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de Vries, C.

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Selection in two-sex stage-structured populations

Charlotte de Vries, Hal Caswell

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Abstract

The outcome of natural selection depends on the demographic processes of birth, death, and development. Here, we derive conditions for protected polymorphism in a population characterized by age- or stage-dependent demography with two sexes. We do so using a novel two-sex matrix population model including basic Mendelian genetics (one locus, two alleles, random mating). Selection may operate on survival, growth, or fertility, any or all of which may differ between the sexes. The model can therefore incorporate genes with arbitrary pleiotropic and sex-specific effects. Conditions for protected polymorphism are expressed in terms of the eigenvalues of the linearization of the model at the homozygote boundary equilibria. We show that in the absence of sexual dimorphism, polymorphism requires heterozygote superiority in the genotypic population growth rate. In the presence of sexual dimorphism, however, heterozygote superiority is not required; an inferior heterozygote may invade, reducing the population growth rate and even leading to extinction (so-called evolutionary suicide). Our model makes no assumptions about separation of time scales between ecological and evolutionary processes, and can thus be used to project sex \times stage \times genotype dynamics of eco-evolutionary processes. Empirical evidence that sexual dimorphism affects extinction risk is growing, yet sex differences are often ignored in evolutionary demography and in eco-evolutionary models. Our analysis highlights the importance of sexual dimorphism and suggest mechanisms by which an allele can be favored by selection, yet drive a population to extinction, as a result of the structure and interdependence of sex- and stage-specific processes.

3.1 Introduction

Among the core results of population genetics are the criteria that determine whether selection leads to fixation of one genetic type, or to coexistence of multiple types in a polymorphism. For viability selection, at a single locus, in discrete generation, random mating, diploid populations, heterozygote advantage in fitness is well known to be a necessary and sufficient condition for a stable polymorphism. However, it is equally well known that the world is populated by species with complex age- or stage-structured life cycles, subject to selection not only on viability but on sex- and stage-specific survival, growth, development, and fertility rates throughout those life cycles.

The original formulations included little of the ecological theatre that hosts the evolutionary play (Hutchinson 1965). Fitness in these models was a lumped parameter, tasked with encapsulating all the life cycle processes determining gene transmission from one generation to the next. Temporal variation, multiple niches, density dependence, and age structure were incorporated in due course (e.g., Giesel 1972; Lewontin and Krakauer 1973; Waples 1989; Levene 1953; MacArthur 1962; Roughgarden 1971, 1979; Charlesworth 1970, 1994; Takada and Nakajima 1992). Developments in quantitative genetics (e.g., Lande and Arnold 1983; Barfield et al. 2011; Coulson and Tuljapurkar 2008; Coulson et al. 2010) and adaptive dynamics (Metz et al. 1992; Diekmann 2004) have led to increased ecological realism but treat genetic processes differently from population genetics.

Much of this theory relies on an implicit or explicit separation of time scales, with ecology assumed to proceed quickly and evolution slowly. It is now recognized that these time scales are not always separated, leading to interest in what has been called ‘eco-evolutionary dynamics’ (Fussmann et al. 2007; Pelletier et al. 2009). Eco-evolutionary studies confront an interdependent set of problems. (1) Time scales: although it is traditional to speak of ecology as acting on short, and evolution on long time scales, some processes operate on the same time scale (e.g., antibiotic and pesticide resistance (Neve et al. 2014), adaptation to urban environments (Schilthuizen 2018)). This requires a model that explicitly incorporates both processes. (2) Sex structure: gene effects may be sex-specific, because of sexual dimorphism or because they affect processes that are specific to one sex (e.g., lactation by females, courtship behavior by males). This requires a model that distinguishes the two sexes. (3) Stage structure: complex life cycles require more elaborate i -state structures than age alone, to accommodate life history characteristics such as maturation, dormancy, dispersal, etc. Genes may have strongly stage-specific effects, and incorporating these requires a model with flexibility in the kinds of structure incorporated. (4) Pleiotropy: genes may affect survival, de-

velopment, fertility, and stage transitions, all in highly stage-specific ways. Such effects can only be incorporated in a model that explicitly incorporates all those processes. (5) Ecological dynamics: genotypic effects on the vital rates operate together with the ecological and demographic processes influencing those rates, including density effects, resource availability, interspecific interactions, and environmental stochasticity. This requires a model that can incorporate or simplify these effects at will.

In this paper, we derive sufficient conditions for a polymorphism in two-sex, stage-structured populations. In doing so, we develop a model that projects eco-evolutionary dynamics of the sex-stage-genotype structure of a population without requiring any assumptions about separation of ecological and evolutionary time scales. We have purposely chosen to keep the genetics simple (one locus, two alleles, random mating), but to make only minimal assumptions about the ecology and demography of the species.

This paper is organized as follows. First we present the sex \times stage \times genotype-classified model. We find sufficient conditions for polymorphism by linearizing this model on the homozygous boundaries of the state space, and contrast these conditions with conclusions based on genotype-specific growth rates. We present a hypothetical example that focuses on intra-locus sexual conflict. Finally, we examine special cases that reveal something about the roles of stage structure and sexual dimorphism.

3.2 A two-sex stage-structured genetic model

Individuals in the population are jointly classified by sex, stage $(1, \dots, \omega)$, and genotype $(1, \dots, g)$. Males and females of each genotype may differ in any demographic parameters; these differences among genotypes in stage- and sex-specific demography are raw material for selection.

We make the standard demographic assumption of female demographic dominance, i.e. that enough males are present to fertilize all the females, and the number of offspring produced in a mating is not affected by the stage or genotype (i.e. the i -state) of the male. This assumption could be relaxed by introducing a marriage function (Keyfitz 1972; Caswell and Weeks 1986; Schoen 1988; Shyu and Caswell 2018a), but this is beyond the scope of the current paper.

The vectors describing the population are listed in Table 3.1. All mathematical objects relating to males are distinguished by a prime (e.g., \mathbf{n}'). The matrix \mathbf{I}_k is the identity matrix of order k , the vector $\mathbf{1}_k$ is a $k \times 1$ vector of ones, \mathbf{e}_k is the k th unit vector, \mathbf{E}_{ij} is a matrix with 1 in the (i, j) entry and zeros elsewhere.

The Kronecker product is denoted \otimes and the vec operator stacks the columns of a matrix to form a vector.

Table 3.1: Mathematical notation. Dimensions are given where relevant.

Symbol	Definition	Dimension
a	Number of alleles (2)	
g	Number of genotypes (3)	
ω	Number of stages	
N	Total population size	
$\tilde{\mathbf{n}}$	Joint sex \times genotype \times stage vector	$2\omega g \times 1$
\mathbf{n}	Female stage \times genotype vector	$\omega g \times 1$
\mathbf{n}'	Male stage \times genotype vector	$\omega g \times 1$
$\tilde{\mathbf{p}}$	Joint sex \times genotype \times stage frequency vector	$2\omega g \times 1$
\mathbf{p}	Female stage \times genotype frequency vector	$\omega g \times 1$
\mathbf{p}'	Male stage \times genotype frequency vector	$\omega g \times 1$
\mathbf{q}_i	Gene frequency vector in genotype i	$a \times 1$
\mathbf{q}_b	Gene frequency vector in breeding population	$a \times 1$

The population vector at t is

$$\tilde{\mathbf{n}}(t) = \begin{pmatrix} \mathbf{n}(t) \\ \mathbf{n}'(t) \end{pmatrix} = \begin{pmatrix} \mathbf{n}_{AA}(t) \\ \mathbf{n}_{Aa}(t) \\ \mathbf{n}_{aa}(t) \\ \mathbf{n}'_{AA}(t) \\ \mathbf{n}'_{Aa}(t) \\ \mathbf{n}'_{aa}(t) \end{pmatrix}. \quad (3.1)$$

where, e.g., \mathbf{n}_{AA} and \mathbf{n}'_{AA} are the stage distribution vectors of females and males of genotype AA , respectively. The proportional population vector is

$$\tilde{\mathbf{p}}(t) = \frac{\tilde{\mathbf{n}}(t)}{\|\mathbf{n}(t)\|} = \begin{pmatrix} \mathbf{p}(t) \\ \mathbf{p}'(t) \end{pmatrix}, \quad (3.2)$$

where $\|\cdot\|$ is the 1-norm. The population vector $\tilde{\mathbf{n}}$ is projected from time t to $t+1$ by an *eco-evolutionary projection matrix* $\tilde{\mathbf{A}}[\tilde{\mathbf{n}}]$, so that

$$\tilde{\mathbf{n}}(t+1) = \tilde{\mathbf{A}}[\tilde{\mathbf{n}}(t)] \tilde{\mathbf{n}}(t). \quad (3.3)$$

The matrix $\tilde{\mathbf{A}}$ is a function of $\tilde{\mathbf{n}}$ because the production of genotypes at $t+1$ depends on genotype distributions at t .

The population projection matrix $\tilde{\mathbf{A}}$ is constructed from a set of matrices that capture the demographic processes for each sex and genotype:

\mathbf{U}_i	survival and transitions for females of genotype i	$i = 1, \dots, g$	$\omega \times \omega$
\mathbf{U}'_i	survival and transitions for males of genotype i	$i = 1, \dots, g$	$\omega \times \omega$
\mathbf{F}_i	fertility matrix for females of genotype i	$i = 1, \dots, g$	$\omega \times \omega$
\mathbf{F}'_i	stage-specific “mating success” matrix for males of genotype i	$i = 1, \dots, g$	$\omega \times \omega$

The \mathbf{F}_i contain stage-specific fertilities for females of genotype i . The matrices \mathbf{F}'_i determine the contribution by males of genotype i to the gamete pool, and therefore to zygotes in the next generation. A genotype that led to male sterility would result in $\mathbf{F}'_i = 0$.

In general these genotype- and sex-specific transition and fertility matrices, \mathbf{U}_i , \mathbf{U}'_i , \mathbf{F}_i , and \mathbf{F}'_i , could be linear or nonlinear, time-invariant or time varying, deterministic or stochastic, and may include dependence on environmental resources or interactions among species. In this paper we restrict attention to linear, time-invariant demography.

The model formally contains matrices describing the transitions of individuals among genotype classes (Caswell et al. 2018), but since individuals do not change genotype these are identity matrices.

We also define matrices $\mathbf{H}_i(\tilde{\mathbf{n}})$ for $i = 1, \dots, \omega$, of dimension $g \times g$, that assign the offspring of a mother in stage i to the genotypes. The (k, ℓ) entry of \mathbf{H}_i is the probability that the offspring of a genotype ℓ mother, of stage i , has genotype k . These probabilities depend on the mating frequencies. We assume that mating is random with respect to stage and genotype, and hence that the parent-offspring map is the same for all stages, i.e. $\mathbf{H}_i(\tilde{\mathbf{n}}) = \mathbf{H}(\tilde{\mathbf{n}})$. Assortative mating by stage would lead to differences among the \mathbf{H}_i .

The male contribution to reproduction

The number of offspring is determined by the female genotype, whereas the male genotype determines the contribution of its genes to zygotes in the next time step. We refer to this male contribution as male “mating success” but it may reflect a range of behavioural or physiological characteristics, such as courtship behavior, gamete production, or gamete viability. Males of each stage and genotype combination contribute differentially to a gamete pool. The allele frequencies in the male gamete pool are obtained from the male stage \times genotype vector:

$$\mathbf{W}'\mathbb{F}'\mathbf{p}' = \begin{pmatrix} \mathbf{1}_\omega^\top & \frac{1}{2}\mathbf{1}_\omega^\top & 0 \\ 0 & \frac{1}{2}\mathbf{1}_\omega^\top & \mathbf{1}_\omega^\top \end{pmatrix} \begin{pmatrix} \mathbf{F}'_{AA} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{F}'_{Aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{F}'_{aa} \end{pmatrix} \begin{pmatrix} \mathbf{p}'_{AA} \\ \mathbf{p}'_{Aa} \\ \mathbf{p}'_{aa} \end{pmatrix}. \quad (3.4)$$

The matrix \mathbb{F}' operates on the vector of male genotype frequencies to give the relative contributions of each genotype to the gamete pool. The matrix \mathbf{W}' converts these relative genotype contributions to allele numbers. Normalizing this vector gives the allele frequencies in the gamete pool,

$$\begin{pmatrix} q'_A \\ q'_a \end{pmatrix} = \frac{\mathbf{W}'\mathbb{F}'\mathbf{p}'}{\|\mathbf{W}'\mathbb{F}'\mathbf{p}'\|} = \frac{\mathbf{W}'\mathbb{F}'\mathbf{n}'}{\|\mathbf{W}'\mathbb{F}'\mathbf{n}'\|}. \quad (3.5)$$

These frequencies determine the distribution of genotypes in the offspring of a female of any genotype.

Genotype distributions in offspring; the matrix $\mathbf{H}(\mathbf{n})$

The matrix $\mathbf{H}(\tilde{\mathbf{n}})$ is given by

$$\mathbf{H}(\tilde{\mathbf{n}}) = \begin{pmatrix} q'_A & \frac{1}{2}q'_A & 0 \\ q'_a & \frac{1}{2} & q'_A \\ 0 & \frac{1}{2}q'_a & q'_a \end{pmatrix}. \quad (3.6)$$

The allele frequencies q'_A and q'_a are given in terms of either $\tilde{\mathbf{p}}$ or $\tilde{\mathbf{n}}$ by (3.5). The first column of $\mathbf{H}(\tilde{\mathbf{n}})$ contains the genotype distribution of the offspring of an AA mother; she produces an AA offspring with probability q'_A and an Aa offspring with probability q'_a . The second and third columns give the genotype distributions for mothers of genotypes Aa and aa .

From (3.6) it follows that $\mathbf{H}(\cdot)$ is a homogenous of degree zero function of its argument; thus it can be written as a function of either $\tilde{\mathbf{n}}$ or $\tilde{\mathbf{p}}$.

3.3 Population projection

The matrix $\tilde{\mathbf{A}}(\tilde{\mathbf{n}})$ that projects the eco-evolutionary dynamics is

$$\tilde{\mathbf{A}}(\tilde{\mathbf{n}}) = \underbrace{\begin{pmatrix} \mathcal{U} & \mathbf{0} \\ \mathbf{0} & \mathcal{U}' \end{pmatrix}}_{\tilde{\mathbf{U}}} + \underbrace{\begin{pmatrix} \alpha\mathcal{F}(\tilde{\mathbf{p}}) & \mathbf{0} \\ (1-\alpha)\mathcal{F}(\tilde{\mathbf{p}}) & \mathbf{0} \end{pmatrix}}_{\tilde{\mathbf{F}}}, \quad (3.7)$$

where α is the fraction of newborn individuals that are female and $\tilde{\mathbf{p}}$ is calculated from $\tilde{\mathbf{n}}$ by (3.2). The blocks correspond to production of males and females by females, and survival of males and females.

To construct $\tilde{\mathbf{A}}$ using the vec-permutation matrix approach (Caswell et al. 2018), create a set of block-diagonal matrices; e.g.,

$$\mathbb{U} = \begin{pmatrix} \mathbf{U}_{AA} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{U}_{Aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa} \end{pmatrix} \quad (3.8)$$

and corresponding matrices \mathbb{U}' , \mathbb{F} , and \mathbb{F}' . Similarly,

$$\mathbb{H}(\tilde{\mathbf{p}}) = \mathbf{I}_\omega \otimes \mathbf{H}(\tilde{\mathbf{p}}) \quad (3.9)$$

The fertility matrix $\mathcal{F}(\tilde{\mathbf{p}})$ in (3.7) is

$$\mathcal{F}(\tilde{\mathbf{p}}) = \mathbf{K}^\top \mathbb{H}(\tilde{\mathbf{p}}) \mathbf{K} \mathbb{F}. \quad (3.10)$$

where \mathbf{K} is the vec-permutation matrix (Henderson and Searle 1981). From right to left, the block-diagonal matrix \mathbb{F} produces offspring as a function of the genotype of the mother, the vec-permutation matrix \mathbf{K} rearranges the vector, the block-diagonal matrix $\mathbb{H}(\tilde{\mathbf{n}})$ allocates the offspring to their genotypes, and \mathbf{K}^\top returns the vector to its original orientation.

Substituting equation (3.6) into equation (3.10) and simplifying yields

$$\mathcal{F}(\tilde{\mathbf{p}}) = \left(\begin{array}{c|c|c} q'_A \mathbf{F}_{AA} & \frac{1}{2} q'_A \mathbf{F}_{Aa} & \mathbf{0} \\ \hline q'_a \mathbf{F}_{AA} & \frac{1}{2} \mathbf{F}_{Aa} & q'_A \mathbf{F}_{aa} \\ \hline \mathbf{0} & \frac{1}{2} q'_a \mathbf{F}_{Aa} & q'_a \mathbf{F}_{aa} \end{array} \right), \quad (3.11)$$

where q'_A and q'_a are given by equation (3.5). For a derivation of equation (3.11) from equation (3.10), see de Vries and Caswell (2018a, Appendix A).

Consider the first block column of $\mathcal{F}(\tilde{\mathbf{p}})$. The first row block produces AA offspring from AA females; this happens when the AA female mates selects allele A from the gamete pool, which happens with probability q'_A . The second row block produces Aa offspring from AA females as a result of selecting allele a from the gamete pool. The other blocks can be interpreted similarly.

Because individuals do not change their genotype once they are born, the male and female survival matrices are block diagonal; $\mathcal{U} = \mathbb{U}$ and $\mathcal{U}' = \mathbb{U}'$.

Combining all the components yields the eco-evolutionary projection matrix

$$\tilde{\mathbf{A}}(\tilde{\mathbf{n}}) = \underbrace{\begin{pmatrix} \mathbf{U}_{AA} & \mathbf{0} & \mathbf{0} & | & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{U}_{Aa} & \mathbf{0} & | & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa} & | & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & | & \mathbf{U}'_{AA} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & | & \mathbf{0} & \mathbf{U}'_{Aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & | & \mathbf{0} & \mathbf{0} & \mathbf{U}'_{aa} \end{pmatrix}}_{\tilde{\mathbf{U}}} + \underbrace{\begin{pmatrix} \alpha q'_A \mathbf{F}_{AA} & \frac{1}{2} \alpha q'_A \mathbf{F}_{Aa} & \mathbf{0} & | & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \alpha q'_a \mathbf{F}_{AA} & \frac{1}{2} \alpha \mathbf{F}_{Aa} & \alpha q'_A \mathbf{F}_{aa} & | & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \frac{1}{2} \alpha q'_a \mathbf{F}_{Aa} & \alpha q'_a \mathbf{F}_{aa} & | & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline (1-\alpha)q'_A \mathbf{F}_{AA} & \frac{1}{2}(1-\alpha)q'_A \mathbf{F}_{Aa} & \mathbf{0} & | & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ (1-\alpha)q'_a \mathbf{F}_{AA} & \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & (1-\alpha)q'_A \mathbf{F}_{aa} & | & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \frac{1}{2}(1-\alpha)q'_a \mathbf{F}_{Aa} & (1-\alpha)q'_a \mathbf{F}_{aa} & | & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix}}_{\mathbf{F}}, \quad (3.12)$$

where q'_A and q'_a are given by (3.5).

3.4 Conditions for protected polymorphism

The eventual fate of an allele depends on its integrated effects, on all the components of the life cycle of both sexes, of all genotypic combinations in which it appears. We approach the problem of allele coexistence by finding sufficient conditions for a protected polymorphism (e.g., Levene 1953; Prout 1968; Nagylaki 1992, Chap. 6). We transform the model for $\tilde{\mathbf{n}}$ in (3.12) into a model for $\tilde{\mathbf{p}}$, and examine the equilibria of $\tilde{\mathbf{p}}$ on the boundary subspaces corresponding to homozygotes. If these boundary equilibria are unstable to perturbations into the interior, then alleles coexist in a protected polymorphism. Therefore, conditions for stability of the boundary equilibria provide conditions for coexistence. These conditions are determined by linearizing the dynamics in the neighborhood of each boundary equilibrium. This is a lengthy exercise in matrix calculus, the details of which are given in Appendix 3.A.

We will compare the results of the stability analysis with genotype-specific population growth rates, defined as

$$\lambda_i = \rho \begin{pmatrix} \mathbf{U}_i + \alpha \mathbf{F}_i & \mathbf{0} \\ (1-\alpha)\mathbf{F}_i & \mathbf{U}'_i \end{pmatrix} \quad i = AA, Aa, aa \quad (3.13)$$

where $\rho(\cdot)$ denotes the spectral radius. It is tempting, but ultimately not completely valid, to think of this growth rate as a simple scalar function that, evaluated for each genotype, will reveal its fate. In classical unstructured models under viability selection, λ reduces to the familiar genotypic fitness, and the criterion for polymorphism is heterozygote advantage in fitness. As we will show (and is well known in other contexts) heterozygote advantage in λ fails as a criterion for genotype coexistence except in special cases (cf. de Vries and Caswell 2018a). The reason is that the matrix (3.13) from which λ_i is calculated allocates all of the reproduction of genotype i to genotype i , whereas in reality each genotype contributes offspring to other genotypes, depending on the population structure. (The same issue applies to genotype-specific values of the net reproductive rate R_0 or the reproductive value). Our approach instead is to derive criteria for allele coexistence directly from the matrix $\tilde{\mathbf{A}}(\tilde{\mathbf{n}})$ which includes all three genotypes and their interactions.

Boundary equilibria

On a homozygous boundary, (3.12) reduces to a linear matrix model. Demographic ergodicity guarantees that the homozygous population will converge to a stable stage distribution and grow exponentially; we assume this degree of ergodicity provided the initial population has a nonzero number of females. As in de Vries and Caswell (2018a), we write an equation for the proportional population vector, so that the boundary state is an equilibrium state even if the original population is shrinking or growing,

$$\tilde{\mathbf{p}}(t+1) = \frac{\tilde{\mathbf{A}}[\tilde{\mathbf{p}}(t)]\tilde{\mathbf{p}}(t)}{\left\| \tilde{\mathbf{A}}[\tilde{\mathbf{p}}(t)]\tilde{\mathbf{p}}(t) \right\|}, \quad (3.14)$$

where $\|\cdot\|$ is the 1-norm. Equilibria of (3.14) satisfy

$$\hat{\mathbf{p}} = \frac{\tilde{\mathbf{A}}[\hat{\mathbf{p}}]\hat{\mathbf{p}}}{\left\| \tilde{\mathbf{A}}[\hat{\mathbf{p}}]\hat{\mathbf{p}} \right\|}. \quad (3.15)$$

Linearization at the boundary equilibria

To evaluate the stability of a boundary equilibrium to invasions by the other allele, we linearize (3.14) in the neighborhood of $\hat{\mathbf{p}}$ and determine the spectral radius (magnitude of the largest eigenvalue) of the Jacobian matrix of the linearization. If the spectral radius exceeds one, the boundary equilibrium is unstable. Because $\hat{\mathbf{p}}$ is stable to small perturbations within the boundary subspace, a spectral radius larger than one must have an associated eigenvector pointing into the interior, which implies that the invading allele increases when rare.

The Jacobian matrix,

$$\mathbf{M} = \left. \frac{d\tilde{\mathbf{p}}(t+1)}{d\tilde{\mathbf{p}}^\top(t)} \right|_{\tilde{\mathbf{p}}}, \quad (3.16)$$

is obtained by differentiating equation (3.14) and evaluating the resulting derivative at the boundary equilibrium. The calculations are simplified if i -states in the population vector are arranged by genotype first, then sex, and finally by stage. Then \mathbf{M} becomes a block-structured matrix with blocks corresponding to genotypes

$$\tilde{\mathbf{M}} = \left(\begin{array}{c|c|c} \mathbf{M}_{11} & \mathbf{M}_{12} & \mathbf{M}_{13} \\ \hline \mathbf{M}_{21} & \mathbf{M}_{22} & \mathbf{M}_{23} \\ \hline \mathbf{M}_{31} & \mathbf{M}_{32} & \mathbf{M}_{33} \end{array} \right), \quad (3.17)$$

where block \mathbf{M}_{11} represents the contribution of perturbations in the AA direction to growth or decline of perturbations in the AA direction, block \mathbf{M}_{12} represents the contribution of perturbations in the Aa direction to growth or decline of perturbations in the AA direction, etc. All of the block terms in the Jacobian are given, with their derivation, in Appendix 3.A.

We consider the Jacobian at the AA boundary; the expression at the aa boundary follows by symmetry. At the AA boundary, $\tilde{\mathbf{M}}$ is block upper triangular, with $\mathbf{M}_{21} = \mathbf{M}_{31} = \mathbf{M}_{32} = \mathbf{0}$; see equation (3.A64) in Appendix 3.A. Thus the eigenvalues of \mathbf{M} are the eigenvalues of the diagonal blocks \mathbf{M}_{11} , \mathbf{M}_{22} , and \mathbf{M}_{33} . Block \mathbf{M}_{11} projects perturbations within the AA boundary. Since $\tilde{\mathbf{p}}$ is stable to such perturbations, the spectral radius of \mathbf{M}_{11} must be smaller than one.

Block \mathbf{M}_{33} projects perturbations in the aa direction. In the neighbourhood 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.

The stability of the AA boundary equilibrium therefore depends on \mathbf{M}_{22} , which is

$$\mathbf{M}_{22} = \frac{1}{\lambda_{AA}} \rho \left(\begin{array}{cc} \mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} & \frac{1}{2}\alpha\mathbf{D}_{AA} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & \mathbf{U}'_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA} \end{array} \right) \quad (3.18)$$

where we define matrices

$$\mathbf{D}_{AA} = \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{p}}'_{AA}} \quad (3.19)$$

$$\mathbf{D}_{aa} = \frac{(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{aa} \hat{\mathbf{p}}'_{aa}} \quad (3.20)$$

and λ_{AA} is the AA homozygote population growth rate, given by (3.13). See Appendix 3.A for derivation.

The dominant eigenvalues of the Jacobian matrices at the AA boundary is therefore

$$\tilde{\zeta}_{AA} = \frac{1}{\lambda_{AA}} \rho \left(\begin{array}{cc} \mathbf{U}_{Aa} + \frac{1}{2}\alpha \mathbf{F}_{Aa} & \frac{1}{2}\alpha \mathbf{D}_{AA} \\ \frac{1}{2}(1-\alpha) \mathbf{F}_{Aa} & \mathbf{U}'_{Aa} + \frac{1}{2}(1-\alpha) \mathbf{D}_{AA} \end{array} \right). \quad (3.21)$$

By symmetry, the dominant eigenvalue of the Jacobian matrix at the aa boundary, is

$$\tilde{\zeta}_{aa} = \frac{1}{\lambda_{aa}} \rho \left(\begin{array}{cc} \mathbf{U}_{Aa} + \frac{1}{2}\alpha \mathbf{F}_{Aa} & \frac{1}{2}\alpha \mathbf{D}_{aa} \\ \frac{1}{2}(1-\alpha) \mathbf{F}_{Aa} & \mathbf{U}'_{Aa} + \frac{1}{2}(1-\alpha) \mathbf{D}_{aa} \end{array} \right), \quad (3.22)$$

where λ_{aa} is the aa homozygote population growth rate, again given by (3.13)

Theorem 2 *A protected polymorphism occurs when both boundaries are unstable, i.e. when*

$$\tilde{\zeta}_{AA} > 1, \quad (3.23)$$

$$\tilde{\zeta}_{aa} > 1. \quad (3.24)$$

Equations (3.23) and (3.24) are satisfied if and only if

$$\rho \left(\begin{array}{cc} \mathbf{U}_{Aa} + \frac{1}{2}\alpha \mathbf{F}_{Aa} & \frac{1}{2}\alpha \mathbf{D}_{AA} \\ \frac{1}{2}(1-\alpha) \mathbf{F}_{Aa} & \mathbf{U}'_{Aa} + \frac{1}{2}(1-\alpha) \mathbf{D}_{AA} \end{array} \right) > \lambda_{AA}, \quad (3.25)$$

$$\rho \left(\begin{array}{cc} \mathbf{U}_{Aa} + \frac{1}{2}\alpha \mathbf{F}_{Aa} & \frac{1}{2}\alpha \mathbf{D}_{aa} \\ \frac{1}{2}(1-\alpha) \mathbf{F}_{Aa} & \mathbf{U}'_{Aa} + \frac{1}{2}(1-\alpha) \mathbf{D}_{aa} \end{array} \right) > \lambda_{aa}. \quad (3.26)$$

Equations (3.25) and (3.26) give sufficient conditions for a protected genetic polymorphism for a general two-sex structured population. The conditions are a function of the demographic rates (through the \mathbf{U}_i , \mathbf{U}'_i , \mathbf{F}_i , and \mathbf{F}'_i matrices), the proportion of female newborns, α , and the structure of the homozygote equilibrium, $\hat{\mathbf{p}}_{AA}$ and $\hat{\mathbf{p}}'_{AA}$ (operating through the matrix \mathbf{D}_{AA} .)

3.5 A two-sex projection example: intralocus sexual conflict

Alleles that have differential effects on males and females (sexual dimorphism in allele effects) have important evolutionary consequences. For example, in intralocus sexual conflict, an allele has positive effects on one sex and negative effects on the other. Evidence for such conflict was found by Chippindale et al. (2001) in laboratory-adapted *Drosophila melanogaster*. Genotypes with high male fertilization success tended to have low female fecundity, and vice versa. For a review of studies demonstrating intralocus sexual conflict, see Bonduriansky and Chenoweth (2009).

As an example of our model, we construct and analyze a sex \times genotype \times stage-classified model for a hypothetical species with intralocus sexual conflict. Our hypothetical species has two life stages: juveniles and adults. Suppose that allele A is beneficial for females but detrimental for males, and that allele a has the reverse effect. As in the *Drosophila* example, suppose that the effects act only during the adult stage through reproductive success or mating success. The allele does not affect survival and transition rates, which we suppose are identical for males and females, such that

$$\mathbf{U}_i = \mathbf{U}'_i = \begin{pmatrix} \sigma(1-\gamma) & 0 \\ \sigma\gamma & s \end{pmatrix} \quad (3.27)$$

for all i . The allele does affect female fertility and male mating success,

$$\mathbf{F}_i = \begin{pmatrix} 0 & f_i \\ 0 & 0 \end{pmatrix}, \quad (3.28)$$

$$\mathbf{F}'_i = \begin{pmatrix} 0 & f'_i \\ 0 & 0 \end{pmatrix}. \quad (3.29)$$

and we suppose additive allele effects, so that f_i and f'_i are

i	f_i	f'_i
AA	$f + \beta$	$f' - a\beta$
Aa	f	f'
aa	$f - \beta$	$f' + a\beta$

Finally, we assume the sex ratio at birth is even ($\alpha = 0.5$).

Iterating equation (3.3) with the above demographic matrices provides numerical solutions for selection operating on any sex- and/or stage-specific demographic parameters. Figure 3.1 shows two examples of such genotype dynamics during an invasion (MATLAB code is given in the Online Supplementary Materials). In

Figures 3.1a, 3.1b the a allele is introduced into an AA population after a hundred days. The frequency of the a allele, which reduces female fertility, increases until a genetic polymorphism is reached. Since aa individuals have much lower fertility than the resident AA individuals, the population goes from positive to negative growth rate as a increases in frequency (evolutionary suicide). In Figures 3.1c, 3.1d allele A is introduced into an aa population. The frequency of the A allele increases and fixation of the AA genotype results. As the frequency of the A allele increases, the population moves from negative to positive growth rate (evolutionary rescue).

Armed with the result of Theorem 2, we calculate how the boundary stabilities (the largest eigenvalue of the Jacobian matrix evaluated at both boundaries) change as a function of the parameter β , which measures the degree of sexual antagonism (large β means a large positive effect on one sex and a large negative effect on the other sex). Figure 3.2 shows results when effects on females are larger than those on males ($a = 0.6$). For small values of β allele A fixates from any initial condition (except for starting exactly on the aa boundary). A protected polymorphism exists for values of $\beta \gtrsim 2.7$, as shown in Figure 3.2. Larger values of β increase the fecundity of AA females, which increases the growth rate of the AA population on the boundary, but it also benefits an invading a allele because matings between Aa males and AA females create new heterozygotes.

We found that when effects on males and females are equal ($a = 1$), a protected polymorphism exists for any value of β . Although this model is simple, the result suggests that sexual antagonism in a sexually dimorphic species can contribute to the maintenance of genetic variation. Chippindale et al. (2001) found that there are indeed extensive genome-wide polymorphisms for sexually antagonistic alleles in *Drosophila*.

3.6 Sexual dimorphism and stage structure

Distinguishing males and females makes it possible to analyze genes with differential effects on the sexes. In Figure 3.3 the criteria for polymorphism are shown for increasingly simplifying assumptions about the two sexes. When sexual dimorphism in survival and transition probabilities is eliminated ($\mathbf{U}_i = \mathbf{U}'_i$ for all i ; Model 2 in Figure 3.3), the genotype-specific population growth rates (3.13) simplify to

$$\lambda_i = \rho(\mathbf{U}_i + \alpha \mathbf{F}_i) \tag{3.30}$$

The male and female population vectors are equal at equilibrium under this assumption. If in addition $\alpha = 1/2$, then starting from any initial vector with

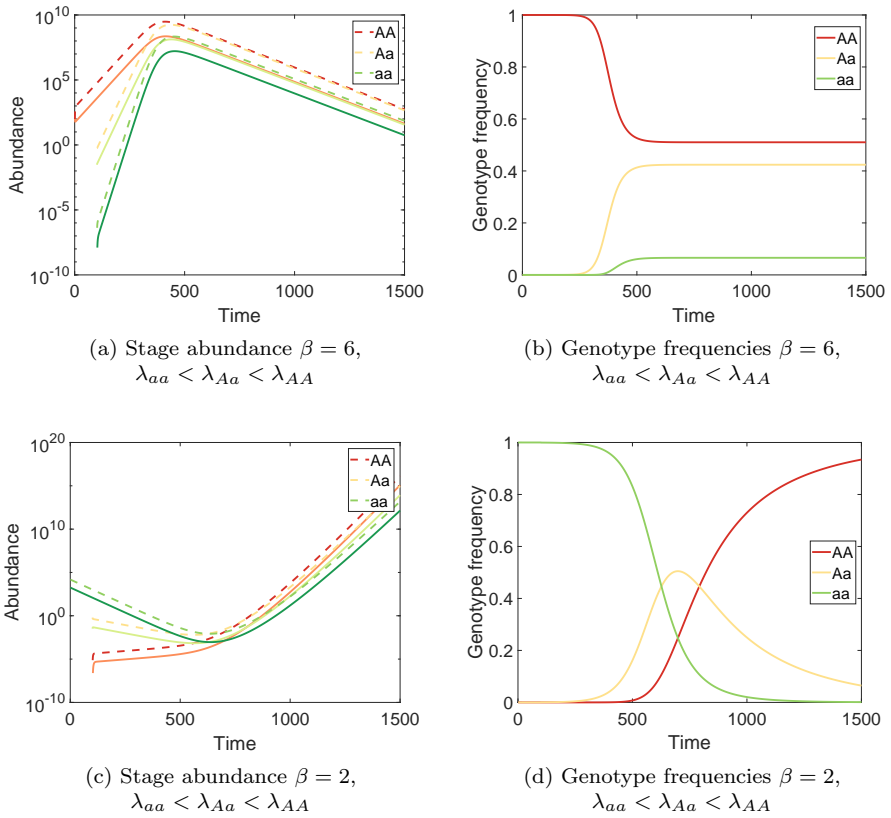


Figure 3.1: Two examples of population dynamics of a two-sex two-stage Mendelian matrix population model. Dashed lines are juvenile abundances; solid lines are adult abundances. 3.1a, 3.1b: Introduction of the a allele leads to a genetic polymorphism and to evolutionary suicide. Male and female population vectors are equal. Parameters used are $\sigma = 0.6$, $s = 0.6$, $\gamma = 0.05$, $f = 8$, $a = 0.6$. 3.1c, 3.1d: Introduction of the A allele leads to evolutionary rescue and fixation of the AA genotype. Parameters used are $\sigma = 0.65$, $s = 0.7$, $\gamma = 0.05$, $f = 8$, $a = 0.6$.

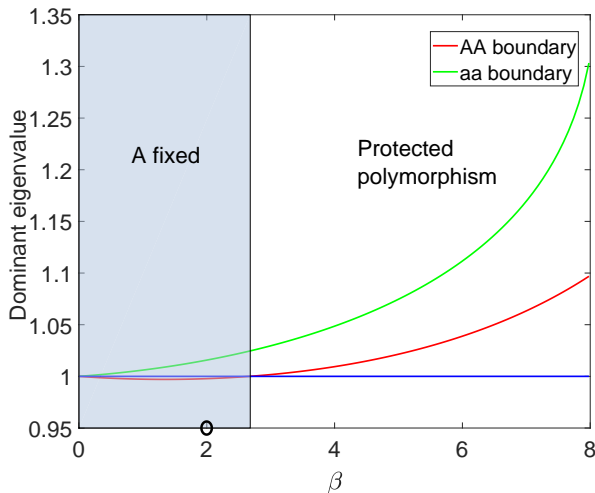


Figure 3.2: The effect of sexual antagonism on polymorphism in the model of Sect. 3.5. For $\beta \lesssim 2.7$ (the grey area), the AA boundary is stable and the A allele is fixed. For larger values of β , both boundaries are unstable (dominant eigenvalue of the determinant is larger than one) and a protected polymorphism exists. The open circle indicates parameter values used in Figures 3.1c and 3.1d. Parameters are $\sigma = 0.65$, $s = 0.7$, $\gamma = 0.05$, $f = 8$, $a = 0.6$.

nonzero numbers of males and females, the male and female population vectors will be identical once the last individual from the initial cohort has died.¹

When sexual dimorphism is reduced further, by making male mating success proportional to female fertility (Model 3B in Figure 3.3), the conditions (3.25) and (3.26) for a protected polymorphism reduce to

$$\rho\left(\mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa}\right) > \rho\left(\mathbf{U}_{AA} + \alpha\mathbf{F}_{AA}\right) \quad (3.31)$$

$$\rho\left(\mathbf{U}_{Aa} + \frac{1}{2}\mathbf{F}_{Aa}\right) > \rho\left(\mathbf{U}_{aa} + \alpha\mathbf{F}_{aa}\right). \quad (3.32)$$

See Appendix 3.B for details. If the female proportion $\alpha = \frac{1}{2}$, then (3.30) implies that the conditions (3.31) and (3.32) reduce to heterozygote superiority in genotype-specific growth rate, λ_i .

Because α occurs only on the right-hand side of these equations, reducing α reduces the stability of the boundaries and extends the parameter range for which a protected polymorphism is obtained. That is, when females are rare (α is small)

¹For an age-structured population where everybody dies after ω time steps, the male and female population vectors are equal after ω time steps. For a model with an open ended last age class or final life stage, the two vectors asymptotically approach each other.

a heterozygote may invade even when it is worse at reproducing and surviving than both homozygotes.

In one-sex population genetic models, the gamete pool is constructed from the female population vector. In the case of structured one-sex population genetics models, it is (implicitly) assumed that each (st)age contributes to the gamete pool proportional to its relative abundance in the population (Coulson et al. 2011; de Vries and Caswell 2018a). The construction of such a one-sex model requires two assumptions: (1) the male and female population vectors are proportional, and (2) male mating success is independent of (st)age and genotype. To describe the mating population, define a vector \mathbf{c}_j whose entries are 1 if that stage of genotype j reproduces, and 0 otherwise. The male mating success matrix then becomes

$$\mathbf{F}_j = \mathbf{e}_1 \otimes \mathbf{c}_j^\top. \quad (3.33)$$

We refer to this as Model 3A and the conditions for a genetic polymorphism are shown in Figure 3.3.

The results in Figure 3.3 are valid for any age or stage structure. If structure is eliminated, the matrices \mathbf{U}_i , \mathbf{F}_i , etc. reduce to scalars u_i , f_i , etc., but the pattern of the conditions for polymorphism remain; see Figure 3.A1 in Appendix 3.B.

3.7 Discussion

Our main result (Theorem 2) gives sufficient conditions for protected polymorphism for sexually dimorphic populations in which selection operates on any demographic rates. These conditions become necessary as well as sufficient if $\lambda_{AA} > 0$ and $\lambda_{aa} > 0$ and if the homozygote projection matrices are primitive.

Sexual dimorphism in survival, fertility, growth, maturation, and other vital rates has been known and studied since Darwin (Darwin 1888). Two-sex demographic models for population dynamics have been extensively studied (e.g., Keyfitz 1972; Caswell and Weeks 1986; Pollak 1990; Vamosi and Otto 2002; Iannelli et al. 2005; Jenouvrier et al. 2010; Plard et al. 2018), as have unstructured models for the evolutionary consequences of sexual dimorphism (Owen 1953; Bodmer 1965; Feldman et al. 1983; Slatkin 1984; Bolnick and Doebeli 2003). Our framework incorporates the ecology and evolution of both sexes for arbitrary life cycle structures.

We have focused on the conditions required for protected polymorphism. These conditions involve the eigenvalues of the linearization near the homozygote boundary equilibria. In general these conditions do not correspond to the genotype-specific population growth rates λ_i . Sexual dimorphism can therefore make it possible for a heterozygote with a lower population growth rate to invade both

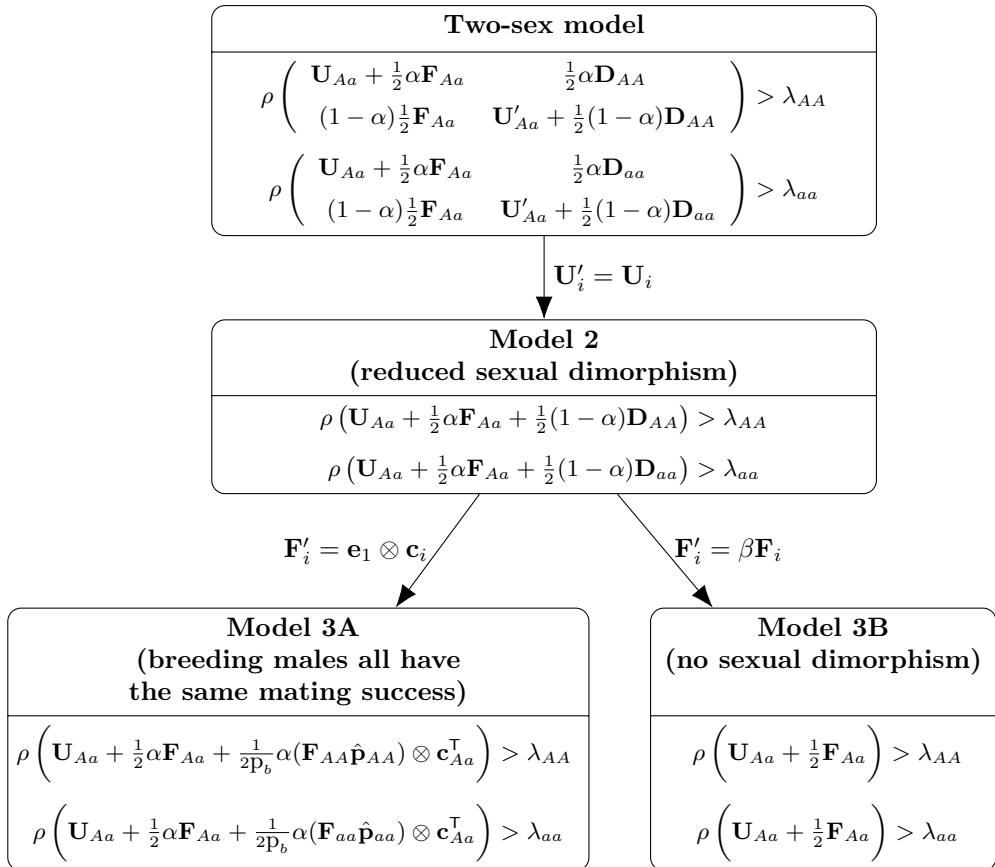


Figure 3.3: Coexistence conditions for the two-sex model and several modifications that reduce sexual dimorphism. The matrices \mathbf{D}_{AA} and \mathbf{D}_{aa} are given by (3.19) and (3.20) and the genotype-specific growth rates are given by (3.13).

homozygote boundaries. This can reduce population growth, and can even lead to extinction (so-called evolutionary suicide; see Figure 3.1a). Interestingly, using fossil records of ostracods, Martins et al. (2018) recently found that species with greater sexual dimorphism exhibit an increased risk of extinction. Similarly, Hasegawa and Arai (2018) estimated perceived extinction risk in 72 species of swallow and found a higher extinction risk for swallows with sexually dimorphic plumage than for species with sexually monomorphic plumage.

Our analysis suggests many mechanisms that could lead to evolutionary suicide. It is well known that intralocus sexual conflict can do so (Kokko and Brooks 2003). We also find that an allele with a higher survival for both males and females but a lower (female) fertility can successfully invade a resident population by taking advantage of the residents' higher fertility during invasion. Once a sta-

ble polymorphism exists with this allele, however, its low fertility can push the population from a positive to a negative growth rate (see de Vries and Caswell (2018a)). Similarly, an allele with a faster maturation rate for both sexes at the cost of lower fertility can lead to evolutionary suicide if survival in the adult stage is much higher than in the juvenile stage (unpublished results). Finally, genes that increase male mating success at the expense of offspring survival can also lead to evolutionary suicide (the “Trojan gene hypothesis” of Muir and Howard 1999).

Kokko and Jennions (2014) define sexual conflict as the existence of a hypothetical tool that allows individuals of sex A to alter what individuals of sex B do at a cost to sex B, and with a selective benefit to sex A. The above mentioned mechanisms for deterministic suicide all fall within this definition of sexual conflict, since they involve a form of intralocus sexual conflict where either both males and females get a benefit but only females pay a cost, or only males get a benefit and females pay the cost. When there is no sexual dimorphism in demography, the interests of males and females are aligned. In this case only genes that improve survival, increase maturation, or increase fertility, i.e., genes that increase population growth rate, can invade.

We have explored a few simplifications of a two-sex stage-structured model in Section 3.6. Under some conditions, the criteria for polymorphism reduce to heterozygote advantage in the genotype-specific growth rate. This result provides an easily calculated demographic quantity that works the same way as fitness in classical population genetic models. However, the hope for such a general scalar measure of fitness seems a chimera. The net reproductive rate and the reproductive value have the same problems as the genotype growth rate: genotypes do not produce copies of themselves only.

Some historical context

Effects of sexual dimorphism are already apparent in unstructured models of fertility selection (e.g., Penrose 1947; Owen 1953; Bodmer 1965; Pollak 1978; Haderler and Liberman 1975; Feldman et al. 1983). For example, both Pollak (1978) and Clark and Feldman (1986) found that mean fitness in the population does not always increase when genotypes differ in fertility as well as survival rates. We have found that this result is still valid in the context of a structured population genetic model.

A few papers have previously addressed evolution in two-sex structured populations. Shyu and Caswell (2016b) investigated sex ratio evolution with multiple maternal conditions by combining nonlinear matrix models with multidimensional adaptive dynamics (see also Shyu and Caswell (2016a)). Childs et al. (2016) com-

bine a two-sex demographic model with quantitative genetics and extend the age-structured Price equation to breeding values and two sexes. Harts et al. (2014) used an individual based, spatially structured model with dispersing juveniles and female demographic dominance to model local adaptation subjected to intralocus sexual conflict and environmentally driven sex ratio biases.

Extensions

Our step by step construction of the projection matrix $\tilde{\mathbf{A}}(\tilde{\mathbf{n}})$ makes it possible to extend the model in a variety of ways. The demographic components (\mathbf{U}_i , \mathbf{F}_i and their male counterparts) can be made density-dependent; conditions for polymorphism can still be obtained by linearizing at boundary equilibria (de Vries and Caswell 2018c). Or the demography could be made time-varying, or environment-dependent. The eco-evolutionary projections could still be carried out, but the conditions for polymorphism would be more complicated.

In species with biparental care, the characteristics of both parents are known to be important for offspring survival (Sheldon 2000; Badyaev and Hill 2002; Rankin and Kokko 2007). Developing a version of the model that explicitly includes pair formation by incorporating a marriage function (Keyfitz 1972; Caswell 2001; Shyu and Caswell 2018a) would make it possible to analyze the genetics of traits related to parental care.

Distortions of the operational sex ratio can lead to limitation of female reproduction by male availability (a “marriage squeeze”) (Schoen 1983; Goldman et al. 1984). Species from a wide range of taxa have adult sex ratios substantially different from one (Altman et al. 1962; Willson et al. 1983; Székely et al. 2014), which is likely to result in marriage squeezes. Modeling species with marriage squeezes would require incorporating a marriage function into the model presented here. The flexibility of the model framework introduced here makes these and other extensions possible.

Acknowledgments

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Appendix 3.A Appendix: Coexistence conditions

The conditions for a protected polymorphism in the two-sex model, equations (3.25) and (3.26), will be derived in this Appendix. The derivation is simplest when the population vector is ordered by genotype first, and then by sex and stage, in contrast to the ordering used in the main text (sex, then genotype, then stage). We will first construct the population projection matrix and then use it to derive coexistence conditions, following closely the logic introduced by de Vries and Caswell (2018a).

Population projection matrix

The population vector is

$$\tilde{\mathbf{n}} = \begin{pmatrix} \mathbf{n}_{AA} \\ \mathbf{n}'_{AA} \\ \mathbf{n}_{Aa} \\ \mathbf{n}'_{Aa} \\ \mathbf{n}_{aa} \\ \mathbf{n}'_{aa} \end{pmatrix}. \quad (3.A1)$$

The population projection matrix $\tilde{\mathbf{A}}$ consists of 3×3 blocks, which act on the genotype-specific population vectors:

$$\tilde{\mathbf{A}} = \tilde{\mathbf{U}} + \tilde{\mathbf{F}} \quad (3.A2)$$

$$= \begin{pmatrix} \mathbf{U}_{AA} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{U}'_{AA} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{U}_{Aa} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}'_{Aa} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}'_{aa} \end{pmatrix} + \begin{pmatrix} q'_A \alpha \mathbf{F}_{AA} & \mathbf{0} & \frac{1}{2} q'_A \alpha \mathbf{F}_{Aa} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ (1 - \alpha) q'_A \mathbf{F}_{AA} & \mathbf{0} & \frac{1}{2} (1 - \alpha) q'_A \mathbf{F}_{Aa} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ q'_a \alpha \mathbf{F}_{AA} & \mathbf{0} & \frac{1}{2} \alpha \mathbf{F}_{Aa} & \mathbf{0} & q'_a \alpha \mathbf{F}_{aa} & \mathbf{0} \\ (1 - \alpha) q'_a \mathbf{F}_{AA} & \mathbf{0} & \frac{1}{2} (1 - \alpha) \mathbf{F}_{Aa} & \mathbf{0} & (1 - \alpha) q'_a \mathbf{F}_{aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \frac{1}{2} q'_a \alpha \mathbf{F}_{Aa} & \mathbf{0} & q'_a \alpha \mathbf{F}_{aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \frac{1}{2} (1 - \alpha) q'_a \mathbf{F}_{Aa} & \mathbf{0} & (1 - \alpha) q'_a \mathbf{F}_{aa} & \mathbf{0} \end{pmatrix}. \quad (3.A3)$$

with symbols defined in the main text. Male and female offspring are produced in a fixed ratio of $\alpha : (1 - \alpha)$. The survival matrices appear on the diagonal because individuals do not change their genotype once they are born. The fertility matrix

incorporates the Mendelian inheritance and is an extension of the fertility matrix derived in de Vries and Caswell (2018a).

The first block column of $\tilde{\mathbf{A}}$ describes the production of offspring by an AA female with stage-specific fertility rates \mathbf{F}_{AA} . The probability of picking an A allele out of the gamete pool, and hence the probability of this AA female producing an AA offspring, is q'_A , as derived in the main text. Conversely, the probability of picking an a allele and producing Aa offspring is q'_a . Similarly, the middle column of block matrices are offspring produced by Aa females, which can produce offspring of all 3 genotypes.

Coexistence conditions

The two-sex Mendelian matrix model defined by equation (3.A3) reduces to a linear matrix model on the boundary (since $q'_A = 1$ and $q'_a = 0$). Provided the initial population contains a nonzero number of females, the population will grow or shrink exponentially after converging to a stable population structure (see Caswell (2001), section 4.5.2.1). Taking advantage of the homogeneity of $\tilde{\mathbf{F}}$, we rewrite the model in terms of the normalized population vector (the frequency vector):

$$\tilde{\mathbf{p}}(t+1) = \frac{\tilde{\mathbf{A}}(\tilde{\mathbf{p}}(t))\tilde{\mathbf{p}}(t)}{\|\tilde{\mathbf{A}}(\tilde{\mathbf{p}}(t))\tilde{\mathbf{p}}(t)\|}, \quad (3.A4)$$

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} . Equilibrium solutions, denoted by $\hat{\mathbf{p}}$, satisfy

$$\hat{\mathbf{p}} = \frac{\tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}}}{\mathbf{1}_{2g\omega}^\top \tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}}}, \quad (3.A5)$$

where the one norm can be replaced by $\mathbf{1}_{2g\omega}^\top \tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}}$ because $\tilde{\mathbf{p}}$ is nonnegative.

Linearization at the boundary equilibria

In this section² we derive the linear approximation to the dynamics in the neighborhood of a homozygote boundary equilibrium. The stability of a such an equilibrium to invasions by the other allele is determined by the magnitude of the largest eigenvalue of the Jacobian matrix of the frequency model evaluated at the equilibrium. If the magnitude of this eigenvalue is larger than one, then the equilibrium is unstable. The Jacobian matrix,

$$\mathbf{M} = \left. \frac{d\tilde{\mathbf{p}}(t+1)}{d\tilde{\mathbf{p}}(t)} \right|_{\hat{\mathbf{p}}}, \quad (3.A6)$$

²This section is modified from Appendix B of de Vries and Caswell (2018a) under the terms of a Creative Commons BY-NC license. The derivation here is modified to account for the presence of the two sexes.

is obtained by differentiating equation (3.A4) and evaluating the resulting derivatives at the boundary equilibrium. This requires a long series of matrix calculus operations, and repeatedly takes advantage of the fact that $\hat{\mathbf{p}}$ at the boundary contains zeros for the blocks corresponding to Aa and aa genotypes.

For notational convenience, first define a matrix \mathbf{B} as

$$\mathbf{B}(\tilde{\mathbf{p}}) = \frac{\tilde{\mathbf{A}}(\tilde{\mathbf{p}})}{\mathbf{1}_{2\omega g}^T \tilde{\mathbf{A}}(\tilde{\mathbf{p}}) \tilde{\mathbf{p}}}, \quad (3.A7)$$

such that

$$\tilde{\mathbf{p}}(t+1) = \mathbf{B}(\tilde{\mathbf{p}}(t)) \tilde{\mathbf{p}}(t). \quad (3.A8)$$

Differentiate equation (3.A8) to obtain

$$d\tilde{\mathbf{p}}(t+1) = \mathbf{B}d\tilde{\mathbf{p}}(t) + \left(d\tilde{\mathbf{B}}\right) \tilde{\mathbf{p}}(t), \quad (3.A9)$$

where the explicit dependence of \mathbf{B} on $\tilde{\mathbf{p}}$ has been omitted to avoid a cluttering of brackets. Multiply the second term by an $2\omega g \times 2\omega g$ identity matrix,

$$d\tilde{\mathbf{p}}(t+1) = \mathbf{B}d\tilde{\mathbf{p}}(t) + \mathbf{I}_{2\omega g} (d\mathbf{B}) \tilde{\mathbf{p}}(t). \quad (3.A10)$$

and apply the vec operator to both sides, remembering that as $\tilde{\mathbf{p}}$ is a vector, $\text{vec}\tilde{\mathbf{p}} = \tilde{\mathbf{p}}$,

$$d\tilde{\mathbf{p}}(t+1) = \mathbf{B}d\tilde{\mathbf{p}}(t) + \text{vec}[\mathbf{I}_{2\omega g} (d\mathbf{B}) \tilde{\mathbf{p}}(t)]. \quad (3.A11)$$

Next apply Roths theorem (Roth 1934), $\text{vec}\mathbf{ABC} = (\mathbf{C}^T \otimes \mathbf{A}) \text{vec}\mathbf{B}$, to replace the vec operator with the Kronecker product:

$$d\tilde{\mathbf{p}}(t+1) = \mathbf{B}d\tilde{\mathbf{p}}(t) + (\tilde{\mathbf{p}}^T(t) \otimes \mathbf{I}_{2\omega g}) d\text{vec}[\mathbf{B}]. \quad (3.A12)$$

Then the first identification theorem and the chain rule together give the following formula for the Jacobian (Magnus and Neudecker 1985; Caswell 2007b),

$$\mathbf{M} = \left. \frac{d\tilde{\mathbf{p}}(t+1)}{d\tilde{\mathbf{p}}(t)} \right|_{\tilde{\mathbf{p}}}, \quad (3.A13)$$

$$= \mathbf{B}(\hat{\mathbf{p}}) + (\hat{\mathbf{p}}^T \otimes \mathbf{I}_{2\omega g}) \left. \frac{\partial \text{vec}\mathbf{B}(\mathbf{p})}{\partial \tilde{\mathbf{p}}^T} \right|_{\hat{\mathbf{p}}}. \quad (3.A14)$$

Our aim is to express the Jacobian matrix \mathbf{M} in terms of the genotype specific matrices, \mathbf{U}_i , \mathbf{F}_i , \mathbf{U}'_i and \mathbf{F}'_i . We choose to analyze the Jacobian at the AA boundary; the expression at the aa boundary can be derived afterwards using symmetry arguments. First it will be convenient to define the scalar $f(\tilde{\mathbf{p}})$ as

$$f(\tilde{\mathbf{p}}) = \frac{1}{\mathbf{1}_{2\omega g}^T \tilde{\mathbf{A}}(\tilde{\mathbf{p}}) \tilde{\mathbf{p}}}, \quad (3.A15)$$

so that

$$\mathbf{B}(\tilde{\mathbf{p}}) = f(\tilde{\mathbf{p}})\tilde{\mathbf{A}}(\tilde{\mathbf{p}}). \quad (3.A16)$$

Where it does not create confusion, we will drop the explicit dependence of $\tilde{\mathbf{A}}$, \mathbf{B} , and f on $\tilde{\mathbf{p}}$. Differentiate equation (3.A16) and take the vec of both sides to obtain

$$\text{dvec}\mathbf{B} = \text{vec}\tilde{\mathbf{A}}df + f\text{dvec}\tilde{\mathbf{A}}, \quad (3.A17)$$

or

$$\frac{\partial \text{vec}\mathbf{B}}{\partial \tilde{\mathbf{p}}^\top} = \text{vec}\tilde{\mathbf{A}}\frac{\partial f}{\partial \tilde{\mathbf{p}}^\top} + f(\tilde{\mathbf{p}})\frac{\partial \text{vec}\tilde{\mathbf{A}}}{\partial \tilde{\mathbf{p}}^\top}. \quad (3.A18)$$

Next differentiate f in equation (3.A15) to obtain

$$df = \frac{-1}{\left(\mathbf{1}_{2\omega g}^\top \tilde{\mathbf{A}}(\tilde{\mathbf{p}})\tilde{\mathbf{p}}\right)^2} \left[\mathbf{1}_{2\omega g}^\top \left(d\tilde{\mathbf{A}} \right) \tilde{\mathbf{p}} + \mathbf{1}_{2\omega g}^\top \tilde{\mathbf{A}} d\tilde{\mathbf{p}} \right]. \quad (3.A19)$$

Since all the terms in the Jacobian are evaluated at the AA boundary, $\tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}} = \lambda_{AA}\hat{\mathbf{p}}$, and therefore

$$\mathbf{1}_{2\omega g}^\top \tilde{\mathbf{A}}(\hat{\mathbf{p}})\hat{\mathbf{p}} = \lambda_{AA}. \quad (3.A20)$$

Evaluate the differential of f at the boundary and use equation (3.A20) to obtain

$$df = \frac{-1}{\lambda_{AA}^2} \left[\mathbf{1}_{2\omega g}^\top \left(d\tilde{\mathbf{A}} \right) \hat{\mathbf{p}} + \mathbf{1}_{2\omega g}^\top \tilde{\mathbf{A}} d\hat{\mathbf{p}} \right]. \quad (3.A21)$$

We will now show that the first term in this sum, $\mathbf{1}_{2\omega g}^\top \left(d\tilde{\mathbf{A}} \right) \hat{\mathbf{p}}$, is equal to zero when evaluated at the boundary. To do so, the population vector analyzed at the AA boundary is necessary,

$$\hat{\mathbf{p}} = \begin{pmatrix} \hat{\mathbf{p}}_{AA} \\ \frac{\hat{\mathbf{p}}'_{AA}}{0} \\ 0 \\ \hline 0 \\ 0 \end{pmatrix}. \quad (3.A22)$$

The last two block columns of the matrix $\left(d\tilde{\mathbf{A}} \right)$, given in equation (3.A3), are therefore multiplied by zero, yielding

$$\mathbf{1}_{2\omega g}^\top \left(d\tilde{\mathbf{A}} \right) \hat{\mathbf{p}} = \mathbf{1}_\omega^\top \mathbf{F}_{AA} \hat{\mathbf{p}}_{AA} (dq'_A + dq'_a), \quad (3.A23)$$

$$= 0, \quad (3.A24)$$

because

$$q'_a + q'_A = 1, \quad (3.A25)$$

$$dq'_a + dq'_A = 0. \quad (3.A26)$$

Substituting equation (3.A21) into equation (3.A17) and evaluating at the boundary yields

$$\text{dvec}\mathbf{B} = \frac{-1}{\lambda_{AA}^2} \text{vec}\tilde{\mathbf{A}} \left[\mathbf{1}_{2\omega g}^\top \tilde{\mathbf{A}} \text{d}\hat{\mathbf{p}} \right] + \frac{1}{\lambda_{AA}} \text{dvec}\tilde{\mathbf{A}}, \quad (3.A27)$$

or

$$\left. \frac{\partial \text{vec}\mathbf{B}}{\partial \hat{\mathbf{p}}^\top} \right|_{\hat{\mathbf{p}}} = \frac{-1}{\lambda_{AA}^2} \left(\text{vec}\tilde{\mathbf{A}} \right) \left(\mathbf{1}_{2\omega g}^\top \tilde{\mathbf{A}} \right) + \frac{1}{\lambda_{AA}} \left. \frac{\partial \text{vec}\tilde{\mathbf{A}}}{\partial \hat{\mathbf{p}}^\top} \right|_{\hat{\mathbf{p}}}. \quad (3.A28)$$

Finally substituting the expression above into equation 3.A14 yields the Jacobian matrix:

$$\mathbf{M} = \mathbf{B}(\hat{\mathbf{p}}) + \underbrace{\left(\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g} \right) \left. \frac{\partial \text{vec}\mathbf{B}}{\partial \hat{\mathbf{p}}^\top} \right|_{\hat{\mathbf{p}}}}_{\textcircled{\text{B}}}, \quad (3.A29)$$

$$\begin{aligned} &= \underbrace{\mathbf{B}(\hat{\mathbf{p}})}_{\textcircled{\text{A}}} - \underbrace{\frac{1}{\lambda_{AA}^2} \left(\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g} \right) \left(\text{vec}\tilde{\mathbf{A}} \right) \left(\mathbf{1}_{2\omega g}^\top \tilde{\mathbf{A}} \right)}_{\textcircled{\text{B}}} \\ &+ \underbrace{\frac{1}{\lambda_{AA}} \left(\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g} \right) \left. \frac{\partial \text{vec}\tilde{\mathbf{A}}}{\partial \hat{\mathbf{p}}^\top} \right|_{\hat{\mathbf{p}}}}_{\textcircled{\text{C}}}, \end{aligned} \quad (3.A30)$$

where we have identified the three terms as $\textcircled{\text{A}}$, $\textcircled{\text{B}}$, and $\textcircled{\text{C}}$.

Components of the Jacobian

The next task is to work out all the terms in the above expression for the Jacobian. We start with $\textcircled{\text{A}}$,

$$\mathbf{B}(\hat{\mathbf{p}}) = \frac{\tilde{\mathbf{A}}(\hat{\mathbf{p}})}{\mathbf{1}_{\omega g}^\top \tilde{\mathbf{A}}(\hat{\mathbf{p}}) \hat{\mathbf{p}}} \quad (3.A31)$$

$$= \frac{1}{\lambda_{AA}} \left(\begin{array}{cc|cc|cc} \mathbf{U}_{AA} + \alpha \mathbf{F}_{AA} & \mathbf{0} & \frac{1}{2} \alpha \mathbf{F}_{Aa} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ (1 - \alpha) \mathbf{F}_{AA} & \mathbf{U}'_{AA} & \frac{1}{2} (1 - \alpha) \mathbf{F}_{Aa} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{U}_{Aa} + \frac{1}{2} \alpha \mathbf{F}_{Aa} & \mathbf{0} & \alpha \mathbf{F}_{aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \frac{1}{2} (1 - \alpha) \mathbf{F}_{Aa} & \mathbf{U}'_{Aa} & (1 - \alpha) \mathbf{F}_{aa} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}'_{aa} \end{array} \right). \quad (3.A32)$$

Next we turn our attention to the second term, $\textcircled{\text{B}}$,

$$\textcircled{\text{B}} = -\frac{1}{\lambda_{AA}^2} \left(\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g} \right) \left(\text{vec}\tilde{\mathbf{A}} \right) \left(\mathbf{1}_{2\omega g}^\top \tilde{\mathbf{A}} \right). \quad (3.A33)$$

Using Roth's theorem, $(\mathbf{C}^\top \otimes \mathbf{A}) \text{vec} \mathbf{B} = \text{vec} \mathbf{ABC}$, we can simplify as follows

$$\begin{aligned} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g}) \text{vec} \left(\tilde{\mathbf{A}}(\hat{\mathbf{p}}) \right) &= \text{vec} \left(\mathbf{I}_{2\omega g} \tilde{\mathbf{A}}(\hat{\mathbf{p}}) \hat{\mathbf{p}} \right) \\ &= \lambda_{AA} \hat{\mathbf{p}}, \end{aligned} \quad (3.A34)$$

which yields

$$\textcircled{\mathbf{B}} = -\frac{1}{\lambda_{AA}} \hat{\mathbf{p}} \left(\mathbf{1}_{\omega g}^\top \tilde{\mathbf{A}}(\hat{\mathbf{p}}) \right). \quad (3.A35)$$

Substituting $\hat{\mathbf{p}}$ from equation (3.A22) into equation (3.A35), defining the temporary $\omega \times 2g\omega$ matrix

$$\mathbf{C} = \left(\hat{\mathbf{p}}_{AA} \otimes \mathbf{1}_\omega^\top \quad \hat{\mathbf{p}}'_{AA} \otimes \mathbf{1}_\omega^\top \mid \mathbf{0} \quad \mathbf{0} \mid \mathbf{0} \quad \mathbf{0} \right) \quad (3.A36)$$

and writing the result in terms of the block matrices yields

$$-\frac{1}{\lambda_{AA}} \mathbf{C} \left(\begin{array}{cc|cc|cc} (\mathbf{U}_{AA} + \alpha \mathbf{F}_{AA}) & \mathbf{U}'_{AA} & (\mathbf{U}_{Aa} + \alpha \mathbf{F}_{Aa}) & \mathbf{U}'_{Aa} & (\mathbf{U}_{aa} + \alpha \mathbf{F}_{aa}) & \mathbf{U}'_{aa} \\ (\mathbf{U}_{AA} + (1-\alpha) \mathbf{F}_{AA}) & \mathbf{U}'_{AA} & (\mathbf{U}_{Aa} + (1-\alpha) \mathbf{F}_{Aa}) & \mathbf{U}'_{Aa} & (\mathbf{U}_{aa} + (1-\alpha) \mathbf{F}_{aa}) & \mathbf{U}'_{aa} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array} \right) \quad (3.A37)$$

To derive term $\textcircled{\mathbf{C}}$ in the Jacobian, we first derive a useful expression for $\text{vec} \tilde{\mathbf{A}}$ in terms of its component block matrices. The matrix $\tilde{\mathbf{A}}$ can be decomposed into $36 \omega \times \omega$ block matrices, as in equation (3.A3), so that for example

$$\mathbf{A}_{11} = \mathbf{U}_{AA} + q'_A \alpha \mathbf{F}_{AA}, \quad (3.A38)$$

$$\mathbf{A}_{22} = \mathbf{U}'_{AA}, \quad (3.A39)$$

and

$$\mathbf{A}_{21} = (1-\alpha) q'_A \mathbf{F}_{AA}, \quad (3.A40)$$

$$\mathbf{A}_{12} = \mathbf{0}. \quad (3.A41)$$

The matrix $\tilde{\mathbf{A}}$ can then be written as

$$\tilde{\mathbf{A}} = \sum_{i,j=1}^6 \mathbf{E}_{ij} \otimes \mathbf{A}_{ij}, \quad (3.A42)$$

$$= \sum_{i,j=1}^6 (\mathbf{e}_i \mathbf{e}_j^\top) \otimes (\mathbf{A}_{ij} \mathbf{I}_\omega), \quad (3.A43)$$

where we have used the definition of the matrix $\mathbf{E}_{ij} = \mathbf{e}_i \mathbf{e}_j^\top$. Using $\mathbf{AC} \otimes \mathbf{BD} = (\mathbf{A} \otimes \mathbf{B})(\mathbf{C} \otimes \mathbf{D})$, equation (3.A43) can be rewritten as

$$\tilde{\mathbf{A}} = \sum_{i,j=1}^6 (\mathbf{e}_i \otimes \mathbf{A}_{ij}) (\mathbf{e}_j^\top \otimes \mathbf{I}_\omega), \quad (3.A44)$$

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 rewrite this again

$$\tilde{\mathbf{A}} = \sum_{i,j=1}^6 (\mathbf{e}_i \otimes \mathbf{I}_\omega) \mathbf{A}_{ij} (\mathbf{e}_j^\top \otimes \mathbf{I}_\omega). \quad (3.A45)$$

This yields the following formula for $\text{vec}\tilde{\mathbf{A}}$:

$$\text{vec}\tilde{\mathbf{A}} = \sum_{i,j}^6 (\mathbf{e}_j \otimes \mathbf{I}_\omega) \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega) \text{vec}\mathbf{A}_{ij}. \quad (3.A46)$$

Armed with this expression for $\text{vec}\tilde{\mathbf{A}}$, we analyze term $\textcircled{\text{C}}$ in the Jacobian. Replace the derivative of $\text{vec}\tilde{\mathbf{A}}$ with equation 3.A46, such that

$$-\frac{1}{\lambda_{AA}} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g}) \frac{\partial \text{vec}\mathbf{A}}{\partial \tilde{\mathbf{p}}^\top} \Big|_{\hat{\mathbf{p}}} = -\frac{1}{\lambda_{AA}} \sum_{i,j=1}^6 (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g}) ((\mathbf{e}_j \otimes \mathbf{I}_\omega) \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega)) \frac{\partial \text{vec}\mathbf{A}_{ij}}{\partial \tilde{\mathbf{p}}^\top} \Big|_{\hat{\mathbf{p}}}. \quad (3.A47)$$

Use $(\mathbf{A} \otimes \mathbf{B})(\mathbf{C} \otimes \mathbf{D}) = \mathbf{AC} \otimes \mathbf{BD}$ to rewrite

$$(\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g}) ((\mathbf{e}_j \otimes \mathbf{I}_\omega) \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega)) = (\hat{\mathbf{p}}^\top (\mathbf{e}_j \otimes \mathbf{I}_\omega)) \otimes (\mathbf{I}_{2\omega g} (\mathbf{e}_i \otimes \mathbf{I}_\omega)), \quad (3.A48)$$

substituting this expression into the right hand side of equation (3.A47) yields

$$\frac{1}{\lambda_{AA}} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g}) \frac{\partial \text{vec}\mathbf{A}}{\partial \tilde{\mathbf{p}}^\top} \Big|_{\hat{\mathbf{p}}} = \frac{1}{\lambda_{AA}} \sum_{i,j=1}^6 (\hat{\mathbf{p}}^\top (\mathbf{e}_j \otimes \mathbf{I}_\omega)) \otimes (\mathbf{I}_{2\omega g} (\mathbf{e}_i \otimes \mathbf{I}_\omega)) \frac{\partial \text{vec}\mathbf{A}_{ij}}{\partial \tilde{\mathbf{p}}^\top} \Big|_{\hat{\mathbf{p}}}. \quad (3.A49)$$

Substitute $\hat{\mathbf{p}}^\top = (\hat{\mathbf{p}}_{AA}^\top, \hat{\mathbf{p}}_{AA}^{\prime\top}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0})$ into the right-hand side of equation (3.A49), so that only terms with $j = 1$ and $j = 2$ are nonzero, yielding

$$\begin{aligned} \frac{1}{\lambda_{AA}} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g}) \frac{\partial \text{vec}\mathbf{A}}{\partial \tilde{\mathbf{p}}^\top} \Big|_{\hat{\mathbf{p}}} &= \frac{1}{\lambda_{AA}} \sum_{i=1}^6 (\hat{\mathbf{p}}_{AA}^\top \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega)) \frac{\partial \text{vec}\mathbf{A}_{i1}}{\partial \tilde{\mathbf{p}}^\top} \Big|_{\hat{\mathbf{p}}} \\ &+ \frac{1}{\lambda_{AA}} \sum_{i=1}^6 (\hat{\mathbf{p}}_{AA}^{\prime\top} \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega)) \frac{\partial \text{vec}\mathbf{A}_{i2}}{\partial \tilde{\mathbf{p}}^\top} \Big|_{\hat{\mathbf{p}}}, \end{aligned} \quad (3.A50)$$

Since none of the \mathbf{A}_{i2} are a function of the frequency vector,

$$\left. \frac{\partial \text{vec} \mathbf{A}_{i2}}{\partial \tilde{\mathbf{p}}^\top} \right|_{\tilde{\mathbf{p}}} = 0, \text{ for all } i. \quad (3.A51)$$

Next write down each term in the sum over i and take the derivative of the $\text{vec} \mathbf{A}_{i1}$'s to obtain

$$\begin{aligned} \frac{1}{\lambda_{AA}} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g}) \left. \frac{\partial \text{vec} \mathbf{A}}{\partial \tilde{\mathbf{p}}^\top} \right|_{\tilde{\mathbf{p}}} &= \frac{\alpha}{\lambda_{AA}} [\hat{\mathbf{p}}_{AA}^\top \otimes (\mathbf{e}_1 \otimes \mathbf{I}_\omega) - \hat{\mathbf{p}}_{AA}^\top \otimes (\mathbf{e}_3 \otimes \mathbf{I}_\omega)] \text{vec}(\mathbf{F}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{p}}^\top} \right|_{\tilde{\mathbf{p}}}, \\ &+ \frac{(1-\alpha)}{\lambda_{AA}} [\hat{\mathbf{p}}_{AA}^\top \otimes (\mathbf{e}_2 \otimes \mathbf{I}_\omega) - \hat{\mathbf{p}}_{AA}^\top \otimes (\mathbf{e}_4 \otimes \mathbf{I}_\omega)] \text{vec}(\mathbf{F}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{p}}^\top} \right|_{\tilde{\mathbf{p}}}, \end{aligned}$$

Finally apply Roths theorem (Roth 1934), $(\mathbf{C}^\top \otimes \mathbf{A}) \text{vec} \mathbf{B} = \text{vec} \mathbf{ABC}$, to the equation above (e.g. $\mathbf{C}^\top = \hat{\mathbf{p}}_{AA}^\top$, $\mathbf{A} = (\mathbf{e}_1 \otimes \mathbf{I}_\omega)$, and $\text{vec} \mathbf{B} = \text{vec} \mathbf{F}_{AA}$) to write this as

$$\begin{aligned} \frac{1}{\lambda_{AA}} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{\omega g}) \left. \frac{\partial \text{vec} \mathbf{A}}{\partial \tilde{\mathbf{p}}^\top} \right|_{\tilde{\mathbf{p}}} &= \frac{\alpha}{\lambda_{AA}} [\text{vec}((\mathbf{e}_1 \otimes \mathbf{I}_\omega) \mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) - \text{vec}((\mathbf{e}_3 \otimes \mathbf{I}_\omega) \mathbf{F}_{AA} \hat{\mathbf{p}}_{AA})] \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{p}}^\top} \right|_{\tilde{\mathbf{p}}} \\ &+ \frac{(1-\alpha)}{\lambda_{AA}} [\text{vec}((\mathbf{e}_2 \otimes \mathbf{I}_\omega) \mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) - \text{vec}((\mathbf{e}_4 \otimes \mathbf{I}_\omega) \mathbf{F}_{AA} \hat{\mathbf{p}}_{AA})] \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{p}}^\top} \right|_{\tilde{\mathbf{p}}}. \end{aligned}$$

Written in terms of block matrices this expression yields

$$\frac{1}{\lambda_{AA}} \begin{pmatrix} \mathbf{0} & \alpha(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{AA}} & \mathbf{0} & \alpha(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{Aa}} & \mathbf{0} & \alpha(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{aa}} \\ \mathbf{0} & (1-\alpha)(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{AA}} & \mathbf{0} & (1-\alpha)(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{Aa}} & \mathbf{0} & (1-\alpha)(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{aa}} \\ \hline \mathbf{0} & -\alpha(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{AA}} & \mathbf{0} & -\alpha(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{Aa}} & \mathbf{0} & -\alpha(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{aa}} \\ \mathbf{0} & -(1-\alpha)(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{AA}} & \mathbf{0} & -(1-\alpha)(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{Aa}} & \mathbf{0} & -(1-\alpha)(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q'_A}{\partial \mathbf{p}'_{aa}} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix}. \quad (3.A52)$$

Equation (3.A52) requires the derivative of the frequency of allele A in the gamete pool with respect to the population frequency vector:

$$\left. \frac{\partial q'_A}{\partial \tilde{\mathbf{p}}^\top} \right|_{\tilde{\mathbf{p}}}. \quad (3.A53)$$

Start with equation (3.5) from the main text:

$$\begin{pmatrix} q'_A \\ q'_a \end{pmatrix} = \frac{\mathbf{W}' \mathbf{F}' \mathbf{n}'}{\|\mathbf{W}' \mathbf{F}' \mathbf{n}'\|}, \quad (3.A54)$$

therefore

$$q'_A = \frac{\mathbf{e}_1^\top \mathbf{W}' \mathbf{F}' \mathbf{p}'}{\mathbf{1}_2^\top \mathbf{W}' \mathbf{F}' \mathbf{p}'}, \quad (3.A55)$$

where we can substitute \mathbf{p}' for \mathbf{n}' because of homogeneity and where the one norm can be replaced by $\mathbf{1}_2^\top \mathbf{W}' \mathbf{F}' \mathbf{p}'$ because \mathbf{p}' is nonnegative. For convenience, we will denote the normalizing factor in the denominator with p_n ,

$$p_n = \mathbf{1}_2^\top \mathbf{W}' \mathbf{F}' \mathbf{p}' \quad (3.A56)$$

Taking the derivative of q'_A yields

$$\frac{\partial q'_A}{\partial \tilde{\mathbf{p}}^\top} = \frac{1}{p_n} \mathbf{e}_1^\top \mathbf{W}' \mathbf{F}' \frac{\partial \mathbf{p}'}{\partial \tilde{\mathbf{p}}^\top} - \frac{\mathbf{e}_1^\top \mathbf{W}' \mathbf{F}' \mathbf{p}'}{p_n^2} \left(\mathbf{1}_2^\top \mathbf{W}' \mathbf{F}' \frac{\partial \mathbf{p}'}{\partial \tilde{\mathbf{p}}^\top} \right). \quad (3.A57)$$

Recall

$$\mathbf{p}' = \begin{pmatrix} \mathbf{p}'_{AA} \\ \mathbf{p}'_{Aa} \\ \mathbf{p}'_{aa} \end{pmatrix}, \quad (3.A58)$$

and

$$\tilde{\mathbf{p}} = \begin{pmatrix} \mathbf{p}_{AA} \\ \frac{\mathbf{p}'_{AA}}{\mathbf{p}_{AA}} \\ \frac{\mathbf{p}'_{Aa}}{\mathbf{p}_{Aa}} \\ \frac{\mathbf{p}'_{aa}}{\mathbf{p}_{aa}} \end{pmatrix}, \quad (3.A59)$$

to calculate

$$\frac{\partial \mathbf{p}'}{\partial \tilde{\mathbf{p}}^\top} = \begin{pmatrix} \mathbf{0} & \mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I} \end{pmatrix}. \quad (3.A60)$$

Finally evaluate $\frac{\partial q'_A}{\partial \tilde{\mathbf{p}}^\top}$ at the boundary to obtain

$$\left. \frac{\partial q'_A}{\partial \tilde{\mathbf{p}}^\top} \right|_{\tilde{\mathbf{p}}} = \frac{1}{p_n} \left(\mathbf{0}, \mathbf{0}, \mathbf{0}, -\frac{1}{2} \mathbf{1}_\omega^\top \mathbf{F}'_{Aa}, \mathbf{0}, -\mathbf{1}_\omega^\top \mathbf{F}'_{aa} \right), \quad (3.A61)$$

where at the boundary

$$p_n = \mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{p}}'_{AA}. \quad (3.A62)$$

Finally, plugging equation (3.A61) into (3.A52) yields

$$\frac{1}{\lambda_{AA}} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{2\omega g}) \frac{\partial \text{vec} \mathbf{A}}{\partial \hat{\mathbf{p}}^\top} \Big|_{\hat{\mathbf{p}}} = \frac{1}{\lambda_{AA}} \left(\begin{array}{cc|cc|cc} \mathbf{0} & \mathbf{0} & \mathbf{0} & -\frac{\alpha}{2p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa} & \mathbf{0} & -\frac{\alpha}{p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{aa} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & -\frac{(1-\alpha)}{2p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa} & \mathbf{0} & -\frac{(1-\alpha)}{p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{aa} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \frac{\alpha}{2p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa} & \mathbf{0} & \frac{\alpha}{p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{aa} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \frac{(1-\alpha)}{2p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa} & \mathbf{0} & \frac{(1-\alpha)}{p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{aa} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array} \right) \quad (3.A63)$$

The Jacobian

Putting it all together, i.e. substituting equations (3.A32), (3.A37), and (3.A63) into equation (3.A30), we get the Jacobian:

$$\mathbf{M} = \frac{1}{\lambda_{AA}} \left(\begin{array}{cc|cc|cc} \mathbf{U}_{AA} + \alpha \mathbf{F}_{AA} & \mathbf{0} & \frac{1}{2} \alpha \mathbf{F}_{Aa} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ (1-\alpha) \mathbf{F}_{AA} & \mathbf{U}'_{AA} & \frac{1}{2} (1-\alpha) \mathbf{F}_{Aa} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{U}_{Aa} + \frac{1}{2} \alpha \mathbf{F}_{Aa} & \mathbf{0} & \alpha \mathbf{F}_{aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \frac{1}{2} (1-\alpha) \mathbf{F}_{Aa} & \mathbf{U}'_{Aa} & (1-\alpha) \mathbf{F}_{aa} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}'_{aa} \end{array} \right)$$

$$- \frac{1}{\lambda_{AA}} \mathbf{C} \left(\begin{array}{cc|cc|cc} (\mathbf{U}_{AA} + \mathbf{F}_{AA}) & \mathbf{U}'_{AA} & (\mathbf{U}_{Aa} + \mathbf{F}_{Aa}) & \mathbf{U}'_{Aa} & (\mathbf{U}_{aa} + \mathbf{F}_{aa}) & \mathbf{U}'_{aa} \\ (\mathbf{U}_{AA} + \mathbf{F}_{AA}) & \mathbf{U}'_{AA} & (\mathbf{U}_{Aa} + \mathbf{F}_{Aa}) & \mathbf{U}'_{Aa} & (\mathbf{U}_{aa} + \mathbf{F}_{aa}) & \mathbf{U}'_{aa} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array} \right)$$

$$+ \frac{1}{\lambda_{AA}} \left(\begin{array}{cc|cc|cc} \mathbf{0} & \mathbf{0} & \mathbf{0} & -\frac{\alpha}{2p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa} & \mathbf{0} & -\frac{\alpha}{p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{aa} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & -\frac{(1-\alpha)}{2p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa} & \mathbf{0} & -\frac{(1-\alpha)}{p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{aa} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \frac{\alpha}{2p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa} & \mathbf{0} & \frac{\alpha}{p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{aa} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \frac{(1-\alpha)}{2p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa} & \mathbf{0} & \frac{(1-\alpha)}{p_n} (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{aa} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array} \right) \quad (3.A64)$$

Eigenvalues of the Jacobian

The Jacobian matrix, given by equation (3.A64), is upper block triangular, so the eigenvalues of \mathbf{M} are the eigenvalues of the diagonal blocks. The largest absolute eigenvalue of the Jacobian, i.e. the spectral radius $\rho(\mathbf{M})$, determines the stability of the boundary equilibrium. We will denote the three nonzero blocks along the diagonal with \mathbf{M}_{11} , \mathbf{M}_{22} , and \mathbf{M}_{33} (see equation (3.17)), such that for example

$$\mathbf{M}_{33} = \begin{pmatrix} \mathbf{U}_{aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{U}'_{aa} \end{pmatrix}. \quad (3.A65)$$

Block \mathbf{M}_{33} projects perturbations in the aa direction. In the neighbourhood 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 $\lambda_{AA} < \rho(\mathbf{M}_{33}) < 1$. 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. The block \mathbf{M}_{11} projects perturbations in the AA boundary, and because $\hat{\mathbf{p}}$ is stable to perturbations in that boundary, $\rho(\mathbf{M}_{11}) < 1$.

The stability of $\hat{\mathbf{p}}$ is thus determined by

$$\mathbf{M}_{22} = \frac{1}{\lambda_{AA}} \begin{pmatrix} \mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} & \frac{\alpha}{2} \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes (\mathbf{1}_\omega^T \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^T \mathbf{F}'_{AA} \hat{\mathbf{p}}'_{AA}} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & \mathbf{U}'_{Aa} + \frac{(1-\alpha)}{2} \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes (\mathbf{1}_\omega^T \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^T \mathbf{F}'_{AA} \hat{\mathbf{p}}'_{AA}} \end{pmatrix}, \quad (3.A66)$$

which is equation (3.18) in the main text. The largest absolute value of the eigenvalues of the Jacobian matrix, the dominant eigenvalue, evaluated at the AA boundary, denoted by ζ_{AA} , is therefore

$$\tilde{\zeta}_{AA} = \frac{1}{\lambda_{AA}} \rho \left(\begin{pmatrix} \mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} & \frac{\alpha}{2} \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes (\mathbf{1}_\omega^T \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^T \mathbf{F}'_{AA} \hat{\mathbf{p}}'_{AA}} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & \mathbf{U}'_{Aa} + \frac{(1-\alpha)}{2} \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes (\mathbf{1}_\omega^T \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^T \mathbf{F}'_{AA} \hat{\mathbf{p}}'_{AA}} \end{pmatrix} \right), \quad (3.A67)$$

equation (3.21) in the main text. By symmetry, the dominant eigenvalue of the Jacobian matrix evaluated at the aa boundary, denoted by $\tilde{\zeta}_{aa}$, is

$$\tilde{\zeta}_{aa} = \frac{1}{\lambda_{aa}} \rho \left(\begin{pmatrix} \mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} & \frac{\alpha}{2} \frac{(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa}) \otimes (\mathbf{1}_\omega^T \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^T \mathbf{F}'_{aa} \hat{\mathbf{p}}'_{aa}} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & \mathbf{U}'_{Aa} + \frac{(1-\alpha)}{2} \frac{(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa}) \otimes (\mathbf{1}_\omega^T \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^T \mathbf{F}'_{aa} \hat{\mathbf{p}}'_{aa}} \end{pmatrix} \right), \quad (3.A68)$$

which is equation (3.22). If both boundaries are unstable, then both alleles will coexist. The coexistence conditions are therefore given by

$$\rho \begin{pmatrix} \mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} & \frac{\alpha}{2} \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{p}}'_{AA}} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & \mathbf{U}'_{Aa} + \frac{(1-\alpha)}{2} \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{p}}'_{AA}} \end{pmatrix} > \lambda_{AA}, \quad (3.A69)$$

$$\rho \begin{pmatrix} \mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} & \frac{\alpha}{2} \frac{(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{aa} \hat{\mathbf{p}}'_{aa}} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & \mathbf{U}'_{Aa} + \frac{(1-\alpha)}{2} \frac{(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{aa} \hat{\mathbf{p}}'_{aa}} \end{pmatrix} > \lambda_{aa}, \quad (3.A70)$$

(equations (3.25) and (3.26)).

Appendix 3.B Coexistence conditions under simplifying assumptions

$$\mathbf{U}_i = \mathbf{U}'_i$$

In this section, we consider a simplification that removes sexual dimorphism in survival and transition rates, $\mathbf{U}_i = \mathbf{U}'_i$. We consider block \mathbf{M}_{22} of the Jacobian matrix, equation (3.A66)

$$\mathbf{M}_{22} = \frac{1}{\lambda_{AA}} \begin{pmatrix} \mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} & \frac{1}{2}\alpha\mathbf{D}_{AA} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & \mathbf{U}_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA} \end{pmatrix}, \quad (3.B1)$$

where we use the following notation (equation (3.19) the main text),

$$\mathbf{D}_{AA} = \frac{(\mathbf{F}_{AA}\hat{\mathbf{P}}_{AA}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{P}}'_{AA}}. \quad (3.B2)$$

Consider an eigenvector of this matrix,

$$\mathbf{v} = \begin{pmatrix} \mathbf{u} \\ \mathbf{u}' \end{pmatrix}, \quad (3.B3)$$

with eigenvalue x , which has to satisfy the following equation

$$\frac{1}{\lambda_{AA}} \begin{pmatrix} \mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} & \frac{1}{2}\alpha\mathbf{D}_{AA} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & \mathbf{U}_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA} \end{pmatrix} \begin{pmatrix} \mathbf{u} \\ \mathbf{u}' \end{pmatrix} = x \begin{pmatrix} \mathbf{u} \\ \mathbf{u}' \end{pmatrix}. \quad (3.B4)$$

We have written the eigenvector in terms of a vector associated with the female direction, \mathbf{u} , and a vector associated with the male direction \mathbf{u}' . Write equation (3.B4) as two separate equations for the male and female directions,

$$\left(\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} \right) \mathbf{u} + \frac{1}{2}\alpha\mathbf{D}_{AA}\mathbf{u}' = \lambda_{AA}x\mathbf{u}, \quad (3.B5)$$

$$\left(\mathbf{U}_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA} \right) \mathbf{u}' + \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa}\mathbf{u} = \lambda_{AA}x\mathbf{u}'. \quad (3.B6)$$

Moving the terms $\mathbf{U}_{Aa}\mathbf{u}$ and $\mathbf{U}_{Aa}\mathbf{u}'$ to the right in the top and bottom equations respectively yields,

$$\frac{1}{2}\alpha [\mathbf{F}_{Aa}\mathbf{u} + \mathbf{D}_{AA}\mathbf{u}'] = (\lambda_{AA}x\mathbf{I}_\omega - \mathbf{U}_{Aa})\mathbf{u}, \quad (3.B7)$$

$$\frac{1}{2}(1-\alpha) [\mathbf{F}_{Aa}\mathbf{u} + \mathbf{D}_{AA}\mathbf{u}'] = (\lambda_{AA}x\mathbf{I}_\omega - \mathbf{U}_{Aa})\mathbf{u}'. \quad (3.B8)$$

Provided the matrix $(\lambda_{AA}x\mathbf{I} - \mathbf{U}_{Aa})$ is non-singular,

$$\mathbf{u} = \frac{1}{2}\alpha (\lambda_{AA}x\mathbf{I}_\omega - \mathbf{U}_{Aa})^{-1} [\mathbf{F}_{Aa}\mathbf{u} + \mathbf{D}_{AA}\mathbf{u}'], \quad (3.B9)$$

$$\mathbf{u}' = \frac{1}{2}(1-\alpha) (\lambda_{AA}x\mathbf{I}_\omega - \mathbf{U}_{Aa})^{-1} [\mathbf{F}_{Aa}\mathbf{u} + \mathbf{D}_{AA}\mathbf{u}'], \quad (3.B10)$$

which implies

$$\mathbf{u}' = \frac{(1-\alpha)}{\alpha} \mathbf{u}. \quad (3.B11)$$

Substituting this relationship between the male and female directions of the eigenvector back into equation (3.B4) yields

$$\frac{1}{\lambda_{AA}} \begin{pmatrix} \mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} & \frac{\alpha}{2}\mathbf{D}_{AA} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & \mathbf{U}_{Aa} + \frac{(1-\alpha)}{2}\mathbf{D}_{AA} \end{pmatrix} \begin{pmatrix} \mathbf{u} \\ \frac{(1-\alpha)}{\alpha}\mathbf{u} \end{pmatrix} = x \begin{pmatrix} \mathbf{u} \\ \frac{(1-\alpha)}{\alpha}\mathbf{u} \end{pmatrix}. \quad (3.B12)$$

Write out the equation for the first block of the eigenvector:

$$\frac{1}{\lambda_{AA}} \left[\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA} \right] \mathbf{u} = x\mathbf{u}. \quad (3.B13)$$

This equation shows that the eigenvalues x of the $2\omega \times 2\omega$ matrix \mathbf{M}_{22} , given by equation (3.B1), are also eigenvalues of the following matrix of dimensions $\omega \times \omega$ (namely, the left-hand side of equation (3.B13)),

$$\frac{1}{\lambda_{AA}} \left[\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA} \right]. \quad (3.B14)$$

Therefore the dominant eigenvalue of the $2\omega \times 2\omega$ matrix \mathbf{M}_{22} is

$$\tilde{\zeta}_{AA} = \frac{1}{\lambda_{AA}} \rho \left[\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA} \right]. \quad (3.B15)$$

Similarly for $\tilde{\zeta}_{aa}$,

$$\tilde{\zeta}_{aa} = \frac{1}{\lambda_{aa}} \rho \left[\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{aa} \right]. \quad (3.B16)$$

The coexistence conditions are then given by

$$\rho \left[\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA} \right] > \lambda_{AA}, \quad (3.B17)$$

$$\rho \left[\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{aa} \right] > \lambda_{aa}, \quad (3.B18)$$

$\mathbf{U}_i = \mathbf{U}'_i$, $\mathbf{F}_i = \beta\mathbf{F}'_i$ and $\alpha = 0.5$

Next we make the additional simplifying assumption that male mating success is proportional (or equal) to female fertility, $\mathbf{F}'_i = \beta\mathbf{F}_i$. Finally, we also set the primary sex to one, i.e. $\alpha = 0.5$. We will show that these simplifying assumptions reduce the coexistence conditions, equations (3.A70) and (3.A69) to heterozygote superiority in genotype-specific population growth rate, i.e. $\lambda_{Aa} > \lambda_{AA}$ and $\lambda_{Aa} > \lambda_{aa}$.

Since males only have one type of offspring, the \mathbf{F}'_i matrices only have one nonzero row. Without loss of generality, we put the newborns in the first stage and hence the first row of the matrix \mathbf{F}'_i is the only nonzero row. Equating male mating succes to female fertility rates, $\mathbf{F}'_i = \beta \mathbf{F}_i$, then implies that females also only produce one type of offspring. Define a vector of fertilities of dimensions $\omega \times 1$ for each genotype, \mathbf{f}_i , such that

$$\mathbf{F}_i = \begin{pmatrix} f_i(1) & \dots & f_i(\omega) \\ 0 & \dots & 0 \\ \vdots & & \vdots \\ \mathbf{0} & \dots & 0 \end{pmatrix}, \quad (3.B19)$$

$$= \mathbf{e}_1 \otimes \mathbf{f}_i^\top. \quad (3.B20)$$

The following equalities hold in this case

$$\mathbf{F}_{AA} \hat{\mathbf{P}}_{AA} = \mathbf{e}_1 \otimes (\mathbf{f}_{AA}^\top \hat{\mathbf{P}}_{AA}), \quad (3.B21)$$

$$\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{P}}_{AA} = \beta \mathbf{f}_{AA}^\top \hat{\mathbf{P}}_{AA}, \quad (3.B22)$$

$$\mathbf{1}_\omega^\top \mathbf{F}'_{Aa} = \beta \mathbf{f}_{Aa}^\top. \quad (3.B23)$$

Substituting these equalities into the \mathbf{D}_{AA} matrix yields

$$\mathbf{D}_{AA} = \frac{(\mathbf{F}_{AA} \hat{\mathbf{P}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa}}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{P}}_{AA}} = \mathbf{e}_1 \otimes \mathbf{f}_{Aa}^\top, \quad (3.B24)$$

$$= \mathbf{F}_{Aa}. \quad (3.B25)$$

Similarly,

$$\mathbf{D}_{aa} = \frac{(\mathbf{F}_{aa} \hat{\mathbf{P}}_{aa}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{aa} \hat{\mathbf{P}}_{aa}} = \mathbf{F}_{Aa}, \quad (3.B26)$$

Substituting this expression for \mathbf{D}_{AA} back into the coexistence conditions derived in the previous section, equations (3.B17) and (3.B18) yields

$$\rho \left(\mathbf{U}_{Aa} + \frac{1}{2} \alpha \mathbf{F}_{Aa} + \frac{1}{2} (1 - \alpha) \mathbf{F}_{Aa} \right) > \rho (\mathbf{U}_{AA} + \alpha \mathbf{F}_{AA}), \quad (3.B27)$$

$$\rho \left(\mathbf{U}_{Aa} + \frac{1}{2} \alpha \mathbf{F}_{Aa} + \frac{1}{2} (1 - \alpha) \mathbf{F}_{Aa} \right) > \rho (\mathbf{U}_{aa} + \alpha \mathbf{F}_{aa}), \quad (3.B28)$$

or

$$\rho \left(\mathbf{U}_{Aa} + \frac{1}{2} \mathbf{F}_{Aa} \right) > \rho (\mathbf{U}_{AA} + \alpha \mathbf{F}_{AA}), \quad (3.B29)$$

$$\rho \left(\mathbf{U}_{Aa} + \frac{1}{2} \mathbf{F}_{Aa} \right) > \rho (\mathbf{U}_{aa} + \alpha \mathbf{F}_{aa}), \quad (3.B30)$$

(equations (3.31) and (3.32) in the main text).

If we define heterozygote population growth rate analogously to the two homozygote population growth rates, then

$$\lambda_{Aa} = \rho(\mathbf{U}_{Aa} + \alpha \mathbf{F}_{Aa}). \quad (3.B31)$$

Therefore when $\alpha = \frac{1}{2}$, the coexistence conditions given by equations (3.B29) and (3.B30) are equal to heterozygote superiority in λ , i.e.

$$\lambda_{Aa} > \lambda_{AA}, \quad (3.B32)$$

$$\lambda_{Aa} > \lambda_{aa}. \quad (3.B33)$$

All breeding males have equal mating success ($\mathbf{F}'_i = \mathbf{e}_1 \otimes \mathbf{c}_i^\top$)

Now we discuss a special case of the one-sex model where we assume that breeding males all have the same mating success, independent of their genotype and stage. This model was introduced in de Vries and Caswell (2018a). The frequencies in the gamete pool, q_A and q_a , are simply equal to the frequencies of these alleles in the breeding part of the population, denoted by q_A^b and q_a^b in de Vries and Caswell (2018a). The mating population is defined by a set of indicator vectors \mathbf{c}_i for $i = 1, \dots, g$ that show which stages of genotype i take part in mating. That is, the entries of \mathbf{c}_i are 1 if that stage of genotype i reproduces, and 0 otherwise.

The genotype specific mating success matrices \mathbf{F}'_i can then be written in terms of these indicator vectors as follows

$$\mathbf{F}'_i = \mathbf{e}_1 \otimes \mathbf{c}_i^\top. \quad (3.B34)$$

If we denote the fraction of the population that is in a breeding stage by p_b , then

$$\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{P}}_{AA} = \mathbf{c}_{AA}^\top \hat{\mathbf{P}}_{AA} = p_b. \quad (3.B35)$$

Substitute this expression into the definition of \mathbf{D}_{AA} ,

$$\mathbf{D}_{AA} = \frac{(\mathbf{F}_{AA} \hat{\mathbf{P}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa}}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{P}}_{AA}} \quad (3.B36)$$

$$= \frac{1}{p_b} (\mathbf{F}_{AA} \hat{\mathbf{P}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa}. \quad (3.B37)$$

Use

$$\mathbf{1}_\omega^\top \mathbf{F}'_{Aa} = \mathbf{1}_\omega^\top (\mathbf{e}_1 \otimes \mathbf{c}_{Aa}^\top) \quad (3.B38)$$

$$= \mathbf{c}_{Aa}^\top, \quad (3.B39)$$

to obtain

$$\zeta_{AA} = \frac{1}{\lambda_{AA}} \rho \left(\mathbf{U}_{Aa} + \frac{1}{2} \alpha \mathbf{F}_{Aa} + \frac{1}{2p_b} (1 - \alpha) (\mathbf{F}_{AA} \hat{\mathbf{P}}_{AA}) \otimes \mathbf{c}_{Aa}^\top \right), \quad (3.B40)$$

and equivalently,

$$\zeta_{aa} = \frac{1}{\lambda_{aa}} \rho \left(\mathbf{U}_{Aa} + \frac{1}{2} \alpha \mathbf{F}_{Aa} + \frac{1}{2p_b} (1 - \alpha) (\mathbf{F}_{aa} \hat{\mathbf{p}}_{aa}) \otimes \mathbf{c}_{Aa}^T \right). \quad (3.B41)$$

These two equations correspond exactly with the results reported in de Vries and Caswell (2018a) for $\alpha = 0.5$, where α is absorbed into the definition of the fertility matrix in the one-sex model.

No population structure

In the absence of population structure, the demographic matrices \mathbf{U}_i , \mathbf{U}'_i , \mathbf{F}_i , and \mathbf{F}'_i all reduce to scalars, which we will label as u_i , u'_i , f_i , and f'_i respectively. Figure 3.A1 shows the coexistence conditions for a population without any age or stage structure are shown. The flow diagram follows exactly the same series of simplifications as Figure 3.3. First male and female survival are equated (Model 2). Next polymorphism conditions are shown for two different simplifying assumptions about fertility and mating success. Model 3A assumes the gene does not affect male mating success. We arbitrarily set male mating success equal to one for all genotypes. Finally model 3B assumes that genotype-specific male mating success is equal or proportional to genotype-specific female fertility. The male parameters drop out of the coexistence conditions for both model 3A and 3B.

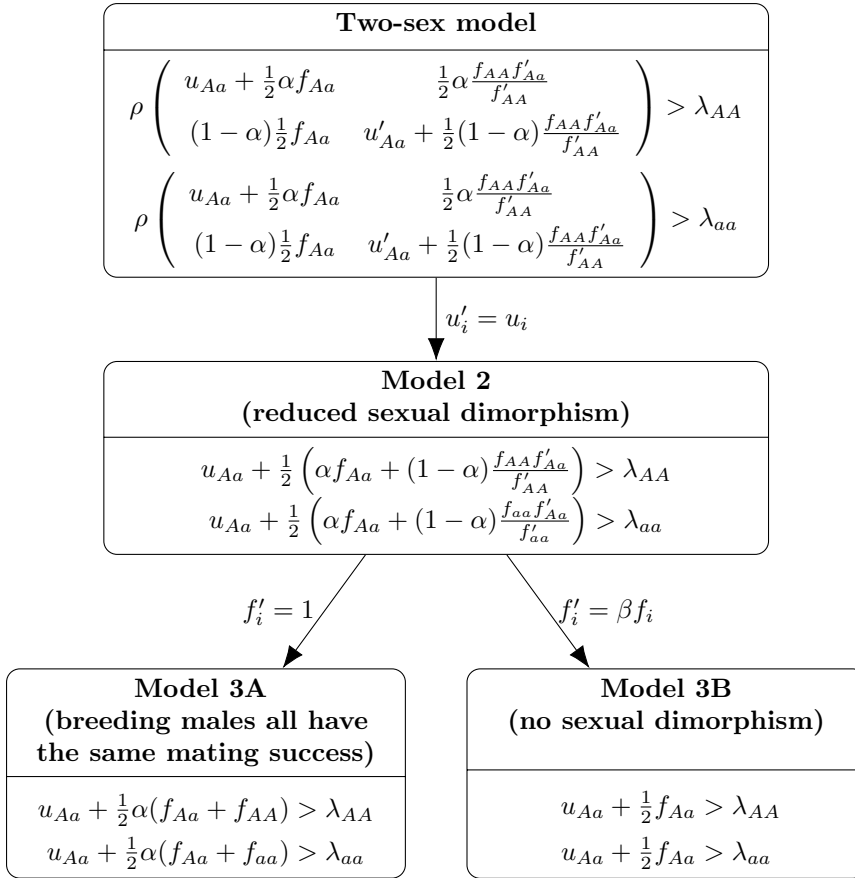


Figure 3.A1: Coexistence conditions for an unstructured two-sex model and several modifications that reduce the extent of sexual dimorphism

Appendix 3.C A females-only model (for $\mathbf{U}_i = \mathbf{U}'_i$ and $\alpha = \frac{1}{2}$)

Consider a gene that affects male mating success, or female fertility, or both, in a species with no sexual dimorphism in survival and transition rates. If males and females are furthermore born at equal proportions, then in this Appendix we show that we can model such a population by keeping track of the females only. We show that under above mentioned simplifying assumptions ($\mathbf{U}'_i = \mathbf{U}_i$, $\alpha = \frac{1}{2}$), it is possible to write down a one-sex model that has the same set of equilibria as the two-sex model and the same boundary stability properties as the two-sex model.

Notation: to distinguish between the dominant eigenvalue of the Jacobian in the two-sex model and the one-sex model, we introduce the following notation,

$\tilde{\zeta}_{ii}$ = Dominant eigenvalue of the Jacobian evaluated at the ii boundary of the two-sex model,

ζ_{ii} = Dominant eigenvalue of the Jacobian evaluated at the ii boundary of the one-sex model.

We start by showing that it is possible to construct a one-sex model with an equilibrium population structure that satisfies the same equation as the equilibrium population structure of the two-sex model when $\mathbf{U}_i = \mathbf{U}'_i$ (assuming such an equilibrium structure exists). Next we verify that the Jacobian of the one-sex model and the Jacobian of the two-sex model have the same dominant eigenvalue at the boundary equilibria, which ensures the models give the same stability conditions for the boundary equilibria.

Stationary distribution

We start by showing that it is possible to write down a model projecting the female vector only with a stationary distribution that satisfies the same equation as the full two-sex model. First, we write the population projection equation of the two-sex model, equation (3.3), as two projection equations, one for males and one for females, using equation (3.7):

$$\mathbf{n}(t+1) = \mathbf{U}\mathbf{n}(t) + \alpha\mathbf{F}(\mathbf{p}')\mathbf{n}(t), \quad (3.C1)$$

$$\mathbf{n}'(t+1) = \mathbf{U}'\mathbf{n}'(t) + (1-\alpha)\mathbf{F}(\mathbf{p}')\mathbf{n}(t). \quad (3.C2)$$

A nonlinear version of the Perron-Frobenius theorem guarantees there exists a nontrivial (nonzero) constant population structure which satisfies the following equation,

$$\tilde{\mathbf{A}} \begin{bmatrix} \hat{\mathbf{n}} \\ \hat{\mathbf{n}} \end{bmatrix} = \lambda \hat{\mathbf{n}}, \quad (3.C3)$$

provided the population projection matrix $\tilde{\mathbf{A}}(\tilde{\mathbf{p}})$ is continuous and does not map any nonzero vector directly to zero (Nussbaum 1986, 1989). The constant population structure can be written in terms of the sex-specific population vectors as follows,

$$\lambda \hat{\mathbf{n}} = \mathbf{U} \hat{\mathbf{n}} + \alpha \mathbf{F}(\hat{\mathbf{p}}) \hat{\mathbf{n}}, \quad (3.C4)$$

$$\lambda \hat{\mathbf{n}}' = \mathbf{U} \hat{\mathbf{n}}' + (1 - \alpha) \mathbf{F}(\hat{\mathbf{p}}) \hat{\mathbf{n}}. \quad (3.C5)$$

A few lines of algebra yield

$$\hat{\mathbf{n}} = \alpha (\lambda \mathbf{I} - \mathbf{U})^{-1} \mathbf{F}(\hat{\mathbf{p}}) \hat{\mathbf{n}}, \quad (3.C6)$$

$$\hat{\mathbf{n}}' = (1 - \alpha) (\lambda \mathbf{I} - \mathbf{U})^{-1} \mathbf{F}(\hat{\mathbf{p}}) \hat{\mathbf{n}}, \quad (3.C7)$$

provided the matrix $(\lambda \mathbf{I} - \mathbf{U})$ is invertible. Equations (3.C6) and (3.C7) imply that $\hat{\mathbf{n}}' = \frac{(1-\alpha)}{\alpha} \hat{\mathbf{n}}$. Since the male and female population vectors are proportional, the male and female frequency vectors are equal. We can therefore replace the male frequency vector $\hat{\mathbf{p}}'$ with the female frequency vector $\hat{\mathbf{p}}$ in equation (3.C4),

$$\lambda \hat{\mathbf{n}} = [\mathbf{U} + \alpha \mathbf{F}(\hat{\mathbf{p}})] \hat{\mathbf{n}}. \quad (3.C8)$$

This condition for the female equilibrium population structure is not a function of the male population vector. It is therefore possible to write down a one-sex model with an equilibrium population structure that satisfies the same equation as the equilibrium population structure of the two-sex model, namely:

$$\mathbf{n}(t+1) = [\mathbf{U} + \alpha \mathbf{F}(\mathbf{p}(t))] \mathbf{n}(t), \quad (3.C9)$$

where the population vector is

$$\mathbf{n} = \begin{pmatrix} \mathbf{n}_{AA} \\ \mathbf{n}_{Aa} \\ \mathbf{n}_{aa} \end{pmatrix}. \quad (3.C10)$$

The fertility matrix is the same as for the two-sex model, except now the frequencies in the gamete pool are calculated from the female population vector, i.e. we replace q'_A and q'_a by q_A and q_a ,

$$\begin{pmatrix} q_A \\ q_a \end{pmatrix} = \frac{\mathbf{W}' \mathbf{F}' \mathbf{n}}{\|\mathbf{W}' \mathbf{F}' \mathbf{n}\|}, \quad (3.C11)$$

and

$$\mathbf{F}(\mathbf{p}) = \begin{pmatrix} q_A \mathbf{F}_{AA} & \frac{1}{2} q_A \mathbf{F}_{Aa} & \mathbf{0} \\ q_a \mathbf{F}_{AA} & \frac{1}{2} \mathbf{F}_{Aa} & q_a \mathbf{F}_{aa} \\ \mathbf{0} & \frac{1}{2} q_a \mathbf{F}_{Aa} & q_a \mathbf{F}_{aa} \end{pmatrix}. \quad (3.C12)$$

Although the two models have constant population structures that satisfy the same equation (equation (3.C8)), the stability of this equilibrium structure in the two models is not guaranteed to be the same. To check whether the boundary equilibria have the same stability properties in the two models, we check that the dominant eigenvalue of the Jacobian of the one-sex model is indeed equal to the dominant eigenvalue of the two-sex model in section 3.C, which turns out to be the case when $\alpha = 0.5$.

Coexistence conditions in the females-only model (i.e. $\mathbf{U}_i = \mathbf{U}'_i$)

The derivation of the one-sex model is almost identical to the derivation in de Vries and Caswell (2018a). The derivations diverge only when dealing with the allele frequencies in the gamete pool and derivatives thereof.

We start from equation (3.C9), here repeated

$$\mathbf{n}(t+1) = [\mathbb{U} + \alpha\mathbb{F}(\mathbf{p}(t))] \mathbf{n}(t), \quad (3.C13)$$

$$= \mathbf{A}[\mathbf{p}(t)] \mathbf{n}(t). \quad (3.C14)$$

The population projection matrix can be written in terms of nine $\omega \times \omega$ matrices,

$$\mathbf{A}(\mathbf{p}) = \left(\begin{array}{c|c|c} \mathbf{U}_{AA} + \alpha q_A \mathbf{F}_{AA} & \frac{1}{2} \alpha q_A \mathbf{F}_{Aa} & \mathbf{0} \\ \hline \alpha q_a \mathbf{F}_{AA} & \mathbf{U}_{Aa} + \frac{1}{2} \alpha \mathbf{F}_{Aa} & \alpha q_A \mathbf{F}_{aa} \\ \hline \mathbf{0} & \frac{1}{2} \alpha q_a \mathbf{F}_{Aa} & \mathbf{U}_{aa} + \alpha q_a \mathbf{F}_{aa} \end{array} \right). \quad (3.C15)$$

As before, we define the frequency model as follows

$$\mathbf{p}(t+1) = \frac{\mathbf{A}[\mathbf{p}(t)]\mathbf{p}(t)}{\mathbf{1}_{g\omega}^\top \mathbf{A}[\mathbf{p}(t)]\mathbf{p}(t)}, \quad (3.C16)$$

The Jacobian matrix is obtained by differentiating equation (3.C16) and evaluating the resulting derivative at the boundary equilibrium,

$$\mathbf{M} = \left. \frac{d\mathbf{p}(t+1)}{d\mathbf{p}^\top(t)} \right|_{\hat{\mathbf{p}}}. \quad (3.C17)$$

In de Vries and Caswell (2018a) it is shown that this method yields the following expression for the Jacobian matrix:

$$\begin{aligned} \mathbf{M} &= \underbrace{\frac{1}{\lambda_{AA}} \mathbf{A}(\hat{\mathbf{p}})}_{\text{(A)}} - \underbrace{\frac{1}{\lambda_{AA}^2} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{\omega g}) (\text{vec} \mathbf{A}) (\mathbf{1}_{\omega g}^\top \mathbf{A})}_{\text{(B)}} \\ &+ \underbrace{\frac{1}{\lambda_{AA}} (\hat{\mathbf{p}}^\top \otimes \mathbf{I}_{\omega g}) \frac{\partial \text{vec} \mathbf{A}}{\partial \mathbf{p}^\top} \Big|_{\hat{\mathbf{p}}}}_{\text{(C)}}, \end{aligned} \quad (3.C18)$$

where we have identified the three terms as \textcircled{A} , \textcircled{B} , and \textcircled{C} .

The next task is to work out all the terms in the above expression for the Jacobian. For \textcircled{A} and \textcircled{B} we can simply use the results derived in de Vries and Caswell (2018a),

$$\textcircled{A} = \frac{1}{\lambda_{AA}} \left(\begin{array}{c|c|c} \mathbf{U}_{AA} + \alpha \mathbf{F}_{AA} & \frac{1}{2} \alpha \mathbf{F}_{Aa} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{U}_{Aa} + \frac{1}{2} \alpha \mathbf{F}_{Aa} & \alpha \mathbf{F}_{aa} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa} \end{array} \right), \quad (3.C19)$$

$$\textcircled{B} = -\frac{1}{\lambda_{AA}} \left(\begin{array}{c|c|c} \hat{\mathbf{p}}_{AA} \otimes \mathbf{1}_\omega^\top (\mathbf{U}_{AA} + \alpha \mathbf{F}_{AA}) & \hat{\mathbf{p}}_{AA} \otimes \mathbf{1}_\omega^\top (\mathbf{U}_{Aa} + \alpha \mathbf{F}_{Aa}) & \hat{\mathbf{p}}_{AA} \otimes \mathbf{1}_\omega^\top (\mathbf{U}_{aa} + \alpha \mathbf{F}_{aa}) \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array} \right). \quad (3.C20)$$

For term \textcircled{C} we can use the following result, where we have replaced q_A^b and q_a^b from de Vries and Caswell (2018a) with q_A and q_a ,

$$\textcircled{C} = \frac{1}{\lambda_{AA}} \left(\begin{array}{c|c|c} \alpha (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q_A}{\partial \mathbf{p}_{AA}^\top} & \alpha (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q_A}{\partial \mathbf{p}_{Aa}^\top} & \alpha (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q_A}{\partial \mathbf{p}_{aa}^\top} \\ \hline -\alpha (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q_A}{\partial \mathbf{p}_{AA}^\top} & -\alpha (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q_A}{\partial \mathbf{p}_{Aa}^\top} & -\alpha (\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \frac{\partial q_A}{\partial \mathbf{p}_{aa}^\top} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array} \right). \quad (3.C21)$$

Equation (3.C21) requires the derivative of the frequency of allele A in the gamete pool with respect to the population frequency vector:

$$\left. \frac{\partial q_A}{\partial \mathbf{p}^\top} \right|_{\mathbf{p}}. \quad (3.C22)$$

Start with equation (3.C11):

$$\begin{pmatrix} q_A \\ q_a \end{pmatrix} = \frac{\mathbf{W}' \mathbf{F}' \mathbf{n}}{\|\mathbf{W}' \mathbf{F}' \mathbf{n}\|}, \quad (3.C23)$$

therefore

$$q_A = \frac{\mathbf{e}_1^\top \mathbf{W}' \mathbf{F}' \mathbf{p}}{\mathbf{1}_2^\top \mathbf{W}' \mathbf{F}' \mathbf{p}}, \quad (3.C24)$$

where we can substitute \mathbf{p} for \mathbf{n} because of homogeneity and where the one norm can be replaced by $\mathbf{1}_2^\top \mathbf{W}' \mathbf{F}' \mathbf{p}$ because \mathbf{p} is nonnegative. For convenience, we will denote the normalizing factor in the denominator with p_n ,

$$p_n = \mathbf{1}_2^\top \mathbf{W}' \mathbf{F}' \mathbf{p} \quad (3.C25)$$

Taking the derivative of q_A yields

$$\frac{\partial q_A}{\partial \mathbf{p}^\top} = \frac{1}{p_n} \mathbf{e}_1^\top \mathbf{W}' \mathbf{F}' \frac{\partial \mathbf{p}}{\partial \mathbf{p}^\top} - \frac{\mathbf{e}_1^\top \mathbf{W}' \mathbf{F}' \mathbf{p}}{p_n^2} \left(\mathbf{1}_2^\top \mathbf{W}' \mathbf{F}' \frac{\partial \mathbf{p}}{\partial \mathbf{p}^\top} \right). \quad (3.C26)$$

Evaluate this expression at the boundary, where

$$\mathbf{p}_n = \mathbf{1}'_\omega \mathbf{F}'_{AA} \hat{\mathbf{p}}_{AA}, \quad (3.C27)$$

to obtain

$$\left. \frac{\partial q_A}{\partial \mathbf{p}^\top} \right|_{\hat{\mathbf{p}}} = \frac{1}{\mathbf{p}_n} \left(\mathbf{0}, -\frac{1}{2} \mathbf{1}'_\omega \mathbf{F}'_{Aa}, -\mathbf{1}'_\omega \mathbf{F}'_{aa} \right). \quad (3.C28)$$

Finally substituting equation (3.C28) into equation (3.C21) yields

$$\textcircled{\mathbf{C}} = \frac{1}{\lambda_{AA}} \left(\begin{array}{c|c|c} \mathbf{0} & -\frac{1}{2} \alpha \frac{(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}'_\omega \mathbf{F}'_{Aa}}{\mathbf{1}'_\omega \mathbf{F}'_{AA} \hat{\mathbf{p}}_{AA}} & -\alpha \frac{(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}'_\omega \mathbf{F}'_{aa}}{\mathbf{1}'_\omega \mathbf{F}'_{AA} \hat{\mathbf{p}}_{AA}} \\ \mathbf{0} & \frac{1}{2} \alpha \frac{(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}'_\omega \mathbf{F}'_{Aa}}{\mathbf{1}'_\omega \mathbf{F}'_{AA} \hat{\mathbf{p}}_{AA}} & \alpha \frac{(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}'_\omega \mathbf{F}'_{aa}}{\mathbf{1}'_\omega \mathbf{F}'_{AA} \hat{\mathbf{p}}_{AA}} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array} \right). \quad (3.C29)$$

Putting it all together, i.e. substituting equations (3.C19), (3.C20), and (3.C29) into equation (3.A30), we get the following Jacobian:

$$\begin{aligned} \mathbf{M} &= \frac{1}{\lambda_{AA}} \left(\begin{array}{c|c|c} \mathbf{U}_{AA} + \alpha \mathbf{F}_{AA} & \frac{1}{2} \alpha \mathbf{F}_{Aa} & \mathbf{0} \\ \mathbf{0} & \mathbf{U}_{Aa} + \frac{1}{2} \alpha \mathbf{F}_{Aa} & \alpha \mathbf{F}_{aa} \\ \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa} \end{array} \right) \\ &- \frac{1}{\lambda_{AA}} \left(\begin{array}{c|c|c} \hat{\mathbf{p}}_{AA} \otimes \mathbf{1}'_\omega (\mathbf{U}_{AA} + \alpha \mathbf{F}_{AA}) & \hat{\mathbf{p}}_{AA} \otimes \mathbf{1}'_\omega (\mathbf{U}_{Aa} + \alpha \mathbf{F}_{Aa}) & \hat{\mathbf{p}}_{AA} \otimes \mathbf{1}'_\omega (\mathbf{U}_{aa} + \alpha \mathbf{F}_{aa}) \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array} \right) \\ &+ \frac{1}{\lambda_{AA}} \left(\begin{array}{c|c|c} \mathbf{0} & -\frac{1}{2} \alpha \frac{(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}'_\omega \mathbf{F}'_{Aa}}{\mathbf{1}'_\omega \mathbf{F}'_{AA} \hat{\mathbf{p}}_{AA}} & -\alpha \frac{(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}'_\omega \mathbf{F}'_{aa}}{\mathbf{1}'_\omega \mathbf{F}'_{AA} \hat{\mathbf{p}}_{AA}} \\ \mathbf{0} & \frac{1}{2} \alpha \frac{(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}'_\omega \mathbf{F}'_{Aa}}{\mathbf{1}'_\omega \mathbf{F}'_{AA} \hat{\mathbf{p}}_{AA}} & \alpha \frac{(\mathbf{F}_{AA} \hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}'_\omega \mathbf{F}'_{aa}}{\mathbf{1}'_\omega \mathbf{F}'_{AA} \hat{\mathbf{p}}_{AA}} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \end{array} \right) \end{aligned} \quad (3.C30)$$

Eigenvalues of the Jacobian

The Jacobian matrix, given by equation (3.C30), is upper block triangular, so the eigenvalues of \mathbf{M} are the eigenvalues of the diagonal blocks. The largest absolute eigenvalue of the Jacobian, i.e. the spectral radius $\rho(\mathbf{M})$, determines the stability of the boundary equilibrium. We will denote the three nonzero blocks along the diagonal with \mathbf{M}_{11} , \mathbf{M}_{22} , and \mathbf{M}_{33} , such that for example

$$\mathbf{M}_{33} = \frac{1}{\lambda_{AA}} \mathbf{U}_{aa}. \quad (3.C31)$$

Block \mathbf{M}_{33} projects perturbations in the aa direction but close to the equilibrium, aa homozygotes are negligible to first order. The block \mathbf{M}_{11} projects perturbations in the AA boundary, and because $\hat{\mathbf{p}}$ is stable to perturbations in that boundary, $\rho(\mathbf{M}_{11}) < 1$.

The stability of $\hat{\mathbf{p}}$ is thus determined by

$$\mathbf{M}_{22} = \frac{1}{\lambda_{AA}} \left(\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}\alpha \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_{\omega}^{\top}\mathbf{F}'_{Aa}}{\mathbf{1}_{\omega}^{\top}\mathbf{F}'_{AA}\hat{\mathbf{p}}_{AA}} \right). \quad (3.C32)$$

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

$$\zeta_{AA} = \frac{1}{\lambda_{AA}} \rho \left(\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}\alpha \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_{\omega}^{\top}\mathbf{F}'_{Aa}}{\mathbf{1}_{\omega}^{\top}\mathbf{F}'_{AA}\hat{\mathbf{p}}_{AA}} \right). \quad (3.C33)$$

By symmetry, the dominant eigenvalue of the Jacobian matrix evaluated at the aa boundary, denoted by ζ_{aa} , is

$$\zeta_{aa} = \frac{1}{\lambda_{aa}} \rho \left(\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}\alpha \frac{(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa}) \otimes \mathbf{1}_{\omega}^{\top}\mathbf{F}'_{Aa}}{\mathbf{1}_{\omega}^{\top}\mathbf{F}'_{aa}\hat{\mathbf{p}}_{aa}} \right). \quad (3.C34)$$

If both boundaries are unstable, then both alleles will coexist. The conditions for a genetic polymorphism are therefore given by

$$\rho \left(\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}\alpha \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_{\omega}^{\top}\mathbf{F}'_{Aa}}{\mathbf{1}_{\omega}^{\top}\mathbf{F}'_{AA}\hat{\mathbf{p}}_{AA}} \right) > \lambda_{AA}, \quad (3.C35)$$

$$\rho \left(\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}\alpha \frac{(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa}) \otimes \mathbf{1}_{\omega}^{\top}\mathbf{F}'_{Aa}}{\mathbf{1}_{\omega}^{\top}\mathbf{F}'_{aa}\hat{\mathbf{p}}_{aa}} \right) > \lambda_{aa}. \quad (3.C36)$$

Compare this to the polymorphism conditions from the two-sex model when $\mathbf{U}_i = \mathbf{U}'_i$, equations (3.B17) and (3.B18), here repeated for convenience

$$\rho \left[\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}(1-\alpha) \frac{(\mathbf{F}_{AA}\hat{\mathbf{p}}_{AA}) \otimes \mathbf{1}_{\omega}^{\top}\mathbf{F}'_{Aa}}{\mathbf{1}_{\omega}^{\top}\mathbf{F}'_{AA}\hat{\mathbf{p}}_{AA}} \right] > \lambda_{AA}, \quad (3.C37)$$

$$\rho \left[\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2}(1-\alpha) \frac{(\mathbf{F}_{aa}\hat{\mathbf{p}}_{aa}) \otimes \mathbf{1}_{\omega}^{\top}\mathbf{F}'_{Aa}}{\mathbf{1}_{\omega}^{\top}\mathbf{F}'_{aa}\hat{\mathbf{p}}_{aa}} \right] > \lambda_{aa}. \quad (3.C38)$$

These two sets of coexistence conditions are identical when $1 - \alpha = \alpha$, i.e. when $\alpha = 0.5$.