean ontogenetic development had a smaller impact on population fitness suggesting that environmental change is more likely to impact survival and fertility rates rather than character trait distribution within the population.

(iii) Heritability estimates

In many ungulates early development mass is a good predictor of reproductive potential (Albon et al. 1987, Clutton-Brock et al. 1992) and affects life-history traits and population dynamics (Clutton-Brock et al. 1992, Post et al. 1997, Rose et al. 1998). In the bighorn sheep Festa-Bianchet et al. (2000) found a positive correlation between mass during early development and lifetime reproductive success. Since body mass is a heritable character in the sheep (e.g. Coltman et al. 2005), and climate change is predicted to be

particularly strong in mountainous habitat (Oechel et al. 1997), it follows that understanding how environmental changes, including climate change, can impact heritability of body mass in the bighorn ewes is important in a conservation perspective of the population. Here the heritability of body mass is estimated at the approximate time of weaning in September of the first year of life. The heritability estimates are based on the phenotypic covariance between parents and their offspring. Each cohort of new recruits to the population is followed through years: one can record the number density distribution of offspring trait values produced by each stage-class within the same cohort through years (Coulson et al. 2010). Estimating heritability from the IPM presents some differences from estimating the heritabilities using the animal model. The animal model corrects for contributions from maternal effects, and non-additive genetic variance (e.g. Kruuk 2004). At the opposite, the estimate of heritability from the IPM does not distinguish between different components of variance and therefore the estimate of additive genetic variance may not be as precise. However it is noteworthy that the relative difference between the heritability of body mass predicted by the model and the heritability estimated from the animal model is small. Similarly, Coulson et al. (2010) estimated heritability of body mass without correcting for maternal effects in the Soay sheep (*Ovis aries*) through the implementation of an IPM and found their estimates matched well with those obtained from the application of the animal model. This is perhaps no surprising: in spite of the advantages the animal model offers, heritability estimates with and without correcting for specific components of variance have often similar magnitude (Kruuk 2004). Despite the above mentioned limitations of the IPM, the implementation of matrix modeling and perturbation analysis allows a mechanistic understanding of the heritability of body mass. This is a clear advantage if one aims to test the relative importance of vital rates on influencing the heritability of body mass, or to link population dynamics with evolutionary processes considerations.

(iv) Perturbation analysis and heritability estimates

The perturbation analysis showed that heritability of body mass is most strongly affected by ontogenetic development and fertility functions, and also that different age-classes respond differently to environmental changes. For example increasing the slope of ontogenetic development in mothers younger than 8 years of age decreases the character heritability estimate. In females of 2 years of age or younger this is due mainly to a decrease

in the additive phenotypic variance. In terms of adjustment of energy allocation between reproduction and ontogenetic development (e.g. Murray et al. 2009), a reduced additive phenotypic variance estimate in response to increased mean development rate implies that younger mothers invest more on growing faster than on producing offspring as big as they were at weaning. This strategy might pose an ecological advantage if mothers' fitness depends more on their own survival and future reproductive success rather than on reproductive success in a given year (Gaillard et al. 2003). In temperate environments juvenile survival is particularly constrained during winter and depends not only on body mass in late autumn but also on resource availability during winter (Gaillard et al. 2000a). Given that weather is extremely unpredictable during winter, low reproductive effort should be favored to avoid compromising maternal survival over lamb survival (Gaillard et al. 2003). In females from 3 to 8 years of age the decrease in heritability estimate is more complex and related with strong increases in both the additive genetic variance and phenotypic variance among mothers: the resemblance in body mass between mothers and newborns increases, and also the phenotypic variation among parents increases. This suggests that energetically favorable conditions lower individual differences, so that more females produce offspring of similar body mass as they were themselves at weaning. A similar result was found by Coltman et al. (2001) in the Soay sheep: heritability of parasite resistance did not differ in favorable and unfavorable conditions, but additive genetic variance was higher in favorable ones. Finally perturbation of the slope for body mass in the growth function in individuals of 9 years of age or older causes an increase in both heritability and additive variance estimates. An increase of heritability of size-related traits under favorable conditions has been found also in birds (Gebhardthenrich and Vannoordwijk 1991, Hoffmann and Merila 1999, Charmantier and Garant 2005). An hypothesis proposed to explain this trend is that increasing growth conditions enhances the genetic potential (Gebhardthenrich and Vannoordwijk 1991). Moreover, in good conditions residual or environmental variance tends to decrease, because the effects of local environmental differences are diminished compared with the genetic effects (Vannoordwijk and Marks 1998). It is perhaps easier to think at the opposite situation: in stressful environmental conditions, offspring size should be determined more from food abundance than any developmental genetic program (Vannoordwijk and Marks 1998). In the bighorn ewes, when growth conditions become more favorable oldest females can invest more energy on reproduction and produce lamb of similar size as they were

themselves at weaning. Another interesting result is that heritability and parent-offspring covariance estimates are negatively affected by increasing the fertility function in most of the ages (females from 2 to 12 years of age, and females older than 12 years). This implies that if females produce more lambs, they will invest less energy in each reproductive event and produce lambs of different body mass as they were themselves at birth. These findings show that the relation between environmental change, vital rates, life-history stages and character heritability are extremely complex.

(v) Conclusion

The analysis has provided several insights. First, changes in the function of survival, fertility and ontogenetic development in each life-history stage had different impacts in the quantities calculated from the model. Second, population fitness is more strongly related with survival and recruitment rates, than with individual ontogenetic development or inheritance of body mass. Third, changing fertility rates and mean ontogenetic development had strong impact on heritability of body mass and parent-offspring phenotypic covariance, but the magnitude of these impacts depended also on the age class considered. This suggests that the amount of additive genetic variation on which evolution could act varies not only according to environmental conditions but also to life-history stages. Finally, this study is consistent with research by Coulson et al. (2010) and Ozgul et al. (2009, 2012), and confirm that populations and individuals respond to environmental change in complex ways depending on which character-demography association is altered and on age. It remains to test how density-dependence and environmental stochasticity would influence these predictions.

Acknowledgments

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Supplementary information

(i) Appendix A1

In this appendix I explain and show mathematical equations to calculate life-history and quantitative genetics quantities from an IPM.

The survivorship function describes the probability of individuals in a cohort to survive to at least age a . In the model, cohort dynamics are simulated by iterating eqn (2): $n(a+1, t+1, z) = \int dz' G(z|a, t, z') S(a, t, z') n(a, t, z')$; $a \geq 1$. Let $\tilde{\mathbf{G}}(a, t)$ and $\tilde{\mathbf{S}}(a, t)$ represent the integral operator of the ontogenetic development and survival functions (integral operators are denoted by tildes). Between age 1 and 2, changes in a cohort are described by the integral operator $\tilde{\mathbf{G}}(1, t) \tilde{\mathbf{S}}(1, t)$ as in eqn (2)). Between ages 2 and 3, the corresponding integral operator is $\tilde{\mathbf{G}}(2, t) \tilde{\mathbf{S}}(2, t)$, and so on. By combining these transitions for each age, I obtain the survivorship functions, which are defined as follow:

$$\tilde{\mathbf{L}}(1, t) = \tilde{\mathbf{I}} \tag{eqn 7}$$

$$\tilde{\mathbf{L}}(a+1, t+a-1) = \left(\tilde{\mathbf{G}}(a, t) \tilde{\mathbf{S}}(a, t) \right) \circ \tilde{\mathbf{L}}(a, t) \tag{eqn 8}$$

where $\tilde{\mathbf{I}}$ is the identity matrix. That means for a cohort $\mathbf{n}_c(1, t) = \int dz' n(z', 1, t)$ giving the number of newborns at time t , the number of survivors of age a , denoted by $\mathbf{n}_c(a, t) = \int dz' n(z', a, t)$ can be obtained via iteration:

$$\tilde{\mathbf{L}}(1, t) [\mathbf{n}_c(1, t)] = \mathbf{n}_c(1, t) \tag{eqn 9}$$

$$\begin{aligned} \mathbf{n}_c(a+1, t+1) &= \tilde{\mathbf{L}}(a+1, t+1) [\mathbf{n}_c(a, t)] = \tilde{\mathbf{G}}(a, t) \tilde{\mathbf{S}}(a, t) [\mathbf{n}_c(a, t)] \\ &= \int dz dz' G(z|z', a, t) S(z', a, t) n(z', a, t) \end{aligned} \tag{eqn 10}$$

I can write eqn (9) and (10) for a cohort structured by age (discrete) and a continuous trait z in a continuous notation:

$$\tilde{\mathbf{L}}(x, 1, t) = \delta(z - x) \tag{eqn 11}$$

such that

$$\tilde{\mathbf{L}}(x, 1, t)[\mathbf{n}_c(z, 1, t)] = \mathbf{n}(x, 1, t) = \int dz \delta(z - x)n(z, 1, t) =: n_c(x, 1, t) \quad \text{eqn 12}$$

and

$$\begin{aligned} \tilde{\mathbf{L}}(z, a + 1, t + 1)[\mathbf{n}_c(x, 1, t)] &= \int dz' G(z|z', a, t)S(z', a, t)n_c(z', a, t) \\ &=: n_c(z, a + 1, t + 1) \end{aligned} \quad \text{eqn 13}$$

where $\delta(z - x)$ is the Dirac delta function, x is the character value at age 1, z' represents the character value at time t and z the character value at time $t + 1$.

The expected number density of offspring with character value z produced at age a by a parent born at time t with a character value x , $M(z|a, t + a - 1, x)$ is given by:

$$\tilde{\mathbf{M}}(a, t + a - 1) = \tilde{\mathbf{D}}(a, t)\tilde{\mathbf{R}}(a, t)^\circ \tilde{\mathbf{L}}(a, t + a - 1) \quad \text{eqn 14}$$

The lifetime reproduction $\tilde{\mathbf{M}}_L$ of a parent born at time t with character value x is given by:

$$\tilde{\mathbf{M}}_L(t) = \sum_{a=1}^A \tilde{\mathbf{M}}(a, t + a - 1) \quad \text{eqn 15}$$

where A is a large maximum age A . In the bighorn ewes case, by allowing parent to reproduce until a maximum age of 50 years I make sure that the estimates of $\tilde{\mathbf{M}}_L(t)$ settle down to the equilibrium.

The $\tilde{\mathbf{G}}(a, t)$ operator describes how each stage-class at age a and time t contributes to different stage classes at age $a + 1$ and time $t + 1$. The $\tilde{\mathbf{D}}(a, t)$ operator describes how each stage-class among mothers of age a contribute to the stage classes of age 1 offspring at time $t + 1$.

Generation length T_c is given by the identity $T_c = \exp(rT)$ where r is the asymptotic growth rate and T is the dominant eigenvalue of $\tilde{\mathbf{M}}_L$ in eqn (14). The asymptotic growth rate r is calculated from eqn (13) at the stationary stable stage. In the stationary state these operators do not depend on time. Using matrix notation it can be written as $\mathbf{T}_c = \frac{\mathbf{aL}(a)\mathbf{M}(a)}{L(1)}$; where \mathbf{a} is a vector of ages and $\mathbf{L}(a)$, $L(1)$ and $\mathbf{M}(a)$ are defined as above.

Demographic dispersion of reproduction σ_d^2 is given by $\sigma_d^2 = \frac{\mathbf{a}^2\mathbf{L}(a)\mathbf{M}(a)}{L(1)} - T_c$.

It remains to specify how to compute h^2 of body mass from the IPM. Let z denote the offspring character value, and x the parental character value at age 1. The lifetime reproduction of a cohort born at time t is $\tilde{M}_L(t)$, and $\tilde{M}_L(z|t)$ is the distribution across character values of all offspring of that cohort. Considering all offspring produced over a lifetime, the joint number density distribution of offspring character value z is proportional to $\tilde{M}_L(z|t)[n(1, t, x)]$.

From the joint number density distribution it is possible to calculate the mean character values of parents:

$$\mu^p = \frac{\int dx xn(1, t, x)}{\int dx n(1, t, x)} \quad \text{eqn 16}$$

and the mean character values of offspring:

$$\mu^0 = \frac{\int dzdxzM_L(z|x, t)n(1, t, x)}{\int dzdxM_L(z|x, t)n(1, t, x)} \quad \text{eqn 17}$$

The parent –offspring covariance is then given by:

$$Cov(Z^0, Z^p) = \frac{\int dzdx(z - \mu^0)(x - \mu^p)M_L(z|x, t)n(1, t, x)}{\int dzdxM_L(z|x, t)n(1, t, x)} \quad \text{eqn 18}$$

and the variance among parents is given by:

$$VarZ^p = \frac{\int dx(x - \mu^p)^2n(1, t, x)}{\int dxn(1, t, x)} \quad \text{eqn 19}$$

From eqn(18) and (19) it is possible to compute h^2 by eqn(5): $h^2/2 = Cov(Z^0, Z^p)/Var Z^p$. All the integral equations here presented are approximated by discrete matrices and iterated using numerical integration methods.

(ii) Appendix A2: Numerical implementation

This appendix provides more information about numerical methods for implementing an *age x size* integral model. The model written in eqns (1) and (2) in the text is a series of one-dimensional integrals. To solve an IPM it is necessary to write it in matrix form and implement numerical integration (Easterling et al. 2000).

The \mathbf{K} matrix in $\mathbf{n}(t + 1) = \mathbf{K} \mathbf{n}(t)$ (eqn (3)) is used to iterate $\mathbf{n}(t)$ to $\mathbf{n}(t + 1)$. It contains a set of squared matrices consisting of an array of age-specific matrices. Each component of the square age matrix corresponds to two meshpoints (z_i, z_j) . The meshpoints are equally spaced and q in number, so the square age matrices have dimension $q \times q$.

The term $\mathbf{n}(t)$ in eqn (3) can then be written as:

$$\mathbf{n}(t) = (n(a_1, t, z'_1), \dots, n(a_1, t, z'_q), \dots, n(a_m, t, z'_1), \dots, n(a_m, t, z'_q))^T \quad \text{eqn 20}$$

The parameter a denotes age, while the parameter m denotes the maximum possible age in the model. Definitions for other parameters are in tab. 1 in the text. Each element of this vector represents the number of individuals in a specific age-class a and character class j . Each age-class is further separated into the same number of character classes. The character class j in $\mathbf{n}(t)$ is set to 0 if there are no individuals of weight z in age class a .

I define the following equalities:

$$\mathbf{DR}(a) := \mathbf{D}(z'_i, z'_j | a, t, z_i, z_j) \mathbf{R}(a, t, z_i, z_j) \quad \text{eqn 21}$$

and

$$\mathbf{GS}(a) := \mathbf{G}(z'_i, z'_j | a, t, z_i, z_j) \mathbf{S}(a, t, z_i, z_j) \quad \text{eqn 22}$$

where $i = 1, \dots, q$, and $j = 1, \dots, q$. It follows that

$$\mathbf{K} = \begin{pmatrix} \mathbf{DR}(1) & \mathbf{DR}(2) & \dots & \mathbf{DR}(m-1) & \mathbf{DR}(m) \\ \mathbf{GS}(1) & 0 & & 0 & 0 \\ 0 & \mathbf{GS}(2) & & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & & \mathbf{GS}(m-1) & \mathbf{GS}(m) \end{pmatrix} \quad \text{eqn 23}$$

The whole \mathbf{K} matrix has then dimensions $(q \times m) \times (q \times m)$. Age m is an absorbing age class. In fact $\mathbf{GS}(m)$ in the \mathbf{K} matrix represents survival and ontogenetic development of individuals $m+$ years old who will still have age $m+$ the following year if they survive. $\mathbf{DR}(m)$ represent fertility and inheritance of body mass of $m+$ years old individuals.

In the time transition from lamb to yearling females do not reproduce, thus $DR(1)$ is equal to a null matrix of $q \times q$ dimensions.

The equations above correspond to those in Coulson et al. (2010), but follow a different mathematical notation.

(iii) Appendix A3: Parameter values

The parameter values describing the relationship between September body mass and demographic and trait transition rates are shown in tab. 3. As explained in the methods, to increase the fit of the statistical models to the data I grouped ages in different age classes. Tab. 4 shows the Akaike information criterion (AIC, e.g. Burhman and Andersan 2004) values in the full statistical model with 14 ages and in the age- structured models. In the survival function females are grouped with respect to age as follow: (i) lambs and yearling; (ii) prime aged adults between 2 and 8 years of age; (iii) adults between 9 and 13 years of age; (iv) senescent of 14+ years of age. In the function of development of body mass females are grouped in four age classes: (i) lambs and yearlings; (ii) 2 years old adults; (iii) adults between 3 and 8 years of age; and (iv) senescent individuals older than 9 years. Lambs are not included in the fertility and inheritance functions because lambs are not sexually mature. Therefore the probability of reproduce in the time step between lamb and yearling is 0. The age structure differentiates individuals of (i) 1 year of age; (ii) 2-12 years of age; and (iii) 13-14 years of age based on their probability of reproduce at time $t + 1$ given their body mass at time t . In the inheritance function age classes are grouped as follow: (i) yearlings; and (ii) all the individuals older than 2, but the slopes for mother body mass don't differ between the two age classes. When ages are grouped in a specific function, the parameter values in the IPM for those specific ages are identical. For example, if lambs and yearlings have the same probability to survive in a time step given their body mass, the intercepts and slopes for body mass in the survival functions $S(1, t, z')$ and $S(2, t, z')$ are set to be identical.

Parameter:		S	G Mean	G Variance	R	D Mean	D Variance
	Age						
Intercept	a = 1	-1.3336	26.7286	24.6153	0	0	0
Intercept	a = 2	-1.3336	26.7286	24.6153	-13.9874	13.6512	5.5222
Intercept	a = 3	3.4342	36.3546	30.0608	-3.1370	15.0133	5.9658
Intercept	a = 4	3.4342	23.9293	19.4668	-3.1370	15.0133	5.9658
Intercept	a = 5	3.4342	23.9293	19.4668	-3.1370	15.0133	5.9658
Intercept	a = 6	3.4342	23.9293	19.4668	-3.1370	15.0133	5.9658
Intercept	a = 7	3.4342	23.9293	19.4668	-3.1370	15.0133	5.9658
Intercept	a = 8	3.4342	23.9293	19.4668	-3.1370	15.0133	5.9658
Intercept	a = 9	3.4342	23.9293	19.4668	-3.1370	15.0133	5.9658
Intercept	a = 10	-6.5999	19.4634	9.0613	-3.1370	15.0133	5.9658
Intercept	a = 11	-6.5999	19.4634	9.0613	-3.1370	15.0133	5.9658
Intercept	a = 12	-6.5999	19.4634	9.0613	-3.1370	15.0133	5.9658
Intercept	a = 13	-6.5999	19.4634	9.0613	-3.1370	15.0133	5.9658
Intercept	a = 14	-6.5999	19.4634	9.0613	-11.7587	15.0133	5.9658
Intercept	a = 15	-5.8961	19.4634	9.0613	-11.7587	15.0133	5.9658
Slope for z	a = 1	0.0796	0.7038	-0.1911	0	0	0
Slope for z	a = 2	0.0796	0.7038	-0.1911	0.2322	0.1963	0.1043
Slope for z	a = 3	-0.0058	0.5001	-0.1880	0.0348	0.1963	0.1043
Slope for z	a = 4	-0.0058	0.6910	-0.0660	0.0348	0.1963	0.1043
Slope for z	a = 5	-0.0058	0.6910	-0.0660	0.0348	0.1963	0.1043
Slope for z	a = 6	-0.0058	0.6910	-0.0660	0.0348	0.1963	0.1043
Slope for z	a = 7	-0.0058	0.6910	-0.0660	0.0348	0.1963	0.1043
Slope for z	a = 8	-0.0058	0.6910	-0.0660	0.0348	0.1963	0.1043
Slope for z	a = 9	-0.0058	0.6910	-0.0660	0.0348	0.1963	0.1043
Slope for z	a = 10	0.1189	0.7476	0.0496	0.0348	0.1963	0.1043
Slope for z	a = 11	0.1189	0.7476	0.0496	0.0348	0.1963	0.1043
Slope for z	a = 12	0.1189	0.7476	0.0496	0.0348	0.1963	0.1043
Slope for z	a = 13	0.1189	0.7476	0.0496	0.0348	0.1963	0.1043
Slope for z	a = 14	0.1189	0.7476	0.0496	0.1370	0.1963	0.1043
Slope for z	a = 15	0.0910	0.7476	0.0496	0.1370	0.1963	0.1043
Slope for N		-0.0042	-0.0189	-0.0726	-0.0041	-0.0530	-0.0520
Year effect σ_s		0.4418	1.9572	7.1342	0.4758	2.3299	0.0037

Tab. 3. Parameter estimates describing relationship between body mass and probability of survival (S), recruitment (R), ontogenetic development (G) and inheritance (D) of body mass. (z = body mass, N = population size, σ_s = standard error year effect). In the recruitment and inheritance functions parameters estimates for lambs are set to dummy values because lambs do not reproduce.

	full model	age-structured model	
Statistical model:	AIC	AIC	ΔAIC
Survival	1731	1718	-13
Fertility	1706	1679	-27
Mean body mass development	10180	10122	-58
Mean offspring body mass	2024	2022	-2

Tab. 4. *AIC values of statistical models describing associations between body-mass and: survival and fertility rates, and mean growth and offspring body mass transitions. The table shows: AIC values in the full model accounting for 14 ages (1st column), AIC values in the age-structured model (2nd column), and AIC values difference (Δ AIC) between the competing models.*

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