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**Density-dependent selection in two-sex
stage-structured populations.**

Charlotte de Vries

Abstract

It is often stated that evolution maximizes growth rate in the absence of density-dependence, and equilibrium population density in the presence of density regulation, provided there are no frequency-dependent processes. Although originally derived in unstructured models, both maximization principles have been extended to age-structured populations. However, these models have always assumed the sexes have identical demographic rates, thereby excluding the potential for intralocus sexual conflict. In this chapter, we combine sex-specific density-dependent demography with basic Mendelian genetics. That is, we combine the models in Chapters 3 and 4. Using this model, we show that density-dependent selection in the presence of sexual dimorphism does not maximize any stage abundance or any weighted sum of stage abundances. We derive a set of necessary and sufficient conditions for a protected polymorphism. Heterozygote superiority in population growth rate evaluated at the equilibrium density of both homozygotes is a necessary and sufficient condition for a protected polymorphism in the absence of sexual dimorphism and when the primary sex ratio is one.

5.1 Introduction

Life-history traits like longevity and life-time reproductive output vary hugely, both within and between species. Corals can live thousands of years. Females of the mayfly *Dolania americana* have an adult lifespan that can be as short as 5 minutes. In most organisms the majority of newborns die before they can reproduce, and a few individuals live long and contribute many offspring to the next generation (Newton 1985; Snyder and Ellner 2018). This leads to very skewed distributions of life-time reproductive success (Moran and Clark 2012), i.e. it leads to lots of intraspecific variation.

Differences in life-history strategies have been explained by different levels of environmental perturbations experienced by populations (MacArthur and Wilson 1967). Populations in highly perturbed environments rarely reach densities high enough to lead to competition for resources or space, and therefore rarely experience density-dependent selection (Caswell 1982). These populations are said to be selected for fast growth and short lifespans (growth selected or r -selected). Large fractions of plankton communities in intertidal pools are washed out by waves every day, for example, thereby generally keeping densities for below carrying capacity (Sousa 1979). Populations in very stable environments, on the other hand, will grow until competition for food and space becomes fierce (carrying capacity or K -selected). As a consequence, the controversial but highly influential theory of $r - K$ selection predicts that fast life-histories with short lifespans will evolve in highly perturbed environments (r -selected), and slow life-histories with long lifespans will evolve in stable environments.

Two maximization principles are derived from models of r - K selection: evolution maximizes growth rates in the absence of density regulation, and equilibrium population density in the presence of density regulation (see for example, Lande (1982*b*); Engen and Sæther (2017)). Many of these models have implemented evolutionary change in population-level parameters like habitat-specific intrinsic growth rates r or carrying capacities K (MacArthur 1962; MacArthur and Wilson 1967; Roughgarden 1971; Lande et al. 2009). Rueffler et al. (2006) show that two dangers are lurking when evolutionary predictions are based on population level parameters. First, population-level parameters are treated as independent in these models, whereas the individual level processes that the parameters are supposed to capture might lead to correlations between them. Second, the mapping from individual level traits to higher-level parameters might be nonlinear, such that trade-off curvatures are not inherited from the individual level to the population level.

A further problem with modeling evolution at the population level is that it ignores the evolutionary consequences of interindividual variation. Individuals of the same species differ, among others, with respect to their age, size, sex, immunocompetence, and marital status. Since individuals differ, a trait that is beneficial for one individual can be disadvantageous for another. Some of these differences, such as age and stage, have been incorporated in models of density-dependent selection (Charlesworth 1994; Takada and Nakajima 1998), and density-independent selection (Lande 1982*a,b*; Tuljapurkar 1982; Charlesworth 1994). But a general framework that includes density-dependent selection, genetics, sex differences, and any other relevant individual differences has been lacking. Here, we introduce such a framework by combining a two-sex matrix population model with any age- or stage-structured density-dependent demography with basic Mendelian genetics.

Some of the most extravagant interindividual differences in sexually reproducing populations are differences between males and females. Due to these sex differences, males and females often have different trait optima. In collared flycatchers (*Ficedula albicollis*), for example, male nestlings have a higher survival if they are relatively small, whereas female nestlings do better if they are relatively large (Merilä et al. 1997). In zebra finches, males with the reddest bill color have the highest fitness because females like red bills. Females with red bills, on the other hand, experience reduced survival relative to females with less intense colours (Price and Burley 1994).

Intralocus sexual conflict arises if the evolution of a trait is constrained by the shared genetic architecture of the two sexes (Van Doorn 2009). Once a gene has invaded that benefits sex A at the expense of sex B, there is selection pressure on the losing sex (B) to evolve ways of suppressing or silencing the gene. An intraspecific Red Queen race between males and females can result from this process (Rice and Holland 1997). Since females are usually more important for population growth, population fitness is expected to suffer if females are losing the conflict (Kokko and Jennions 2014). In sexually reproducing populations, it is therefore highly doubtful that evolution will maximize growth rates or equilibrium population densities.

In this paper, we will answer two questions: (1) Does selection maximize equilibrium population size in a density-dependent, two-sex demographic model with Mendelian genetics? (2) Under which conditions does density-dependent selection lead to a protected polymorphism in a two-sex structured population? To answer these questions, we use a model with arbitrarily complex demographic structure, but with simple one locus, two allele genetics.

Allelic effects have to cascade through several mappings to result in a population level change: from gene to enzymes and their regulation, from enzymes to

the development of physical characteristics like plumage colour or immune competency, from physical characteristics to individual demographic rates, and finally from demographic rates to population level characteristics. A complete understanding of evolution would therefore require knowledge of this entire cascade of mappings (Lewontin 1974; Rueffler et al. 2006; Coulson et al. 2006). Theoretical biologists have traditionally solved this problem by either ignoring the genotype-phenotype map altogether (quantitative genetics, adaptive dynamics, game theory, and optimization models), or by assuming an extremely simplified genotype-phenotype map by assigning fixed fitness values to alleles (population genetics). The framework in this paper fits squarely in the tradition of population genetics, but expands the phenotype from a single scalar fitness value to the entire life cycle of the organism. It can therefore incorporate genes with arbitrarily many pleiotropic and sex-specific effects.

We use matrix calculus (Caswell 2007*b*, 2018) to derive a set of necessary and sufficient conditions for a protected polymorphism. We define a protected polymorphism by the stability of the two homozygote boundaries to invasion by the other allele: if both boundaries are unstable to invasion by the other allele, then the population can never return to a homozygote state once both alleles are present (since both alleles grow when rare). We show that the conditions for a protected polymorphism reduce to heterozygote superiority in genotype-specific population growth rate in the absence of sexual dimorphism. If density-dependence is exerted by one stage or one weighted sum of stages, and if the population growth rate is a monotonically decreasing function of this weighted sum of stages, we find that heterozygote superiority in population growth rate at the boundaries is equivalent to heterozygote superiority in equilibrium density of this stage or weighted sum of stages.

5.2 Model construction

The two-sex density-dependent model in this chapter is a combination of the two-sex density-independent model in Chapter 3 with the density-dependent one-sex genetic model in Chapter 4. This model construction section follows the model construction as presented in these two earlier chapters closely. For notational reasons, we denote the total population vector by $\tilde{\mathbf{m}}$ in this chapter, and the entries of $\tilde{\mathbf{m}}$ by m_i . The purpose of this modified notation is to be able to refer to a stage abundance of an unspecified sex, whereas n_i and n'_i refer to a male and female stage abundance, respectively.

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 the source of selective differences. In this section we consider general density dependence without specifying a functional dependence. In section 5.4 we consider a case study.

We make the standard demographic assumption of female demographic dominance, i.e. that there are enough males to fertilize all the females, and that 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 2018b), but this is beyond the scope of the current paper.

The vectors describing the population are listed in Table 5.1. All mathematical objects relating to males (demographic rates, population vectors, etc) are denoted with a prime. The total population vector of size $2\omega g \times 1$ is denoted with $\tilde{\mathbf{m}}$; the sex-specific population vectors of size $\omega g \times 1$ are denoted with \mathbf{n} and \mathbf{n}' . Finally the genotype- and sex-specific vectors of size $\omega \times 1$ are indicated with a subscript, \mathbf{n}_i and \mathbf{n}'_i . 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 5.1: Mathematical notation used in this paper. Dimensions of vectors and matrices 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	
$\tilde{\mathbf{m}}$	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 vector	$\omega g \times 1$
\mathbf{p}'	Male stage \times genotype 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	$a \times 1$

A population vector is constructed by ordering the densities in each sex \times stage \times genotype combination and placing them in a column vector. The com-

plete population vector is

$$\tilde{\mathbf{m}}(t) = \left(\frac{\mathbf{n}(t)}{\mathbf{n}'(t)} \right) = \begin{pmatrix} \mathbf{n}_{AA}(t) \\ \mathbf{n}_{Aa}(t) \\ \mathbf{n}_{aa}(t) \\ \mathbf{n}'_{AA}(t) \\ \mathbf{n}'_{Aa}(t) \\ \mathbf{n}'_{aa}(t) \end{pmatrix}. \quad (5.1)$$

where \mathbf{n}_{AA} is the stage distribution vector of females of genotype AA and \mathbf{n}'_{AA} is the stage distribution vector of males of genotype AA; both are of size $\omega \times 1$. The proportional population vector is

$$\tilde{\mathbf{p}}(t) = \frac{\tilde{\mathbf{m}}(t)}{\|\tilde{\mathbf{m}}(t)\|} = \left(\frac{\mathbf{p}(t)}{\mathbf{p}'(t)} \right), \quad (5.2)$$

where $\|\cdot\|$ is the 1-norm.

The model projects the population vector $\tilde{\mathbf{m}}$ from time t to $t + 1$ by an *eco-evolutionary projection matrix* $\tilde{\mathbf{A}}[\tilde{\mathbf{m}}]$, so that

$$\tilde{\mathbf{m}}(t + 1) = \tilde{\mathbf{A}}[\tilde{\mathbf{m}}(t)] \tilde{\mathbf{m}}(t). \quad (5.3)$$

Component matrices

The population projection matrix $\tilde{\mathbf{A}}[\tilde{\mathbf{m}}]$ is constructed from matrices that capture the demographic processes for each sex and genotype. We define

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

where explicit time-dependence of the population vector, $\tilde{\mathbf{m}}(t)$, has been dropped to avoid a proliferation of brackets. As in the previous chapters, the $\mathbf{F}_i(\tilde{\mathbf{m}})$ matrices contain stage-specific fertilities for females of genotype i . The matrices $\mathbf{F}'_i(\tilde{\mathbf{m}})$ determine the contribution by males of genotype i to the gamete pool, and therefore to zygotes in the next generation.

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

Finally, we define matrices $\mathbf{H}_i(\tilde{\mathbf{m}})$, of dimension $g \times g$, that map the genotype of a mother in stage i to the genotype of her offspring. 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 . For the purpose of this paper, we assume that mating is random with respect to stage and hence that the parent-offspring map is the same for all stages, i.e. $\mathbf{H}_i(\tilde{\mathbf{m}}) = \mathbf{H}(\tilde{\mathbf{m}})$ (assortative mating by stage would lead to differences among the \mathbf{H}_i).

Mating: from genotypes of parents to genotypes of offspring (the parent-offspring map $\mathbf{H}(\tilde{\mathbf{m}})$)

We construct the parent-offspring map in exactly the same way as in Chapter 3, except that now male mating success can be a function of the population vector. To model the differential contribution of genes to the next generation by males, a gamete pool is constructed. Males of each stage and genotype combination contribute differentially to the gamete pool according to the $\mathbf{F}'_i(\tilde{\mathbf{m}})$ matrices. The allele frequencies in the male gamete pool are obtained from a vector of relative contributions to the gamete pool

$$\mathbf{W}'\mathbb{F}'\tilde{\mathbf{p}}(t) = \begin{pmatrix} \mathbf{1}_\omega^\top & \frac{1}{2}\mathbf{1}_\omega^\top & 0 \\ 0 & \frac{1}{2}\mathbf{1}_\omega^\top & \mathbf{1}_\omega^\top \end{pmatrix} \begin{pmatrix} \mathbf{F}'_{AA}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{F}'_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{F}'_{aa}(\tilde{\mathbf{m}}) \end{pmatrix} \begin{pmatrix} \mathbf{p}'_{AA}(t) \\ \mathbf{p}'_{Aa}(t) \\ \mathbf{p}'_{aa}(t) \end{pmatrix}. \quad (5.4)$$

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 numbers to allele numbers. Normalizing this vector gives the allele frequencies in the gamete pool,

$$\begin{pmatrix} q'_A \\ q'_a \end{pmatrix} = \frac{\mathbf{W}'\mathbb{F}'(\tilde{\mathbf{m}})\mathbf{p}'}{\|\mathbf{W}'\mathbb{F}'\mathbf{p}'\|} = \frac{\mathbf{W}'\mathbb{F}'\mathbf{n}'}{\|\mathbf{W}'\mathbb{F}'\mathbf{n}'\|}. \quad (5.5)$$

When a female randomly picks an allele out of the gamete pool, she will pick allele A with probability q'_A , and allele a with probability q'_a . These probabilities therefore determine the distribution of genotypes in her offspring, which is captured in the matrix $\mathbf{H}(\tilde{\mathbf{p}})$,

$$\mathbf{H}(\tilde{\mathbf{p}}) = \begin{pmatrix} q'_A & \frac{1}{2}q'_A & 0 \\ q'_a & \frac{1}{2} & q'_A \\ 0 & \frac{1}{2}q'_a & q'_a \end{pmatrix}. \quad (5.6)$$

The first column of $\mathbf{H}(\tilde{\mathbf{p}})$ 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 .

5.3 Population projection

The matrix that projects the eco-evolutionary dynamics is created from the $\mathbf{U}_i(\tilde{\mathbf{m}})$, $\mathbf{U}'_i(\tilde{\mathbf{m}})$, $\mathbf{F}_i(\tilde{\mathbf{m}})$, $\mathbf{F}'_i(\tilde{\mathbf{m}})$, and $\mathbf{H}(\tilde{\mathbf{p}})$. We write it as

$$\tilde{\mathbf{A}}(\tilde{\mathbf{m}}) = \underbrace{\begin{pmatrix} \mathcal{U}(\tilde{\mathbf{m}}) & \mathbf{0} \\ \mathbf{0} & \mathcal{U}'(\tilde{\mathbf{m}}) \end{pmatrix}}_{\tilde{\mathbf{U}}} + \underbrace{\begin{pmatrix} \alpha\mathcal{F}(\tilde{\mathbf{m}}) & \mathbf{0} \\ (1-\alpha)\mathcal{F}(\tilde{\mathbf{m}}) & \mathbf{0} \end{pmatrix}}_{\tilde{\mathbf{F}}}, \quad (5.7)$$

where α is the fraction of newborn individuals that are female. The blocks correspond to survival of males and females, and production of males and females by females.

Following the same sequence of steps as in Section 3.3 in chapter 3, we arrive at the following eco-evolutionary projection matrix

$$\tilde{\mathbf{A}}(\tilde{\mathbf{m}}) = \underbrace{\begin{pmatrix} \mathbf{U}_{AA}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{U}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}'_{AA}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}'_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}'_{aa}(\tilde{\mathbf{m}}) \end{pmatrix}}_{\tilde{\mathbf{U}}} + \underbrace{\begin{pmatrix} \alpha q'_A \mathbf{F}_{AA}(\tilde{\mathbf{m}}) & \frac{1}{2} \alpha q'_A \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \alpha q'_a \mathbf{F}_{AA}(\tilde{\mathbf{m}}) & \frac{1}{2} \alpha \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \alpha q'_A \mathbf{F}_{aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \frac{1}{2} \alpha q'_a \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \alpha q'_a \mathbf{F}_{aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ (1-\alpha) q'_A \mathbf{F}_{AA}(\tilde{\mathbf{m}}) & \frac{1}{2} (1-\alpha) q'_A \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ (1-\alpha) q'_a \mathbf{F}_{AA}(\tilde{\mathbf{m}}) & \frac{1}{2} (1-\alpha) \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & (1-\alpha) q'_A \mathbf{F}_{aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \frac{1}{2} (1-\alpha) q'_a \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & (1-\alpha) q'_a \mathbf{F}_{aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix}}_{\tilde{\mathbf{F}}}, \quad (5.8)$$

where, again, q'_A and q'_a are given by (5.5). This matrix provides numerical solutions for selection operating on any of the sex- and stage-specific demographic parameters. In the next section, we show an example of the type of evolutionary dynamics in this model.

5.4 A two-sex projection example: density-dependent fertility-survival trade-off

As a simple example, consider a two stage (juvenile and adult) model, in which fecundity decreases exponentially as total population abundance increases. The

nonlinearity could be due to cannibalism, competition for food, competition for nesting sites, etc. Males and females have the same genotype-specific survival and transition rates,

$$\mathbf{U}_i = \mathbf{U}'_i = \beta_i \begin{pmatrix} \sigma(1-\gamma) & 0 \\ \sigma\gamma & s \end{pmatrix}, \quad (5.9)$$

where σ denotes juvenile survival, s is adult survival, γ is the maturation probability, and β_i is a genotype-specific factor that scales the entire survival matrix. Female fertility is density-dependent with a genotype-specific density parameter, r_i ,

$$\mathbf{F}_i = e^{-r_i \|\mathbf{a}\|} \begin{pmatrix} 0 & f_i \\ 0 & 0 \end{pmatrix}, \quad (5.10)$$

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} . Adult males all have the same mating success, independent of genotype,

$$\mathbf{F}'_i = \begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}. \quad (5.11)$$

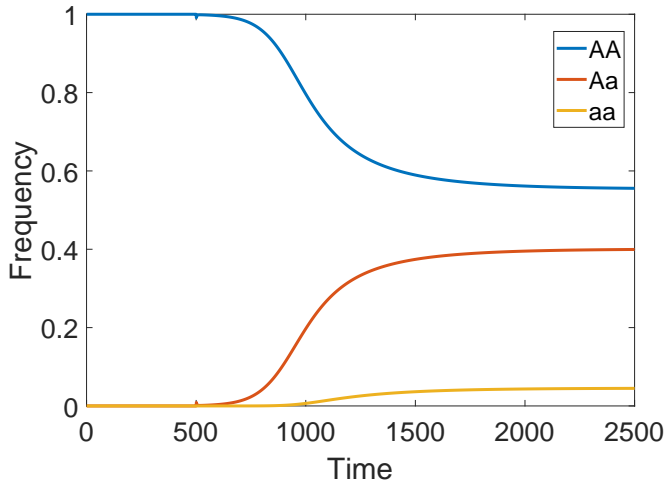
We introduce a survival-fertility trade-off by hypothesizing an allele a that increases survival (β_i) but reduces fertility by increasing the density-dependent rate r_i and reducing the fecundity f_i as follows

i	β_i	r_i	f_i
AA	0.3	0.3	6.0
Aa	0.5	0.5	1.5
aa	0.6	0.6	1.25

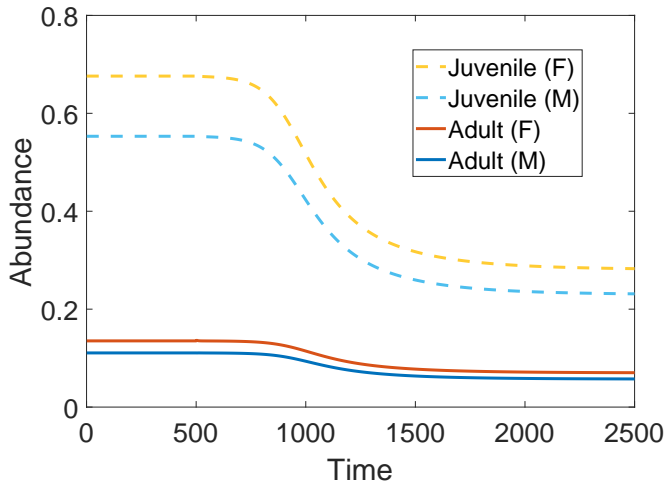
Figure 5.1 shows the genotype \times stage \times sex dynamics of this model. The simulation is initialized on the AA boundary. At $t = 500$ a small fraction of heterozygote female juveniles is introduced. The a allele (with higher survival and lower fertility) increases until a polymorphic equilibrium is reached with lower abundances of juveniles and adults for both sexes. This example shows that an allele can invade even if the invasion results in lower stage abundances for all stages. In the next section we calculate invasion criteria.

5.5 Conditions for genotype coexistence

In this section, we return to the important question of genotype coexistence. The question becomes more complicated, but no less important, when two sexes, demographic structure and nonlinearity are included. In this section, we present a general analytical criterion for determining the outcome of selection in a two-sex



(a) Genotype frequencies.



(b) Stage abundances.

Figure 5.1: At $t = 500$ a small fraction of heterozygote female juveniles is introduced. The new allele increases in frequency and a polymorphic equilibrium is reached with lower equilibrium abundances in each stage for both sexes. The model is defined by equations (5.9)-(5.11) with the following parameters: $\sigma = 0.8$, $\gamma = 0.1$, $s = 0.85$, $\beta_{AA} = 0.3$, $\beta_{Aa} = 0.5$, $\beta_{aa} = 0.6$, $f_{AA} = 6$, $f_{Aa} = 1.5$, $f_{aa} = 1.25$, $r_{AA} = 0.3$, $r_{Aa} = 0.5$, and $r_{aa} = 0.6$. We used a primary sex ratio of $\alpha = 0.55$.

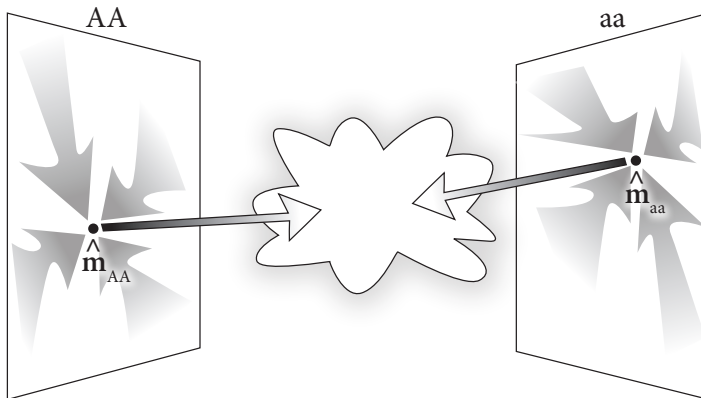


Figure 5.2: Graphical depiction of the $2\omega g$ -dimensional space defined by combinations of ω stages and g genotypes. If both the homozygous boundaries are unstable, then a homozygote state can never be reached again once both alleles are present in the population (since both alleles grow when rare). In general, we do not know what the dynamics in the interior space are, there could be multiple equilibria, strange attractors, cycles, etc. Image by Jan van Arkel.

density-dependent model. We follow the logic presented in the previous chapters closely.

The dynamics of $\tilde{\mathbf{m}}$ take place in a $2\omega g$ -dimensional space defined by combinations of ω stages, 2 sexes, and g genotypes (with $g = 3$ in the present context, see Figure 5.2). In the absence of mutation, the 2ω -dimensional boundary subspaces defined by the homozygous genotypes AA and aa are invariant under the dynamics specified by $\tilde{\mathbf{A}}[\tilde{\mathbf{m}}]$, and are given by the nonlinear projection matrices for the homozygous genotypes.

We assume the existence of a single equilibrium on each boundary, and that this equilibrium is stable with respect to perturbations in the boundary subspace. We use the following notation for the vectors evaluated at the boundary equilibria,

$$\hat{\mathbf{m}}_{AA}^T = (\hat{\mathbf{n}}_{AA}, \mathbf{0}, \mathbf{0}, \hat{\mathbf{n}}'_{AA}, \mathbf{0}, \mathbf{0}), \quad (5.12)$$

$$\hat{\mathbf{m}}_{aa}^T = (\mathbf{0}, \mathbf{0}, \hat{\mathbf{n}}_{aa}, \mathbf{0}, \mathbf{0}, \hat{\mathbf{n}}'_{aa}). \quad (5.13)$$

The growth rate on the AA boundary at equilibrium is equal to one,

$$\lambda_{AA}(\hat{\mathbf{m}}) = \rho \left(\begin{array}{cc} \mathbf{U}_{AA}(\hat{\mathbf{m}}) + \alpha \mathbf{F}_{AA}(\hat{\mathbf{m}}) & \mathbf{0} \\ (1 - \alpha) \mathbf{F}_{AA}(\hat{\mathbf{m}}) & \mathbf{U}'_{AA}(\hat{\mathbf{m}}) \end{array} \right) = 1, \quad (5.14)$$

where $\rho(\cdot)$ denotes the largest eigenvalue of a matrix. Similarly on the aa boundary,

$$\lambda_{aa}(\hat{\mathbf{m}}) = \rho \begin{pmatrix} \mathbf{U}_{aa}(\hat{\mathbf{m}}) + \alpha \mathbf{F}_{aa}(\hat{\mathbf{m}}) & \mathbf{0} \\ (1 - \alpha) \mathbf{F}_{aa}(\hat{\mathbf{m}}) & \mathbf{U}'_{aa}(\hat{\mathbf{m}}) \end{pmatrix} = 1. \quad (5.15)$$

By analogy, we can define a hypothetical heterozygote growth rate as,

$$\lambda_{Aa}(\tilde{\mathbf{m}}) = \rho \begin{pmatrix} \mathbf{U}_{Aa}(\tilde{\mathbf{m}}) + \alpha \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} \\ (1 - \alpha) \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{U}'_{Aa}(\tilde{\mathbf{m}}) \end{pmatrix}. \quad (5.16)$$

This hypothetical heterozygote growth rate turns out to be relevant when we consider the conditions for boundary stability in the absence of sexual dimorphism in Section 5.6.

Coexistence of the two alleles in a protected polymorphism (Levene 1953; Prout 1968; see Nagylaki 1992, Chap. 6) results when both boundary subspaces are unstable to perturbations into the interior. That is, if allele A can invade a population of aa individuals and allele a can invade a population of AA individuals, then a homozygote state can never be reached again once both alleles are present in the population (since both alleles grow when rare). Mutual invasibility therefore leads to a protected genetic polymorphism.

As in chapter 4, the dynamics in the interior are unknown, and could include multiple equilibria, strange attractors, cycles, etc. Provided both boundary subspaces are unstable to perturbations into the interior, we refer to any of the possible exotic dynamics in the interior as a protected polymorphism. And as before, we will restrict our discussion to models with a unique equilibrium on the boundary, ignoring more complicated attractors for the purpose of this paper. Extending the analysis to include a k -cycle on the boundary can be accomplished by transforming the k -point cycle into an equilibrium of the k -point map, but is not considered here.

Stability of the homozygote boundaries

Again, following very closely in the footsteps of previous chapters, we analyze the stability of the boundaries by calculating the largest of the eigenvalues of the Jacobian matrix evaluated at the boundary equilibrium, denoted by ζ_{AA} and ζ_{aa} for the AA and aa boundary respectively. If the spectral radius of the Jacobian matrix evaluated at the boundary equilibrium is less than one, then the boundary equilibrium is stable; if the spectral radius is larger than one, the boundary equilibrium is unstable. We have restricted our discussion to boundary equilibria that are locally stable to perturbations within the boundary subspace. Therefore if the dominant eigenvalue of the Jacobian is larger in magnitude than one, the

associated eigenvector must be pointing into the interior which implies that the invading allele increases when rare.

The Jacobian matrix,

$$\mathbf{M} = \left. \frac{d\tilde{\mathbf{m}}(t+1)}{d\tilde{\mathbf{m}}^\top(t)} \right|_{\hat{\mathbf{m}}}, \quad (5.17)$$

is obtained by differentiating equation (5.3) 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. In Appendix 5.A the Jacobian matrix at the AA boundary is derived,

$$\begin{aligned} \mathbf{M} = & \tilde{\mathbf{A}}(\hat{\mathbf{m}}) + \left(\mathbf{e}_1 \otimes \hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{U}_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} + \left(\mathbf{e}_2 \otimes \hat{\mathbf{n}}_{AA}^{\prime\top} \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{U}'_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \left. \vphantom{\frac{\partial \text{vec}(\mathbf{U}_{AA})}{\partial \tilde{\mathbf{m}}^\top}} \right\} \text{ecological} \\ & + \alpha \left(\mathbf{e}_1 \otimes \hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{F}_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} + (1-\alpha) \left(\mathbf{e}_2 \otimes \hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{F}_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \left. \vphantom{\frac{\partial \text{vec}(\mathbf{F}_{AA})}{\partial \tilde{\mathbf{m}}^\top}} \right\} \text{nonlinearities} \\ & + \alpha \left(\mathbf{e}_1 \otimes \mathbf{I}_\omega \right) (\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} + (1-\alpha) \left(\mathbf{e}_2 \otimes \mathbf{I}_\omega \right) (\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \left. \vphantom{\frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top}} \right\} \text{genetic} \\ & - \alpha \left(\mathbf{e}_3 \otimes \mathbf{I}_\omega \right) (\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} - (1-\alpha) \left(\mathbf{e}_4 \otimes \mathbf{I}_\omega \right) (\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \left. \vphantom{\frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top}} \right\} \text{nonlinearities}, \end{aligned} \quad (5.18)$$

where the AA boundary population vector is written as $\hat{\mathbf{m}}^\top(t) = (\hat{\mathbf{n}}_{AA}^\top, \hat{\mathbf{n}}_{AA}^{\prime\top}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0})$. The linearization reflects the two sources of nonlinearity in the model: nonlinearities due to ecological density-dependence and nonlinearities due to the genetic frequency-dependence. Consequently, the linearization reflects these two components and contains derivatives of the demographic matrices and derivatives of the allele frequencies, which are functions of the normalized population vector.

As before, the Jacobian matrix \mathbf{M} at the AA boundary is block upper triangular, with

$$\mathbf{M}_{21} = \mathbf{M}_{31} = \mathbf{M}_{32} = \mathbf{0}, \quad (5.19)$$

(See equation (5.A43) in Appendix 5.A). Thus the spectral radius of \mathbf{M} depends on the eigenvalues of the diagonal blocks. Block \mathbf{M}_{33} projects perturbations in the aa direction and is bounded by one in the density-dependent model, see equation (5.A43) in Appendix 5.A. Block \mathbf{M}_{11} projects perturbations in the AA boundary. Since we have restricted our discussion to boundary equilibria that are stable to perturbations in the boundary, the spectral radius of \mathbf{M}_{11} is also bounded by one. The stability of the AA boundary equilibrium therefore depends on the eigenvalues

of \mathbf{M}_{22} (derived in Appendix 5.A),

$$\mathbf{M}_{22} = \begin{pmatrix} \mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \frac{\alpha}{2} \frac{(\mathbf{F}_{AA}\hat{\mathbf{n}}_{AA}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{n}}'_{AA}} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \mathbf{U}'_{Aa}(\hat{\mathbf{m}}) + \frac{(1-\alpha)}{2} \frac{(\mathbf{F}_{AA}\hat{\mathbf{n}}_{AA}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{n}}'_{AA}} \end{pmatrix}, \quad (5.20)$$

where all the demographic matrices, \mathbf{U}_i , \mathbf{U}'_i , \mathbf{F}_i , \mathbf{F}'_i , are evaluated at the boundary equilibrium, $\hat{\mathbf{m}}$, but the dependence on $\hat{\mathbf{m}}$ is sometimes dropped to avoid a proliferation of brackets. For notational convenience, we define matrices,

$$\mathbf{D}_{AA}(\hat{\mathbf{m}}) = \frac{(\mathbf{F}_{AA}\hat{\mathbf{n}}_{AA}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{n}}'_{AA}}, \quad (5.21)$$

$$\mathbf{D}_{aa}(\hat{\mathbf{m}}) = \frac{(\mathbf{F}_{aa}\hat{\mathbf{n}}_{aa}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{aa} \hat{\mathbf{n}}'_{aa}}. \quad (5.22)$$

The spectral radius of the Jacobian matrix, evaluated at the AA boundary, denoted by ζ_{AA} , is

$$\zeta_{AA} = \rho \begin{pmatrix} \mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \frac{1}{2}\alpha\mathbf{D}_{AA}(\hat{\mathbf{m}}) \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \mathbf{U}'_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA}(\hat{\mathbf{m}}) \end{pmatrix}. \quad (5.23)$$

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

$$\zeta_{aa} = \rho \begin{pmatrix} \mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \frac{1}{2}\alpha\mathbf{D}_{aa}(\hat{\mathbf{m}}) \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \mathbf{U}'_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{aa}(\hat{\mathbf{m}}) \end{pmatrix}. \quad (5.24)$$

Criteria for a polymorphism A protected polymorphism occurs when both boundaries are unstable, i.e. when the spectral radius of the Jacobian is larger than 1 at both boundaries,

$$\zeta_{AA} > 1, \quad (5.25)$$

$$\zeta_{aa} > 1, \quad (5.26)$$

or

$$\rho \begin{pmatrix} \mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \frac{1}{2}\alpha\mathbf{D}_{AA}(\hat{\mathbf{m}}) \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \mathbf{U}'_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA}(\hat{\mathbf{m}}) \end{pmatrix} > 1, \quad (5.27)$$

$$\rho \begin{pmatrix} \mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \frac{1}{2}\alpha\mathbf{D}_{aa}(\hat{\mathbf{m}}) \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \mathbf{U}'_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{aa}(\hat{\mathbf{m}}) \end{pmatrix} > 1. \quad (5.28)$$

Equations (5.27) and (5.28) give the conditions for a genetic polymorphism for a structured population with nonlinear demographic rates. The conditions are a function of the nonlinear demographic rates of both the invading heterozygote and the resident homozygote (through the \mathbf{U}_i , \mathbf{U}'_i , \mathbf{F}_i , and \mathbf{F}'_i matrices), and of the stable population structure of the homozygote equilibrium, $\hat{\mathbf{n}}_{AA}$ or $\hat{\mathbf{n}}_{aa}$.

Note that none of the derivatives in equation (5.18) due to ecological nonlinearities appear in these coexistence conditions. The derivatives of the nonlinear demographic rates therefore have no influence on the success or failure of invasion, and the invasion conditions are remarkably similar to the invasion conditions for linear demography in Chapter 3. This is reminiscent of invasion calculations in adaptive dynamics (Diekmann 2004), in which the growth of the invading phenotype is described by a linear model.

5.6 Simplifications

Eliminating sexual dimorphism

We explore the same sequence of simplifications of the model introduced in Chapter 3. As in the linear case, eliminating sexual dimorphism in survival and transition probabilities significantly simplifies the coexistence conditions (Model 2 in Figure 5.4). The genotype-specific population growth rates (5.14)-(5.15) simplify to

$$\lambda_i(\hat{\mathbf{m}}) = \rho\left(\mathbf{U}_i(\hat{\mathbf{m}}) + \alpha\mathbf{F}_i(\hat{\mathbf{m}})\right) \quad (5.29)$$

A few lines of algebra show that the male and female population vectors are equal at equilibrium under this assumption. If in addition the primary sex ratio is equal to a half, then starting from any initial vector with 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.

If sexual dimorphism is reduced further by making genotype-specific male mating success proportional to female fertility (Model 3B in Figure 5.4), it can be shown (Appendix 5.B) that the conditions (5.27) and (5.28) for a protected polymorphism reduce to

$$\rho\left(\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\mathbf{F}_{Aa}(\hat{\mathbf{m}})\right) > \rho\left(\mathbf{U}_{AA}(\hat{\mathbf{m}}) + \alpha\mathbf{F}_{AA}(\hat{\mathbf{m}})\right) \quad (5.30)$$

$$\rho\left(\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\mathbf{F}_{Aa}(\hat{\mathbf{m}})\right) > \rho\left(\mathbf{U}_{aa}(\hat{\mathbf{m}}) + \alpha\mathbf{F}_{aa}(\hat{\mathbf{m}})\right). \quad (5.31)$$

If the proportion of females at birth is a half, $\alpha = \frac{1}{2}$, then (5.29) implies that the conditions (5.30) and (5.31) reduce to heterozygote superiority in growth rate λ .

If all breeding males have the same mating success, independent of their (st)age or genotype as in Chapters 2 and 4, then the mating population can be described by 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 simply becomes

$$\mathbf{F}_j = \mathbf{e}_1 \otimes \mathbf{c}_j. \quad (5.32)$$

We refer to this as Model 3A and the conditions for a genetic polymorphism are shown in Figure 5.4.

Heterozygote superiority in (hypothetical) equilibrium stage abundance

MacArthur (1962) and Roughgarden (1971) showed that density-dependent selection maximizes population size, assuming logistic-like density effects and an unstructured population. Charlesworth (1994) extended this result to age-structured populations and showed that density-dependent selection maximizes the abundance of the age class that is exerting the density-dependent pressure on the population. For example, if adults are cannibalizing juveniles and juvenile mortality is a nonlinear function of adult density, then a successful invasion will always lead to a higher adult density. In deriving this result, Charlesworth assumes males and females have identical demographic rates, i.e. there is no sexual dimorphism in any life-history characteristics.

Figure 5.1b in Chapter 5 shows that density-dependent selection does not maximize stage abundance or any sum of stage abundances in the presence of sexual dimorphism. The coexistence conditions derived in this thesis allow us to ask whether selection in our model always leads to a higher growth rate in the linear model and higher equilibrium abundances in the nonlinear model in the absence of sexual dimorphism, independent of the demography of the specific species.

In the absence of sexual dimorphism, and when the primary sex ratio is a half, the conditions for coexistence reduce to heterozygote superiority in population growth rate. Consider the case where the demographic matrices are a function of one stage, m_i , or of one weighted sum of several stages,

$$\bar{m} = \sum_i \beta_i m_i. \quad (5.33)$$

The invasion condition on the AA boundary is,

$$\lambda_{Aa}(\bar{m}_{AA}) > \lambda_{AA}(\bar{m}_{AA}), \quad (5.34)$$

where $\lambda_{AA}(\bar{m}_{AA}) = 1$, and the stage abundances in \bar{m}_{AA} are all evaluated on the AA boundary. Likewise on the aa boundary, we must have

$$\lambda_{Aa}(\bar{m}_{aa}) > \lambda_{aa}(\bar{m}_{aa}), \quad (5.35)$$

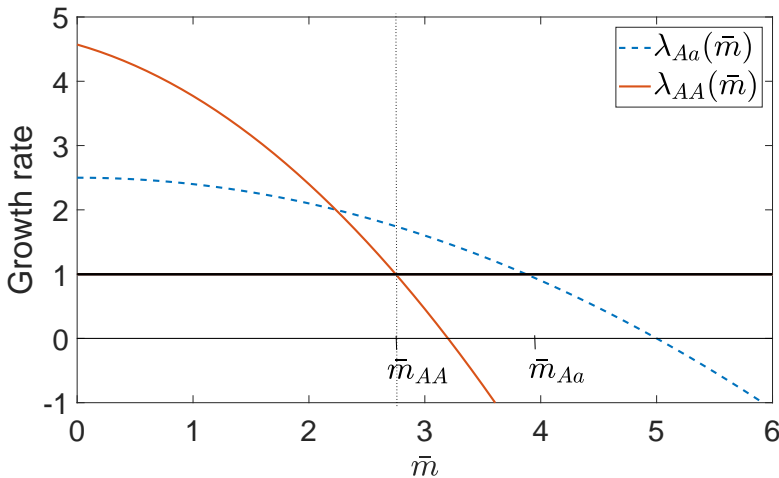


Figure 5.3: Growth rate as a function of the density-dependence exerting stage or sum of stages, \bar{m} . The thick black line indicates the border between growth and decline.

where $\lambda_{aa}(\bar{m}_{aa}) = 1$, and the stage abundances in \bar{m}_{AA} are all evaluated on the aa boundary. If the population growth rate is a monotonically decreasing function of \bar{m} , a heterozygote can only invade if its hypothetical equilibrium value \bar{m}_{Aa} is larger than that of the resident, as Figure 5.3 demonstrates for two hypothetical growth rate functions. This means that the coexistence conditions, equations (5.34) and (5.35), are equivalent to,

$$\bar{m}_{Aa} > \bar{m}_{AA}, \quad (5.36)$$

$$\bar{m}_{Aa} > \bar{m}_{aa}. \quad (5.37)$$

Therefore a heterozygote can only invade if its hypothetical equilibrium density, \bar{m}_{Aa} , is larger than both actual equilibrium densities of the two homozygotes when there is no sexual dimorphism in demographic rates, when the demographic rates only depend on one weighted sum of stage abundances, and when the population growth rate is a monotonically decreasing function of this weighted sum of stage abundances.

This does not prove that the asymptotic equilibrium density after invasion will be larger than the two boundary equilibrium densities under these conditions, however. To prove that the weighted density \bar{m} will increase after an invasion requires proving that the weighted density at the coexistence equilibrium, \bar{m}_c , is larger than both \bar{m}_{AA} and \bar{m}_{aa} . To the best of our knowledge, it is impossible

to get a general analytical expression for the internal equilibrium. Therefore we have been unable to prove that $\bar{m}_c > \bar{m}_{AA}$ and $\bar{m}_c > \bar{m}_{aa}$ when there is no sexual dimorphism, although both intuition and simulations suggest it is true.

Eliminating stage structure

In Figure 5.5 the coexistence conditions for a population without any age or stage structure are shown. The flow diagram follows the same series of simplifications as Figure 5.4. 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.

5.7 Discussion

We have shown that density-dependent selection in the presence of sexual dimorphism need not maximize any stage abundance or any weighted sum of stage abundances. Instead, intralocus sexual conflict can lead to lower population abundances if a trait invades that benefits males at the expense of females. Lower population abundances increase the risk of extinction through demographic stochasticity. Heterozygote superiority in population growth rate at the equilibrium density of both homozygotes is only a necessary and sufficient condition for a protected polymorphism in the absence of sexual dimorphism and when the primary sex ratio is one.

Selection can operate at different levels: from genes to individuals to (arguably) populations (Okasha 2006). Selection at a lower level can promote genes that do not benefit higher levels. The most striking example of this are selfish genetic elements, which encode traits beneficial to their own transmission at the expense of fitness costs to the organisms carrying them (Werren et al. 1988; Hatcher 2000). Genes that benefit males at the expense of females are another example of selfish genes.

When there is no sexual dimorphism in demographic rates, genes effectively only live in one type of individual. Therefore a gene can only increase in frequency by producing heterozygotes with higher individual survival and/or fertility. In the absence of sexual dimorphism, the interests of the three different levels of selection (genes, individuals, and populations) are thus aligned in our model (unless we introduce other sources of conflict or selfish behaviors, like cannibalism, in the

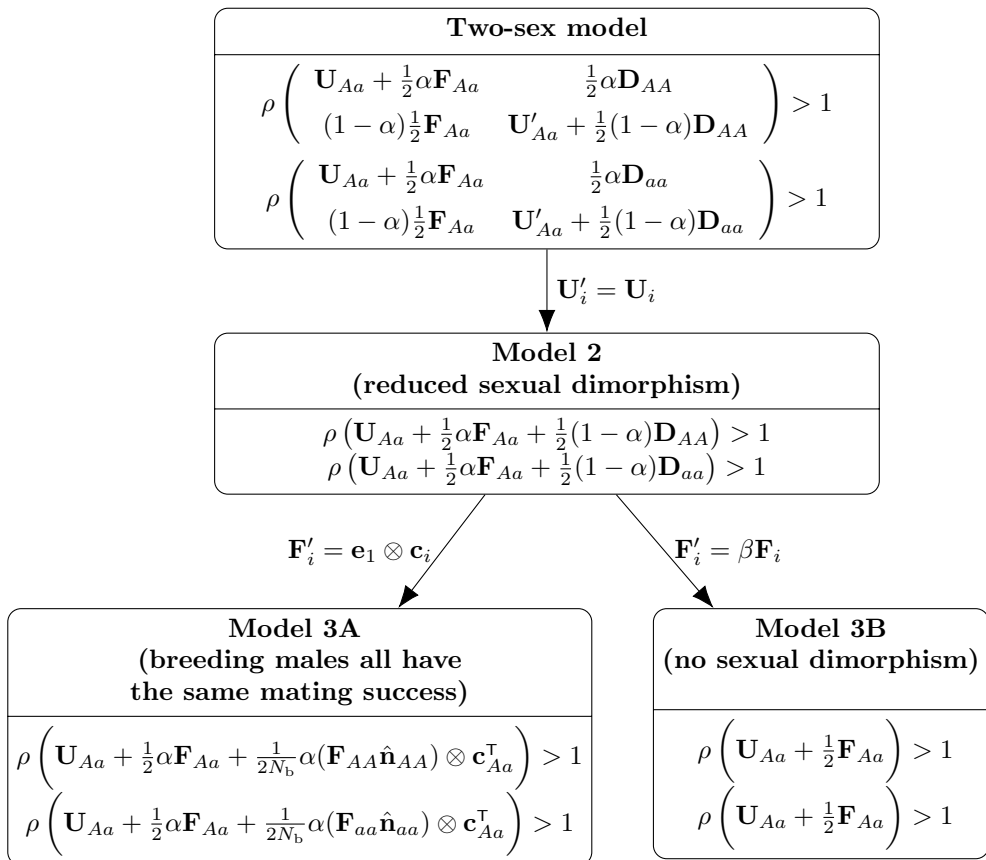


Figure 5.4: Coexistence conditions for the two-sex model, the general one-sex model, the one-sex model when all breeding males have the same mating success, and the one-sex model when males and females have equal, or proportional demographic rates. The symbols \mathbf{D}_{AA} and \mathbf{D}_{aa} are used as a short-hand for the following matrices,

$$\mathbf{D}_{AA} = \frac{(\mathbf{F}_{AA}\hat{\mathbf{n}}_{AA}) \otimes (\mathbf{1}_\omega^T \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^T \mathbf{F}'_{AA} \hat{\mathbf{n}}'_{AA}},$$

$$\mathbf{D}_{aa} = \frac{(\mathbf{F}_{aa}\hat{\mathbf{n}}_{aa}) \otimes (\mathbf{1}_\omega^T \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^T \mathbf{F}'_{aa} \hat{\mathbf{n}}'_{aa}}.$$

N_b is the number of individuals that is in a breeding stage at the stationary distribution of the boundary homozygote,

$$N_b = \sum_{j=1}^g (\mathbf{e}_j^T \otimes \mathbf{c}_j^T) \tilde{\mathbf{m}}. \quad (5.38)$$

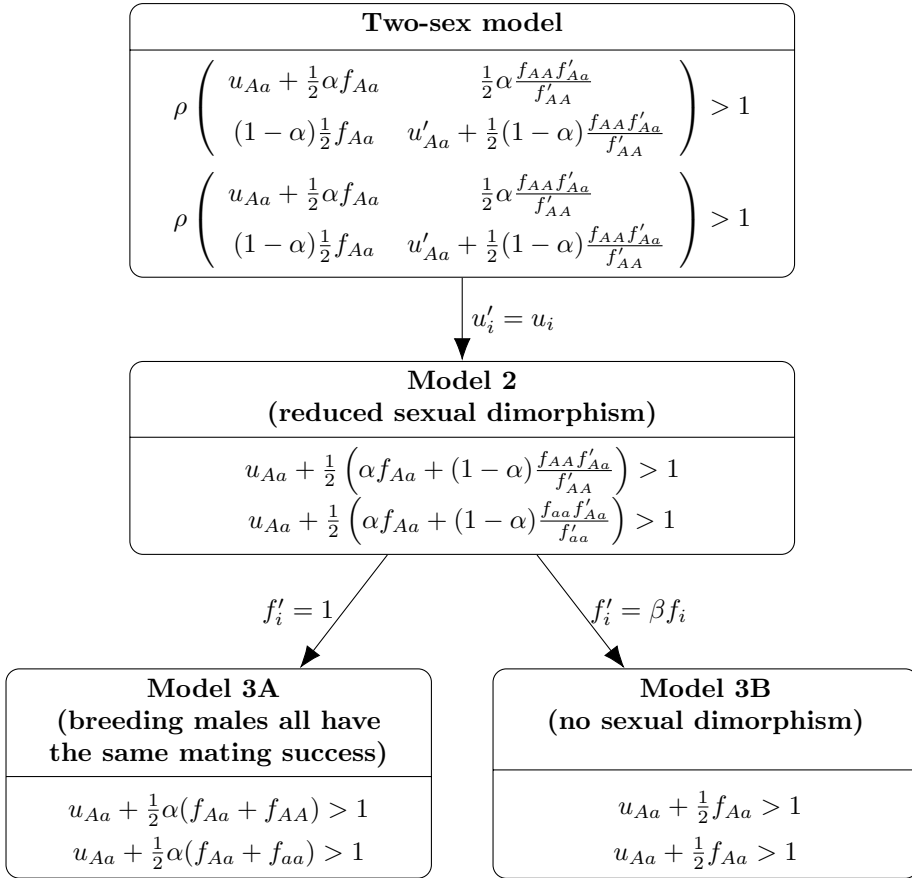


Figure 5.5: Coexistence conditions for an unstructured two-sex model, an unstructured one-sex model, an unstructured one-sex model when breeding males of the different genotypes have the same mating success, and an unstructured one-sex model when males and females have equal, or proportional demographic rates.

model). In the presence of sexual dimorphism, on the contrary, the interests of males and females are not necessarily aligned, and this conflict can reduce stage densities in the nonlinear model, and population growth rate in the linear model (de Vries and Caswell 2018a).

Sexual dimorphism is both the cause of, and the solution to, sexual conflict. If the sexes were somehow locked into the exact same life-history strategy, then sexual conflict can not happen because their interests are forced to be aligned. If this symmetry is broken, it opens up the evolutionary playing field for genetic elements that benefit one sex over the other. As a consequence, mechanisms to stop the expression of genes in one of the sexes have an evolutionary advantage,

thereby enhancing sexual dimorphism, and so an intraspecies Red Queen race begins (Rice and Holland 1997; McDaniel 2005; Harano et al. 2010).

If the Red Queen does not run fast enough to suppress selfish genes, or whilst she is catching up, the population is likely to decrease in size. This might make highly sexually dimorphic populations more vulnerable to extinction as a consequence of demographic stochasticity. Empirical evidence for this idea is contradictory with some papers confirming the hypothesis (Martins et al. 2018; Hasegawa and Arai 2018), and some showing no effect (Morrow and Fricke 2004).

Extensions In this paper, we have assumed that there are enough males to fertilize all the females, and that 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 is likely to be regularly violated. For example, when the sex ratio is highly skewed towards females, a lack of males can limit female fertilisation (referred to as a “marriage squeeze” in the human demography literature). Furthermore, 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 2018*b*) would make it possible to analyze the genetics of traits related to parental care, or populations experiencing a marriage squeeze.

The model can be extended to include more ecological processes by including intraspecific interactions, resources, time-varying demographic rates, or environmentally driven demographic rates. Polymorphic dispersal strategies are found in many plant and animal species and the maintenance of such genetic variation in dispersal strategies is subject of much debate (Fronhofer et al. 2011; Saastamoinen et al. 2018). Distinct heritable dispersal strategies could be modeled by adding a dispersal kernel to the (two-sex) structured genetic model (Sullivan et al. 2017). Such a two-sex genetic dispersal model allows an analytical evaluation of the conditions for the spread of an allele which affects dispersal rate (Neubert and Caswell 2000).

The genetic component of the model can be expanded to include more than two alleles, nonrandom mating, or mutations (de Vries and Caswell 2018*a*; de Vries 2019).

Conclusion Genes that can get more copies of themselves in the next generation increase in frequency. Sometimes this happens at the expense of population size or growth rate. Only when the interests of all levels of selection and all individuals

in a population align, we might expect natural selection to maximize some fitness proxy (Mylius and Metz 2004).

In this paper, we focused on the effect of sex differences on eco-evolutionary dynamics in the presence of density-dependence. Our results suggest that ignoring sexual dimorphism in demographic rates can lead to erroneous predictions of the trajectory of an invading allele. The importance of sex differences has been shown before (Møller 2003; Kokko and Brooks 2003), but it has rarely been considered in the context of structured population models, see (Lindström and Kokko 1998; Harts et al. 2014) for exceptions. Including population structure means including development, growth, and maturation; these are fundamental biological processes that affect both population dynamics and evolution.

Appendix 5.A Coexistence conditions

The conditions for a protected polymorphism in the two-sex model, equations (5.27) and (5.28), will be derived in this Appendix. The derivation for the coexistence conditions 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). First, we will construct the population projection matrix for this ordering, then we will use this projection matrix to derive coexistence conditions, following the logic introduced by de Vries and Caswell (2018*b*) and de Vries and Caswell (2018*c*) closely.

Population projection matrix for genotype×sex×stage ordering

The population vector is organized by genotype first, then by sex and then by stage,

$$\tilde{\mathbf{m}} = \begin{pmatrix} \mathbf{n}_{AA} \\ \mathbf{n}'_{AA} \\ \mathbf{n}_{Aa} \\ \mathbf{n}'_{Aa} \\ \mathbf{n}_{aa} \\ \mathbf{n}'_{aa} \end{pmatrix}. \quad (5.A1)$$

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

$$\begin{aligned} \tilde{\mathbf{A}} &= \tilde{\mathbf{U}}(\tilde{\mathbf{m}}) + \tilde{\mathbf{F}}(\tilde{\mathbf{m}}) \quad (5.A2) \\ &= \left(\begin{array}{cc|cc|cc} \mathbf{U}_{AA}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{U}'_{AA}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{U}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}'_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}_{aa}(\tilde{\mathbf{m}}) & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{U}'_{aa}(\tilde{\mathbf{m}}) \end{array} \right) \\ &+ \left(\begin{array}{cc|cc|cc} q'_A \alpha \mathbf{F}_{AA}(\tilde{\mathbf{m}}) & \mathbf{0} & \frac{1}{2} q'_A \alpha \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ (1-\alpha) q'_A \mathbf{F}_{AA}(\tilde{\mathbf{m}}) & \mathbf{0} & \frac{1}{2} (1-\alpha) q'_A \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hline q'_a \alpha \mathbf{F}_{AA}(\tilde{\mathbf{m}}) & \mathbf{0} & \frac{1}{2} \alpha \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & q'_A \alpha \mathbf{F}_{aa} & \mathbf{0} \\ (1-\alpha) q'_a \mathbf{F}_{AA}(\tilde{\mathbf{m}}) & \mathbf{0} & \frac{1}{2} (1-\alpha) \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & (1-\alpha) q'_A \mathbf{F}_{aa} & \mathbf{0} \\ \hline \mathbf{0} & \mathbf{0} & \frac{1}{2} q'_a \alpha \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & q'_a \alpha \mathbf{F}_{aa}(\tilde{\mathbf{m}}) & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \frac{1}{2} (1-\alpha) q'_a \mathbf{F}_{Aa}(\tilde{\mathbf{m}}) & \mathbf{0} & (1-\alpha) q'_a \mathbf{F}_{aa}(\tilde{\mathbf{m}}) & \mathbf{0} \end{array} \right). \quad (5.A3) \end{aligned}$$

As before, male and female offspring are produced at a constant ratio of $\alpha : (1-\alpha)$. The survival matrices are along 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 $\tilde{\mathbf{F}}$ contains the offspring produced 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.

Derivation of Jacobian matrix, general nonlinear model

The stability of a boundary equilibrium to invasions by the other allele is determined by the largest absolute eigenvalue (spectral radius) of the Jacobian matrix of the nonlinear matrix model evaluated at the boundary equilibrium. We denote the spectral radius of the Jacobian at the AA boundary by x_{AA} , and at the aa boundary by x_{aa} . If the magnitude of the dominant eigenvalue of the Jacobian matrix is larger than one when evaluated at an equilibrium, then this equilibrium is unstable. The Jacobian matrix,

$$\mathbf{M} = \left. \frac{d\tilde{\mathbf{m}}(t+1)}{d\tilde{\mathbf{m}}^\top(t)} \right|_{\tilde{\mathbf{m}}}, \quad (5.A4)$$

is obtained by differentiating equation (5.3),

$$\tilde{\mathbf{m}}(t+1) = \tilde{\mathbf{A}}[\tilde{\mathbf{m}}] \tilde{\mathbf{m}}(t), \quad (5.A5)$$

and evaluating the resulting derivative at the boundary equilibrium. This requires a long series of matrix calculus operations, and repeatedly takes advantage of the fact that $\hat{\mathbf{m}}$ at the AA boundary contains zeros for the blocks corresponding to Aa and aa genotypes.

Differentiate equation (5.A5) to obtain

$$d\tilde{\mathbf{m}}(t+1) = \tilde{\mathbf{A}}d\tilde{\mathbf{m}}(t) + \left(d\tilde{\mathbf{A}} \right) \tilde{\mathbf{m}}(t), \quad (5.A6)$$

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

$$d\tilde{\mathbf{m}}(t+1) = \tilde{\mathbf{A}}d\tilde{\mathbf{m}}(t) + \mathbf{I}_{2\omega g} \left(d\tilde{\mathbf{A}} \right) \tilde{\mathbf{m}}(t). \quad (5.A7)$$

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

$$d\tilde{\mathbf{m}}(t+1) = \tilde{\mathbf{A}}d\tilde{\mathbf{m}}(t) + \text{vec} \left[\mathbf{I}_{2\omega g} \left(d\tilde{\mathbf{A}} \right) \tilde{\mathbf{m}}(t) \right]. \quad (5.A8)$$

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

$$d\tilde{\mathbf{m}}(t+1) = \tilde{\mathbf{A}}d\tilde{\mathbf{m}}(t) + (\tilde{\mathbf{m}}^\top(t) \otimes \mathbf{I}_{2\omega g}) \text{dvec} \left[\tilde{\mathbf{A}} \right]. \quad (5.A9)$$

The matrix $\tilde{\mathbf{A}}$ can be decomposed into $36 \omega \times \omega$ block matrices, which are the blocks in equation (5.A3). The blocks are denoted by \mathbf{A}_{ij} , so that for example

$$\mathbf{A}_{11} = \mathbf{U}_{AA}(\tilde{\mathbf{m}}) + q'_A \mathbf{F}_{AA}(\tilde{\mathbf{m}}), \quad (5.A10)$$

and

$$\mathbf{A}_{31} = \mathbf{0}. \quad (5.A11)$$

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

$$\tilde{\mathbf{A}} = \sum_{i,j=1}^6 \mathbf{E}_{ij} \otimes \mathbf{A}_{ij}, \quad (5.A12)$$

$$= \sum_{i,j=1}^6 (\mathbf{e}_i \mathbf{e}_j^\top) \otimes (\mathbf{A}_{ij} \mathbf{I}_\omega), \quad (5.A13)$$

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 (5.A13) can be rewritten as

$$\tilde{\mathbf{A}} = \sum_{i,j=1}^6 (\mathbf{e}_i \otimes \mathbf{A}_{ij}) (\mathbf{e}_j^\top \otimes \mathbf{I}_\omega). \quad (5.A14)$$

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

$$\tilde{\mathbf{A}} = \sum_{i,j=1}^6 (\mathbf{e}_i \otimes \mathbf{I}_\omega) \mathbf{A}_{ij} (\mathbf{e}_j^\top \otimes \mathbf{I}_\omega). \quad (5.A15)$$

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

$$\text{vec}\tilde{\mathbf{A}} = \sum_{i,j}^6 (\mathbf{e}_j \otimes \mathbf{I}_\omega) \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega) \text{vec}\mathbf{A}_{ij}. \quad (5.A16)$$

Armed with this expression for $\text{vec}\tilde{\mathbf{A}}$, we analyze the term $(\tilde{\mathbf{m}}^\top(t) \otimes \mathbf{I}_{\omega g}) \text{dvec} \left[\tilde{\mathbf{A}} \right]$ in (5.A9). Replace the derivative of $\text{vec}\tilde{\mathbf{A}}$ with equation 5.A16, such that

$$(\tilde{\mathbf{m}}^\top(t) \otimes \mathbf{I}_{\omega g}) \text{dvec} \left[\tilde{\mathbf{A}} \right] = \sum_{i,j=1}^6 (\tilde{\mathbf{m}}^\top(t) \otimes \mathbf{I}_{\omega g}) \left[(\mathbf{e}_j \otimes \mathbf{I}_\omega) \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega) \right] \text{dvec}\mathbf{A}_{ij} \quad (5.A17)$$

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

$$(\tilde{\mathbf{m}}^\top(t) \otimes \mathbf{I}_{\omega g}) \left[(\mathbf{e}_j \otimes \mathbf{I}_\omega) \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega) \right] = (\tilde{\mathbf{m}}^\top(\mathbf{e}_j \otimes \mathbf{I}_\omega)) \otimes (\mathbf{I}_{\omega g}(\mathbf{e}_i \otimes \mathbf{I}_\omega)), \quad (5.A18)$$

substituting this expression into the right hand side of equation (5.A17) yields

$$(\tilde{\mathbf{m}}^\top(t) \otimes \mathbf{I}_{\omega g}) \text{dvec} \left[\tilde{\mathbf{A}} \right] = \sum_{i,j=1}^6 (\tilde{\mathbf{m}}^\top(\mathbf{e}_j \otimes \mathbf{I}_\omega)) \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega) \text{dvec} \mathbf{A}_{ij}. \quad (5.A19)$$

When we evaluate this expression on the boundary (since we are interested in the Jacobian evaluated at the equilibrium on the boundary), there are only AA individuals in the population, i.e.

$$\tilde{\mathbf{m}}^\top(t) = (\hat{\mathbf{n}}_{AA}^\top, \hat{\mathbf{n}}_{AA}^{\prime\top}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0}). \quad (5.A20)$$

Substituting this expression for $\tilde{\mathbf{m}}^\top(t)$ into equation (5.A19), so that only terms $j = 1$ and $j = 2$ are nonzero, yields

$$\begin{aligned} \left[(\tilde{\mathbf{m}}^\top(t) \otimes \mathbf{I}_{\omega g}) \text{dvec} \tilde{\mathbf{A}} \right] \Big|_{\tilde{\mathbf{m}}} &= \sum_i^6 \hat{\mathbf{n}}_{AA}^\top \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega) \text{dvec} \mathbf{A}_{i1} \Big|_{\tilde{\mathbf{m}}} \\ &+ \sum_i^6 \hat{\mathbf{n}}_{AA}^{\prime\top} \otimes (\mathbf{e}_i \otimes \mathbf{I}_\omega) \text{dvec} \mathbf{A}_{i2} \Big|_{\tilde{\mathbf{m}}}. \end{aligned} \quad (5.A21)$$

The \mathbf{A}_{i1} matrices are the matrices in the first block column of $\tilde{\mathbf{A}}$, see equation (5.A3), i.e.

$$\mathbf{A}_{11} = \mathbf{U}_{AA}(\tilde{\mathbf{m}}) + \alpha q'_A \mathbf{F}_{AA}(\tilde{\mathbf{m}}), \quad (5.A22)$$

$$\mathbf{A}_{21} = (1 - \alpha) q'_A \mathbf{F}_{AA}(\tilde{\mathbf{m}}), \quad (5.A23)$$

$$\mathbf{A}_{31} = \alpha q'_a \mathbf{F}_{AA}(\tilde{\mathbf{m}}), \quad (5.A24)$$

$$\mathbf{A}_{41} = (1 - \alpha) q'_a \mathbf{F}_{AA}(\tilde{\mathbf{m}}). \quad (5.A25)$$

There is only one nonzero \mathbf{A}_{i2} matrix, namely

$$\mathbf{A}_{22} = \mathbf{U}'_{AA}(\tilde{\mathbf{m}}). \quad (5.A26)$$

Finally, using these expressions for the \mathbf{A}_{i1} and \mathbf{A}_{i2} matrices, and equation (5.A21) to evaluate equation (5.A9) on the AA boundary, we obtain

$$\begin{aligned} d\tilde{\mathbf{m}}(t+1) &= \tilde{\mathbf{A}} d\tilde{\mathbf{m}}(t) + \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_1 \otimes \mathbf{I}_\omega \right) \text{dvec} [\mathbf{U}_{AA}(\tilde{\mathbf{m}})] \Big|_{\tilde{\mathbf{m}}} + \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_2 \otimes \mathbf{I}_\omega \right) \text{dvec} [\mathbf{U}'_{AA}(\tilde{\mathbf{m}})] \Big|_{\tilde{\mathbf{m}}} \\ &+ \alpha \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_1 \otimes \mathbf{I}_\omega \right) \text{dvec} [q'_A \mathbf{F}_{AA}(\tilde{\mathbf{m}})] \Big|_{\tilde{\mathbf{m}}} + (1 - \alpha) \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_2 \otimes \mathbf{I}_\omega \right) \text{dvec} [q'_A \mathbf{F}_{AA}(\tilde{\mathbf{m}})] \Big|_{\tilde{\mathbf{m}}} \\ &+ \alpha \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_3 \otimes \mathbf{I}_\omega \right) \text{dvec} [q'_a \mathbf{F}_{AA}(\tilde{\mathbf{m}})] \Big|_{\tilde{\mathbf{m}}} + (1 - \alpha) \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_4 \otimes \mathbf{I}_\omega \right) \text{dvec} [q'_a \mathbf{F}_{AA}(\tilde{\mathbf{m}})] \Big|_{\tilde{\mathbf{m}}} \end{aligned} \quad (5.A27)$$

where the differentials are all evaluated at the boundary equilibrium. To continue, note that

$$q'_a + q'_A = 1, \quad (5.A28)$$

$$dq'_a + dq'_A = 0. \quad (5.A29)$$

Finally, using the first identification theorem and the chain rule gives the following formula for the Jacobian (Magnus and Neudecker 1985; Caswell 2007b),

$$\begin{aligned} \mathbf{M} &= \left. \frac{d\tilde{\mathbf{n}}(t+1)}{d\tilde{\mathbf{m}}(t)} \right|_{\hat{\mathbf{m}}}, \quad (5.A30) \\ &= \tilde{\mathbf{A}}(\hat{\mathbf{m}}) + \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_1 \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{U}_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} + \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_2 \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{U}_{AA'})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \\ &+ \alpha \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_1 \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{F}_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} + \alpha \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_1 \otimes \mathbf{I}_\omega \right) \text{vec}(\mathbf{F}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \\ &+ (1-\alpha) \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_2 \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{F}_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \\ &+ (1-\alpha) \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_2 \otimes \mathbf{I}_\omega \right) \text{vec}(\mathbf{F}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \\ &- \alpha \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_3 \otimes \mathbf{I}_\omega \right) \text{vec}(\mathbf{F}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \\ &- (1-\alpha) \left(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_4 \otimes \mathbf{I}_\omega \right) \text{vec}(\mathbf{F}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \quad (5.A31) \end{aligned}$$

Use $\mathbf{ab}^\top = \mathbf{a} \otimes \mathbf{b}^\top = \mathbf{b}^\top \otimes \mathbf{a}$ for two vectors \mathbf{a} and \mathbf{b} to write $(\hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{e}_i \otimes \mathbf{I}_\omega)$ as $(\mathbf{e}_i \otimes \hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{I}_\omega)$. Also note that the two terms with partial derivatives of q'_A can be rewritten using $(\mathbf{Z}^\top \otimes \mathbf{X}) \text{vec} \mathbf{Y} = \text{vec}(\mathbf{X}\mathbf{Y}\mathbf{Z})$ to obtain the following expression

$$\begin{aligned} \mathbf{M} &= \tilde{\mathbf{A}}(\hat{\mathbf{m}}) + \left(\mathbf{e}_1 \otimes \hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{U}_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} + \left(\mathbf{e}_2 \otimes \hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{U}'_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \\ &+ \alpha \left(\mathbf{e}_1 \otimes \hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{F}_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} + (1-\alpha) \left(\mathbf{e}_2 \otimes \hat{\mathbf{n}}_{AA}^\top \otimes \mathbf{I}_\omega \right) \left. \frac{\partial \text{vec}(\mathbf{F}_{AA})}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \\ &+ \alpha \left(\mathbf{e}_1 \otimes \mathbf{I}_\omega \right) (\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} + (1-\alpha) \left(\mathbf{e}_2 \otimes \mathbf{I}_\omega \right) (\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \\ &- \alpha \left(\mathbf{e}_3 \otimes \mathbf{I}_\omega \right) (\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} - (1-\alpha) \left(\mathbf{e}_4 \otimes \mathbf{I}_\omega \right) (\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\hat{\mathbf{m}}} \quad (5.A32) \end{aligned}$$

Equation (5.A32) requires the derivative of the frequency of allele A in the gamete pool with respect to the population frequency vector:

$$\left. \frac{\partial q'_A}{\partial \tilde{\mathbf{p}}^\top} \right|_{\hat{\mathbf{p}}}. \quad (5.A33)$$

Start with equation (5.5) from the main text:

$$\begin{pmatrix} q'_A \\ q'_a \end{pmatrix} = \frac{\mathbf{W}'\mathbf{F}'\mathbf{n}'}{\|\mathbf{W}'\mathbf{F}'\mathbf{n}'\|}, \quad (5.A34)$$

therefore

$$q'_A = \frac{\mathbf{e}_1^\top \mathbf{W}'\mathbf{F}'\mathbf{n}'}{\mathbf{1}_2^\top \mathbf{W}'\mathbf{F}'\mathbf{n}'}, \quad (5.A35)$$

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

$$N_b = \mathbf{1}_2^\top \mathbf{W}'\mathbf{F}'\mathbf{n}' \quad (5.A36)$$

Taking the derivative of q'_A yields

$$\frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} = \frac{1}{N_b} \mathbf{e}_1^\top \mathbf{W}'\mathbb{F}' \frac{\partial \mathbf{n}'}{\partial \tilde{\mathbf{m}}^\top} - \frac{\mathbf{e}_1^\top \mathbf{W}'\mathbf{F}'\mathbf{n}'}{N_b^2} \left(\mathbf{1}_2^\top \mathbf{W}'\mathbb{F}' \frac{\partial \mathbf{n}'}{\partial \tilde{\mathbf{m}}^\top} \right). \quad (5.A37)$$

Recall

$$\mathbf{n}' = \begin{pmatrix} \mathbf{n}'_{AA} \\ \mathbf{n}'_{Aa} \\ \mathbf{n}'_{aa} \end{pmatrix}, \quad (5.A38)$$

and

$$\tilde{\mathbf{m}} = \begin{pmatrix} \mathbf{n}_{AA} \\ \frac{\mathbf{n}'_{AA}}{\mathbf{n}_{AA}} \\ \mathbf{n}_{Aa} \\ \frac{\mathbf{n}'_{Aa}}{\mathbf{n}_{Aa}} \\ \mathbf{n}_{aa} \\ \mathbf{n}'_{aa} \end{pmatrix}, \quad (5.A39)$$

to calculate

$$\frac{\partial \mathbf{n}'}{\partial \tilde{\mathbf{m}}^\top} = \begin{pmatrix} \mathbf{0} & \mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I} \end{pmatrix}. \quad (5.A40)$$

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

$$\left. \frac{\partial q'_A}{\partial \tilde{\mathbf{m}}^\top} \right|_{\tilde{\mathbf{m}}} = \frac{1}{N_b} \left(\mathbf{0}, \mathbf{0}, \mathbf{0}, -\frac{1}{2} \mathbf{1}_\omega^\top \mathbf{F}'_{Aa}, \mathbf{0}, -\mathbf{1}_\omega^\top \mathbf{F}'_{aa} \right), \quad (5.A41)$$

where at the boundary

$$N_b = \mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{n}}'_{AA}. \quad (5.A42)$$

Finally, plug equation (5.A41) back into the expression for the Jacobian, equation (5.A32), to write the Jacobian in terms of its block components, see equation (5.A43) on the next page. Note that all the demographic matrices, \mathbf{U}_i , \mathbf{U}'_i , \mathbf{F}_i , and \mathbf{F}'_i , are evaluated at the equilibrium, but the explicit dependence on the population vector is left out to avoid a proliferation of brackets.

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Appendix 5.B Coexistence conditions under simplifying assumptions

$$\mathbf{U}_i(\hat{\mathbf{m}}) = \mathbf{U}'_i(\hat{\mathbf{m}})$$

In this section, we consider a simplification that removes sexual dimorphism in survival and transition rates, $\mathbf{U}_i(\hat{\mathbf{m}}) = \mathbf{U}'_i(\hat{\mathbf{m}})$ for any $\hat{\mathbf{m}}$. We consider block \mathbf{M}_{22} of the Jacobian matrix, equation (5.20)

$$\mathbf{M}_{22} = \begin{pmatrix} \mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \frac{1}{2}\alpha\mathbf{D}_{AA}(\hat{\mathbf{m}}) \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA}(\hat{\mathbf{m}}) \end{pmatrix}, \quad (5.B44)$$

where we use the following notation (equation (5.21) the main text),

$$\mathbf{D}_{AA} = \frac{(\mathbf{F}_{AA}\hat{\mathbf{n}}_{AA}) \otimes (\mathbf{1}_\omega^T \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^T \mathbf{F}'_{AA} \hat{\mathbf{n}}'_{AA}}. \quad (5.B45)$$

Consider an eigenvector of this matrix,

$$\mathbf{v} = \begin{pmatrix} \mathbf{u} \\ \mathbf{u}' \end{pmatrix}, \quad (5.B46)$$

with eigenvalue x , which has to satisfy the following equation

$$\begin{pmatrix} \mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \frac{1}{2}\alpha\mathbf{D}_{AA}(\hat{\mathbf{m}}) \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa}(\hat{\mathbf{m}}) & \mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA}(\hat{\mathbf{m}}) \end{pmatrix} \begin{pmatrix} \mathbf{u} \\ \mathbf{u}' \end{pmatrix} = x \begin{pmatrix} \mathbf{u} \\ \mathbf{u}' \end{pmatrix}. \quad (5.B47)$$

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 (5.B47) as two separate equations for the male and female directions (dropping the explicit dependence on $\hat{\mathbf{m}}$ to avoid a proliferation of brackets),

$$\left(\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} \right) \mathbf{u} + \frac{1}{2}\alpha\mathbf{D}_{AA}\mathbf{u}' = x\mathbf{u}, \quad (5.B48)$$

$$\left(\mathbf{U}_{Aa} + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA} \right) \mathbf{u}' + \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa}\mathbf{u} = x\mathbf{u}'. \quad (5.B49)$$

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,

$$\frac{1}{2}\alpha[\mathbf{F}_{Aa}\mathbf{u} + \mathbf{D}_{AA}\mathbf{u}'] = (x\mathbf{I}_\omega - \mathbf{U}_{Aa})\mathbf{u}, \quad (5.B50)$$

$$\frac{1}{2}(1-\alpha)[\mathbf{F}_{Aa}\mathbf{u} + \mathbf{D}_{AA}\mathbf{u}'] = (x\mathbf{I}_\omega - \mathbf{U}_{Aa})\mathbf{u}'. \quad (5.B51)$$

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

$$\mathbf{u} = \frac{1}{2}\alpha(x\mathbf{I}_\omega - \mathbf{U}_{Aa})^{-1}[\mathbf{F}_{Aa}\mathbf{u} + \mathbf{D}_{AA}\mathbf{u}'], \quad (5.B52)$$

$$\mathbf{u}' = \frac{1}{2}(1-\alpha)(x\mathbf{I}_\omega - \mathbf{U}_{Aa})^{-1}[\mathbf{F}_{Aa}\mathbf{u} + \mathbf{D}_{AA}\mathbf{u}'], \quad (5.B53)$$

which implies

$$\mathbf{u}' = \frac{(1-\alpha)}{\alpha} \mathbf{u}. \quad (5.B54)$$

Substituting this relationship between the male and female directions of the eigenvector back into equation (5.B47) yields

$$\begin{pmatrix} \mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} & \frac{\alpha}{2}\mathbf{D}_{AA} \\ \frac{1}{2}(1-\alpha)\mathbf{F}_{Aa} & \mathbf{U}_{Aa} + \frac{(1-\alpha)}{2}\mathbf{D}_{AA} \end{pmatrix} \begin{pmatrix} \mathbf{u} \\ \frac{(1-\alpha)}{\alpha}\mathbf{u} \end{pmatrix} = x \begin{pmatrix} \mathbf{u} \\ \frac{(1-\alpha)}{\alpha}\mathbf{u} \end{pmatrix}. \quad (5.B55)$$

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

$$\left[\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA}(\hat{\mathbf{m}}) \right] \mathbf{u} = x\mathbf{u}. \quad (5.B56)$$

This equation shows that the eigenvalues x of the $2\omega \times 2\omega$ matrix \mathbf{M}_{22} , given by equation (5.B44), are also eigenvalues of the following matrix of dimensions $\omega \times \omega$ (namely, the left-hand side of equation (5.B56)),

$$\left[\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA}(\hat{\mathbf{m}}) \right]. \quad (5.B57)$$

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

$$\tilde{\zeta}_{AA} = \rho \left[\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA}(\hat{\mathbf{m}}) \right]. \quad (5.B58)$$

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

$$\tilde{\zeta}_{aa} = \rho \left[\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{aa}(\hat{\mathbf{m}}) \right]. \quad (5.B59)$$

The coexistence conditions are then given by

$$\rho \left[\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{AA}(\hat{\mathbf{m}}) \right] > 1, \quad (5.B60)$$

$$\rho \left[\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}\alpha\mathbf{F}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2}(1-\alpha)\mathbf{D}_{aa}(\hat{\mathbf{m}}) \right] > 1, \quad (5.B61)$$

$\mathbf{U}_i(\tilde{\mathbf{m}}) = \mathbf{U}'_i(\tilde{\mathbf{m}})$, $\mathbf{F}_i(\tilde{\mathbf{m}}) = \beta\mathbf{F}'_i(\tilde{\mathbf{m}})$ and $\alpha = 0.5$

Next we make the additional simplifying assumption that male mating success is proportional (or equal) to female fertility, $\mathbf{F}'_i(\tilde{\mathbf{m}}) = \beta\mathbf{F}_i(\tilde{\mathbf{m}})$. 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 (5.27) and (5.28) to heterozygote superiority in population growth rate, i.e. $\lambda_{Aa}(\hat{\mathbf{m}}) > \lambda_{AA}(\hat{\mathbf{m}})$ and $\lambda_{Aa}(\hat{\mathbf{m}}) > \lambda_{aa}(\hat{\mathbf{m}})$, where $\lambda_{AA}(\hat{\mathbf{m}}) = \lambda_{aa}(\hat{\mathbf{m}}) = 1$.

Since males only have one type of offspring, the $\mathbf{F}'_i(\tilde{\mathbf{m}})$ 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 $\mathbf{F}'_i(\tilde{\mathbf{m}})$ is the only nonzero row. Equating male mating succes to female fertility rates, $\mathbf{F}'_i(\tilde{\mathbf{m}}) = \beta \mathbf{F}_i(\tilde{\mathbf{m}})$, then implies that females also only produce one type of offspring. Define a vector of fertilities of dimensions $\omega \times 1$ for each genotype, $\mathbf{f}_i(\tilde{\mathbf{m}})$, such that

$$\mathbf{F}_i(\tilde{\mathbf{m}}) = \begin{pmatrix} f_i(1) & \dots & f_i(\omega) \\ 0 & \dots & 0 \\ \vdots & & \vdots \\ \mathbf{0} & \dots & 0 \end{pmatrix}, \quad (5.B62)$$

$$= \mathbf{e}_1 \otimes \mathbf{f}_i^\top(\tilde{\mathbf{m}}). \quad (5.B63)$$

The following equalities hold in this case

$$\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA} = \mathbf{e}_1 \otimes (\mathbf{f}_{AA}^\top \hat{\mathbf{n}}_{AA}), \quad (5.B64)$$

$$\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{n}}_{AA} = \beta \mathbf{f}_{AA}^\top \hat{\mathbf{n}}_{AA}, \quad (5.B65)$$

$$\mathbf{1}_\omega^\top \mathbf{F}'_{Aa} = \beta \mathbf{f}_{Aa}^\top. \quad (5.B66)$$

Substituting these equalities into the $\mathbf{D}_{AA}(\hat{\mathbf{m}})$ matrix yields

$$\mathbf{D}_{AA}(\hat{\mathbf{m}}) = \frac{(\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa}}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{n}}_{AA}} = \mathbf{e}_1 \otimes \mathbf{f}_{Aa}^\top, \quad (5.B67)$$

$$= \mathbf{F}_{Aa}. \quad (5.B68)$$

Similarly,

$$\mathbf{D}_{aa}(\hat{\mathbf{m}}) = \frac{(\mathbf{F}_{aa} \hat{\mathbf{n}}_{aa}) \otimes (\mathbf{1}_\omega^\top \mathbf{F}'_{Aa})}{\mathbf{1}_\omega^\top \mathbf{F}'_{aa} \hat{\mathbf{n}}_{aa}} = \mathbf{F}_{Aa}, \quad (5.B69)$$

Substituting this expression for \mathbf{D}_{AA} back into the coexistence conditions derived in the previous section, equations (5.B60) and (5.B61) yields

$$\rho \left(\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2} \alpha \mathbf{F}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2} (1 - \alpha) \mathbf{F}_{Aa}(\hat{\mathbf{m}}) \right) > \rho(\mathbf{U}_{AA}(\hat{\mathbf{m}}) + \alpha \mathbf{F}_{AA}(\hat{\mathbf{m}})), \quad (5.B70)$$

$$\rho \left(\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2} \alpha \mathbf{F}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2} (1 - \alpha) \mathbf{F}_{Aa}(\hat{\mathbf{m}}) \right) > \rho(\mathbf{U}_{aa}(\hat{\mathbf{m}}) + \alpha \mathbf{F}_{aa}(\hat{\mathbf{m}})), \quad (5.B71)$$

or

$$\rho \left(\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2} \mathbf{F}_{Aa}(\hat{\mathbf{m}}) \right) > \rho(\mathbf{U}_{AA}(\hat{\mathbf{m}}) + \alpha \mathbf{F}_{AA}(\hat{\mathbf{m}})), \quad (5.B72)$$

$$\rho \left(\mathbf{U}_{Aa}(\hat{\mathbf{m}}) + \frac{1}{2} \mathbf{F}_{Aa}(\hat{\mathbf{m}}) \right) > \rho(\mathbf{U}_{aa}(\hat{\mathbf{m}}) + \alpha \mathbf{F}_{aa}(\hat{\mathbf{m}})), \quad (5.B73)$$

(equations (5.30) and (5.31)).

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

$$\lambda_{Aa} = \rho(\mathbf{U}_{Aa} + \alpha \mathbf{F}_{Aa}). \quad (5.B74)$$

Therefore when $\alpha = \frac{1}{2}$, the coexistence conditions given by equations (5.B72) and (5.B73) are equal to heterozygote superiority in λ , i.e.

$$\lambda_{Aa} > \lambda_{AA}, \quad (5.B75)$$

$$\lambda_{Aa} > \lambda_{aa}. \quad (5.B76)$$

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

$$\mathbf{F}'_i = \mathbf{e}_1 \otimes \mathbf{c}_i^\top, \quad (5.B77)$$

therefore

$$\mathbf{1}_\omega^\top \mathbf{F}'_{Aa} = \mathbf{1}_\omega^\top (\mathbf{e}_1 \otimes \mathbf{c}_{Aa}^\top) \quad (5.B78)$$

$$= \mathbf{c}_{Aa}^\top. \quad (5.B79)$$

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

$$\mathbf{D}_{AA} = \frac{(\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \otimes \mathbf{1}_\omega^\top \mathbf{F}'_{Aa}}{\mathbf{1}_\omega^\top \mathbf{F}'_{AA} \hat{\mathbf{n}}_{AA}} \quad (5.B80)$$

$$= \frac{1}{N_b} (\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \otimes \mathbf{c}_{Aa}^\top, \quad (5.B81)$$

The largest eigenvalue of the Jacobian matrix evaluated at the AA boundary is therefore,

$$\zeta_{AA} = \rho \left(\mathbf{U}_{Aa} + \frac{1}{2} \alpha \mathbf{F}_{Aa} + \frac{1}{2N_b} (1 - \alpha) (\mathbf{F}_{AA} \hat{\mathbf{n}}_{AA}) \otimes \mathbf{c}_{Aa}^\top \right), \quad (5.B82)$$

and at the aa boundary,

$$\zeta_{aa} = \rho \left(\mathbf{U}_{Aa} + \frac{1}{2}\alpha\mathbf{F}_{Aa} + \frac{1}{2N_b}(1 - \alpha)(\mathbf{F}_{aa}\hat{\mathbf{n}}_{aa}) \otimes \mathbf{c}_{Aa}^\top \right). \quad (5.B83)$$

These two equations correspond exactly with the results reported in de Vries and Caswell (2018c) if we absorb α into the definition of the \mathbf{F}_i matrices.