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Appendix C from M. Barfield et al., "Evolution in Stage-Structured Populations"

(Am. Nat., vol. 177, no. 4, p. 397)

Computational Details for the Two-Stage Example

It can be shown by direct calculation that the asymptotic growth rate (leading eigenvalue) of the population projection matrix

$$\bar{\mathbf{A}} = \begin{pmatrix} \bar{t}_{11} & \bar{f}_{12} \\ \bar{t}_{21} & 0 \end{pmatrix}$$

is

$$\bar{\lambda} = \frac{\bar{t}_{11} + \sqrt{\bar{t}_{11}^2 + 4\bar{f}_{12}\bar{t}_{21}}}{2}. \tag{C1}$$

The vector

$$(w_1, w_2) = \frac{1}{\bar{\lambda} + \bar{t}_{21}}(\bar{\lambda}, \bar{t}_{21}) \tag{C2}$$

describes the corresponding stable stage structure (right eigenvector of $\bar{\mathbf{A}}$), and

$$(v_1, v_2) = \frac{\bar{\lambda} + \bar{t}_{21}}{\bar{\lambda}^2 + \bar{f}_{12}\bar{t}_{21}}(\bar{\lambda}, \bar{f}_{12}) \tag{C3}$$

is the vector of normalized reproductive values (left eigenvector of $\bar{\mathbf{A}}$). The asymptotic rate of evolution shared by both stages (using eq. [8]) for this scenario takes the form

$$\Delta\bar{z} = \frac{1}{\bar{\lambda}}\left[w_1 G_1\left(v_1\bar{t}_{11}\frac{d\ln\bar{t}_{11}}{d\bar{z}_1} + v_2\bar{t}_{21}\frac{d\ln\bar{t}_{21}}{d\bar{z}_1}\right) + w_2 G_2 v_1 \bar{f}_{12}\frac{d\ln\bar{f}_{12}}{d\bar{z}_2}\right], \tag{C4}$$

with $\bar{\lambda}$, w_i, and v_i as defined above. The notation $d/d\bar{z}_i$ indicates that the derivative with respect to the mean phenotype is to be evaluated at the stage-specific mean $\bar{z}_i$.

When it is impossible to repeat stage 1 (i.e., the population is age-structured), $\bar{t}_{11} = 0$ identically. This implies that $d\ln\bar{t}_{11}/d\bar{z}_1 = 0$ and, from equation (C1),

$$\bar{\lambda} = \sqrt{\bar{f}_{12}\bar{t}_{21}} \stackrel{\text{def}}{=} \bar{\lambda}_{\text{age}}. \tag{C5}$$

Additional algebra using equations (C2), (C3), and (C5) shows that the shared rate of evolution (C4) for an age-structured population simplifies to

$$\Delta\bar{z} = \frac{1}{2}\left(G_1\frac{d\ln\bar{t}_{21}}{d\bar{z}_1} + G_2\frac{d\ln\bar{f}_{12}}{d\bar{z}_2}\right) \stackrel{\text{def}}{=} \Delta\bar{z}_{\text{age}}. \tag{C6}$$

If the first stage can be repeated the next year but the trait z has no effect on the probability of repeating (i.e., $\bar{t}_{11} > 0$ but $d\ln\bar{t}_{11}/d\bar{z}_1 = 0$), then the rate of evolution (C4) is

$$\Delta\bar{z} = \frac{2\bar{\lambda}_{\text{age}}^2}{\bar{\lambda}_{\text{age}}^2 + \bar{\lambda}^2}\Delta\bar{z}_{\text{age}}, \tag{C7}$$

where $\bar{\lambda}$ and $\bar{\lambda}_{\text{age}}$ are defined by equations (C1) and (C5), respectively. Because $\bar{\lambda} > \bar{\lambda}_{\text{age}}$, the leading fraction in equation (C7) is less than 1, which implies $\Delta\bar{z} < \Delta\bar{z}_{\text{age}}$. Equation (C7) thus shows that, all else being equal, evolution is slower with repeated stages than without them if the focal trait has no bearing on the probability of repeating a stage. The same comparison also reveals that while the speed is reduced, the direction of adaptation is unaffected.

Finally, consider the rate of adaptation when the probability of repeating the first stage is affected by the phenotype z. This is the same as the last case except that $d\ln\bar{t}_{11}/d\bar{z}_1 \neq 0$. Equation (C4) in this case becomes

$$\Delta\bar{z}_{\text{stage}} = \frac{2\bar{\lambda}_{\text{age}}^2}{\bar{\lambda}_{\text{age}}^2 + \bar{\lambda}^2}\left(\frac{\bar{t}_{11}\bar{\lambda}G_1}{2\bar{\lambda}_{\text{age}}^2}\frac{d\ln\bar{t}_{11}}{d\bar{z}_1} + \Delta\bar{z}_{\text{age}}\right), \tag{C8}$$

which is equivalent to equation (11).

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Appendix D from M. Barfield et al., "Evolution in Stage-Structured Populations"

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Price's Theorem and the General Joint Probability Density Function Method

We show here that the stage-structured version of Price's equation (eq. [13]) can be derived from our general recursions for the distribution of phenotypes and genotypes. By definition,

$$\begin{aligned}\bar{\mathbf{z}}'_i &= \int\int \mathbf{z}p'(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z}\\ &= \frac{T'_i\iint \mathbf{z}\theta_i(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} + F'_i\iint \mathbf{z}\phi_i(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z}}{N'_i}\\ &= \frac{\sum_j N_j\iint \mathbf{z}a_{ij}(\mathbf{z})p_j(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} + \sum_j N_j\iint \mathbf{D}f_{ij}(\mathbf{z})p_j(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z}}{N'_i}\\ &= \sum_j \frac{N_j}{N'_i}\int\int \mathbf{z}a_{ij}(\mathbf{z})p_j(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} + \sum_j \frac{N_j}{N'_i}\int\int \mathbf{d}a_{ij}(\mathbf{z})p_j(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z},\end{aligned} \tag{D1}$$

where $\mathbf{D} = \mathbf{g} - \mathbf{z}$ and $\mathbf{d} = \mathbf{D}f_{ij}/a_{ij}$. (Note that the second line corresponds to an average over the distribution given in eq. [4] in the main text.) The fact that the average phenotype of offspring is the same as their average genotype, which is the same as the average parental genotype, has been used in deriving the second term. The variable $\mathbf{d}$ is the difference between parental and offspring phenotypes due to reproduction. This is $\mathbf{0}$ for stage transitions not involving reproduction, so $\mathbf{d}$ is found by weighting $\mathbf{D}$ by the fraction of a_{ij} that is due to reproduction (f_{ij}/a_{ij}).

The double integrals in the last line of equation (D1) are stage-specific expected values of $\mathbf{z}a_{ij}(\mathbf{z})$ and $\mathbf{d}a_{ij}(\mathbf{z})$, which can be written in terms of covariances as follows:

$$\begin{aligned}\bar{\mathbf{z}}'_i &= \sum_j \frac{N_j}{N'_i}\{\mathrm{E}[\mathbf{z}a_{ij}(\mathbf{z})|j] + \mathrm{E}[\mathbf{d}a_{ij}(\mathbf{z})|j]\}\\ &= \sum_j \frac{N_j}{N'_i}\{\mathrm{E}[\mathbf{z}|j]\mathrm{E}[a_{ij}(\mathbf{z})|j] + \mathrm{Cov}[\mathbf{z},a_{ij}(\mathbf{z})|j] + \mathrm{E}[\mathbf{d}|j]\mathrm{E}[a_{ij}(\mathbf{z})|j] + \mathrm{Cov}[\mathbf{d},a_{ij}(\mathbf{z})|j]\}\\ &= \sum_j \frac{N_j}{N'_i}[\bar{\mathbf{z}}_j\bar{a}_{ij} + \mathrm{Cov}_j(\mathbf{z},a_{ij}) + \bar{\mathbf{d}}_j\bar{a}_{ij} + \mathrm{Cov}_j(\mathbf{d},a_{ij})],\end{aligned} \tag{D2}$$

where $\bar{\mathbf{z}}_j = \mathrm{E}(\mathbf{z}|j)$, $\bar{a}_{ij} = E[a_{ij}(\mathbf{z})|j]$, and $\mathrm{Cov}_j(\mathbf{z},a_{ij}) = \mathrm{Cov}[\mathbf{z},a_{ij}(\mathbf{z})|j]$ (similar expressions apply to the $\mathbf{d}$ terms).

The overall mean phenotype is $\bar{\mathbf{z}} = \sum_j \bar{\mathbf{z}}_j N_j/N = \sum_j c_j \bar{\mathbf{z}}_j$, where $c_j = N_j/N$ is the proportion of the population in stage j. The recursion for overall mean phenotype is then

$$\begin{aligned}\bar{\mathbf{z}}' &= \sum_i \frac{N_i'}{N'}\bar{\mathbf{z}}_i' \\ &= \sum_i \frac{N_i'}{N'}\sum_j \frac{N_j}{N_i'}\left[\bar{\mathbf{z}}_j\bar{a}_{ij} + \mathrm{Cov}_j(\mathbf{z}, a_{ij}) + \bar{\mathbf{d}}_j\bar{a}_{ij} + \mathrm{Cov}_j(\mathbf{d}, a_{ij})\right] \\ &= \sum_i\sum_j \frac{N_j}{N'}\left[\bar{\mathbf{z}}_j\bar{a}_{ij} + \mathrm{Cov}_j(\mathbf{z}, a_{ij}) + \bar{\mathbf{d}}_j\bar{a}_{ij} + \mathrm{Cov}_j(\mathbf{d}, a_{ij})\right] \\ &= \frac{1}{\bar{w}}\sum_i\sum_j \frac{N_j}{N}\left[\bar{\mathbf{z}}_j\bar{a}_{ij} + \mathrm{Cov}_j(\mathbf{z}, a_{ij}) + \bar{\mathbf{d}}_j\bar{a}_{ij} + \mathrm{Cov}_j(\mathbf{d}, a_{ij})\right],\end{aligned} \tag{D3}$$

where we have used $N' = \bar{w}N$, with $\bar{w}$ being the mean fitness of the population. Letting $w_j = w_j(\mathbf{z}) = \sum_i a_{ij}(\mathbf{z})$ be the fitness of $\mathbf{z}$ in stage j and $\bar{w}_j = \sum_i \bar{a}_{ij}$ be the average fitness of stage j individuals, then $\bar{w} = \mathrm{E}[\bar{w}_j] = \sum_j c_j\bar{w}_j$. Equation (D3) is then

$$\begin{aligned}\bar{\mathbf{z}}' &= \frac{1}{\bar{w}}\sum_j \frac{N_j}{N}[\bar{\mathbf{z}}_j\bar{w}_j + \mathrm{Cov}_j(\mathbf{z}, w_j) + \bar{\mathbf{d}}_j\bar{w}_j + \mathrm{Cov}_j(\mathbf{d}, w_j)] \\ &= \frac{1}{\bar{w}}\sum_j c_j[\bar{\mathbf{z}}_j\bar{w}_j + \mathrm{Cov}_j(\mathbf{z}, w_j) + \bar{\mathbf{d}}_j\bar{w}_j + \mathrm{Cov}_j(\mathbf{d}, w_j)].\end{aligned} \tag{D4}$$

The change in the mean is thus

$$\begin{aligned}\Delta\bar{\mathbf{z}} &= \bar{\mathbf{z}}' - \bar{\mathbf{z}} \\ &= \sum_j c_j\left[\bar{\mathbf{z}}_j\frac{\bar{w}_j}{\bar{w}} + \mathrm{Cov}_j\left(\mathbf{z}, \frac{w_j}{\bar{w}}\right)\right] + \sum_j c_j\left[\bar{\mathbf{d}}_j\frac{\bar{w}_j}{\bar{w}} + \mathrm{Cov}_j\left(\mathbf{d}, \frac{w_j}{\bar{w}}\right)\right] - \bar{\mathbf{z}} \\ &= \left[\sum_j c_j\bar{\mathbf{z}}_j\frac{\bar{w}_j}{\bar{w}} - \bar{\mathbf{z}}\right] + \sum_j c_j\,\mathrm{Cov}_j\left(\mathbf{z}, \frac{w_j}{\bar{w}}\right) + \left[\sum_j c_j\bar{\mathbf{d}}_j\frac{\bar{w}_j}{\bar{w}} - \bar{\mathbf{d}}\right] + \bar{\mathbf{d}} + \sum_j c_j\,\mathrm{Cov}_j\left(\mathbf{d}, \frac{w_j}{\bar{w}}\right).\end{aligned} \tag{D5}$$

The first term in brackets describes the covariance between mean phenotype and mean relative fitness over stages, which we write as $\mathrm{Cov}(\bar{\mathbf{z}}_j, \bar{w}_j/\bar{w})$. (The covariance of $\bar{\mathbf{z}}_j$ and $\bar{w}_j/\bar{w}$ is $\mathrm{E}[\bar{\mathbf{z}}_j\bar{w}_j/\bar{w}] - \mathrm{E}[\bar{\mathbf{z}}_j]\mathrm{E}[\bar{w}_j/\bar{w}] = \sum_j c_j\bar{\mathbf{z}}_j\bar{w}_j/\bar{w} - \bar{\mathbf{z}}$; simplification of the second term used the facts that $\mathrm{E}[\bar{\mathbf{z}}_j] = \bar{\mathbf{z}}$ and $\mathrm{E}[\bar{w}_j/\bar{w}] = 1$ by definition.) The second term in brackets is the same for $\bar{\mathbf{d}}_j$. The second summation is the average within-stage covariance between phenotype and relative fitness, $\mathrm{E}[\mathrm{Cov}_j(\mathbf{z}, w_j/\bar{w})]$, and the last term is the same for $\mathbf{d}$. Thus, the stage-structured version of Price's equation is

$$\Delta\bar{\mathbf{z}} = \mathrm{Cov}\left(\bar{\mathbf{z}}_j, \frac{\bar{w}_j}{\bar{w}}\right) + \mathrm{E}\left[\mathrm{Cov}_j\left(\mathbf{z}, \frac{w_j}{\bar{w}}\right)\right] + \mathrm{Cov}\left(\bar{\mathbf{d}}_j, \frac{\bar{w}_j}{\bar{w}}\right) + \bar{\mathbf{d}} + \mathrm{E}\left[\mathrm{Cov}_j\left(\mathbf{d}, \frac{w_j}{\bar{w}}\right)\right]. \tag{D6}$$

This is the formula (slightly rewritten) shown in the main text and there arrived at more simply using the law of total covariance.