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# The Dynamics of a Quantitative Trait in an Age-Structured Population Living in a Variable Environment

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ABSTRACT: Time series of rapid phenotypic change have been documented in age-structured populations living in the wild. Researchers are often interested in identifying the processes responsible for such change. We derive an equation to exactly decompose change in the mean value of a phenotypic trait into contributions from fluctuations in the demographic structure and age-specific viability selection, fertility selection, phenotypic plasticity, and differences between offspring and parental trait values. We treat fitness as a sum of its components rather than as a scalar and explicitly consider age structure by focusing on short time steps, which are appropriate for describing phenotypic change in species with overlapping generations. We apply the method to examine stasis in birth weight in a well-characterized population of red deer. Stasis is achieved because positive viability selection for an increase in birth weight is countered by parents producing offspring that are, on average, smaller than they were at birth. This is one of many ways in which equilibria in the mean value of a phenotypic trait can be maintained. The age-structured Price equation we derive has the potential to provide considerable insight into the processes generating now frequently reported cases of rapid phenotypic change.

*Keywords:* birth weight, Price equation, red deer, selection differential.

The probability that an individual survives a period of time and successfully reproduces can be dependent on aspects of its phenotype, including quantitative traits such

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as body size and condition (Jorgenson et al. 1993; Gaillard et al. 1997; Larsson et al. 1998; Yoccoz and Mesnager 1998; Wikelski and Romero 2003). One consequence of this is that average survival and recruitment rates can, in part, be dependent on the distribution of quantitative traits within the population (Vaupel et al. 1979). Associations between trait values and individual survival and reproductive rates can vary with the environment (Jorgenson et al. 1993; Benton and Beckerman 2005). This means that the contribution of the distribution of quantitative traits to mean survival and recruitment, and consequently to population growth, can vary over time (Pelletier et al. 2007). Demographic rates can therefore be considered as phenotype by environment interactions (Coulson et al. 2006).

If individuals with specific trait values are more likely to survive or successfully reproduce than individuals with other trait values, then the trait is subject to selection (Arnold and Wade 1984). Within populations, viability selection will alter the distribution of trait values over time within a cohort (Vaupel et al. 1979). If the trait has an additive genetic component, fertility selection can alter the distribution of trait values across generations (Falconer 1960). The strength of both viability and fertility selection can vary with the environment (Hairston and Dillon 1990; Ellner et al. 1999), which means that the magnitude of change in trait distributions can vary with time.

These observations imply that the dynamics of populations and the dynamics of quantitative traits subject to selection must be intimately linked. This means that it should be possible to write an expression to exactly describe change in the mean value of a quantitative trait in an age-structured population over a time step in a way similar to that used to describe observed population growth in terms of survival and recruitment (Caswell 2001). Such an expression will allow for the retrospective decomposition of observed temporal fluctuations in the mean value of a quantitative trait into contributions from survival and reproduction, and it will also allow for the identification of how factors such as density dependence and climatic variation explain temporal variation in these

contributions. Similar approaches have provided understanding into the dynamics of populations (Coulson et al. 2001; Tuljapurkar et al. 2003). The decomposition of trait dynamics is desirable because there are a growing number of reports of quantitative trait distributions changing rapidly over time within populations (Law 2000; Reale et al. 2003; Hairston et al. 2005; Grant and Grant 2006; Edeline et al. 2007; Wilson et al. 2007). Theory has been developed to predict changes in phenotypic trait distributions as a result of fertility selection and viability selection (Falconer 1960; Lande 1982; Lande and Arnold 1983; Charlesworth 1993), but it is not sufficient to provide a comprehensive retrospective description of the observed dynamics of phenotypic traits in age-structured populations. In this article, we begin to develop this theory. A second reason to do this is a retrospective understanding of observed dynamics are useful for guiding the development of theory to predict future change in altered environments (for population dynamic models, see, e.g., Coulson et al. 2001; Tuljapurkar et al. 2003).

Among vertebrates, rapid phenotypic change has been reported in fish (Reznick and Endler 1982; Law 2000), reptiles (Sinervo and Lively 1996), birds (Grant and Grant 1995), and mammals (Coulson et al. 2003). In a population of bighorn sheep living in Alberta, Canada, mean body weight of 4-year-old rams declined at a rate of 650 g year$^{-1}$, while their horn lengths declined by just under 33% over a period of 30 years. The ultimate cause of this decline was trophy hunting of large individuals, while the proximate cause is believed to be genetic (Coltman et al. 2003). Other than hunting, a range of ecological processes can generate rapid phenotypic change, including environmental variation: global climate change has led to births occurring earlier in the year in mammals (Reale et al. 2003) and has advanced laying date in birds (Both et al. 2004) and the timing of flowering in vascular plants (Fitter and Fitter 2002). Species interactions are another cause of rapid phenotypic change: the introduction of predatory fish into ecosystems containing daphnia leads to the expression of an armored helmet and an extended tail spine (Gilbert 1966). In general, such phenotypic change can be caused by (1) viability selection preferentially removing individuals from one part of the phenotype distribution compared with other parts (Vaupel et al. 1979); (2) fertility selection leading to some genotypes contributing more to reproduction than others (Lande and Arnold 1983); (3) genetic, maternal, and environmental effects influencing offspring size (Roach and Wulff 1987); (4) phenotypic plasticity within the life span (Niva and Jokela 2000); and (5) fluctuations in the demographic composition of the population (Charlesworth 1994). A detailed understanding of why phenotypic distributions change with time requires consideration of each of these processes and identification of the relative contributions of each process. In this article, we demonstrate how these processes can be combined to provide an exact description of observed change in the mean value of a quantitative trait over a time step.

## Descriptions of Quantitative Trait Dynamics

### Quantitative Genetics and the Breeder's Equation

The effects of selection (expressed in terms of variation in a Malthusian parameter, or lifetime fitness) and heredity on changes in the distribution of quantitative traits have been described by the univariate (Falconer 1960) and the multivariate (Lande and Arnold 1983) breeder's equation. These equations assume nonoverlapping generations.

The univariate breeder's equation states that the change $\Delta \overline{Z}$ in the mean of a quantitative trait over a generation is the product of a selection differential on the trait, $\text{Cov}(Z, W)/\overline{W}$, and the heritability of the trait, defined as the ratio of the additive genetic variance to the phenotypic variance: $V_A/V_P$. Individual $i$ has a trait value $z_i$; fitness, $w_i = w(z_i)$, is defined as the Malthusian parameter for an individual with trait value $z_i$; and the mean fitness $\overline{W}$ and the covariance $\text{Cov}(Z, W)$ are computed across all individuals within the population. The selection differential is the difference between the mean of the distribution of parents (in which an individual is represented once for each offspring it produces) and the mean of the overall population before selection. To describe change in a trait distribution, the selection differential must be multiplied by a heritability that is related to the genetic architecture of the trait.

Each individual's trait value is considered to consist of two components: a breeding value, which describes the additive genetic contribution to the individual's focal trait, and an environmental component (Falconer 1960). The trait's heritability is the proportion of phenotypic variation attributable to breeding values. It is assumed that the mean of the breeding value distribution of parents (after selection) is equal to the mean of the phenotypic distribution among offspring (Lande and Arnold 1983). The breeder's equation consequently describes how the mean of the breeding value distribution changes within a generation as a result of fertility selection and then makes an assumption concerning the similarity between parents and their offspring. Further assumptions include independence between individual breeding values and the individual environmental components and that traits in parents and offspring are normally distributed (Bulmer 1980).

The breeder's equation would be a useful tool to describe changes from one year to the next only for annual species with nonoverlapping generations and satisfying the assumptions above, but it does not apply when generations

overlap. To address this limitation, Lande (1982) and Charlesworth (1993) derive age-structured versions of the breeder's equation for traits that change with age under the additional assumption of weak selection and a stable age structure. Their approach incorporates the effects of viability and fertility selection on change in the mean of the trait distribution. We do not consider their derivations here because we are primarily interested in decomposing observed phenotypic change without making the restrictive assumptions that they used to make prospective predictions analytically tractable. In "Viability Selection and Frailty," we consider another approach that has examined how viability selection will alter a trait distribution within a generation.

### Viability Selection and Frailty

Vaupel et al. (1979) developed life table methods for cases when individual survival probabilities vary with age as a function of a phenotypic trait, $Z$. The trait they focus on is termed "frailty"; its value in an individual is fixed throughout life and simply influences the individual's chance of survival. They show that estimates of key life table statistics are biased if individual heterogeneity in the trait exists and is ignored. They also demonstrate that viability selection on a trait changes the mean ($\overline{Z}(a)$) of the trait distribution within a cohort as individuals within the cohort age. Such viability selection has the potential to alter the distribution of the trait rapidly within generations.

The consequences of intracohort viability selection due to variation in frailty may be followed using a simple form of the Price equation (Price 1970 and below), which yields the difference between mean frailties at ages $a$ and $a + 1$ as

$$\Delta \overline{Z} = \overline{Z}(a + 1) - \overline{Z}(a) = \frac{\mathrm{Cov}\,(Z, S)}{\overline{S}(a)}, \qquad (1)$$

where $s_i(a)$ is a binary variable describing whether individual $i$ of age $a$ survives and $\overline{S}(a)$ is mean survival across individuals of age $a$ within a cohort. As well as viability selection, phenotypic plasticity among surviving individuals could also theoretically contribute to changes in phenotypic trait distributions with time.

### Phenotypic Plasticity and Changes in Trait Means

Frailty, the trait that Vaupel et al. (1979) consider, remains constant throughout life. However, many quantitative traits that influence survival and recruitment are not fixed throughout life. For example, in vertebrates, body weight varies with age, environment, and physiological status. There is little formal theory developed to generalize how the dynamics of trait distributions are influenced by phenotypic plasticity within life, although factors influencing individual rates of phenotypic plasticity have been investigated in a range of species. For example, in numerous mosquito species, environmental drivers including temperature, genetic effects, intra- and interspecific competition for food, and the presence of predators influence growth rates of larvae and the time taken for transitions between instars (Agnew and Koella 1999; Strand et al. 1999; Wallace and Merritt 1999; Braks et al. 2004). Any contribution of phenotypic plasticity to a change in the mean of a trait distribution will need to consider the average difference across trait values of survivors before and after selection. Finally, any formulation describing the dynamics of a quantitative trait over a time step may also need to consider the demographic structure of the population at time $t$.

### Fluctuations in the Demographic Structure

In structured populations, survival and recruitment rates often vary with age. One consequence of this in variable environments is that the demographic structure of the population fluctuates over time (Tuljapurkar 1990; Coulson et al. 2001). This means that average survival and recruitment rates at the level of the population often vary with time as a function of the proportion of individuals within each age class. If the mean of trait values also differs across demographic classes because of past viability selection, the mean value of a trait may also vary as a function of the demographic structure of the population.

Several processes are consequently likely to influence the temporal dynamics of a quantitative trait in an age-structured population living in a variable environment. One equation already describes changes in the mean value of a trait distribution subject to selection: the Price equation (Price 1970). As the final part of this brief review, we consider the properties of this equation, which is typically considered in relation to populations with nonoverlapping generations.

### The Price Equation

Price (1970) showed that change in the mean value of a phenotypic trait between one generation and the next can be described exactly as a sum of two quantities. The first quantity describes the difference in the mean trait value of individuals selected to be parents and the mean trait value across all individuals within the population. The second quantity describes the difference in the mean trait value between offspring and their parents. There are var-

ious ways in which this equation can be written. The individual trait value may be a scalar or a vector, and individual fitness, $W$, is a scalar. Fitness is typically considered to be lifetime offspring production assuming nonoverlapping generations, so this form of the equation cannot sensibly be applied to populations with overlapping generations. In "Age-Structured Price Equation," we develop a version of the Price equation where fitness is decomposed into age-specific survival and recruitment. As a prelude, it is useful to discuss the Price equation in detail for an annual organism, in which case the time interval in the equation is a year and $W = R$, the number of offspring.

There are, say, $n$ individuals in a particular year $t$. Individual $i$ has trait value $z_i$ and produces $r_i \geq 0$ offspring, so the mean trait value in year $t$ is $\overline{Z}(t) = (1/n)\sum_i z_i$, and the average number of offspring produced by all potential parents is $\overline{R} = (1/n)\sum_i r_i$. Write the trait value of the $j$th offspring of individual $i$ as $y_{ij} = z_i + d_{ij}$. The mean trait value in the next year is the mean trait value of offspring,

$$\overline{Z}(t+1) = \left(\frac{1}{\overline{R}n}\right)\sum_{i=1}^{n}\sum_{j=1}^{r_i}[z_i + d_{ij}]. \tag{2}$$

Here, the first term in square brackets on the right side is just

$$\left(\frac{\overline{ZR}}{\overline{R}}\right) = \overline{Z}(t) + \frac{\text{Cov}(Z, R)}{\overline{R}}. \tag{3}$$

The covariance term describes selection via the effect of trait $Z$ on fertility.

The second term in square brackets on the right side of equation (2) describes any infidelity in the transmission of mean phenotype from parents to offspring. Let $\overline{d}_i$ be the difference between the mean trait value of individual $i$'s offspring and its own (parental) trait value $z_i$. To average over all potential parents, we follow Price (1970) and set $\overline{d}_i$ to the observed value for parents (for whom $r_i > 0$) and $\overline{d}_i = 0$ for individuals who produce no offspring (for whom $r_i = 0$). Then the second term in square brackets on the right side of equation (2) yields

$$\left(\frac{1}{\overline{R}n}\right)\sum_{i=1}^{n} r_i\overline{d}_i = \overline{D} + \frac{\text{Cov}(D, R)}{\overline{R}}. \tag{4}$$

The first term above describes the average difference in the mean of the phenotypic trait between offspring and their parents, and the second term describes any interaction between fertility and the intergenerational differ-

ence in trait mean. Combining terms, the Price equation is

$$\Delta\overline{Z} = \frac{\text{Cov}(Z, R)}{\overline{R}} + \overline{D} + \frac{\text{Cov}(D, R)}{\overline{R}}. \tag{5}$$

To repeat, averages here are computed over all $n$ potential parents.

A different and useful perspective is to consider only parents, that is, individuals observed to have $r_i > 0$. There are $n_p \leq n$ parents, and we use a plus sign to denote averages over these parents. Thus, the average number of offspring is

$$\overline{R}_+ = \left(\frac{1}{n_p}\right)\sum_{i:r_i>0} r_i = \left(\frac{1}{n_p}\right)\sum_+ r_i.$$

The mean phenotype in year $t + 1$, written as average over parents, is

$$\overline{Z}(t+1) = \left(\frac{1}{\overline{R}_+n_p}\right)\sum_{i=1}^{n_p}\sum_{j=1}^{r_i:r_i>0}[z_i + d_{ij}]. \tag{6}$$

The first term on the right side yields

$$\left(\frac{1}{\overline{R}_+n_p}\right)\sum_{i=1}^{n_p} r_iz_i = \overline{Z}_+ + \frac{\text{Cov}_+(Z, R)}{\overline{R}_+}. \tag{7}$$

However,

$$\sum_{i=1}^{n_p} r_iz_i = \sum_{i=1}^{n} r_iz_i,$$

because individuals with $r_i = 0$ do not contribute to the sum. Also, the total number of offspring is $\overline{R}_+n_p = \overline{R}n$. Hence

$$\left(\frac{1}{\overline{R}_+n_p}\right)\sum_{i=1}^{n_p} r_iz_i = \left(\frac{1}{\overline{R}n}\right)\sum_{i=1}^{n_p} r_iz_i$$

$$= \left(\frac{1}{\overline{R}n}\right)\sum_{i=1}^{n} r_iz_i,$$

which implies that

$$\overline{Z}_+ + \frac{\text{Cov}_+(Z, R)}{\overline{R}_+} = \overline{Z} + \frac{\text{Cov}(Z, R)}{\overline{R}}. \tag{8}$$

The second term in square brackets on the right side of equation (6) is

$$\overline{D}_+ + \frac{\text{Cov}_+ (D, R)}{\overline{R}_+}.$$

Recalling that $\bar{d}_i = 0$ for individuals who do not reproduce, an argument similar to the one above shows that

$$\overline{D}_+ + \frac{\text{Cov}_+ (D, R)}{\overline{R}_+} = \overline{D} + \frac{\text{Cov} (D, R)}{\overline{R}}. \qquad (9)$$

Putting things together, we can rewrite the Price equation (eq. [5]) as

$$\Delta\overline{Z} = [\overline{Z}_+ - \overline{Z}] + \frac{\text{Cov}_+ (Z, R)}{\overline{R}_+} + \left[\overline{D}_+ + \frac{\text{Cov}_+ (D, R)}{\overline{R}_+}\right]. \qquad (10)$$

On the right, the first term in square brackets represents the selection of parents from among all individuals, the middle term is the effect of fertility selection among parents with different phenotypes, and the last term in square brackets describes the difference in mean trait value between offspring and their parents.

In the empirical literature, it is often assumed that the breeder's equation will accurately describe $\Delta\overline{Z}$ in the same way that the Price equation does. However, the assumptions underlying the breeder's equation imply that it will yield the same results as the Price equation only under rather restrictive circumstances (Feldman and Lewontin 1975; Jacquard 1983; Frank 1997; Heywood 2005). This failure of the breeder's equation is sometimes interpreted by empiricists as evidence of selection on unmeasured correlated characters (Merila et al. 2001). However, as Heywood (2005) shows, several other factors may prevent the breeder's and the Price equations from giving the same value of $\Delta\overline{Z}$, including a spurious response to selection and various types of transmission bias.

### Age-Structured Price Equation

Using the logic above but with fitness divided into its age-specific survival and recruitment components and demographic weights, we derive a version of the Price equation in appendix A in the online edition of the *American Naturalist*. We provide two versions of the final expression: first, using our non-"+" notation, where values of growth $g_i$ and the difference between offspring and their parents, $d_i$, are set to 0 for individuals that did not survive or reproduce, and second, using our "+" notation, where $g_i$ and $d_i$ are not defined for those individuals that died or did not breed. Definitions are given in table 1, and the interpretation of each term is provided in table 2. The

change in the mean of the trait distribution across all individuals within the population is

$$\Delta\overline{Z}(t) = \overline{Z}(t + 1) - \overline{Z}(t)$$

$$= \sum_{a=1}^{\omega-1} [\Delta c(a, t)]\overline{Z}(a, t) - c(\omega, t)\overline{Z}(\omega, t) \qquad (11a)$$

$$+ \sum_{a=1}^{\omega-1} \left(\frac{c(a, t)}{\overline{W}(t)}\right)[\text{Cov} (Z, S)(a, t) \qquad (11b)$$

$$+ \overline{SG}(a, t)] \qquad (11c)$$

$$+ \sum_{a=1}^{\omega} \left(\frac{c(a, t)}{\overline{W}(t)}\right)[\overline{R}(a, t)\overline{Z}(a, t) \qquad (11d)$$

$$+ \overline{R}(a, t)\overline{D}(a, t) \qquad (11e)$$

$$+ \text{Cov} (D, R)(a, t) \qquad (11f)$$

$$+ \text{Cov} (Z, R)(a, t)]. \qquad (11g)$$

With the "+" notation,

$$\Delta\overline{Z}(t) = \sum_{a=1}^{\omega-1} [\Delta c(a, t)]\overline{Z}(a, t) - c(\omega, t)\overline{Z}(\omega, t) \qquad (12a)$$

$$+ \sum_{a=1}^{\omega-1} \left(\frac{c(a, t)\overline{S}(a, t)}{\overline{W}(t)}\right)\left[\frac{\text{Cov} (Z, S)(a, t)}{\overline{S}(a, t)} \qquad (12b)$$

$$+ \overline{G}_+(a, t)\right] \qquad (12c)$$

$$+ \sum_{a=1}^{\omega} \left(\frac{c(a, t)\overline{R}(a, t)}{\overline{W}(t)}\right)[\overline{Z}(a, t) \qquad (12d)$$

$$+ \frac{\text{Cov} (Z, R)(a, t)}{\overline{R}(a, t)} \qquad (12e)$$

$$+ \overline{D}_+(a, t) \qquad (12f)$$

$$+ \frac{\text{Cov}_+ (D, R)(a, t)}{\overline{R}_+(a, t)}\right]. \qquad (12g)$$

We now consider some of the properties of these expressions by considering how equilibria can arise.

### Conditions for Equilibrium of the Mean Phenotype

Equation (A14) in appendix A defines general conditions under which the mean trait value in a population is maintained over time (at an equilibrium value) or changes directionally in one time step. To explore these conditions, we examine several cases, starting with the simplest.

**Table 1:** Definition of variables used in the text

| Variable | Definition |
| --- | --- |
| $a$ | Age class (discrete units); $a = 1$ for newborns |
| $t$ | Time (discrete units) |
| $i, j$ | Indices for individuals or offspring |
| $n(a, t)$ | Number of individuals in age class $a$ at time $t$ |
| $N(t)$ | Total number of individuals at time $t$ |
| $c(a, t)$ | Proportion of individuals in age class $a$ at time $t$ |
| $\lambda(t) = \overline{W}(t)$ | Population's growth rate between $t$ and $t + 1$; also the mean fitness |
| $z_i$ | Trait value of individual $i$ |
| $Z$ | Random trait value of an individual (values are $z_i$) |
| $s_i$ | Binary survival rate (0 or 1) of individual $i$ (function of $a, t$) |
| $S$ | Random survival rate (0 or 1) of an individual (values are $s_i$, a function of $a, t$) |
| $r_i$ | Number of offspring produced by individual $i$ (function of $a, t$) |
| $R$ | Random number of offspring produced by an individual (values are $r_i$, a function of $a, t$) |
| $y_{ij}$ | Trait value of $j$th offspring of individual $i$ (function of $a, t$) |
| $d_{ij} = y_{ij} - z_i$ | Difference between trait value between offspring $j$ of individual $i$ and parent's trait value (function of $a, t$) |
| $\bar{d}$ | For individuals who reproduce (with $r_i > 0$), the difference between the average trait values of all offspring $j$ of individual $i$ and parent's trait value $z_i$; for individuals who do not reproduce (with $r_i = 0$), defined as $\bar{d} = 0$ (function of $a, t$) |
| $D$ | Random difference between average offspring trait value and parental trait value (values are $\bar{d}$, a function of $a, t$) |
| $\overline{D}$ | Mean of $D$ (equivalently of $\bar{d}$) over all individuals (function of $a, t$) |
| $g_i$ | Phenotypic plasticity of trait value of individual $i$ (function of $a, t$) |
| $G$ | Random phenotypic plasticity of trait value of an individual (function of $a, t$) |

### Equilibrium with No Selection

Suppose that fertility, survival, and rates of phenotypic plasticity are constant in time, the population's demographic structure is stable, and there is no selection. At time $t$, the mean trait value is

$$\overline{Z}(t) = c(1)\overline{Z}(1) + \sum_{1}^{\omega-1} c(a + 1)[\overline{Z}(a) + \overline{G}(a)]. \quad (13)$$

Demographic stability means that the age structure and the growth rate $\overline{W}$ do not change with $t$, that equation (A12) becomes

$$c(a + 1) = \frac{c(a)\overline{S}(a)}{\overline{W}}$$

for $a \geq 1$, and that the fraction of newborns is

$$c(1) = \sum_{1}^{\omega} \frac{c(a)\overline{R}(a)}{\overline{W}}.$$

The absence of selection means that the covariance terms in equation (A14) are all 0. Using the two equations above, equation (A14) shows that

$$\overline{Z}(t + 1) = \sum_{1}^{\omega-1} c(a + 1)[\overline{Z}(a) + \overline{G}(a)]$$

$$+ \sum_{a=1}^{\omega} \left(\frac{c(a)\overline{R}(a)}{\overline{W}}\right)[\overline{Z}(a) + \overline{D}(a)].$$

Compare this with equation (13) to see that the mean trait value stays constant if

$$\overline{Z}(a) + \overline{D}(a) = \overline{Z}(1). \quad (14)$$

In other words, this condition means that parents of age $a$ have to produce offspring whose mean trait value is constant over time. Recalling equation (A5), this means that there can be no difference between mean offspring and parental trait values and that phenotypic plasticity at every age is perfectly offset in the mean traits of offspring.

### Equilibrium with Directional Selection on Traits Fixed at Birth

Now consider a trait such as frailty (Vaupel et al. 1979) that is fixed at birth and is positively correlated with survival rates at every age. In this case, there is no change in trait value through life, so $\overline{D}(a)$ is just the difference in mean trait value between offspring and their parents age $a$. To keep things simple, suppose that the demographic structure does not change between times $t$ and $t + 1$ and

**Table 2:** Biological interpretation of terms

| Equation | Expression | What it means |
|---|---|---|
| (11a), (12a) | $\Delta c(a, t)\overline{Z}(a, t) - c(\omega, t)\overline{Z}(\omega, t)$ | Change in ($\overline{Z}$) due to aging |
| | $\dfrac{c(a, t)\overline{S}(a, t)}{\overline{W}(t)}$ | Contribution of age-specific survival to population growth |
| | $\dfrac{c(a, t)\overline{R}(a, t)}{\overline{W}(t)}$ | Contribution of age-specific recruitment to population growth |
| (11b), (12b) | $\dfrac{\text{Cov}(Z, S)(a, t)}{\overline{S}(a, t)}$ | Survival selection differential on $z$ across all individuals in $a, t$ |
| (11c) | $\dfrac{\overline{SG}(a, t)}{\overline{S}(a, t)}$ | Mean phenotypic plasticity calculated across all individuals in $a, t$ |
| (11d), (12d) | $\overline{Z}(a, t)$ | Mean trait value of individuals in $a, t$ |
| (11e) | $\overline{D}(a, t)$ | Mean difference between offspring and parental trait values calculated across all individuals in $a, t$; $d_i = 0$ when $r_i = 0$ |
| (11f) | $\text{Cov}(D, R)(a, t)$ | Covariation between offspring size and offspring number calculated across all individuals in $a, t$; $d_i = 0$ when $r_i = 0$ |
| (11g), (12c) | $\text{Cov}(Z, R)(a, t)$ | Selection differential on recruitment calculated across all individuals in $a, t$ |
| (12c) | $\overline{G}_+(a, t)$ | Mean phenotypic plasticity calculated across individuals in $a, t$ that survive |
| (12f) | $\overline{D}_+(a, t)$ | Average difference between offspring and parental trait values calculated across observed $a, t$ parents, $r_i > 0$ |
| (12g) | $\dfrac{\text{Cov}_+(D, R)(a, t)}{\overline{R}_+(a, t)}$ | Covariation between offspring size and offspring number calculated across observed parents in $a, t$, $r_i > 0$ |

that there is no selection via fertility. Then equation (A14) shows that

$$\overline{Z}(t + 1) = \sum_{1}^{\omega-1} c(a + 1)\overline{Z}(a)$$

$$+ \sum_{a=1}^{\omega}\left(\frac{c(a)\overline{R}(a)}{\overline{W}}\right)[\overline{Z}(a) + \overline{D}(a)]$$

$$+ \sum_{a=1}^{\omega-1} c(a + 1)\frac{\text{Cov}(Z, S)(a)}{\overline{S}(a)}.$$

Condition (14) is not sufficient to hold the mean trait value fixed; even if it applies, $\overline{Z}(t + 1) > \overline{Z}(t)$ because $\text{Cov}(Z, S)(a) > 0$ as a result of directional selection on the trait via survival. To maintain equilibrium requires a difference between offspring and parental trait means that balances the selection differential,

$$\sum_{a=1}^{\omega}\left(\frac{c(a)\overline{R}(a)}{\overline{W}}\right)[\overline{Z}(a) - \overline{Z}(1) + \overline{D}(a)] =$$

$$- \sum_{a=1}^{\omega-1} c(a + 1)\frac{\text{Cov}(Z, S)(a)}{\overline{S}(a)}. \tag{15}$$

Here age structure and fertility at age $a$ weight the difference between mean offspring and parental trait, and age structure weights the strength of directional selection.

Difference between offspring and parental trait means

is also necessary for equilibrium in the mean of a trait fixed at birth that is positively correlated with fertility and survival. To obtain the equilibrium condition in that case, just add to the right-hand side of equation (15) the selection on fertility involving $\text{Cov}(Z, R)(a) > 0$. In a detailed analysis of data on a natural population ("Application to Red Deer"), we consider a case in which a trait is positively correlated with both survival and fertility, and we show that the difference between offspring and parental trait means is indeed the balancing factor maintaining mean trait value.

### Equilibrium with Survival-Fertility Trade-Offs

Traits such as birth weight or provisioning that are set at birth often positively influence early survival, but in many cases, we expect a trade-off (genetic or physiological) between early survival and reproduction at those or later ages. In such cases, a trait that is positively selected via its effect on current survival will, because of the trade-off, be selected against when it negatively influences current or future reproduction. If differences between offspring and parental trait values are negligible, a mean trait value $\overline{Z}(t)$ can be maintained if survival selection, acting through a positive $\text{Cov}(Z, S)(a, t)$ at ages $a = 1, 2, \ldots, A$, is balanced by fertility selection, acting via a negative value of $\text{Cov}(Z, R)(a', t)$ at ages $a' \geq A$. An equilibrium in mean trait value in such cases does not require differences between offspring and parental trait values. Assuming that

equation (14) applies, so there is no difference between offspring and parental trait means, and that demography is stable, the equilibrium condition with a trade-off becomes

$$\sum_{a=1}^{A} c(a+1)\frac{\text{Cov}\,(Z,S)(a)}{\overline{S}(a)} =$$
$$-\sum_{a=1}^{\omega-1} c(a+1)\frac{\text{Cov}\,(Z,R)(a)}{\overline{S}(a)}.$$

### Equilibrium with Growth-Mediated Trade-Offs

A different kind of trade-off occurs when a trait fixed at birth is positively correlated with survival alone (or reproduction alone) at one age and negatively correlated with survival (respectively, reproduction) at a later age. Such an effect may be mediated by a growth-mortality trade-off. An example of such a trait is otolith size at hatching (a measure of larval size and provisioning) in the marine fish *Pomacentrus amboinensis* (Gagliano et al. 2007). In these fish, larvae with smaller otoliths have slow growth rates at early ages (a pelagic phase) and high growth rates at later ages (settlement into adult habitat and after). Selection favors slow growth in the early ages and fast growth at later ages. Assuming no difference between the mean of offspring traits and parental traits, demographic stability, and that selection acts only via growth, the condition for maintaining mean otolith size at equilibrium is

$$\sum_{a=1}^{\omega-1} c(a+1)\frac{\text{Cov}\,(S,G)(a)}{\overline{S}(a)} = 0.$$

### Equilibrium with Temporal Variation in Selection

The equilibrium conditions above assume that age-specific selection (the covariances) are constant in time. In practice, we can expect that both the strength and direction of selection can vary with environmental conditions. For example, a positive covariance between a trait such as size and fertility in resource-rich years can be reversed in resource-poor years, when larger and more fertile individuals incur but cannot compensate for a high energetic cost of reproduction. Thus, the annual shift in a trait mean, $\Delta\overline{Z}(t)$, can average to 0 over a long period if selection differentials fluctuate over time.

We now use the age-structured Price equation to decompose fluctuations in the mean of a phenotypic trait in a population of red deer (*Cervus elaphus*).

### Application to Red Deer

We use data collected from marked red deer living in the North Block of the island of Rum, Scotland (Clutton-Brock et al. 1982). More than 95% of individuals seen in North Block censuses are marked (Coulson et al. 1997). The rut takes place in September and October, and births occur between May 15 and the end of June. Natural mortality predominantly occurs in late winter (February–April). We consider a postbreeding census date of July 1. Individuals are caught within hours of birth, and capture weight is recorded. Residual birth weight is defined as an individual's residual from a regression line between capture weight (kg) and capture date (h). At first capture, individuals are uniquely marked with ear tags and/or collars. They are then followed throughout life, and complete life histories are constructed. Age is known for all marked females; population estimates of the study area at the census date are close to error free; date of death is known to the day for most females and to the month for those who were not found dead within days of death. Full methodological details have been published elsewhere and are not repeated here (Clutton-Brock et al. 1982; Coulson et al. 2004). We use birth weight and life-history data collected between July 1, 1974, and June 30, 2006.

Using these data, we compiled a file with rows representing each year a female with a known birth weight was in the population. The columns in the file contained data on individual identity, year, age, residual birth weight, a binary variable describing whether the individual survived the year, number of recruits produced, and residual mean birth weights of these recruits. From this file, we estimated each of the terms in equations (12) (R code in app. B in the online edition of the *American Naturalist*).

The average number of females in our data set with known birth weights alive in the population at each census point is 145.3 (range 38–224). On average, residual birth weight was estimated for 28 female calves each year (range 16–44), giving a total of 886 individual females with known birth weights. Over the course of the study, there was no significant temporal trend in residual birth weights among female calves, although there were year-to-year fluctuations (variance across years in mean residual birth weight of female calves $= 0.173$; fig. 1a). Mean residual birth weight of all living individuals fluctuated less than fluctuations in calf residual birth weight (temporal variance $= 0.0087$; fig. 1a). Despite the lower variance, changes in mean residual birth weight from one year to the next fluctuated between a decrease of 0.25 kg and an increase of 0.19 kg (fig. 1b). Most of the change in $\Delta\overline{Z}$ was attributable to fluctuations in calf birth weights (fig. 1c), with an $r^2$ between $\Delta\overline{Z}$ and mean residual calf birth weight in that year of 0.74.

Some of the terms in our derivation of the age-structured Price equation are 0 in the case of residual birth weight in the red deer. Because birth weight is fixed throughout life, all age-specific phenotypic plasticity terms, $\overline{G}_+(a, t)$, are 0. Similarly, because maximum litter size is 1, the covariance terms $\mathrm{Cov}_+(D, R)(a, t)$ are also 0. All other terms are calculable. In figure 2, we show the viability selection differentials $\mathrm{Cov}(Z, S)(a, t)$, the fertility selection differentials $\mathrm{Cov}(Z, R)(a, t)$, the difference between mother's trait value and offspring value $\overline{D}_+(a, t)$, and change due to demographic fluctuations $\Delta c(a, t)\overline{Z}(a, t) - c(\omega, t)\overline{Z}(\omega, t)$ summed across all age classes for each year. Viability selection differentials tend to be positive, with a mean of 42 g per year. Fertility selection differentials are lower, with a mean of 10 g. Combined with the term $\overline{Z}(t)$, recruitment contributes on average +26 g to $\Delta\overline{Z}$. This means that, on average, approximately 70% of selection occurs through survival. Fluctuations in the demographic structure, on average, explain only an increase of 2 g, although there is considerable temporal variation in their contribution. Between them, these terms predict an annual average increase of 70 g a year, constituting more than 1% of mean female calf birth weights. This might not sound like much, but over the course of the study, this would equate to a more than 25% increase in birth weights. This increase is not achieved because female calf weights are, on average, less than the birth weights of their mothers; on average, the term $\overline{D}(a, t)$ constitutes an annual decrease in $\overline{Z}$ of 71 g.

These results describe the sum of each term over age classes. We next examined how the selection differentials and mother-offspring difference terms varied with age. We do not report age-specific contributions from demographic change because this term is easily interpreted only at the level of the entire population. Much of the viability selection we observed occurs in the first 2 years of life (fig. 3a). A consequence of this is that the mean birth weight of individuals surviving to age $a$ increased with $a$. Heavier-born individuals tended to live longer, which meant that the mean residual birth weight of survivors within a cohort increased with age throughout life. Viability selection results in mothers' residual birth weights being approximately 330 g greater than the mean birth weight of their cohort at birth (fig. 3a). Because we have not seen a change in mean birth weight over the course of the study, mothers must produce offspring that are lighter than they were—they must produce offspring with residual birth weights closer to the population mean birth weight of calves ($\overline{Z}(1)$) rather than the mean birth weight of the selected group of mothers. The difference between offspring and maternal residual birth weight was greatest in young and old individuals (fig. 3b). Only those individuals in the prime of life were able to produce offspring that, on av-
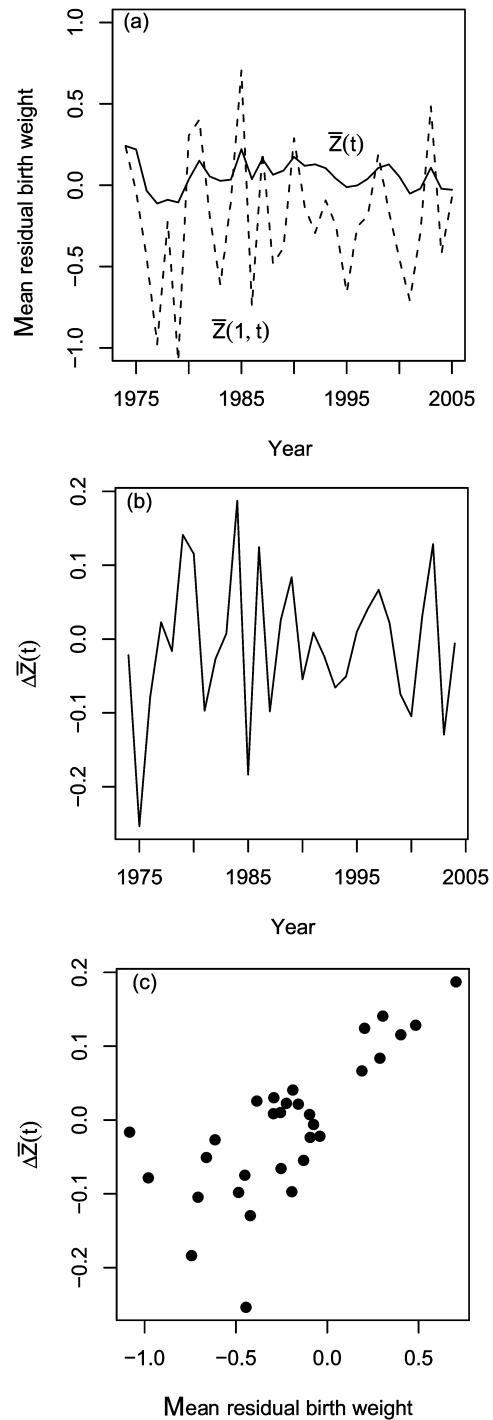


**Figure 1:** Time series of residual birth weight statistics. *a*, Temporal fluctuations in the mean of residual birth weight for the entire population ($\overline{Z}(t)$) and for calves ($\overline{Z}(1, t)$). *b*, Time series of changes in the mean of residual birth weight across all living individuals ($\Delta\overline{Z}(t)$). *c*, Correlation between residual birth weight of calves and $\Delta Z(t)$, demonstrating that most of the fluctuations in $\Delta\overline{Z}(t)$ are due to fluctuations in calf residual birth weight.

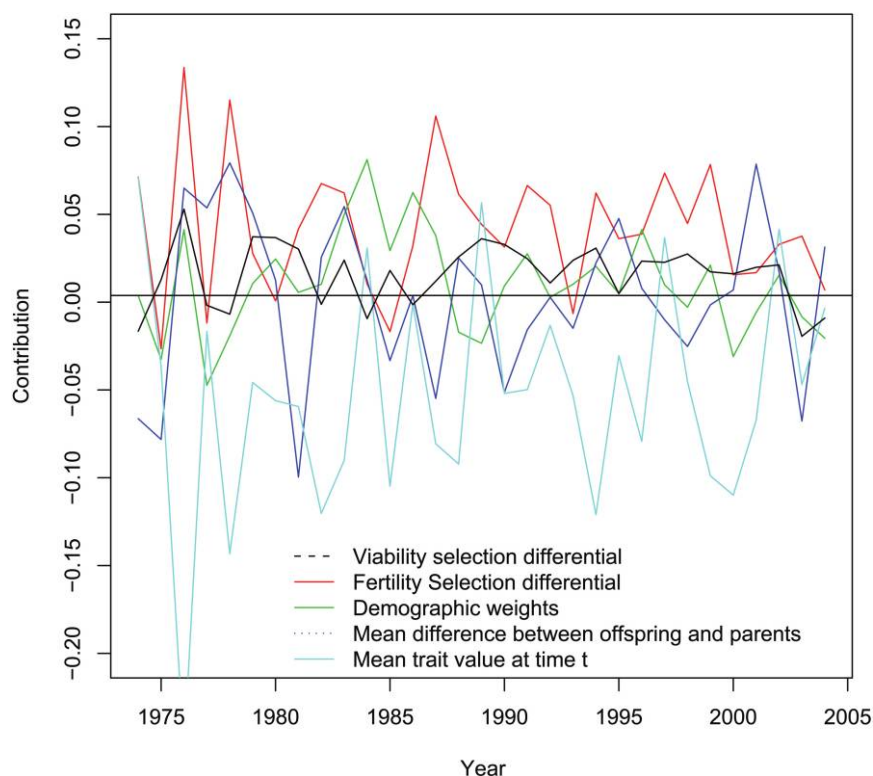**Figure 2:** Time series of the contribution of different terms to $\Delta \overline{Z}(t)$. Each quantity is calculated from equation (12). The horizontal line depicts the mean change in $\Delta \overline{Z}(t)$ over a time step.

erage, had the same birth weight that they did. There was little age-related variation in fertility selection (results not shown).

## Discussion

There are a growing number of examples where population biologists report rapid change in the mean value of phenotypic traits in age-structured populations living in variable environments (Law 2000; Coltman et al. 2003; Reale et al. 2003; Hairston et al. 2005; Grant and Grant 2006; Edeline et al. 2007; Wilson et al. 2007). In this article, we derive an expression to exactly describe change in the mean value of a quantitative trait over a time step into contributions from viability and fertility selection, phenotypic plasticity, the mean difference between offspring and parental trait values, and fluctuations in the demographic structure. We use this expression to decompose temporal variation in the mean value of birth weight in a well-studied population of red deer, and we show that the effects of viability selection are countered by offspring being, on average, smaller than their parents were at birth. Our method has the potential to provide considerable insight

into the processes associated with the dynamics of quantitative traits in variable environments.

Our biologically intuitive equation provides a demography for phenotypic change. The equation extends the work of Price (1970), who developed an equation describing the change in the mean of a phenotypic trait over a time step as a function of individual fitness defined as a scalar. Our work makes several important advances. First, we do not consider fitness as a scalar but instead work with fitness components. Second, as a direct consequence of the first advance, we can consider the contribution of specific demographic classes to observed phenotypic change. Third, by focusing on short time steps, we are able to examine how the relative contributions of different demographic processes that generate change vary with time. Finally, we provide the first comprehensive description of the processes generating fluctuations in the mean of a fitness-related phenotypic trait in an age-structured population living in a stochastic environment.

The age-structured Price equation we derive contains four terms for each age: a viability selection differential on the trait, a fertility selection differential on the trait, a term describing the average rate of phenotypic plasticity,
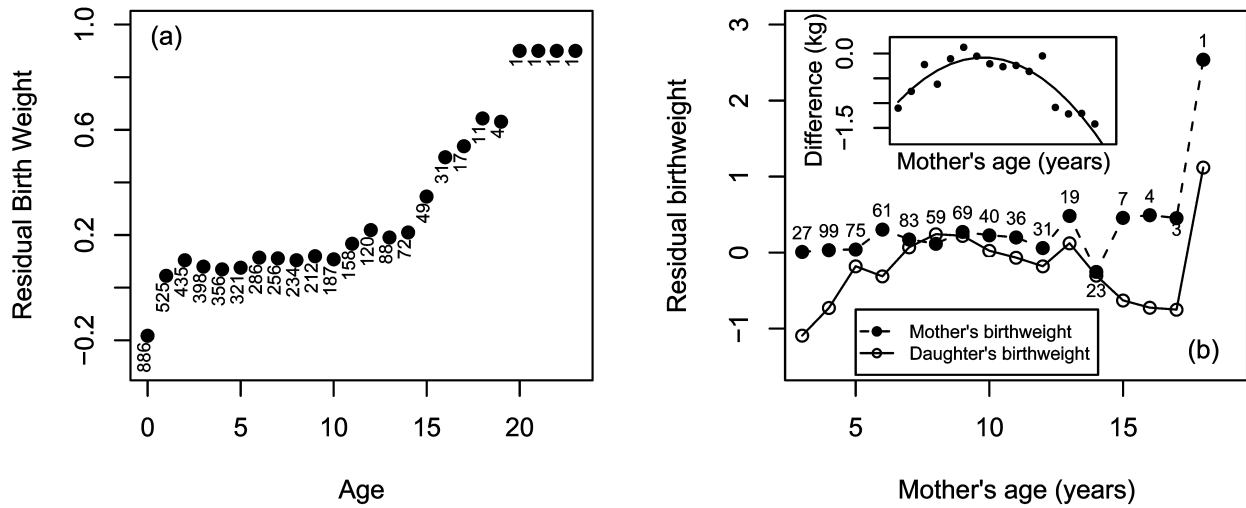
**Figure 3:** Age-related patterns. *a*, The viability selection differential removes small individuals from the distribution of residual birth weights. This leads to an increase in mean residual birth weight among surviving individuals within a cohort as they age. Data are pooled across years. *b*, Mean difference between offspring and mother's residual birth weight pooled across years. Only prime-aged mothers are able to produce offspring with average residual birth weights that are the same as their birth weights. Young and older individuals tend to produce offspring with smaller birth weights than they had. This relationship is well described with a quadratic function.

and a term describing the mean difference between offspring and parental trait values. Each of these terms is weighted by the contribution of age-specific survival and recruitment to population growth. These weighted terms are then summed before being combined with a term describing change in the mean of the trait caused solely by aging. Two of these terms require further discussion: first, the phenotypic plasticity term $\overline{G}(a, t)$, which describes the mean age-specific change in trait value over a time step across surviving individuals. In traits that remain fixed throughout life, this term is 0; however, for traits such as body size, which change over time, this term will be non-zero. There are various factors that can influence individual phenotypic plasticity, $g_i$, including competition for food, climate, reproductive status, and genotype. ANOVAs of $g_i$ would identify factors that influence $\overline{G}_+(a, t)$.

The second term worthy of discussion is the $\overline{D}_+(a, t)$ term. This describes the difference in the mean trait value between offspring and parents. There are many factors that can influence this term, including additive genetic effects, maternal environmental effects, and resource availability. As with the $g_i$'s, the $d_i$'s can be statistically analyzed with individual- and population-level variables. We do not report analyses of these two terms here but will in future work.

In the population of red deer we analyzed with equation (12), we found that viability selection changed the mean of the trait distribution as individuals aged. Fertility selection was weaker. This result suggests that previously

reported selection on birth weight using lifetime measures of fitness (Clutton-Brock and Albon 1982; Clutton-Brock et al. 1982, 1987, 1997; Kruuk et al. 1999; Clutton-Brock and Coulson 2002) is generated primarily by viability selection and not fertility selection. In itself, this result is not unexpected, since Clutton-Brock (1988) reported a decomposition of variation in lifetime reproductive success across a range of vertebrates, showing that longevity was typically the dominant component. However, our results demonstrate that a richer picture of selection and phenotypic change can be achieved by decomposing fitness into its constituent components.

The viability selection we report is countered by a substantial difference in the mean value of parental and offspring traits; this difference varies with age, being greatest at young and old ages. Parents tend to produce offspring that are more similar to the population mean than they are to themselves. Although it is not surprising that young and old mothers produce smaller individuals than those at prime age, the observation that this means parental birth weights are, on average, greater than offspring birth weights has not previously been described. The reasons for the difference are not clear but could be a result of developmental or energetic constraints (Smith et al. 1985; Moran 1992; Wagner and Altenberg 1996), which may or may not have additive genetic components. Previous analyses of the red deer population have reported significant heritabilities of birth weight (Kruuk et al. 2000; Coulson

et al. 2003), which suggest that the $\overline{D}(a, t)$ term incorporates additive genetic variation.

In the red deer study, equilibrium of the trait mean is primarily maintained because the viability selection differential is countered by differences between offspring and parental trait values. In Price's (1970) original equation, this form of equilibrium can arise when the first term is positive and the second term is negative, which can be interpreted to describe a trade-off between recruitment and survival. In the age-structured Price equation, we have derived explicit conditions describing further routes to equilibrium. These include selection operating in different directions, possibly mediated by a trade-off via survival and fertility, as in the original Price equation; selection operating via a covariance between survival and growth rates but in opposite directions at different ages; and the direction and route via which selection acts varying with the environment (Lande 1982; van Tienderen 2000). Coulson et al. (2003) demonstrated that for birth weight in this population, all of these processes operate to prevent evolution of the trait mean. The framework we develop will enable researchers to examine the processes that lead to stasis in the mean of a trait value, despite apparent positive selection (Merila et al. 2001), as well as changes in trait value in the apparent absence of selection.

Our derivation of an age-structured Price equation provides a useful step in characterizing the dynamics of the mean of a phenotypic trait in an age-structured population living in a variable environment. However, there are clearly obvious areas for future research. First, because evolutionary ecologists are often interested in changes in the variance in a trait distribution (Turelli and Barton 1994) as well as the mean, extending our derivations for higher moments of trait distributions is desirable. This work is already under way (extending the work of Rice [2004] in the non-age-structured case). Second, in order to generate dynamic equations, each term could be replaced by functions describing how the term is influenced by environmental variables. Such an approach has proved illuminating in understanding the temporal dynamics of population size and population growth and should prove insightful in identifying processes associated with phenotypic change (Coulson et al. 2001). Finally, in order to use our equations to describe genetic change, our derivation would need to be linked to models describing the genotype-phenotype map. An obvious starting point would be the additive genetic model. Such work should allow unprecedented insights into evolutionary change of fitness-related phenotypic traits in age-structured populations living in variable environments.

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