

Appendix B from M. E. Orive et al., “Effects of Clonal Reproduction on Evolutionary Lag and Evolutionary Rescue” (Am. Nat., vol. 190, no. 4, p. 469)

Part A. Derivation of Recursions for Mean Genotype and Mean Phenotype

Recursion for Mean Genotype

We begin the derivation of the recursion for mean genotype given in equation (1) with $\bar{\mathbf{g}}'_i = \iint \mathbf{g} p'_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z}$, and using equation (A3) in appendix A, part A, for $p'_i(\mathbf{g}, \mathbf{z})$ we can write

$$\bar{\mathbf{g}}'_i = \frac{T'_i}{N'_i} \iint \mathbf{g} \theta_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} + \frac{F'_i}{N'_i} \iint \mathbf{g} \phi_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} + \frac{C'_i}{N'_i} \iint \mathbf{g} \kappa_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z}. \quad (\text{B1})$$

Focusing on each of the three terms in equation (B1) in turn, we note that equation (A1) in Barfield et al. (2011), $\theta_i(\mathbf{g}, \mathbf{z}) = \sum_j N_j t_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) / T'_i$, allows us to write the first term as

$$\frac{T'_i}{N'_i} \iint \mathbf{g} \left[\frac{1}{T'_i} \sum_j N_j t_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) \right] d\mathbf{g} d\mathbf{z} = \frac{1}{N'_i} \sum_j N_j \int t_{ij}(\mathbf{z}) \int \mathbf{g} p_j(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z}.$$

Equation (A2) in Barfield et al. (2011) gives the distribution of \mathbf{g} among parents of sexual offspring born into stage i , which is $\Phi_i(\mathbf{g}) = \sum_j N_j \int f_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) d\mathbf{z} / F'_i$. We assume that the average genotype of stage i sexually produced offspring, $\iint \mathbf{g} \phi_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z}$, is equal to the average genotype of their parents, $\int \mathbf{g} \Phi_i(\mathbf{g}) d\mathbf{g}$, so the second term in equation (B1) becomes

$$\frac{F'_i}{N'_i} \int \mathbf{g} \Phi_i(\mathbf{g}) d\mathbf{g} = \frac{1}{N'_i} \int \mathbf{g} \sum_j N_j \int f_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) d\mathbf{z} d\mathbf{g}.$$

For the final term in equation (B1), we assume that the average genotype of stage i clonal offspring is equal to the average genotype of their parents; this is equivalent to an assumption of no directional bias to the somatic mutations that cause clonal offspring to differ in genotype from their parents. If this is true, the third term in equation (B1) is $(C'_i/N'_i) \int \mathbf{g} K_i(\mathbf{g}) d\mathbf{g}$, where $K_i(\mathbf{g})$ is the distribution of genotypes among the parents of stage i clonal offspring. Following similar reasoning as for equation (A2) in Barfield et al. (2011), we find that

$$K_i(\mathbf{g}) = \sum_j \frac{1}{\bar{c}_{ij}} \int c_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) d\mathbf{z} \frac{\bar{c}_{ij} N_j}{C'_i} = \frac{1}{C'_i} \sum_j N_j \int c_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) d\mathbf{z}. \quad (\text{B2})$$

Substituting this into the last term of equation (B1) gives

$$\begin{aligned} \frac{C'_i}{N'_i} \int \mathbf{g} K_i(\mathbf{g}) d\mathbf{g} &= \frac{C'_i}{N'_i} \int \mathbf{g} \left[\frac{1}{C'_i} \sum_j N_j \int c_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) d\mathbf{z} \right] d\mathbf{g} \\ &= \frac{1}{N'_i} \sum_j N_j \int c_{ij}(\mathbf{z}) \int \mathbf{g} p_j(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z}. \end{aligned}$$

Combining all three terms and using $a_{ij}(\mathbf{z}) = t_{ij}(\mathbf{z}) + f_{ij}(\mathbf{z}) + c_{ij}(\mathbf{z})$ leads to the following equation:

$$\begin{aligned} \bar{\mathbf{g}}'_i &= \frac{1}{N'_i} \sum_j N_j \int [t_{ij}(\mathbf{z}) + f_{ij}(\mathbf{z}) + c_{ij}(\mathbf{z})] \int \mathbf{g} p_j(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} \\ &= \frac{1}{N'_i} \sum_j N_j \int a_{ij}(\mathbf{z}) \int \mathbf{g} p_j(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z}. \end{aligned} \quad (\text{B3})$$

Equation (B3) now has the same form as the middle line of equation (5) in Barfield et al. (2011), with the difference in the definition of the total transition rate $a_{ij}(\mathbf{z})$. We now define $d_{ij} = \bar{a}_{ij} N_j / N'_i$ as the fraction of stage i individuals in the

next time step contributed by stage j , where the overbar indicates the expected values over the distribution of stage j (to avoid notational confusion, we note that this quantity was written as c_{ij} in Barfield et al. [2011], but here we are using c_{ij} for the production of clonal offspring instead). Following the same derivation as given in Barfield et al. (2014) allows equation (B3) to be written as

$$\bar{\mathbf{g}}'_i = \frac{1}{N'_i} \sum_j N_j \int \mathbf{g} p_j(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} = \sum_j d_{ij} \bar{\mathbf{g}}_j + \sum_j d_{ij} \mathbf{G}_j \nabla_{\mathbf{z}_j} \ln \bar{a}_{ij}, \quad (\text{B4})$$

which is equation (1). As in Barfield et al. (2011), $\nabla_{\mathbf{z}_j} = (\partial/\partial\bar{z}_1, \partial/\partial\bar{z}_2, \dots, \partial/\partial\bar{z}_m)^\top$ is the gradient operator with respect to trait means evaluated at $\bar{\mathbf{z}}_j$, the multivariate mean phenotype of stage j individuals. Here, the first sum of the last expression in equation (B4) is a weighted average of stage-specific mean genotypes contributing to stage i , and the second sum describes the combined effects of selection.

Recursion for Mean Phenotype

For the change in mean phenotype, we start with $\bar{\mathbf{z}}'_i = \iint \mathbf{z} p'_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z}$ and again use the equation for the next-generation joint PDF given in equation (A3). This leads to

$$\begin{aligned} \bar{\mathbf{z}}'_i &= \iint \mathbf{z} \left[\theta_i(\mathbf{g}, \mathbf{z}) \frac{T'_i}{N'_i} + \phi_i(\mathbf{g}, \mathbf{z}) \frac{F'_i}{N'_i} + \kappa_i(\mathbf{g}, \mathbf{z}) \frac{C'_i}{N'_i} \right] d\mathbf{g} d\mathbf{z} \\ &= \frac{T'_i}{N'_i} \iint \mathbf{z} \theta_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} + \frac{F'_i}{N'_i} \iint \mathbf{z} \phi_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} + \frac{C'_i}{N'_i} \iint \mathbf{z} \kappa_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z}. \end{aligned} \quad (\text{B5})$$

We denote the three terms in equation (B5) as A , B , and C , respectively. Term A gives the contribution to the mean phenotype of stage i individuals in the next generation arising from transitions, term B gives the contribution arising from sexual reproduction, and term C gives the contribution arising from clonal reproduction. We note that A and B are identical to A and B given in equations (A6) and (A9) of Barfield et al. (2014), allowing us to write them as

$$A = \frac{T'_i}{N'_i} \iint \mathbf{z} \theta_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} = \sum_j d'_{ij} (\bar{\mathbf{z}}_j + \bar{t}_{ij}^{-1} \mathbf{P}_j \nabla_{\mathbf{z}_j} \bar{t}_{ij}), \quad (\text{B6a})$$

$$B = \frac{F'_i}{N'_i} \iint \mathbf{z} \phi_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} = \sum_j d^f_{ij} (\bar{\mathbf{g}}_j + \bar{f}_{ij}^{-1} \mathbf{G}_j \nabla_{\mathbf{z}_j} \bar{f}_{ij}), \quad (\text{B6b})$$

where we use the definitions $d'_{ij} = \bar{t}_{ij} N_j / N'_i$ and $d^f_{ij} = \bar{f}_{ij} N_j / N'_i$ (these were given as c'_{ij} and c^f_{ij} in Barfield et al. [2014]).

Now turning to term C , we use the clonal offspring joint PDF $\kappa_i(\mathbf{g}, \mathbf{z})$ from equation (A4) in appendix A, part A (with $S_{ij}(\mathbf{g}, \mathbf{z} | \mathbf{g}^*, \mathbf{z}^*) = X_{ij}(\mathbf{g} | \mathbf{g}^*) Y_{ij}(\mathbf{z} | \mathbf{g}, \mathbf{g}^*, \mathbf{z}^*)$) to write

$$\begin{aligned} C &= \frac{C'_i}{N'_i} \iint \mathbf{z} \kappa_i(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} \\ &= \frac{1}{N'_i} \iint \mathbf{z} \sum_j N_j \left[\iint X_{ij}(\mathbf{g} | \mathbf{g}^*) Y_{ij}(\mathbf{z} | \mathbf{g}, \mathbf{g}^*, \mathbf{z}^*) c_{ij}(\mathbf{z}^*) p_j(\mathbf{g}^*, \mathbf{z}^*) d\mathbf{g}^* d\mathbf{z}^* \right] d\mathbf{g} d\mathbf{z}. \end{aligned}$$

Rearranging and using equation (A7) from appendix A, part A, gives

$$\begin{aligned} C &= \frac{1}{N'_i} \int \sum_j N_j \left[\iint X_{ij}(\mathbf{g} | \mathbf{g}^*) \left\{ \int \mathbf{z} Y_{ij}(\mathbf{z} | \mathbf{g}, \mathbf{g}^*, \mathbf{z}^*) d\mathbf{z} \right\} c_{ij}(\mathbf{z}^*) p_j(\mathbf{g}^*, \mathbf{z}^*) d\mathbf{g}^* d\mathbf{z}^* \right] d\mathbf{g} \\ &= \frac{1}{N'_i} \int \sum_j N_j \left[\iint X_{ij}(\mathbf{g} | \mathbf{g}^*) \left\{ \mathbf{g} + \mathbf{R}_{ij}(\mathbf{z}^* - \mathbf{g}^*) \right\} c_{ij}(\mathbf{z}^*) p_j(\mathbf{g}^*, \mathbf{z}^*) d\mathbf{g}^* d\mathbf{z}^* \right] d\mathbf{g}, \end{aligned}$$

where once again \mathbf{R}_{ij} is a matrix whose diagonal entries are ρ_{ijk} and all other entries are 0. We rearrange the last expression and use the assumption that the mean of $X_{ij}(\mathbf{g}|\mathbf{g}^*) = \mathbf{g}^*$ (mean clonal offspring genotype equals that of their parents, as is the case for eq. [A5]), leading to

$$\begin{aligned} C &= \frac{1}{N'_i} \sum_j N_j \iint \left\{ \int X_{ij}(\mathbf{g}|\mathbf{g}^*)[\mathbf{g} + \mathbf{R}_{ij}(\mathbf{z}^* - \mathbf{g}^*)]d\mathbf{g} \right\} c_{ij}(\mathbf{z}^*) p_j(\mathbf{g}^*, \mathbf{z}^*) d\mathbf{g}^* d\mathbf{z}^* \\ &= \frac{1}{N'_i} \sum_j N_j \iint \left\{ (\mathbf{I} - \mathbf{R}_{ij})\mathbf{g}^* + \mathbf{R}_{ij}\mathbf{z}^* \right\} c_{ij}(\mathbf{z}^*) p_j(\mathbf{g}^*, \mathbf{z}^*) d\mathbf{g}^* d\mathbf{z}^*, \end{aligned}$$

where \mathbf{I} is the $m \times m$ identity matrix. (The integral in braces is the mean of $X_{ij}(\mathbf{g}|\mathbf{g}^*)$ plus $\mathbf{R}_{ij}(\mathbf{z}^* - \mathbf{g}^*)$ times the integral of $X_{ij}(\mathbf{g}|\mathbf{g}^*)$, which is 1 since this is a PDF.) Therefore, after rearranging and dropping the asterisks (since, in the last expression for C above, \mathbf{g} and \mathbf{z} do not appear and \mathbf{g}^* and \mathbf{z}^* are dummy variables),

$$C = (\mathbf{I} - \mathbf{R}_{ij}) \sum_j \frac{N_j}{N'_i} \iint \mathbf{g} c_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} + \mathbf{R}_{ij} \sum_j \frac{N_j}{N'_i} \iint \mathbf{z} c_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z}. \quad (\text{B7})$$

We will focus on the two terms in equation (B7) separately and denote them as D (the first term) and E (the second), so $C = D + E$.

Note that $p_j(\mathbf{g}, \mathbf{z}) = p_j(\mathbf{g}|\mathbf{z})p_j(\mathbf{z})$, where, for stage j , $p_j(\mathbf{g}|\mathbf{z})$ is the conditional PDF of \mathbf{g} given \mathbf{z} and $p_j(\mathbf{z})$ is the marginal distribution of \mathbf{z} , which is given by

$$p_j(\mathbf{z}) = \frac{1}{\sqrt{(2\pi)^m |\mathbf{P}_j|}} \exp \left\{ -\frac{1}{2} (\mathbf{z} - \bar{\mathbf{z}}_j)^\top \mathbf{P}_j^{-1} (\mathbf{z} - \bar{\mathbf{z}}_j) \right\},$$

from which it follows that $\nabla_{\mathbf{z}} p_j(\mathbf{z}) = \mathbf{P}_j^{-1} (\mathbf{z} - \bar{\mathbf{z}}_j) p_j(\mathbf{z})$.

Substituting $p_j(\mathbf{g}, \mathbf{z}) = p_j(\mathbf{g}|\mathbf{z})p_j(\mathbf{z})$ into D (the first term of C) gives

$$\begin{aligned} D &= (\mathbf{I} - \mathbf{R}_{ij}) \sum_j \frac{N_j}{N'_i} \iint \mathbf{g} c_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} \\ &= \sum_j \frac{N_j}{N'_i} (\mathbf{I} - \mathbf{R}_{ij}) \iint \mathbf{g} c_{ij}(\mathbf{z}) p_j(\mathbf{g}|\mathbf{z}) p_j(\mathbf{z}) d\mathbf{g} d\mathbf{z} \\ &= \sum_j \frac{N_j}{N'_i} (\mathbf{I} - \mathbf{R}_{ij}) \int c_{ij}(\mathbf{z}) \left[\int \mathbf{g} p_j(\mathbf{g}|\mathbf{z}) d\mathbf{g} \right] p_j(\mathbf{z}) d\mathbf{z}. \end{aligned}$$

Since \mathbf{g} and \mathbf{z} in stage j are jointly Gaussian with phenotypic covariance matrix \mathbf{P}_j and covariance between components of \mathbf{g} and \mathbf{z} given by matrix \mathbf{G}_j , the term in brackets (the expected value of \mathbf{g} given \mathbf{z}) is equal to $\bar{\mathbf{g}}_j + \mathbf{G}_j \mathbf{P}_j^{-1} (\mathbf{z} - \bar{\mathbf{z}}_j)$, and we can write D as

$$D = \sum_j \frac{N_j}{N'_i} (\mathbf{I} - \mathbf{R}_{ij}) \int c_{ij}(\mathbf{z}) \left[\bar{\mathbf{g}}_j + \mathbf{G}_j \mathbf{P}_j^{-1} (\mathbf{z} - \bar{\mathbf{z}}_j) \right] p_j(\mathbf{z}) d\mathbf{z},$$

and, since $\bar{c}_{ij} = \int c_{ij}(\mathbf{z}) p_j(\mathbf{z}) d\mathbf{z}$,

$$D = \sum_j \frac{N_j}{N'_i} (\mathbf{I} - \mathbf{R}_{ij}) \left[\bar{\mathbf{g}}_j \bar{c}_{ij} + \mathbf{G}_j \mathbf{P}_j^{-1} \int c_{ij}(\mathbf{z}) (\mathbf{z} - \bar{\mathbf{z}}_j) p_j(\mathbf{z}) d\mathbf{z} \right]. \quad (\text{B8})$$

Using the expression for $\nabla_{\mathbf{z}} p_j(\mathbf{z})$ above, we note that

$$\nabla_{\mathbf{z}} \bar{c}_{ij} = \nabla_{\mathbf{z}} \int c_{ij}(\mathbf{z}) p_j(\mathbf{z}) d\mathbf{z} = \int c_{ij}(\mathbf{z}) \nabla_{\mathbf{z}} p_j(\mathbf{z}) d\mathbf{z} = \int c_{ij}(\mathbf{z}) \mathbf{P}_j^{-1} (\mathbf{z} - \bar{\mathbf{z}}_j) p_j(\mathbf{z}) d\mathbf{z}.$$

Substituting for this integral in equation (B8) gives $D = \sum_j (N_j/N'_i) (\mathbf{I} - \mathbf{R}_{ij}) [\bar{\mathbf{g}}_j \bar{c}_{ij} + \mathbf{G}_j \nabla_{\mathbf{z}} \bar{c}_{ij}]$. Defining $d_{ij}^c = \bar{c}_{ij} N_j/N'_i$ allows us to write D as

$$D = \sum_j d_{ij}^c (\mathbf{I} - \mathbf{R}_{ij}) (\bar{\mathbf{g}}_j + \bar{c}_{ij}^{-1} \mathbf{G}_j \nabla_{\mathbf{z}} \bar{c}_{ij}). \quad (\text{B9})$$

Now turning to term E ,

$$\begin{aligned} E &= \mathbf{R}_{ij} \sum_j \frac{N_j}{N'_i} \iint \mathbf{z} c_{ij}(\mathbf{z}) p_j(\mathbf{g}, \mathbf{z}) d\mathbf{g} d\mathbf{z} \\ &= \sum_j \frac{N_j}{N'_i} \mathbf{R}_{ij} \int \mathbf{z} c_{ij}(\mathbf{z}) \left[\int p_j(\mathbf{g}, \mathbf{z}) d\mathbf{g} \right] d\mathbf{z} \\ &= \sum_j \frac{N_j}{N'_i} \mathbf{R}_{ij} \int \mathbf{z} c_{ij}(\mathbf{z}) p_j(\mathbf{z}) d\mathbf{z}. \end{aligned}$$

As noted earlier, $\nabla_{\mathbf{z}} \bar{c}_{ij} = \int c_{ij}(\mathbf{z}) \mathbf{P}_j^{-1} (\mathbf{z} - \bar{\mathbf{z}}_j) p_j(\mathbf{z}) d\mathbf{z}$, which can be written as $\mathbf{P}_j^{-1} [\int \mathbf{z} c_{ij}(\mathbf{z}) p_j(\mathbf{z}) d\mathbf{z} - \bar{c}_{ij} \bar{\mathbf{z}}_j]$, so $\int \mathbf{z} c_{ij}(\mathbf{z}) p_j(\mathbf{z}) d\mathbf{z} = \mathbf{P}_j \nabla_{\mathbf{z}} \bar{c}_{ij} + \bar{\mathbf{z}}_j \bar{c}_{ij}$. Therefore,

$$E = \sum_j \frac{N_j}{N'_i} \mathbf{R}_{ij} [\bar{\mathbf{z}}_j \bar{c}_{ij} + \mathbf{P}_j \nabla_{\mathbf{z}} \bar{c}_{ij}] = \sum_j d_{ij}^c \mathbf{R}_{ij} (\bar{\mathbf{z}}_j + \bar{c}_{ij}^{-1} \mathbf{P}_j \nabla_{\mathbf{z}} \bar{c}_{ij}). \quad (\text{B10})$$

Substituting equations (B9) and (B10) into equation (B7), which is $C = D + E$, gives

$$C = \sum_j d_{ij}^c \left\{ (\mathbf{I} - \mathbf{R}_{ij}) (\bar{\mathbf{g}}_j + \bar{c}_{ij}^{-1} \mathbf{G}_j \nabla_{\mathbf{z}} \bar{c}_{ij}) + \mathbf{R}_{ij} (\bar{\mathbf{z}}_j + \bar{c}_{ij}^{-1} \mathbf{P}_j \nabla_{\mathbf{z}} \bar{c}_{ij}) \right\}. \quad (\text{B11})$$

Finally, combining A , B , and C (eqq. [B6] and [B11]) gives

$$\begin{aligned} \bar{\mathbf{z}}'_i &= \sum_j d_{ij}^t (\bar{\mathbf{z}}_j + \bar{t}_{ij}^{-1} \mathbf{P}_j \nabla_{\mathbf{z}} \bar{t}_{ij}) + \sum_j d_{ij}^f (\bar{\mathbf{g}}_j + \bar{f}_{ij}^{-1} \mathbf{G}_j \nabla_{\mathbf{z}} \bar{f}_{ij}) \\ &\quad + \sum_j d_{ij}^c \left\{ (\mathbf{I} - \mathbf{R}_{ij}) (\bar{\mathbf{g}}_j + \bar{c}_{ij}^{-1} \mathbf{G}_j \nabla_{\mathbf{z}} \bar{c}_{ij}) + \mathbf{R}_{ij} (\bar{\mathbf{z}}_j + \bar{c}_{ij}^{-1} \mathbf{P}_j \nabla_{\mathbf{z}} \bar{c}_{ij}) \right\}. \end{aligned} \quad (\text{B12})$$

We note that $d_{ij}/\bar{a}_{ij} = d_{ij}^t/\bar{t}_{ij} = d_{ij}^f/\bar{f}_{ij} = d_{ij}^c/\bar{c}_{ij} = N_j/N'_i$, so we can simplify the equation for the change in mean phenotype to

$$\begin{aligned} \bar{\mathbf{z}}'_i &= \sum_j \left[(d_{ij}^t + \mathbf{R}_{ij} d_{ij}^c) \bar{\mathbf{z}}_j + (d_{ij}^f + (\mathbf{I} - \mathbf{R}_{ij}) d_{ij}^c) \bar{\mathbf{g}}_j \right] \\ &\quad + \sum_j \frac{d_{ij}}{\bar{a}_{ij}} (\mathbf{P}_j \nabla_{\mathbf{z}} \bar{t}_{ij} + \mathbf{G}_j \nabla_{\mathbf{z}} \bar{f}_{ij} + \mathbf{R}_{ij} \mathbf{P}_j \nabla_{\mathbf{z}} \bar{c}_{ij} + (\mathbf{I} - \mathbf{R}_{ij}) \mathbf{G}_j \nabla_{\mathbf{z}} \bar{c}_{ij}) \\ &= \sum_j \left[(d_{ij}^t + \mathbf{R}_{ij} d_{ij}^c) \bar{\mathbf{z}}_j + (d_{ij}^f + (\mathbf{I} - \mathbf{R}_{ij}) d_{ij}^c) \bar{\mathbf{g}}_j \right] \\ &\quad + \sum_j \frac{d_{ij}}{\bar{a}_{ij}} \left[\mathbf{P}_j \nabla_{\mathbf{z}} (\bar{t}_{ij} + \mathbf{R}_{ij} \bar{c}_{ij}) + \mathbf{G}_j \nabla_{\mathbf{z}} (\bar{f}_{ij} + (\mathbf{I} - \mathbf{R}_{ij}) \bar{c}_{ij}) \right], \end{aligned}$$

which parallels equation (6) of Barfield et al. (2011), given the correction from Barfield et al. (2014). Recalling that $\nabla_{\mathbf{z}} = (\partial/\partial \bar{z}_1, \partial/\partial \bar{z}_2, \dots, \partial/\partial \bar{z}_m)^\top$, we note that $\nabla_{\mathbf{z}} \ln x = x^{-1} \nabla_{\mathbf{z}} x$, so letting $x = \bar{t}_{ij}, \bar{f}_{ij}$, and \bar{c}_{ij} allows equation (B12) to be written as

$$\begin{aligned} \bar{\mathbf{z}}'_i = & \sum_j \left[(d_{ij}^t + \mathbf{R}_{ij} d_{ij}^c) \bar{\mathbf{z}}_j + (d_{ij}^f + (\mathbf{I} - \mathbf{R}_{ij}) d_{ij}^c) \bar{\mathbf{g}}_j \right] \\ & + \sum_j \left[d_{ij}^t \mathbf{P}_j \nabla_{\mathbf{z}} \ln \bar{l}_{ij} + d_{ij}^f \mathbf{G}_j \nabla_{\mathbf{z}} \ln \bar{f}_{ij} + \mathbf{R}_{ij} d_{ij}^c \mathbf{P}_j \nabla_{\mathbf{z}} \ln \bar{c}_{ij} + (\mathbf{I} - \mathbf{R}_{ij}) d_{ij}^c \mathbf{G}_j \nabla_{\mathbf{z}} \ln \bar{c}_{ij} \right], \end{aligned} \quad (\text{B13})$$

which is equation (2).

Part B. Assumption of Gaussian Genotypic and Phenotypic Distributions

As mentioned in the section giving recursions for mean genotype (eq. [1]) and phenotype (eq. [2]) under the assumption that the genotypic and phenotypic distributions are Gaussian with fixed covariances, this Gaussian assumption is likely to become less accurate with increasing clonality. To examine this possibility, we compared the results of simulations using the individual-based model with results using equations with the Gaussian assumption at various levels of clonality (r, ρ). The results given here are for nonoverlapping generations and a step change in the phenotypic optimum.

The parameters we use (following Burger and Lynch [1995] and our previous work) have a random component of phenotype (introduced during sexual reproduction and clonal reproduction with $\rho = 0$) that is high relative to the expected genetic variance. Since this random component of phenotype is Gaussian and tends to dominate the phenotype, the Gaussian assumption for the phenotype is likely to be met in most cases, the possible exception being when clonal reproduction (r_c) and ρ are high (with high ρ , the random part of the phenotype still has a relatively high value, but most of it is determined by the parent's random component, and therefore the new independent part is smaller). The distribution of the genotype is more likely to be affected by clonality (with or without correlation), but since the genotypic variance is lower, this deviation would be less likely to affect the accuracy of using the Gaussian assumption.

We compared the two methods at three levels of clonality, $r, \rho = 0.25, 0.5$, and 0.81 , in figure B1 (in all cases, r_c and ρ were assumed to be equal, so each was $0.5, 0.707$, and 0.9 for the three cases). There was fairly good agreement for population size in all three cases, with the biggest deviation for the lowest clonality, probably due to the lower population sizes reached (which could produce deviations from Gaussian distributions) as well as the fact that some simulated populations became extinct and the population size is averaged only over populations that persisted. For genotype and phenotype, there was quite good agreement for the lowest clonality used (which, note, was 50% clonality and correlation and so was not low), there was reasonable agreement for the middle level of clonality, and there were large discrepancies (slower increase in genotype and phenotype in the simulations) only at the highest clonality (90% clonality and correlation).

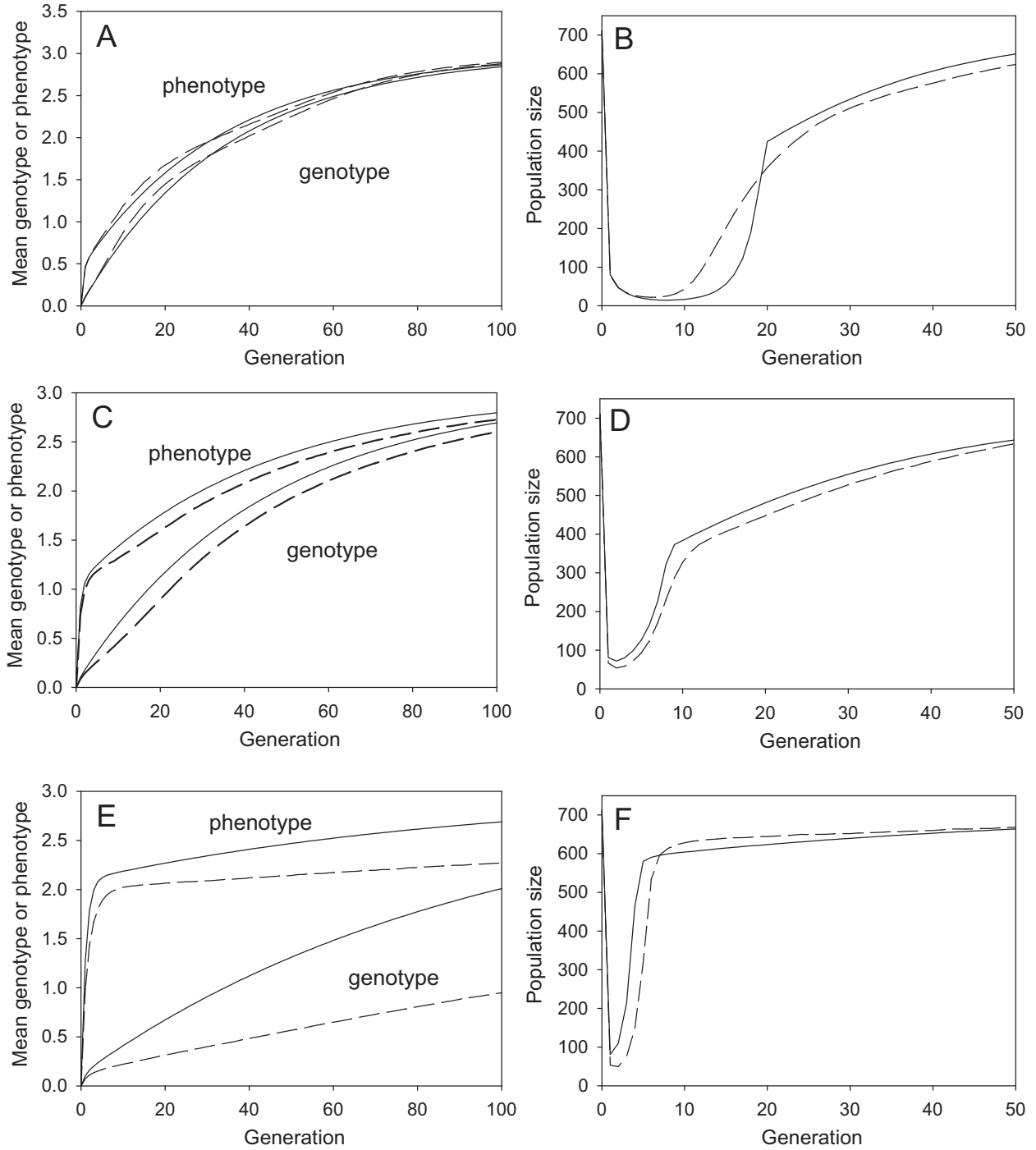


Figure B1: Comparison of analytical results using the assumption of Gaussian distributions for genotype and phenotype (solid lines) with results from the individual-based model (IBM; dashed lines). Shown are mean phenotype and genotype (A) and population size (B) for $r_c \rho = 0.25$, for $r_c \rho = 0.5$ (C, D), and for $r_c \rho = 0.81$ (E, F). For the IBM, $K = 256$, $f = 4$, $\omega^2 = 1$, $n = 10$, $\mu_g = 0.001$, $\mu_s = 0.00001$, $\alpha^2 = 0.05$, $\delta = 1$, $\theta = 3$, and $r_c = \rho$ (0.5 each for A, B; 0.7071 for C, D; and 0.9 for E, F). For the analytical results, parameters were chosen to be comparable using the expected genetic variance (as in Burger and Lynch 1995) and were $P = 1.07$, $G = 0.07$, $\theta = 3$, $f = 4$, $\omega^2 = 2.07$, $t_{\max} = 0.695$, and, initially, $\bar{g} = \bar{z} = 0$, and the population size was 712 (with a maximum of 256 reproducing individuals).

Part C. Relative Importance of Varying Some Parameters on Evolutionary Rescue

Using our individual-based model, we examined the effect of varying various parameters related to clonal reproduction and stage structure on evolutionary rescue, which raises the question of the relative importance of each of these factors. This will likely depend on detailed aspects of the life history in question and the exact conditions being considered, and a thorough investigation is beyond the scope of this article. However, as a first step in this direction we performed simulations with the individual-based model and a step change in the optimal phenotype in a baseline case and then changed four parameters in turn by a modest, consistent amount (0.1). The parameters and their baseline values were the association constant ρ (0.5), clonal fraction r_c (0.5), relative effort for clonal offspring δ (1), and adult survival p_s (0). The results are shown in figure B2. Increasing ρ , r_c , or p_s increased persistence, with a small increase for r_c , a larger increase for ρ , and the largest increase for p_s (about twice the increase for increasing r_c but only slightly larger than that for increasing ρ). Increasing the effort for a clonal offspring, of course, decreased the probability of persistence, by an amount approximately the same as the increase observed by increasing r_c . Note, however, that baseline δ was twice the baseline r_c , so the fractional change in δ was only half as much. Therefore, in terms of fractional change the magnitude of the change resulting from increased δ is probably comparable to that seen when increasing ρ (we did not equalize the fractional change because the baseline p_s was 0).

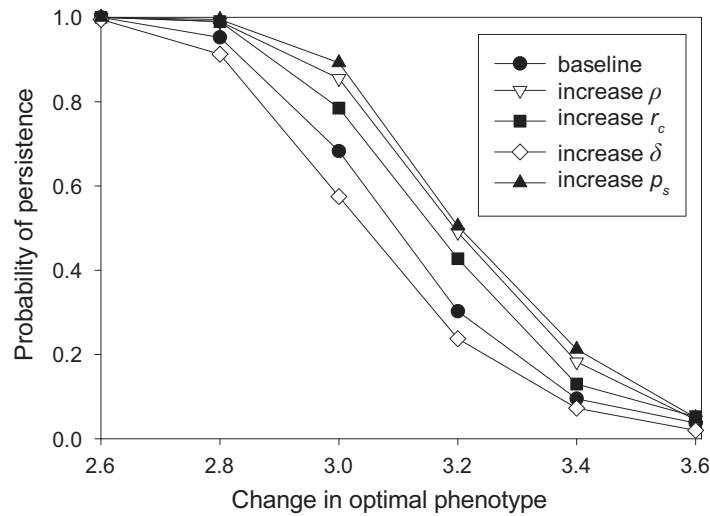


Figure B2: Comparison of the effect of changing various parameters on the probability of population persistence after a one-step change in optimal phenotype as a function of the magnitude of the change (θ), using the individual-based model with parameters $K = 256$, $f = 4$, $\omega^2 = 1$, $n = 10$, $\mu_g = 0.001$, $\mu_s = 0.00001$, $\alpha^2 = 0.05$, and $G = 1,000$. The baseline (filled circles) was $\rho = 0.5$, $r_c = 0.5$, $\delta = 1$, and p_s (adult survival) = 0. Each parameter was then in turn increased by 0.1, with the others at their baseline values.