DOI: 10.1086/591693

Appendix A from T. Coulson and S. Tuljapurkar, "The Dynamics of a Quantitative Trait in an Age-Structured Population Living in a Variable Environment"

(Am. Nat., vol. 172, no. 5, p. 599)

Derivation of the Age-Structured Price Equation

We track trait values, population numbers, survival, fertility, and phenotypic plasticity by age (notation is summarized in table 1). Here the term "phenotypic plasticity" includes developmental changes in a trait, such as changes in physiological function or degenerative change in organs. Age classes are labeled by index a; newborns are in age class $a = 1$. There are $n(a, t)$ individuals in age class a at time t with phenotypes z_i, $i = 1, \dots, n(a, t)$; z_i may be a scalar or a vector. Total population size is $N(t)$; age structure proportions are $c(a, t) = n(a, t)/N(t)$. Individual i in age class a at time t has phenotype z_i and produces $r_i(a, t)$ offspring. The survival rate of individual i in age class a at time t is $s_i(a, t)$. At time t, the mean phenotype in age class a is $\bar{Z}(a, t)$. The mean phenotype in the whole population is

$$\bar{Z}(t) = \sum_a c(a, t)\bar{Z}(a, t). \tag{A1}$$

At time $t + 1$, phenotypic distributions at ages $2, 3, \dots$ are determined by selection through survival on the phenotypes already present at t in ages $1, 2, \dots$. But the newborn phenotypes in age class 1 at $t + 1$ depend on all parents at t, through their phenotypes and fertility, and on the transmission of phenotypes from parents to offspring. At time $t + 1$ for $a \geq 1$, the $n(a + 1, t + 1)$ individuals in age class $a + 1$ are survivors of the $n(a, t)$:

$$n(a + 1, t + 1) = \sum_{i=1}^{n(a,t)} s_i(a, t) = n(a, t)\bar{S}(a, t). \tag{A2}$$

Here $\bar{S}(a, t)$ is an average of $s_i(a, t)$ over the original a, t individuals. Suppose that an a, t individual with phenotype z_i who survives has a phenotype $z_i + g_i$, where g_i is growth or reversion. Set $g_i = 0$ for individuals that do not survive. The mean phenotype of $a + 1, t + 1$ individuals is

$$\begin{aligned} \bar{Z}(a + 1, t + 1) &= \frac{\overline{(S(Z + G))(a, t)}}{\bar{S}(a, t)}, \\ &= \bar{Z}(a, t) + \frac{\operatorname{Cov}(Z, S)(a, t)}{\bar{S}(a, t)} + \frac{\overline{SG}(a, t)}{\bar{S}(a, t)}. \end{aligned} \tag{A3}$$

As in our discussion of the non-age-structured Price equation, the second term above can be calculated only over individuals that actually survive:

$$\bar{Z}(a + 1, t + 1) = \bar{Z}(a, t) + \frac{\operatorname{Cov}(Z, S)(a, t)}{\bar{S}(a, t)} + \bar{G}_+(a, t), \tag{A4}$$

where $\bar{G}_+(a, t)$ is the mean of $Z(a + 1, t + 1) - Z(a, t)$ calculated across survivors. For offspring, we use an age-specific version of the notation in the preceding discussion of the Price equation. Individual i in age class a at time t has trait value $z_i(a, t)$ and produces $r_i(a, t) \geq 0$ offspring; the average number of offspring produced by a, t individuals is $\bar{R}(a, t)$. The trait value of the jth offspring of individual i in age class a at time t is $y_{ij}(a, t) =$

$z_i(a,t) + d_{ij}(a,t)$, and $\bar{d}(a,t)$ is the difference between the mean trait value of individual i's offspring and its own (parental) trait value $z_i(a,t)$. It is important to note that here $d_{ij}(a,t)$ and $\bar{d}(a,t)$ include both transmission infidelity and any difference in trait values between parents and offspring that is purely due to phenotypic plasticity. To see why, notice that individual i's trait value at a, t is related to its own trait value at birth, $z_i(1, t-a+1)$, by

$$z_i(a,t) = z_i(1, t-a+1) + g_i^c(a,t),$$

where $g_i^c(a,t)$ is the cumulative phenotypic plasticity of the trait value between ages 1 and a. The average size at birth of the offspring of this individual is

$$\bar{y}_i(a,t) = z_i(a,t) + \bar{d}(a,t) = z_i(1, t-a+1) + g_i^c(a,t) + \bar{d}(a,t),$$

and thus

$$\bar{d}_i(a,t) = [\bar{y}_i(a,t) - z_i(1, t-a+1)] - g_i^c(a,t). \tag{A5}$$

The term in square brackets on the right measures the mean difference between offspring and parental trait values, and the other term measures phenotypic plasticity. Let $\bar{Y}(1|a)$ be the mean trait value of the offspring produced by a, t individuals, and use equation (5) to see that

$$\bar{Y}(1|a) - \bar{Z}(a,t) = \frac{\mathrm{Cov}\,(Z,R)(a,t)}{\bar{R}(a,t)} + \bar{D}(a,t) + \frac{\mathrm{Cov}\,(D,R)(a,t)}{\bar{R}(a,t)}. \tag{A6}$$

Averages here are computed over all a, t individuals, that is, all potential parents. Alternatively, we can use equation (10) to write

$$\bar{Y}(1|a) - \bar{Z}(a,t) = [\bar{Z}_+(a,t) - \bar{Z}(a,t)] + \frac{\mathrm{Cov}_+\,(Z,R)(a,t)}{\bar{R}_+(a,t)} + \left[\bar{D}_+(a,t) + \frac{\mathrm{Cov}_+\,(D,R)(a,t)}{\bar{R}_+(a,t)}\right]. \tag{A7}$$

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 mean difference between offspring and parental trait values and differences due to phenotypic plasticity. The total number of newborns at time t is

$$n(1, t+1) = \sum_a \bar{R}(a,t)n(a,t). \tag{A8}$$

The mean trait value of all offspring is an average of $\bar{Y}(1|a)$ across all parental ages, weighted by reproductive output:

$$\bar{Z}(1, t+1) = \sum_a \left(\frac{\bar{R}(a,t)n(a,t)}{n(1,t+1)}\right)\left[\bar{Z}(a,t) + \bar{D}(a,t) + \frac{\mathrm{Cov}\,(Z,R)(a,t)}{\bar{R}(a,t)} + \frac{\mathrm{Cov}\,(D,R)(a,t)}{\bar{R}(a,t)}\right]. \tag{A9}$$

The population's mean phenotype at $t+1$ is

$$\bar{Z}(t+1) = \left(\frac{1}{N(t+1)}\right)\sum_a n(a, t+1)\bar{Z}(a, t+1). \tag{A10}$$

We follow standard demography in killing off the last age class at time t, call it age class ω, by time $t+1$; it is straightforward to modify the results if individuals can stay on in the terminal age class. Define the population growth rate $\bar{W}(t)$, which is also the mean fitness, by

$$N(t+1) = \overline{W}(t)N(t). \tag{A11}$$

For $a \geq 1$,

$$c(a+1, t+1) = \frac{\overline{S}(a,t)c(a,t)}{\overline{W}(t)}, \tag{A12}$$

$$\frac{n(a,t)}{n(1,t+1)} = \frac{c(a,t)}{\overline{W(t)}c(1,t+1)}. \tag{A13}$$

When we use these to combine equation (A9) with equation (A3) across all age classes, it is algebraically inevitable that

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

$$\sum_{a=1}^{\omega-1}\left(\frac{c(a,t)\overline{S}(a,t)}{\overline{W}(t)}\right)[\overline{Z}(a,t)] \tag{A14a}$$

$$+\sum_{a=1}^{\omega}\left(\frac{c(a,t)\overline{R}(a,t)}{\overline{W}(t)}\right)[\overline{Z}(a,t)+\overline{D}(a,t)] \tag{A14b}$$

$$+\sum_{a=1}^{\omega-1}\left(\frac{c(a,t)\overline{S}(a,t)}{\overline{W}(t)}\right)\left[\frac{\mathrm{Cov}\,(Z,S)(a,t)}{\overline{S}(a,t)}+\frac{\mathrm{Cov}\,(S,G)(a,t)}{\overline{S}(a,t)}\right] \tag{A14c}$$

$$\sum_{a=1}^{\omega}\left(\frac{c(a,t)\overline{R}(a,t)}{\overline{W}(t)}\right)\left[\frac{\mathrm{Cov}\,(D,R)(a,t)}{\overline{R}(a,t)}+\frac{\mathrm{Cov}\,(Z,R)(a,t)}{\overline{R}(a,t)}\right]. \tag{A14d}$$

To write the change in the mean trait value for the entire population, define the change in population structure:

$$\Delta c(a,t) = c(a+1,t+1) - c(a,t). \tag{A15}$$

Using this, we arrive at equations (11) and (12).