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Appendix A from C. de Vries and H. Caswell, "Stage-Structured Evolutionary Demography: Linking Life Histories, Population Genetics, and Ecological Dynamics" (Am. Nat., vol. 193, no. 4, p. 545)

The Projection Matrix $\tilde{\mathbf{A}}$

In this appendix, we will derive equation (32), repeated here for convenience:

$$\tilde{\mathbf{A}}(\tilde{\mathbf{p}}) = \left[\begin{array}{c|c|c} \mathbf{U}_{AA} + q_A^{\mathrm{b}}\mathbf{F}_{AA} & \frac{1}{2}q_A^{\mathrm{b}}\mathbf{F}_{Aa} & \mathbf{0} \\ \hline q_a^{\mathrm{b}}\mathbf{F}_{AA} & \mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa} & q_A^{\mathrm{b}}\mathbf{F}_{aa} \\ \hline \mathbf{0} & \frac{1}{2}q_a^{\mathrm{b}}\mathbf{F}_{Aa} & \mathbf{U}_{aa} + q_a^{\mathrm{b}}\mathbf{F}_{aa} \end{array}\right] \tag{A1}$$

$$= \tilde{\mathbf{U}} + \tilde{\mathbf{F}}. \tag{A2}$$

We start with the survival and transition matrix, $\tilde{\mathbf{U}}$. Substituting equation (24),

$$\mathbb{U} = \sum_{i=1}^{g} \mathbf{E}_{ii} \otimes \mathbf{U}_i, \tag{A3}$$

into the equation for $\tilde{\mathbf{U}}$ yields

$$\tilde{\mathbf{U}} = \sum_{i=1}^{g} \mathbf{K}^{\top}\mathbb{D}\mathbf{K}(\mathbf{E}_{ii} \otimes \mathbf{U}_i). \tag{A4}$$

Because individuals do not change their genotype once they are born,

$$\tilde{\mathbf{U}} = \left[\begin{array}{c|c|c} \mathbf{U}_{AA} & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{U}_{Aa} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa} \end{array}\right], \tag{A5}$$

where we have set $g = 3$.

The fertility matrix, $\tilde{\mathbf{F}}$, is rewritten in a similar way. We substitute equation (25),

$$\mathbb{F} = \sum_{i=1}^{g} \mathbf{E}_{ii} \otimes \mathbf{F}_i, \tag{A6}$$

and equation (27),

$$\mathbb{H} = \mathbf{I}_{\omega} \otimes \mathbf{H}(\tilde{\mathbf{n}}), \tag{A7}$$

into the fertility part of equation (A2), yielding

$$\tilde{\mathbf{F}} = \mathbf{K}^{\top}\mathbb{H}(\tilde{\mathbf{n}})\,\mathbf{K}\mathbb{F} \tag{A8}$$

$$= \sum_{i=1}^{g} \mathbf{K}^{\top}(\mathbf{I}_{\omega} \otimes \mathbf{H})\mathbf{K}(\mathbf{E}_{ii} \otimes \mathbf{F}_i), \tag{A9}$$

where the explicit dependence of the matrix $\mathbf{H}$ on $\tilde{\mathbf{n}}$ was dropped to avoid a proliferation of brackets. Note that $\mathbf{K}^{\top}(\mathbf{A}\otimes\mathbf{B})\mathbf{K} = \mathbf{B}\otimes\mathbf{A}$ (Magnus and Neudecker 1979), so

$$\tilde{\mathbf{F}} = \sum_{i=1}^{g}(\mathbf{H}\otimes\mathbf{I}_{\omega})(\mathbf{E}_{ii}\otimes\mathbf{F}_{i}). \tag{A10}$$

Finally, use $(\mathbf{A}\otimes\mathbf{B})(\mathbf{C}\otimes\mathbf{D}) = \mathbf{AC}\otimes\mathbf{BD}$ to write

$$\tilde{\mathbf{F}} = \sum_{i=1}^{g}(\mathbf{HE}_{ii})\otimes\mathbf{F}_{i}. \tag{A11}$$

To continue, the entries of the parent-offspring matrix, $\mathbf{H}$, are needed. The parent-offspring matrix is defined as

$$\mathbf{H} = (\,\mathbf{p}_1' \quad \mathbf{p}_2' \quad \mathbf{p}_3'\,), \tag{A12}$$

where $\mathbf{p}_i'$ is the genotype frequency vector in the offspring of a parent of genotype i. We ignore mutations, so that the gene frequencies in the gametes are the same as the gene frequencies in the breeding population:

$$\mathbf{r}_i = \mathbf{q}_i, \tag{A13}$$

$$\mathbf{r}_{\mathrm{b}} = \mathbf{q}_{\mathrm{b}}. \tag{A14}$$

The offspring are formed by the random combination of gametes when a parent of genotype i mates with a member of the breeding population, so that

$$\mathbf{p}_i' = \mathbf{Z}(\mathbf{q}_i\otimes\mathbf{q}_{\mathrm{b}}), \tag{A15}$$

where $\mathbf{q}_i$ and $\mathbf{q}_{\mathrm{b}}$ are respectively the vector of gene frequencies in gametes of genotype i and the vector of gene frequencies in gametes of the entire breeding population. The matrix $\mathbf{Z}$ is

$$\mathbf{Z} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}. \tag{A16}$$

The three genotypes have the following gene-frequency vectors:

$$\mathbf{q}_{AA} = \begin{bmatrix} 1 \\ 0 \end{bmatrix} \quad \mathbf{q}_{Aa} = \begin{bmatrix} \frac{1}{2} \\ \frac{1}{2} \end{bmatrix} \quad \mathbf{q}_{AA} = \begin{bmatrix} 0 \\ 1 \end{bmatrix}. \tag{A17}$$

We denote the entries of $\mathbf{q}_{\mathrm{b}}$, the vector of gene frequencies in gametes of the entire breeding population, as

$$\mathbf{q}_{\mathrm{b}} = \begin{bmatrix} q_A^{\mathrm{b}} \\ q_a^{\mathrm{b}} \end{bmatrix}. \tag{A18}$$

Finally, substituting $\mathbf{Z}$ and $\mathbf{q}_{AA}$ into equation (A17) for $i = 1$ yields

$$\mathbf{p}_1' = \mathbf{Z}(\mathbf{r}_1\otimes\mathbf{r}_{\mathrm{b}}) = \begin{bmatrix} q_A^{\mathrm{b}} \\ q_a^{\mathrm{b}} \\ 0 \end{bmatrix}. \tag{A19}$$

Similarly, $\mathbf{p}_2'$ and $\mathbf{p}_3'$ can be expressed in terms of the parental genotype frequencies; this yields the following matrix **H**:

$$\mathbf{H} = \begin{bmatrix} q_A^{\mathrm{b}} & \frac{1}{2}q_A^{\mathrm{b}} & 0 \\ q_a^{\mathrm{b}} & \frac{1}{2} & q_A^{\mathrm{b}} \\ 0 & \frac{1}{2}q_a^{\mathrm{b}} & q_a^{\mathrm{b}} \end{bmatrix}. \tag{A20}$$

The final step is to substitute the above expression for **H** into equation (A11), which yields

$$\tilde{\mathbf{F}}(\tilde{\mathbf{p}}) = \left[\begin{array}{c|c|c} q_A^{\mathrm{b}}\mathbf{F}_{AA} & \frac{1}{2}q_A^{\mathrm{b}}\mathbf{F}_{Aa} & \mathbf{0} \\ \hline q_a^{\mathrm{b}}\mathbf{F}_{AA} & \frac{1}{2}\mathbf{F}_{Aa} & q_A^{\mathrm{b}}\mathbf{F}_{aa} \\ \hline \mathbf{0} & \frac{1}{2}q_a^{\mathrm{b}}\mathbf{F}_{Aa} & q_a^{\mathrm{b}}\mathbf{F}_{aa} \end{array}\right]. \tag{A21}$$

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Appendix B from C. de Vries and H. Caswell, "Stage-Structured Evolutionary Demography: Linking Life Histories, Population Genetics, and Ecological Dynamics"
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Coexistence Conditions

In this appendix, we will derive the linearization of the model defined by the transition matrix (28) at the boundary equilibria and prove that the eigenvalues of the Jacobian matrix $\mathbf{M}$ are given by theorem 1.

Linear Demography, Any Number of Reproducing Stages

We consider first the general case, in which demography is described by an age- or stage-structured life cycle with any number of reproducing stages. We assume that the demographic component of the model is linear (nonlinear demography will be considered elsewhere). The dynamics of the population frequency vector are

$$\tilde{\mathbf{p}}(t+1) = \frac{\tilde{\mathbf{A}}(\tilde{\mathbf{p}}(t))\tilde{\mathbf{p}}(t)}{\|\tilde{\mathbf{A}}(\tilde{\mathbf{p}}(t))\tilde{\mathbf{p}}(t)\|}, \tag{B1}$$

where $\|\mathbf{a}\|$ indicates the 1-norm of the vector $\mathbf{a}$, defined as the sum of the absolute values of the entries of the vector $\mathbf{a}$. The matrix $\tilde{\mathbf{A}}$ is given by equation (32):

$$\tilde{\mathbf{A}}(\tilde{\mathbf{p}}) = \left[\begin{array}{c|c|c} \mathbf{U}_{AA} + q_A^{\mathrm{b}}\mathbf{F}_{AA} & \frac{1}{2}q_A^{\mathrm{b}}\mathbf{F}_{Aa} & \mathbf{0} \\ \hline q_a^{\mathrm{b}}\mathbf{F}_{AA} & \mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa} & q_A^{\mathrm{b}}\mathbf{F}_{aa} \\ \hline \mathbf{0} & \frac{1}{2}q_a^{\mathrm{b}}\mathbf{F}_{Aa} & \mathbf{U}_{aa} + q_a^{\mathrm{b}}\mathbf{F}_{aa} \end{array}\right]. \tag{B2}$$

An equilibrium solution, $\hat{\mathbf{p}}$, must satisfy

$$\hat{\mathbf{p}} = \frac{\tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}}}{\mathbf{1}_{g\omega}^{\mathsf{T}}\tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}}}, \tag{B3}$$

where the 1-norm can be replaced by $\mathbf{1}_{g\omega}^{\mathsf{T}}\tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}}$ because $\tilde{\mathbf{p}}$ is nonnegative.

The Jacobian matrix at an equilibrium $\hat{\mathbf{p}}$ is

$$\mathbf{M} = \left.\frac{d\tilde{\mathbf{p}}(t+1)}{d\tilde{\mathbf{p}}^{\mathsf{T}}(t)}\right|_{\hat{\mathbf{p}}}. \tag{B4}$$

This differentiation is carried out using matrix calculus; for details on the methodology, see Magnus and Neudecker (1985, 1988); for ecological presentations, see Caswell (2007, 2008, 2019). Matrix calculus makes extensive use of the vec operator, which stacks the columns of a matrix; for example,

$$\operatorname{vec}\begin{bmatrix} a & b \\ c & d \end{bmatrix} = \begin{bmatrix} a \\ c \\ b \\ d \end{bmatrix}. \tag{B5}$$

It also makes extensive use of the fact that

$$\operatorname{vec}\mathbf{ABC} = (\mathbf{C}^{\mathsf{T}} \otimes \mathbf{A})\operatorname{vec}\mathbf{B} \tag{B6}$$

for any conformable matrices $\mathbf{A}$, $\mathbf{B}$, and $\mathbf{C}$, where $\otimes$ is the Kronecker product.

For notational convenience, define a matrix **B** as

$$\mathbf{B}(\tilde{\mathbf{p}}) = \frac{\tilde{\mathbf{A}}(\tilde{\mathbf{p}})}{\mathbf{1}^{\top}_{g\omega}\tilde{\mathbf{A}}(\tilde{\mathbf{p}})\tilde{\mathbf{p}}}, \tag{B7}$$

so that

$$\tilde{\mathbf{p}}(t+1) = \mathbf{B}(\tilde{\mathbf{p}}(t))\tilde{\mathbf{p}}(t). \tag{B8}$$

Differentiate equation (B8) to obtain

$$\mathrm{d}\tilde{\mathbf{p}}(t+1) = \mathbf{B}\mathrm{d}\tilde{\mathbf{p}}(t) + (\mathrm{d}\tilde{\mathbf{B}})\tilde{\mathbf{p}}(t), \tag{B9}$$

where the explicit dependence of **B** on $\tilde{\mathbf{p}}$ has been omitted to avoid a cluttering of brackets. Apply the vec operator to both sides, to obtain

$$\mathrm{d}\tilde{\mathbf{p}}(t+1) = \mathbf{B}\mathrm{d}\tilde{\mathbf{p}}(t) + (\tilde{\mathbf{p}}^{\top}(t)\otimes\mathbf{I}_{\omega g})\mathrm{d}\mathrm{vec}\mathbf{B}. \tag{B10}$$

Thus,

$$\mathbf{M} = \left.\frac{\mathrm{d}\tilde{\mathbf{p}}(t+1)}{\mathrm{d}\tilde{\mathbf{p}}(t)}\right|_{\hat{\mathbf{p}}} \tag{B11}$$

$$= \mathbf{B}(\hat{\mathbf{p}}) + (\hat{\mathbf{p}}^{\top}\otimes\mathbf{I}_{\omega g})\left.\frac{\partial\mathrm{vec}\mathbf{B}(\mathbf{p})}{\partial\tilde{\mathbf{p}}^{\top}}\right|_{\hat{\mathbf{p}}} \tag{B12}$$

(Verdy and Caswell 2008).

We will express the Jacobian matrix **M** in terms of the genotype-specific matrices, $\mathbf{U}_i$ and $\mathbf{F}_i$; the genotype-specific growth rates; and the boundary equilibrium population structures. We choose to analyze the Jacobian at the *AA* boundary; the expression at the *aa* boundary can be derived afterward by symmetry.

We define the scalar function $f(\tilde{\mathbf{p}})$ as

$$f(\tilde{\mathbf{p}}) = \frac{1}{\mathbf{1}^{\top}_{\omega g}\tilde{\mathbf{A}}(\tilde{\mathbf{p}})\tilde{\mathbf{p}}} \tag{B13}$$

so that

$$\mathbf{B}(\tilde{\mathbf{p}}) = f(\tilde{\mathbf{p}})\tilde{\mathbf{A}}(\tilde{\mathbf{p}}). \tag{B14}$$

Where it does not create confusion, we will drop the explicit dependence of $\tilde{\mathbf{A}}$, **B**, and f on $\tilde{\mathbf{p}}$. Differentiate equation (B14) and take the vec of both sides to obtain

$$\mathrm{d}\mathrm{vec}\mathbf{B} = \mathrm{vec}\tilde{\mathbf{A}}(\mathrm{d}f) + f\mathrm{d}\mathrm{vec}\tilde{\mathbf{A}}, \tag{B15}$$

or

$$\frac{\partial\mathrm{vec}\mathbf{B}}{\partial\tilde{\mathbf{p}}^{\top}} = \mathrm{vec}\tilde{\mathbf{A}}\frac{\partial f}{\partial\tilde{\mathbf{p}}^{\top}} + f(\tilde{\mathbf{p}})\frac{\partial\mathrm{vec}\tilde{\mathbf{A}}}{\partial\tilde{\mathbf{p}}^{\top}}. \tag{B16}$$

Differentiating f in equation (B13) gives

$$\mathrm{d}f = \frac{-1}{(\mathbf{1}^{\top}_{\omega g}\tilde{\mathbf{A}}(\tilde{\mathbf{p}})\tilde{\mathbf{p}})^2}[\mathbf{1}^{\top}_{\omega g}(\mathrm{d}\tilde{\mathbf{A}})\tilde{\mathbf{p}} + \mathbf{1}^{\top}_{\omega g}\tilde{\mathbf{A}}\mathrm{d}\tilde{\mathbf{p}}]. \tag{B17}$$

At the AA boundary, $\tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}} = \lambda_{AA}\hat{\mathbf{p}}$, and therefore

$$\mathbf{1}_{\omega g}^{\top}\tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}} = \lambda_{AA}. \tag{B18}$$

Evaluate the differential of f at the boundary and use equation (B18) to obtain

$$\mathrm{d}f = \frac{-1}{\lambda_{AA}^2}\left[\mathbf{1}_{\omega g}^{\top}(\mathrm{d}\tilde{\mathbf{A}})\hat{\mathbf{p}} + \mathbf{1}_{\omega g}^{\top}\tilde{\mathbf{A}}\mathrm{d}\tilde{\mathbf{p}}\right]. \tag{B19}$$

The first term in this sum, $\mathbf{1}_{\omega g}^{\top}(\mathrm{d}\tilde{\mathbf{A}})\hat{\mathbf{p}}$, equals zero when evaluated at the boundary. To see this, recall that the population vector at the AA boundary is

$$\hat{\mathbf{p}} = \begin{bmatrix} \hat{\mathbf{p}}_{AA} \\ 0 \\ 0 \end{bmatrix}. \tag{B20}$$

The last two block columns of the matrix $\mathrm{d}\tilde{\mathbf{A}}$ are therefore multiplied by zero, yielding

$$\mathbf{1}_{\omega g}^{\top}(\mathrm{d}\tilde{\mathbf{A}})\hat{\mathbf{p}} = \mathbf{1}_{\omega}^{\top}\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}(\mathrm{d}q_A^{\mathrm{b}} + \mathrm{d}q_a^{\mathrm{b}}) \tag{B21}$$

$$= 0, \tag{B22}$$

because

$$q_a^{\mathrm{b}} + q_A^{\mathrm{b}} = 1, \tag{B23}$$

$$\mathrm{d}q_a^{\mathrm{b}} + \mathrm{d}q_A^{\mathrm{b}} = 0. \tag{B24}$$

Substituting equation (B19) into equation (B15) and evaluating at the boundary yields

$$\mathrm{dvec}\mathbf{B} = \frac{-1}{\lambda_{AA}^2}\mathrm{vec}\tilde{\mathbf{A}}[\mathbf{1}_{\omega g}^{\top}\tilde{\mathbf{A}}\mathrm{d}\tilde{\mathbf{p}}] + \frac{1}{\lambda_{AA}}\mathrm{dvec}\tilde{\mathbf{A}}, \tag{B25}$$

or

$$\left.\frac{\partial\mathrm{vec}\mathbf{B}}{\partial\tilde{\mathbf{p}}^{\top}}\right|_{\hat{\mathbf{p}}} = \frac{-1}{\lambda_{AA}^2}(\mathrm{vec}\tilde{\mathbf{A}})(\mathbf{1}_{\omega g}^{\top}\tilde{\mathbf{A}}) + \frac{1}{\lambda_{AA}}\left.\frac{\partial\mathrm{vec}\tilde{\mathbf{A}}}{\partial\tilde{\mathbf{p}}^{\top}}\right|_{\hat{\mathbf{p}}}. \tag{B26}$$

Finally, substituting the expression above into equation (B12) yields an expression for the Jacobian matrix:

$$\mathbf{M} = \mathbf{B}(\hat{\mathbf{p}}) + (\hat{\mathbf{p}}^{\top}\otimes\mathbf{I}_{\omega g})\left.\frac{\partial\mathrm{vec}\mathbf{B}}{\partial\tilde{\mathbf{p}}^{\top}}\right|_{\hat{\mathbf{p}}} \tag{B27}$$

$$= \underbrace{\mathbf{B}(\hat{\mathbf{p}})}_{Ⓐ} \underbrace{- \frac{1}{\lambda_{AA}^2}(\hat{\mathbf{p}}^{\top}\otimes\mathbf{I}_{\omega g})(\mathrm{vec}\tilde{\mathbf{A}})(\mathbf{1}_{\omega g}^{\top}\tilde{\mathbf{A}})}_{Ⓑ} + \underbrace{\frac{1}{\lambda_{AA}}(\hat{\mathbf{p}}^{\top}\otimes\mathbf{I}_{\omega g})\left.\frac{\partial\mathrm{vec}\tilde{\mathbf{A}}}{\partial\tilde{\mathbf{p}}^{\top}}\right|_{\hat{\mathbf{p}}}}_{Ⓒ}, \tag{B28}$$

where we have identified the three terms as Ⓐ, Ⓑ, and Ⓒ. We address each of these in turn.

Derivation of Term Ⓐ

Evaluating $\mathbf{B}(\hat{\mathbf{p}})$ from equation (B14), we find that

$$\mathbf{B}(\hat{\mathbf{p}}) = \frac{1}{\lambda_{AA}} \left[\begin{array}{c|c|c} \mathbf{U}_{AA} + \mathbf{F}_{AA} & \frac{1}{2}\mathbf{F}_{Aa} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa} & \mathbf{F}_{aa} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa} \end{array} \right]. \tag{B29}$$

Derivation of Term Ⓑ

This term is given by

$$Ⓑ = -\frac{1}{\lambda_{AA}^2} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{\omega g})(\mathrm{vec}\tilde{\mathbf{A}})(\mathbf{1}_{\omega g}^\top \tilde{\mathbf{A}}). \tag{B30}$$

Using Roth's theorem, this simplifies to

$$\begin{aligned} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{\omega g})\mathrm{vec}(\tilde{\mathbf{A}}(\hat{\mathbf{p}})) &= \mathrm{vec}(\mathbf{I}_{\omega g}\tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}}) \\ &= \lambda_{AA}\hat{\mathbf{p}}, \end{aligned} \tag{B31}$$

so that

$$Ⓑ = -\frac{1}{\lambda_{AA}} \hat{\mathbf{p}}(\mathbf{1}_{\omega g}^\top \tilde{\mathbf{A}}(\hat{\mathbf{p}})). \tag{B32}$$

Substituting $\hat{\mathbf{p}}$ from equation (B20) into equation (B32) and writing the result in terms of the block matrices yields

$$Ⓑ = -\frac{1}{\lambda_{AA}} \left[\begin{array}{c|c|c} \hat{\mathbf{p}}_{AA} \otimes \mathbf{1}_\omega^\top (\mathbf{U}_{AA} + \mathbf{F}_{AA}) & \hat{\mathbf{p}}_{AA} \otimes \mathbf{1}_\omega^\top (\mathbf{U}_{Aa} + \mathbf{F}_{Aa}) & \hat{\mathbf{p}}_{AA} \otimes \mathbf{1}_\omega^\top (\mathbf{U}_{aa} + \mathbf{F}_{aa}) \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array} \right]. \tag{B33}$$

Derivation of Term ©

Term © requires the most elaborate derivation. We first derive a useful expression for $\mathrm{vec}\tilde{\mathbf{A}}$ in terms of its component block matrices. Recall that $\tilde{\mathbf{A}}$ can be decomposed into nine $\omega \times \omega$ block matrices, as in equation (32):

$$\tilde{\mathbf{A}}(\tilde{\mathbf{p}}) = \left[\begin{array}{c|c|c} \mathbf{U}_{AA} + \mathbf{F}_{AA}q_A^{\mathrm{b}} & \frac{1}{2}\mathbf{F}_{Aa}q_A^{\mathrm{b}} & \mathbf{0} \\ \hline \mathbf{F}_{AA}q_a^{\mathrm{b}} & \mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa} & \mathbf{F}_{aa}q_A^{\mathrm{b}} \\ \hline \mathbf{0} & \frac{1}{2}\mathbf{F}_{Aa}q_a^{\mathrm{b}} & \mathbf{U}_{aa} + \mathbf{F}_{aa}q_a^{\mathrm{b}} \end{array} \right]. \tag{B34}$$

Denote the blocks by $\mathbf{A}_{ij}$, so that $\tilde{\mathbf{A}}$ can be written as

$$\tilde{\mathbf{A}} = \sum_{i,j=1}^{3} \mathbf{E}_{ij} \otimes \mathbf{A}_{ij} \tag{B35}$$

$$= \sum_{i,j=1}^{3} (\mathbf{e}_i \mathbf{e}_j^\top) \otimes (\mathbf{A}_{ij} \mathbf{I}_\omega), \tag{B36}$$

where we have used the definition of the matrix $\mathbf{E}_{ij} = \mathbf{e}_i\mathbf{e}_j^\top$. Using the fact that $\mathbf{AC}\otimes\mathbf{BD} = (\mathbf{A}\otimes\mathbf{B})(\mathbf{C}\otimes\mathbf{D})$, equation (B36) can be rewritten as

$$\tilde{\mathbf{A}} = \sum_{i,j=1}^{3}(\mathbf{e}_i\otimes\mathbf{A}_{ij})(\mathbf{e}_j^\top\otimes\mathbf{I}_\omega). \tag{B37}$$

Next use the identity $\sum_i(\mathbf{e}_i\otimes\mathbf{I}_\omega)\mathbf{A}_{ij} = \sum_i\mathbf{e}_i\otimes\mathbf{A}_{ij}$ to write

$$\tilde{\mathbf{A}} = \sum_{i,j=1}^{3}(\mathbf{e}_i\otimes\mathbf{I}_\omega)\mathbf{A}_{ij}(\mathbf{e}_j^\top\otimes\mathbf{I}_\omega) \tag{B38}$$

and apply the vec operator to obtain

$$\mathrm{vec}\tilde{\mathbf{A}} = \sum_{i,j=1}^{3}(\mathbf{e}_j\otimes\mathbf{I}_\omega)\otimes(\mathbf{e}_i\otimes\mathbf{I}_\omega)\mathrm{vec}\mathbf{A}_{ij}. \tag{B39}$$

Armed with this expression for vec**A**, we analyze term © in the Jacobian. Replace the derivative of vec**A** with equation (B39), such that

$$\frac{1}{\lambda_{AA}}(\hat{\mathbf{p}}^\top\otimes\mathbf{I}_{\omega g})\frac{\partial\mathrm{vec}\mathbf{A}}{\partial\tilde{\mathbf{p}}^\top} = \frac{1}{\lambda_{AA}}\sum_{i,j=1}^{3}(\hat{\mathbf{p}}^\top\otimes\mathbf{I}_{\omega g})[(\mathbf{e}_j\otimes\mathbf{I}_\omega)\otimes(\mathbf{e}_i\otimes\mathbf{I}_\omega)]\frac{\partial\mathrm{vec}\mathbf{A}_{ij}}{\partial\tilde{\mathbf{p}}^\top}, \tag{B40}$$

where all derivatives are evaluated at $\hat{\mathbf{p}}$. Use $(\mathbf{A}\otimes\mathbf{B})(\mathbf{C}\otimes\mathbf{D}) = \mathbf{AC}\otimes\mathbf{BD}$ to rewrite

$$(\hat{\mathbf{p}}^\top\otimes\mathbf{I}_{\omega g})[(\mathbf{e}_j\otimes\mathbf{I}_\omega)\otimes(\mathbf{e}_i\otimes\mathbf{I}_\omega)] = [\hat{\mathbf{p}}^\top(\mathbf{e}_j\otimes\mathbf{I}_\omega)]\otimes[\mathbf{I}_{\omega g}(\mathbf{e}_i\otimes\mathbf{I}_\omega)]. \tag{B41}$$

Substituting this expression into the right-hand side of equation (B40) yields

$$\frac{1}{\lambda_{AA}}(\hat{\mathbf{p}}^\top\otimes\mathbf{I}_{\omega g})\frac{\partial\mathrm{vec}\mathbf{A}}{\partial\tilde{\mathbf{p}}^\top} = \frac{1}{\lambda_{AA}}\sum_{i,j=1}^{3}[\hat{\mathbf{p}}^\top(\mathbf{e}_j\otimes\mathbf{I}_\omega)]\otimes[\mathbf{I}_{\omega g}(\mathbf{e}_i\otimes\mathbf{I}_\omega)]\frac{\partial\mathrm{vec}\mathbf{A}_{ij}}{\partial\tilde{\mathbf{p}}^\top}. \tag{B42}$$

Substitute $\hat{\mathbf{p}}^\top = (\hat{\mathbf{p}}_{AA}^\top, \mathbf{0}, \mathbf{0})$ into the right-hand side of equation (B42), so that only terms with $j = 1$ are nonzero, yielding

$$\frac{1}{\lambda_{AA}}(\hat{\mathbf{p}}^\top\otimes\mathbf{I}_{\omega g})\frac{\partial\mathrm{vec}\mathbf{A}}{\partial\tilde{\mathbf{p}}^\top} = \frac{1}{\lambda_{AA}}\sum_{i=1}^{3}[\hat{\mathbf{p}}_{AA}^\top\otimes(\mathbf{e}_i\otimes\mathbf{I}_\omega)]\frac{\partial\mathrm{vec}\mathbf{A}_{i1}}{\partial\tilde{\mathbf{p}}^\top}. \tag{B43}$$

Write down each term in the sum over i and take the derivative of $\mathrm{vec}\mathbf{A}_{11} = \mathrm{vec}(\mathbf{U}_{AA} + q_A^{\mathrm{b}}\mathbf{F}_{AA})$ and $\mathrm{vec}\mathbf{A}_{21} = \mathrm{vec}(q_a^{\mathrm{b}}\mathbf{F}_{AA})$ to obtain

$$\frac{1}{\lambda_{AA}}(\hat{\mathbf{p}}^\top\otimes\mathbf{I}_{\omega g})\frac{\partial\mathrm{vec}\mathbf{A}}{\partial\tilde{\mathbf{p}}^\top} = \frac{1}{\lambda_{AA}}[\hat{\mathbf{p}}_{AA}^\top\otimes(\mathbf{e}_1\otimes\mathbf{I}_\omega) - \hat{\mathbf{p}}_{AA}^\top\otimes(\mathbf{e}_2\otimes\mathbf{I}_\omega)]\mathrm{vec}(\mathbf{F}_{AA})\frac{\partial q_A^{\mathrm{b}}}{\partial\tilde{\mathbf{p}}^\top}. \tag{B44}$$

Finally, apply Roth's (1934) theorem, $(\mathbf{C}^\top\otimes\mathbf{A})\mathrm{vec}\mathbf{B} = \mathrm{vec}\mathbf{ABC}$, to the equation above (with $\mathbf{C}^\top = \hat{\mathbf{p}}_{AA}^\top$, $\mathbf{A} = (\mathbf{e}_1\otimes\mathbf{I}_\omega)$, and $\mathrm{vec}\mathbf{B} = \mathrm{vec}\mathbf{F}_{AA}$) to write

$$\frac{1}{\lambda_{AA}}(\hat{\mathbf{p}}^\top\otimes\mathbf{I}_{\omega g})\frac{\partial\mathrm{vec}\mathbf{A}}{\partial\tilde{\mathbf{p}}^\top} = \frac{1}{\lambda_{AA}}[\mathrm{vec}((\mathbf{e}_1\otimes\mathbf{I}_\omega)\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) - \mathrm{vec}((\mathbf{e}_2\otimes\mathbf{I}_\omega)\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})]\frac{\partial q_A^{\mathrm{b}}}{\partial\tilde{\mathbf{p}}^\top}, \tag{B45}$$

where throughout all derivatives are evaluated at $\hat{\mathbf{p}}$. Written in terms of block matrices, this expression yields

$$\frac{1}{\lambda_{AA}}(\hat{\mathbf{p}}^{\top}\otimes\mathbf{I}_{\omega g})\frac{\partial\text{vec}\mathbf{A}}{\partial\tilde{\mathbf{p}}^{\top}} =$$

$$\frac{1}{\lambda_{AA}}\left[\begin{array}{c|c|c} (\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\dfrac{\partial q_A^{\mathrm{b}}}{\partial\mathbf{p}_{AA}^{\top}} & (\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\dfrac{\partial q_A^{\mathrm{b}}}{\partial\mathbf{p}_{Aa}^{\top}} & (\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\dfrac{\partial q_A^{\mathrm{b}}}{\partial\mathbf{p}_{aa}^{\top}} \\ \hline -(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\dfrac{\partial q_A^{\mathrm{b}}}{\partial\mathbf{p}_{AA}^{\top}} & -(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\dfrac{\partial q_A^{\mathrm{b}}}{\partial\mathbf{p}_{Aa}^{\top}} & -(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\dfrac{\partial q_A^{\mathrm{b}}}{\partial\mathbf{p}_{aa}^{\top}} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array}\right]. \tag{B46}$$

Equation (B46) requires the derivative of the frequency of allele A in the gamete pool with respect to the population frequency vector:

$$\frac{\partial q_A^{\mathrm{b}}}{\partial\tilde{\mathbf{p}}^{\top}}. \tag{B47}$$

Differentiating equation (11),

$$q_A^{\mathrm{b}} = \mathbf{e}_1^{\top}\mathbf{q}_{\mathrm{b}} = \mathbf{e}_1^{\top}\mathbf{W}\mathbf{p}_{\mathrm{b}}, \tag{B48}$$

yields

$$\frac{\partial q_A^{\mathrm{b}}}{\partial\tilde{\mathbf{p}}^{\top}} = \mathbf{e}_1^{\top}\mathbf{W}\frac{\partial\mathbf{p}_{\mathrm{b}}}{\partial\tilde{\mathbf{p}}^{\top}}. \tag{B49}$$

Combine equations (5) and (7) to write

$$\mathbf{p}_{\mathrm{b}} = \frac{\sum_{i=1}^{g}(\mathbf{E}_{ii}\otimes\mathbf{c}_i^{\top})\tilde{\mathbf{p}}}{\sum_{j=1}^{g}(\mathbf{e}_j^{\top}\otimes\mathbf{c}_j^{\top})\tilde{\mathbf{p}}}, \tag{B50}$$

where we can substitute $\tilde{\mathbf{p}}$ for $\tilde{\mathbf{n}}$ because of homogeneity. The denominator gives the fraction of individuals in the total population that are in a breeding stage:

$$\sum_{j=1}^{g}(\mathbf{e}_j^{\top}\otimes\mathbf{c}_j^{\top})\tilde{\mathbf{p}} = p_{\mathrm{b}}. \tag{B51}$$

Taking the derivative of $\mathbf{p}_{\mathrm{b}}$ yields

$$\left.\frac{\partial\mathbf{p}_{\mathrm{b}}}{\partial\tilde{\mathbf{p}}^{\top}}\right|_{\hat{\mathbf{p}}} = \frac{p_{\mathrm{b}}\sum_{i=1}^{3}(\mathbf{E}_{ii}\otimes\mathbf{c}_i^{\top}) - \sum_{i=1}^{3}(\mathbf{E}_{ii}\otimes\mathbf{c}_i^{\top})\hat{\mathbf{p}}\sum_{j=1}^{3}(\mathbf{e}_j^{\top}\otimes\mathbf{c}_j^{\top})}{\mathrm{p}_{\mathrm{b}}^2}. \tag{B52}$$

Writing the above expression as a matrix yields

$$\left.\frac{\partial\mathbf{p}_{\mathrm{b}}}{\partial\tilde{\mathbf{p}}^{\top}}\right|_{\hat{\mathbf{p}}} = \frac{1}{p_{\mathrm{b}}}\begin{bmatrix} \mathbf{0} & -\mathbf{c}_{Aa}^{\top} & -\mathbf{c}_{aa}^{\top} \\ \mathbf{0}_{\omega}^{\top} & \mathbf{c}_{Aa}^{\top} & \mathbf{0}_{\omega}^{\top} \\ \mathbf{0}_{\omega}^{\top} & \mathbf{0}_{\omega}^{\top} & \mathbf{c}_{aa}^{\top} \end{bmatrix}. \tag{B53}$$

Substituting equation (B53) into equation (B49) leads to

$$\left.\frac{\partial q^{\mathrm{b}_A}}{\partial\tilde{\mathbf{p}}^{\top}}\right|_{\hat{\mathbf{p}}} = \mathbf{e}_1^{\top}\mathbf{W}\left.\frac{\partial\mathbf{p}_{\mathrm{b}}}{\partial\tilde{\mathbf{p}}^{\top}}\right|_{\hat{\mathbf{p}}} \tag{B54}$$

$$= \begin{bmatrix} \mathbf{0} & -\frac{1}{2}\frac{\mathbf{c}_{Aa}^{\top}}{p_{\mathrm{b}}} & -\frac{\mathbf{c}_{aa}^{\top}}{p_{\mathrm{b}}} \end{bmatrix}. \tag{B55}$$

Finally, plugging equation (B55) into (B46) yields

$$\frac{1}{\lambda_{AA}}(\hat{\mathbf{p}}^{\top}\otimes\mathbf{I}_{\omega g})\frac{\partial\mathrm{vec}\mathbf{A}}{\partial\tilde{\mathbf{p}}^{\top}}\bigg|_{\hat{\mathbf{p}}} = \frac{1}{\lambda_{AA}}\left[\begin{array}{c|c|c} \mathbf{0} & -\frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{Aa}^{\top} & -\frac{1}{p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{aa}^{\top} \\ \hline \mathbf{0} & \frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{Aa}^{\top} & \frac{1}{p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{aa}^{\top} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array}\right]. \tag{B56}$$

The Jacobian Matrix

Combining the terms by substituting equations (B29), (B33), and (B56) into equation (B28), we obtain the Jacobian:

$$\begin{aligned} \mathbf{M} = {} & \frac{1}{\lambda_{AA}}\left[\begin{array}{c|c|c} \mathbf{U}_{AA}+\mathbf{F}_{AA} & \frac{1}{2}\mathbf{F}_{Aa} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{U}_{Aa}+\frac{1}{2}\mathbf{F}_{Aa} & \mathbf{F}_{aa} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa} \end{array}\right] \\ & -\frac{1}{\lambda_{AA}}\left[\begin{array}{c|c|c} \hat{\mathbf{p}}_{AA}\otimes\mathbf{1}_{\omega}^{\top}(\mathbf{U}_{AA}+\mathbf{F}_{AA}) & \hat{\mathbf{p}}_{AA}\otimes\mathbf{1}_{\omega}^{\top}(\mathbf{U}_{Aa}+\mathbf{F}_{Aa}) & \hat{\mathbf{p}}_{AA}\otimes\mathbf{1}_{\omega}^{\top}(\mathbf{U}_{aa}+\mathbf{F}_{aa}) \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array}\right] \\ & +\frac{1}{\lambda_{AA}}\left[\begin{array}{c|c|c} \mathbf{0} & -\frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{Aa}^{\top} & -\frac{1}{p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{aa}^{\top} \\ \hline \mathbf{0} & \frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{Aa}^{\top} & \frac{1}{p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{aa}^{\top} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array}\right]. \end{aligned} \tag{B57}$$

Eigenvalues of the Jacobian

The Jacobian matrix, given by equation (B57), is upper block triangular, so the eigenvalues of $\mathbf{M}$ are the eigenvalues of the diagonal blocks:

$$\mathbf{M}_{11} = \frac{1}{\lambda_{AA}}(\mathbf{U}_{AA}+\mathbf{F}_{AA}-\hat{\mathbf{p}}_{AA}\otimes\mathbf{1}_{s}^{\top}(\mathbf{U}_{AA}+\mathbf{F}_{AA})), \tag{B58}$$

$$\mathbf{M}_{22} = \frac{1}{\lambda_{AA}}\left(\mathbf{U}_{Aa}+\frac{1}{2}\mathbf{F}_{Aa}+\frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{Aa}^{\top}\right), \tag{B59}$$

$$\mathbf{M}_{33} = \frac{1}{\lambda_{AA}}\mathbf{U}_{aa}. \tag{B60}$$

The largest absolute eigenvalue of the Jacobian, that is, the spectral radius $\rho(\mathbf{M})$, determines the stability of the boundary equilibrium. The block $\mathbf{M}_{11}$ projects perturbations within the *AA* boundary, and because $\hat{\mathbf{p}}$ is stable to perturbations in that boundary, $\rho(\mathbf{M}_{11}) < 1$. Block $\mathbf{M}_{33}$ projects perturbations in the *aa* direction. In the neighborhood of the *AA* equilibrium, *aa* homozygotes are negligibly rare, and thus $\mathbf{M}_{33}$ normally does not determine the stability of $\mathbf{M}$. An exception occurs when $\lambda_{AA} < \rho(\mathbf{U}_{aa}) < 1$. That is, if the *AA* population is declining sufficiently rapidly, the *aa* homozygote may increase in frequency simply by declining to extinction more slowly. If the homozygous *AA* population is stable or increasing, so that $\lambda_{AA} \geq 1$, this cannot happen. Similarly, if $\mathbf{U}_{aa}$ is age classified with a maximum age, $\rho(\mathbf{U}_{aa}) = 0$, and the phenomenon can not happen. We neglect this pathological case in our discussions.

We thus focus our stability analysis on growth in the *Aa* direction, which means we focus on the middle block:

$$\mathbf{M}_{22} = \frac{1}{\lambda_{AA}}\left(\mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa} + \frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{Aa}^{\top}\right). \tag{B61}$$

The largest absolute value of the eigenvalues of this matrix, the dominant eigenvalue, evaluated at the *AA* boundary, denoted by ζ_{AA}, is

$$\zeta_{AA} = \frac{1}{\lambda_{AA}}\rho\left(\mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa} + \frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{Aa}^{\top}\right). \tag{B62}$$

By symmetry, at the *aa* boundary

$$\zeta_{aa} = \frac{1}{\lambda_{aa}}\rho\left(\mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa} + \frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{aa}\hat{\mathbf{p}}_{\alpha\alpha})\otimes\mathbf{c}_{Aa}^{\top}\right). \tag{B63}$$

If both boundaries are unstable, then both alleles will coexist. The coexistence conditions are therefore given by

$$\rho\left(\mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa} + \frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{Aa}^{\top}\right) > \lambda_{AA}, \tag{B64}$$

$$\rho\left(\mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa} + \frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa})\otimes\mathbf{c}_{Aa}^{\top}\right) > \lambda_{aa}. \tag{B65}$$

This completes the derivation of theorem 1.

Special Case: A Single Reproducing Stage

Corollary 1 uses the eigenvalues ζ_{AA} and ζ_{aa} for the special case in which the life cycle contains only a single breeding stage but with no restrictions on the newborn and juvenile stages.

Our goal is to simplify the final term in the expressions for ζ_{AA} and ζ_{aa} by showing that

$$\frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{c}_{Aa}^{\top} = \frac{1}{2}\mathbf{F}_{AA}, \tag{B66}$$

$$\frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa})\otimes\mathbf{c}_{Aa}^{\top} = \frac{1}{2}\mathbf{F}_{aa}. \tag{B67}$$

Without loss of generality, let the reproducing stage be the last stage, stage ω, for all three genotypes. Then $\mathbf{c}_i = \mathbf{c} = \mathbf{e}_\omega$, $\hat{\mathbf{p}}_{AA}(\omega) = p_{\mathrm{b}}$, and $\hat{\mathbf{p}}_{aa}(\omega) = p_{\mathrm{b}}$. The matrix $\mathbf{F}_{AA}$ has a single nonzero column, denoted by $\mathbf{f}_{AA}$, giving the production of the various types of offspring produced by the reproducing stage, that is,

$$\mathbf{F}_{AA} = [\,\mathbf{0} \quad \cdots \quad \mathbf{0} \quad \mathbf{f}_{AA}\,]. \tag{B68}$$

Thus,

$$\frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA})\otimes\mathbf{e}_{\omega}^{\top} = \frac{1}{2p_{\mathrm{b}}}p_{\mathrm{b}}\mathbf{f}_{AA}\otimes\mathbf{e}_{\omega}^{\top}, \tag{B69}$$

$$= \frac{1}{2}\mathbf{F}_{AA}. \tag{B70}$$

Likewise,

$$\frac{1}{2p_{\mathrm{b}}}(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa})\otimes\mathbf{e}_{\omega}^{\top} = \frac{1}{2p_{\mathrm{b}}}p_{\mathrm{b}}\mathbf{f}_{aa}\otimes\mathbf{e}_{\omega}^{\top}, \tag{B71}$$

$$= \frac{1}{2}\mathbf{F}_{aa}. \tag{B72}$$

Substituting equations (B70) and (B72) into ζ_{AA} and ζ_{aa} yields corollary 1.