A TWO-SEX, AGE-STRUCTURED POPULATION MODEL IN DISCRETE-TIME

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This work examines how the life history parameters effect the stable age distribution of the different classes and compares these results with the standard single sex model. The conditions necessary for a population projected forward in time to reach a stable age distribution is analyzed. The conditions for existence are dependent on the nature of the mating function, i.e. the rate at which the two sexes find each other and mate. In addition, the assumptions under which these mating functions are constructed have important implications for the dynamics of the population and ultimate age distribution, stable or not. An analysis of when including both sexes becomes essential to the understanding of reproductive strategies, examination of whether a population fulfils the necessary assumptions about mating to make certain statements about population growth, growth rates and relative fitness, and outlining an accessible approach to modeling the joint life histories will be of practical value. Toward this end, a framework for discrete-time two-sex models with age structure is developed. In addition a marriage (mating) function based on an analogy with foraging theory and preferences based on the predispositions of one age group for another is proposed. Some of the properties of these models and their solutions are also investigated.

BIOGRAPHICAL SKETCH

Stephen Eric Tennenbaum was born on November 15, 196 in Baltimore Maryland, and subsequently moved every two years until the age of 14 where he was forcibly settled in New Jersey. He studied Biology and General Science at Rutgers University, Camden. He worked for a few years as a lab technician at Thomas Jefferson University Hospital in the Psychology and Neurology departments before returning to Graduate school at the University of Florida. He received a Masters of Science in Environmental Engineering under Howard Odum in 1988. He then started a PhD program at the University of Maryland in Ecological Economics with Robert Costanza where he stayed a year before he transferred to Cornell University. Here he had the good fortune to meet Carlos Castillo-Chavez who soon became his advisor and mentor. Stephen interrupted his PhD program shortly after passing his "A" exam in order to work full time managing the Mathematical and Theoretical Biology Institute. He did this for seven years until Carlos (and MTBI) moved to Arizona State University. In October of 2004 Stephen followed Carlos to Arizona in order to complete his Doctoral Program.

In memory of Arthur Lionel Tennenbaum 1926 - 2002

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Introduction

1.1 History and Motivation

I will examine how the life history parameters effect the stable age distribution of the different classes and compare these results with the standard single sex model. The more the life history of the sexes diverge the more important the tracking of both sexes become. Although this may seem an obvious conclusion, the fact remains that structured two sex models are not very commonplace. Analyses are often of the population projected forward in time to some stable age distribution. However, conditions under which such a stable age structure can exist are dependent on the nature of the mating function, that is the rate at which the two sexes find each other and mate. In addition the assumptions under which these functions are constructed has important implications for the dynamics of the population and ultimate age distribution, stable or not. An analysis of when including both sexes becomes essential to the understanding of reproductive strategies, examination of whether a population fulfils the necessary assumptions about mating to make certain statements about population growth, growth rates and relative fitness, and outlining an accessible approach to modeling the joint life histories will be of practical value. To date most of the work in this area has been done for age-structured continuous time models or non age-structured discrete time population models for example see Castillo-Chavez, et al. [4], R. Pollak [37], [38], [39], Hoppensteadt [18], Caswell [5], Kendall [23], Keyfitz [24], [25], [26], Fredrickson [11], Hadeler [13], [14], [15], M. Iannelli [21], M. Martcheva [30], F.A. Milner [33], and others.

Population models have broad application in general, not only the obvious field of demography but ecology, forestry, fisheries, epidemiology, population genetics, sociology, and economics to name a few. Clearly many applications can benefit from having a two-sex age structured framework. In particular population genetics and sexually transmitted diseases require inclusion of both sexes and the addition of age structure can increase the accuracy of both the distribution and timing of the spread of genes or infection respectively. Demography has a long history and even the concept of stable age structure can be traced back to the eighteenth century with its introduction by Leonard Euler [8]. The first purely mathematical model of a population is attributed to Thomas Malthus[28] in 1798. The combination of the two, stable age structure and rigorous mathematical treatment came at the beginning of the twentieth century with A. J. Lotka and F. R. Sharpe [44] with an integral equation approach. McKendrick [32] and later von Foerester [10] reformulated the problem in terms of PDE's. The two approaches are referred to as the Sharpe–Lotka and McKendrick–von Foerester models.

Two sex models first appeared with a model by Kendall in 1949 [23]. There is no age structure in this model, but he introduces three possibilities for a marriage function (a function for predicting the number of marriages between males and females per unit of time). These are proportional to geometric mean, arithmetic mean, and minimum of the total number of single males and single females in the population. Fredrickson [11] later (1971) suggested the harmonic mean as function that satisfied, what he considered the self-evident conditions that if there are no singles of either sex there are no marriages and that the number of marriages must change in proportion to the total population size (the marriage function is homogeneous of degree one). His two sex model also included age structure. Further development followed with work by Hoppensteadt [18] and Hadeler [13]. Hadeler, in his model, includes the duration of marriage. McFarland [31] reviews marriage functions and proposes seven additional conditions ("axioms") that a marriage function should satisfy. These deal with existence, non-negativity, and the signs of the partial derivatives of the marriage function (see 'Properties for a "nice" marriage function' below). Martcheva [29] examines the existence, uniqueness and well-posedness of marriage functions in the Fredrickson-Hoppensteadt model.

Marriage and mixing functions have been used extensively in the modeling of sexually transmitted diseases, Heathcote and Yorke [17] used the idea of preferences to explain like-with-like mixing patterns. Blythe and Castillo-Chavez [2] develop generalized one-sex mixing functions as perturbations of proportionate mixing. Castillo-Chavez and Busenberg [3] formulate a two-sex mixing approach for populations with preferences for fixed characteristics. In both the one-sex and two-sex cases preferences are measured as deviations from random mixing. Hsu Schmitz and Castillo-Chavez [19] further develop non-random mixing with the use of male and female affinity matrices to describe the preferences that one group has for another. Castillo-Chavez, et al. [4] discuss discrete-time two-sex models without age structure and investigate some of the properties of the models and their solutions.

1.1.1 Goals of this dissertation

In this work I will attempt to develop a framework for discrete-time two-sex models with age structure. In addition I will develop a marriage function based on an analogy with foraging theory and preferences based on the predispositions of one age group for another. I also investigate some of the properties of these models and their solutions.

1.2 A Select Chronology of Population Modeling and Demography

(Adapted from M. Iannelli, M. Martcheva, and F.A. Milner [22] with some additions relevant to the current work).

c.3800BC Babylonia. First recorded census

225BC Emilius Mercer (Roman Jurisconsul) Romans took a census every 5 years. Recorded mortalities or life expectancy - very inaccurate.

c.200BC Ulpian (successor to Mercer) updated tables, much more accurate, used for 1600yrs.

1086 Domesday book. William the Conqueror (Census)

1208 Leonado Pisano (Fibenacci). Rabbit populations in "Liberabaci"

1570 Girolamo Cardano. Formula for expectancy of life

1662 John Graunt. "Natural and Political Observations Upon Bills of Mortality" (Life table concept)

1693 Edmund Halley. "Estimation of the Degrees of the Mortality of Mankind." First "modern" life table.

1760 L. Euler. "A general investigation into the mortality and multiplication of the human species" Stable age distribution. Enabled population projections from incomplete data.

1766 Daniel Bernoulli. Continous analysis (continuous age dependent force of mortality)

1798 Thomas Malthus. First formal mathematical model of population growth

1825 Benjamin Gompertz. "On the nature of the function expressive of the law of human mortality." (Density dependence)

1837 Aldolphe Quetelet "Sur L'homme et le development de ses faculté" (Logistic equation suggested)

1838 Pierre-Francois Verhulst. "A note on the law of population growth" (Logistic equation)

1860, 1867 William Makeham. "On the law of mortality" Variations on Gompertz

1886 Richard Böckh. "Statistisches Jahrbuch der Stadt Berlin" Net reproductive rate.

1911 F.R Sharpe & A.J. Lotka. "A problem in age-distribution" (Integral equations)

1922 A.J. Lotka. "Stability of the Normal Age Distribution"

1926 A.C. McKendrick "Applications of mathematics to medical problems" PDE approach

1928 R. Pearl. "The rate of living; being an account of some experimental studies on the biology of life duration." Life tables for *Drosophila* (first animal population life table?)

1938 V. Volterra. "Population growth, equilibria, and extinction under specified breeding conditions: a development and extention of the theory of the logistic curve."

1938 F.S. Bodenheimer "Problems of animal ecology" Life tables for several species

1941 William Feller. "On the integral equation of renewal theory" (Rigorous proof of stable age distribution)

1945 P.H. Leslie. "On the use of matrices in certain population mathematics."

1947 P.H. Karmel. "The relations between male and female reproductive rates"

1947 E.S. Deevey Jr. "Life tables for natural populations of animals"

1949 W.C. Allee "Principles of animal ecology"

1954 Lamont Cole "The population consequences of life history phenomena"

1959 H. Von Foerster. "Some remarks on changing populations" (More on the PDE approach)

1967 N. Keyfetz "Reconciliation of population models: matrix, integral equation and partial fraction."

1969 J.H. Pollard "Continous-time and discrete-time models of population growth."

1971 A. Fredrickson "A mathematical theory of age structure in sexual populations: Random mating and monogamous marriage models".

1975 F. Hoppensteadt. "Mathematical theories of populations: Demographics, Genetics and Epidemics."

1987 R. Pollak "The two-sex model with persistent unions: a generalization of the birth matrix-mating rule model".

1989 K. Hadeler. "Pair formation in age structured populations"

1989 C. Castillo-Chavez, S Busenberg, K. Gerow. "Pair formation in structured populations"

1996 C. Castillo-Chavez, W. Huang, and J. Li. "On the existence of stable pairing distributions."

2005 M. Iannelli, M. Martcheva, F.A. Milner. "Gender-structured Population Modeling"

Chapter 2

Notation and Definitions

I will try to adhere to the following conventions: Roman upper case are un-scaled state variables, upper case Fraktur font is for sets, and Calligraphic font (usually upper case) is for functions of state variables (these will always be specified). Lower case Roman, Greek and Fraktur are constant parameter values, time, and scaled state variables. A tilde ($\tilde{}$) will be placed over male symbols when necessary to distinguish them from female symbols.

For age notation relating to couples I will use subscripts to indicate current age and superscripts to indicate ages at which the individuals were mated. Although the two conventions are equivalent there are occasions when the manipulation of expressions are more convenient in one form versus the other.

Finally, when we deal with a population that has reached a stable age distribution we will use an underscore to indicate the value of a variable at some arbitrary base time or a variable that becomes constant withe respect to time. For example for a population with a stable age distribution $F_i(0) \equiv \underline{F}_i$ and $\mathcal{B}_i(t) = \underline{\mathcal{B}}_i$. For variables that are defined only for a population at a stable age distribution no underscore is used, e.g. x_i.

2.1 State variables

$F_i(t)$	number or density of females in age class i at time t
$M_j(t)$	number or density of males in age class j at time t
$C_h^{i,j}(t)$	number or density of reproductive couples, at time t females mated at age i, males mated at age j for h units of time

$F_i^s(t)$ number or density of single females in age class i at time t

$M_j^s(t)$ number or density of single males in age class j at time t

$F_A(t)$ number or density of all adult (reproductive age classes) females at time t

$M_A(t)$ number or density of all adult (reproductive age classes) males at time t

$F^s(t)$ number or density of all adult single females at time t

$M^s(t)$ number or density of all adult single males at time t

$F(t)$ number or density of all females at time t

$M(t)$ number or density of all males at time t

$C(t)$ number or density of all reproductive couples, at time t

$\mathcal{S}_{i,j}(t)$ secondary sex ratio of males age j to females age i at time t

$\mathfrak{F}^s(t)$ the set of all adult single female state variables at time t

$\mathfrak{M}^s(t)$ the set of all adult single male state variables at time t

$\mathfrak{C}(t)$ the set of all couple state variables at time t

x_i, y_j proportions of individuals in each age group

x_A, y_A proportions of individuals that are adults

$z_h^{i,j}$ proportions of couples in each age group and length of marriage out of all couples

$\mathfrak{f}_i$, $\mathfrak{m}_j$ fraction of each age class that is single (by sex)

$\langle \mathfrak{f} \rangle$, $\langle \mathfrak{m} \rangle$ proportion of all single female and male adults of reproductive age

$\mathcal{N}^{i,j}(\mathfrak{F}^s(t), \mathfrak{M}^s(t), \mathfrak{C}(t))$ a function determining the number of new pair bondings between females of age i and males of age j at time t

2.2 Parameters

2.2.1 Age

α, $\tilde{\alpha}$ minimum reproductive age classes of females and males

ω, $\tilde{\omega}$ maximum reproductive ages of females and males

Ω, $\tilde{\Omega}$ maximum age of females and males

2.2.2 Survival

p_i, $\tilde{p}_j$ probabilities of survival for females and males from the current age classes, i and j, to the next, i+1 and j+1

$\pi_h^{i,j}$ probability of a pair - female mated at age i, and male at age j remaining mated from the h-1 to the next unit of time

ℓ_i, $\tilde{\ell}_j$ probabilities of survival for females and males from birth to ages i and j respectively

$\mathcal{L}_h^{i,j}$ probability of survival of a marriage for h units of time by a couple mated at the ages of i and j

$\Lambda^{i,j}$ mean expectation of survival of a marriage for a couple that were mated at ages i and j

2.2.3 Reproduction

$f_h^{i,j}$ fecundity (female births) of couples mated at ages i and j for h time units

$\tilde{f}_h^{i,j}$ fecundity (male births) of couples mated at ages i and j for h time units

$\langle f^{i,j}\rangle, \left\langle \tilde{f}^{i,j}\right\rangle$ mean expected fecundities of a couple that were mated at ages i and j averaged over the lifetime of the marriage

$f, \tilde{f}$ maximum fecundity for females and males respectively

$\mathcal{B}_i\left(t\right)$ age specific birthrates of females per female

$\tilde{\mathcal{B}}_j\left(t\right)$ age specific birthrates of males per male

$\sigma_h^{i,j}$ the subjective primary sex ratio (the expected ratio of male births to female births for individual parents that mated at ages i & j and been mated for h time units)

2.2.4 Marriage function

$a_{i,j}$ female age predisposition (probability that a female age j will want to court a male age i upon encountering him)

$\tilde{a}_{i,j}$ male age predisposition (probability that a male age i will want to court a female age j upon encountering her)

$\rho_{i,j}$ joint predisposition (probability that a male age i and female age j will want to court each other)

$\eta_{i,j}$, $1-\eta_{i,j}$ probability that a single male (j) or single female (i) will initiate courtship given an encounter with the opposite sex of indicated age

$w_{i,j}$ preference coefficient of female age i for male age j (time spent in mating activities between i & j per search time attributable to males age j)

$\tilde{w}_{i,j}$ preference coefficient of male age j for female age i (time spent in mating activities between i & j per search time attributable to females age i)

$v_{i,j}$ preference probability (standardized fraction of time that initiating females of age i spend in mating activities with males age j)

$\tilde{v}_{i,j}$ preference probability (standardized fraction of time that initiating males age j spend in mating activities with females of age i)

c_i, $\tilde{c}_j$ average fraction of total time that a single (female or male) spends pursuing mating activities.

$q_{i,j}$ proportion of courting couples that marry

$h_{i,j}$ average "individual-hours" it takes for a courtship between a male age j and a female age i

2.3 Time variables and Rates

$\underline{T}_G, \underline{\tilde{T}}_G$ generation times for females and males

$A, \tilde{A}$ Mean ages of of childbearing in a population with a stable age distribution

$\underline{\mu}_1, \underline{\tilde{\mu}}_1$ Mean ages of childbearing in a cohort

$\underline{\mu}_n, \underline{\tilde{\mu}}_n$ n$^{\text{th}}$ central moments of the maternity functions

T average length of time to successfully find a mate

T_s time devoted to searching for a mate

T_c courting time

T_o time devoted to non-mating activities

$\mathcal{E}_{i,j}$ rate of encounter that single females age i have with single males age j per unit time searched per single female age i

$\tilde{\mathcal{E}}_{i,j}$ rate of encounter that single males age j have with single females age i per unit time searched per single male age j

$k_{i,j}$ rate of encounter that single females age i have with single males age j per unit time searched per single female age i per fraction of single males that are age j

$\tilde{k}_{i,j}$ rate of encounter that single males age j have with single females age i per unit time searched per single male age j per fraction of single females that are age i

$u_{i,j}, \tilde{u}_{i,j}$ maximal rates of marriage between female i & male j for female initiating and males initiating respectively

$Q_{ij}(t)$ potential overall rate of marriage per female i per male j

$\tau_{i,j}(t)$ fraction of time interval before all females age i and/or males age j are mated

$U_{i,j}$ potential marriage rate with respect to fraction of single females (i) and males (j) within each age class

$\mathcal{U}_{i,j}$ realized marriage rate with respect to fraction of single females (i) and males (j) within each age class occuring in $\tau_{i,j}$

λ asymptotic growth rate of the population

Chapter 3

A Brief Example

Suppose we have a sexually reproducing population with a life history where individuals live for a maximum of 3 years and have offspring in second and last years of their life. The usual way of modeling the population would be to follow the dynamics of the females and ignore the males role in determining the overall dynamics of the population. There are three equations governing these dynamics. The first two express the number of females in age classes 1 and 2 at time $t+1$ which have survived from time t (and age classes 0 and 1 respectively). The constants p_0 and p_1 are the fraction of the respective age class that survives the year.

$$F_1(t+1) = p_0 F_0(t), \tag{3.1a}$$

$$F_2(t+1) = p_1 F_1(t). \tag{3.1b}$$

The third equation is

$$F_0(t+1) = \mathcal{B}_1 F_1(t) + \mathcal{B}_2 F_2(t), \tag{3.1c}$$

where $\mathcal{B}_1$ and $\mathcal{B}_2$ are age specific birthrates (fertilities) of females per total number of females aged 1 and 2 (individuals do not reproduce in the first year after they are born so $\mathcal{B}_0 = 0$). Note also that $\mathcal{B}_1$ and $\mathcal{B}_2$ are constants and are fertilities averaged over the entire number of females of each age class regardless whether all the females are actually reproducing.

Looking at the same population but now considering monogomous mating and including males explicitly, we have the same set of equations for survival of the females

$$F_1(t+1) = p_0 F_0(t), \tag{3.2a}$$

$$F_2(t+1) = p_1 F_1(t). \tag{3.2b}$$

And now of course we have the males

$$M_1(t+1) = \tilde{p}_0 M_0(t), \tag{3.2c}$$

$$M_2(t+1) = \tilde{p}_1 M_1(t). \tag{3.2d}$$

In addition we have the number of reproductive couples. First let $C_h^{i,j}(t)$ be the number, at time t, of reproductive females (producing first offspring for this couple at age i) that are paired with males (producing first offspring for this couple at age j) and have been producing offspring for h units of time. The fraction of females and males remaining mated after a single reproductive season is π given that they both survived to the next mating season. Then

$$C_1^{1,1}(t+1) = p_1\,\tilde{p}_1 \pi C_0^{1,1}(t). \tag{3.3}$$

This is the only survival equation for existing marriages since all other couples have at least one member that was already in the last year of reproduction after marrying. There are four equations governing the number of new pair bondings between females of age i and males of age j at time t. The number of new couples at the beginning of time interval $t+1$ coming from mating, and courtship that occurred during the previous time interval t. Consider the following marriage function,

$$C_0^{i+1,j+1}(t+1) = p_i \tilde{p}_j Q_{i,j}(t)\, F_i^s(t)\, M_j^s(t)\, \tau_{i,j}(t), \tag{3.4a}$$

$$Q_{i,j}(t) \equiv \left(\frac{\tilde{u}_{i,j}\tilde{v}_{i,j}}{\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j} F_{i'}^{s}(t)} + \frac{u_{i,j} v_{i,j}}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'} M_{j'}^{s}(t)} \right), \tag{3.4b}$$

$$\tau_{i,j}(t) = \min \left\{ 1, \frac{1}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j'}(t) M_{j'}^{s}(t)}, \frac{1}{\sum_{i'=\alpha-1}^{\omega-1} Q_{i'j}(t) F_{i'}^{s}(t)} \right\}. \tag{3.4c}$$

$Q_{i,j}(t)$ is the potential (or "desired") rate of pair formation. $\tau_{i,j}(t)$ is the fraction of a time interval that it takes, given $Q_{i,j}(t)$, to pair up all the available singles of age i (female) or j (male). In other words $1/\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j'}(t) M_{j'}^{s}(t)$ and $1/\sum_{i'=\alpha-1}^{\omega-1} Q_{i'j}(t) F_{i'}^{s}(t)$ are the expected fractions of a time interval to "use up" all available single females age i or single males age j respectively. If these quotients are greater than one, then the number of singles are not limiting and potential rate is realized. They are less than one if the demand for a particular age-sex exceeds the supply.

The reason that π does not appear in these equations is that I consider a couple mated when they have had sex for reproductive purposes (almost always true for all non-human matings) so the number of couples that are potentially producing offspring is the number that has conceived and survived to the next season, if they had split up after conceiving it would not matter to the math. I will use the term "matings" interchangably with the phrase "pair bonding". In other words, "mating" as used here refers to the semi-permenant union of a male and female over successive reproductive seasons and does not refer to a single reproductive event except as a special case. In addition the accounting is such that the pair formation process is considered over at the *end* of time interval t but the couples resulting from this process are counted as a reproductive couple at the *beginning* of the next time interval $(t+1)$. It is perhaps unfortunate that the mating formulas are called "marriage functions" in the literature since in truth we aren't interested in the social, religious, or legal aspects of pair formation – only the reproductive aspects. In human demography, as currently practiced, it is impossible to separate the two. Be that as it may, I will continue to use the term marriage in the broad sense of the word as a coupling, and it will be used synonymously with reproductive mating. In addition, and with the preceding in mind, when I say a couple is "first mated at ages i and j and has been mated for h units of time" I mean that this couple produced its first offspring at ages i and j and have been producing offspring for h units of time.

$$C_0^{1,1}(t+1) = p_0\tilde{p}_0\tau_{0,0}(t)\,Q_{0,0}(t)\,F_0^s(t)\,M_0^s(t)\,, \tag{3.5a}$$

$$C_0^{1,2}(t+1) = p_0\tilde{p}_1\tau_{0,1}(t)\,Q_{0,1}(t)\,F_0^s(t)\,M_1^s(t)\,, \tag{3.5b}$$

$$C_0^{2,1}(t+1) = p_1\tilde{p}_0\tau_{1,0}(t)\,Q_{1,0}(t)\,F_1^s(t)\,M_0^s(t)\,, \tag{3.5c}$$

$$C_0^{2,2}(t+1) = p_1\tilde{p}_1\tau_{1,1}(t)\,Q_{1,1}(t)\,F_1^s(t)\,M_1^s(t)\,, \tag{3.5d}$$

where $F_i^s(t)$ and $M_j^s(t)$ are the number of singles at time t. The interpretation of the parameters in Equation 3.4b will be dealt with in detail later on, for the time though we note their units. For $\tilde{u}_{i,j}$ units: $\left(= \frac{\text{[marriages between } i \text{ \& } j \text{ (resulting from males initiating)]}}{\text{[single males age } j\text{][time spent in mating activities between female } i \text{ \& male } j\text{]}}\right)$, (similar for $u_{i,j}$). The parameter $\tilde{v}_{i,j}$ is preference probability, i.e. it is the fraction of time that initiating males age j would spend in mating activities with female of age i given equal numbers of all age females (similar for $v_{i,j}$). $\eta_{i,j}$ is the fraction of courtships between females age i and males age j that occur due to male searching and $1-\eta_{i,j}$ is the fraction of courtships between females age i and males age j that occur due to female searching.

The number of single females of a given age are determined by subtracting the total number of paired females from all females of that age

$$F_0^s(t) = F_0(t) \tag{3.6a}$$

$$F_1^s(t) = F_1(t) - C_0^{1,1}(t) - C_0^{1,2}(t) \tag{3.6b}$$

$$F_2^s(t) = F_2(t) - C_0^{2,1}(t) - C_0^{2,2}(t) - C_1^{1,1}(t) \tag{3.6c}$$

and similarly for single males

$$\begin{aligned} M_0^s(t) &= M_0(t) && (3.7a) \\ M_1^s(t) &= M_1(t) - C_0^{1,1}(t) - C_0^{2,1}(t) && (3.7b) \\ M_2^s(t) &= M_2(t) - C_0^{1,2}(t) - C_0^{2,2}(t) - C_1^{1,1}(t) && (3.7c) \end{aligned}$$

The total number of female and male births resulting from reproduction during the time interval t are,

$$F_0(t+1) = f_0^{1,1}C_0^{1,1}(t) + f_0^{1,2}C_0^{1,2}(t) + f_0^{2,1}C_0^{2,1}(t) + f_0^{2,2}C_0^{2,2}(t) + f_1^{1,1}C_1^{1,1}(t) \quad (3.8)$$

$$M_0(t+1) = \tilde{f}_0^{1,1}C_0^{1,1}(t) + \tilde{f}_0^{1,2}C_0^{1,2}(t) + \tilde{f}_0^{2,1}C_0^{2,1}(t) + \tilde{f}_0^{2,2}C_1^{2,2}(t) + \tilde{f}_1^{1,1}C_1^{1,1}(t) \quad (3.9)$$

Here the $f_h^{i,j}$'s are the fecundities (female births) of the couples mated at ages i and j and mated for h time units, and the $\tilde{f}_h^{i,j}$'s are the fecundities (male births). In order to compare the two sex model with single sex models, we calculate the agespecific birthrates (fertilities) of females per female and males per male as follows[1]. If $F_i(t) = 0$ then $\mathcal{B}_i(t) = 0$ and if $M_j(t) = 0$ then $\tilde{\mathcal{B}}_j(t) = 0$ otherwise,

$$\begin{aligned} \mathcal{B}_1(t) &= \frac{1}{F_1(t)}\left(f_0^{1,1}C_0^{1,1}(t) + f_0^{1,2}C_0^{1,2}(t)\right) && (3.10a) \\ \mathcal{B}_2(t) &= \frac{1}{F_2(t)}\left(f_0^{2,1}C_0^{2,1}(t) + f_0^{2,2}C_0^{2,2}(t) + f_1^{1,1}C_1^{1,1}(t)\right) && (3.10b) \end{aligned}$$

[1] There is no reason other than consistency with the single sex (female only) models that I choose to express these as females per female and males per male. I could have just as easily chosen males per female and females per male, or half offspring per male and per female. In fact Pollard ([40] continuous model, [41] discrete model) does define the birthrates as males per female and females per male in his models to ensure matched growth rates in male and female subpopulation when marriage functions are not explicitly include in the models.

$$\tilde{\mathcal{B}}_1(t) = \frac{1}{M_1(t)}\left(\tilde{f}_0^{1,1}C_0^{1,1}(t) + \tilde{f}_0^{2,1}C_0^{2,1}(t)\right) \quad (3.11a)$$

$$\tilde{\mathcal{B}}_2(t) = \frac{1}{M_2(t)}\left(\tilde{f}_0^{1,2}C_0^{1,2}(t) + \tilde{f}_0^{2,2}C_0^{2,2}(t) + \tilde{f}_1^{1,1}C_1^{1,1}(t)\right) \quad (3.11b)$$

Rearranging and substituting these definitions into the generation birth equations we have,

$$F_0(t+1) = \mathcal{B}_1(t)\,F_1(t) + \mathcal{B}_2(t)\,F_2(t) \quad (3.12)$$

$$M_0(t+1) = \tilde{\mathcal{B}}_1(t)\,M_1(t) + \tilde{\mathcal{B}}_2(t)\,M_2(t) \quad (3.13)$$

3.1 Example

I will use the following set of parameter values in the above equations. The suvival probabilities are $p_0 = 0.400$, $p_1 = 0.900$, $\tilde{p}_0 = 0.300$, and $\tilde{p}_1 = 0.800$.Individuals of both sexes can potentially reproduce in their second and third years (ages 1 and 2). The probability that a couple will remain together for both those years (given both the male and female partners were age 1 when they first mated) is $\pi = 0.900$. The maximal rates of pair formation are

$$\begin{bmatrix} u_{0,0} & u_{0,1} \\ u_{1,0} & u_{1,1} \end{bmatrix} = \begin{bmatrix} 0.500 & 0.144 \\ 0.300 & 0.320 \end{bmatrix}, \quad \begin{bmatrix} \tilde{u}_{0,0} & \tilde{u}_{0,1} \\ \tilde{u}_{1,0} & \tilde{u}_{1,1} \end{bmatrix} = \begin{bmatrix} 0.400 & 0.372 \\ 0.500 & 0.500 \end{bmatrix}.$$

The preference probabilities are

$$v = v_{i,j} = \tilde{v}_{i,j} = 0.625.$$

There is no discrimination between ages however there is only a 62.5% chance that given an encounter with the opposite sex the opportunity for courtship will be exploited. The fecundities by age and length of marriage are

$$\begin{bmatrix} f_0^{1,1} & f_0^{1,2} \\ f_0^{2,1} & f_0^{2,2} \end{bmatrix} = \begin{bmatrix} 20 & 40 \\ 40 & 60 \end{bmatrix}, \quad f_1^{1,1} = 50,$$
$$\begin{bmatrix} \tilde{f}_0^{1,1} & \tilde{f}_0^{1,2} \\ \tilde{f}_0^{2,1} & \tilde{f}_0^{2,2} \end{bmatrix} = \begin{bmatrix} 30 & 50 \\ 40 & 70 \end{bmatrix}, \quad \tilde{f}_1^{1,1} = 82.0.$$

Initially there are no couples,

$$C_h^{i,j}(0) = 0.$$

The initial number of singles are

$$\begin{bmatrix} F_0^s(0) \\ F_1^s(0) \\ F_2^s(0) \end{bmatrix} = \begin{bmatrix} F_0(0) \\ 0 \\ 0 \end{bmatrix}; \quad \begin{bmatrix} M_0^s(0) \\ M_1^s(0) \\ M_2^s(0) \end{bmatrix} = \begin{bmatrix} M_0(0) \\ 0 \\ 0 \end{bmatrix}.$$

And the initial (total) number of males and females are

$$\begin{bmatrix} F_0(0) \\ F_1(0) \\ F_2(0) \end{bmatrix} = \begin{bmatrix} 100 \\ 0 \\ 0 \end{bmatrix}; \quad \begin{bmatrix} M_0(0) \\ M_1(0) \\ M_2(0) \end{bmatrix} = \begin{bmatrix} 100 \\ 0 \\ 0 \end{bmatrix}.$$

In order to compare with the single sex case I simulate the two sex case with the above parameters and then calculate the birth rates once a stable age distribution and constant gross fertilities are achieved (Figure 3.1). I do this for two single sex models: female births attributable to females, and male births attributable to males. In the one sex models these fertilities are treated as constants over the entire simulation,

$$\begin{bmatrix} \mathcal{B}_0 \\ \mathcal{B}_1 \\ \mathcal{B}_2 \end{bmatrix} = \begin{bmatrix} 0 \\ 3.5833 \\ 1.9604 \end{bmatrix}; \begin{bmatrix} \tilde{\mathcal{B}}_0 \\ \tilde{\mathcal{B}}_1 \\ \tilde{\mathcal{B}}_2 \end{bmatrix} = \begin{bmatrix} 0 \\ 5.5083 \\ 1.6685 \end{bmatrix}$$

The results of simulation are shown in Figure 3.1. The first two top panels show the fertilities of females ($\mathcal{B}$) and males $\left(\tilde{\mathcal{B}}\right)$ for the two sex model. These vary wildly until the population starts to reach a stable distribution. The values for the single sex case were taken at $t = 30$. In Figure 3.2. the top three panels show the population (log scale) of each of the age classes for females in the two sex case (o's) and one sex case (x's) although the ultimate growth rate achieved is the same ($\lambda = 1.393$) the initial behavior of the two models is quite different with often one model increasing while the other decreases. The bottom three panels are for the males and show similar behavior. Also the total population size is much lower once the systems have stabilized (the one sex model lags the two sex by about 3.9 time steps for females and about 4.8 time steps for males). The reason for this is the large spikes in fertility (Fig.3.1) early on in the two sex model as compared to the single sex models where the fertility is held constant. The two sex model has constant fecundities (births per reproductive couple). The two sexes differ in the details of the growth and sizes of the different age categories due to the differences in their fecundities and survival rates. Yet they eventually achieve the same growth rate by virtue of the fact that reproduction is ultimately controlled by the number of reproductive pairs. . The fertilities of the single sex models are calculated from the two sex model after they have stabled on. Back calculating with these when the population is much smaller and more variable results in the lag in population growth exhibited by the single sex vs. two sex model where the births can track the rapid increase in the number of couples forming early on.

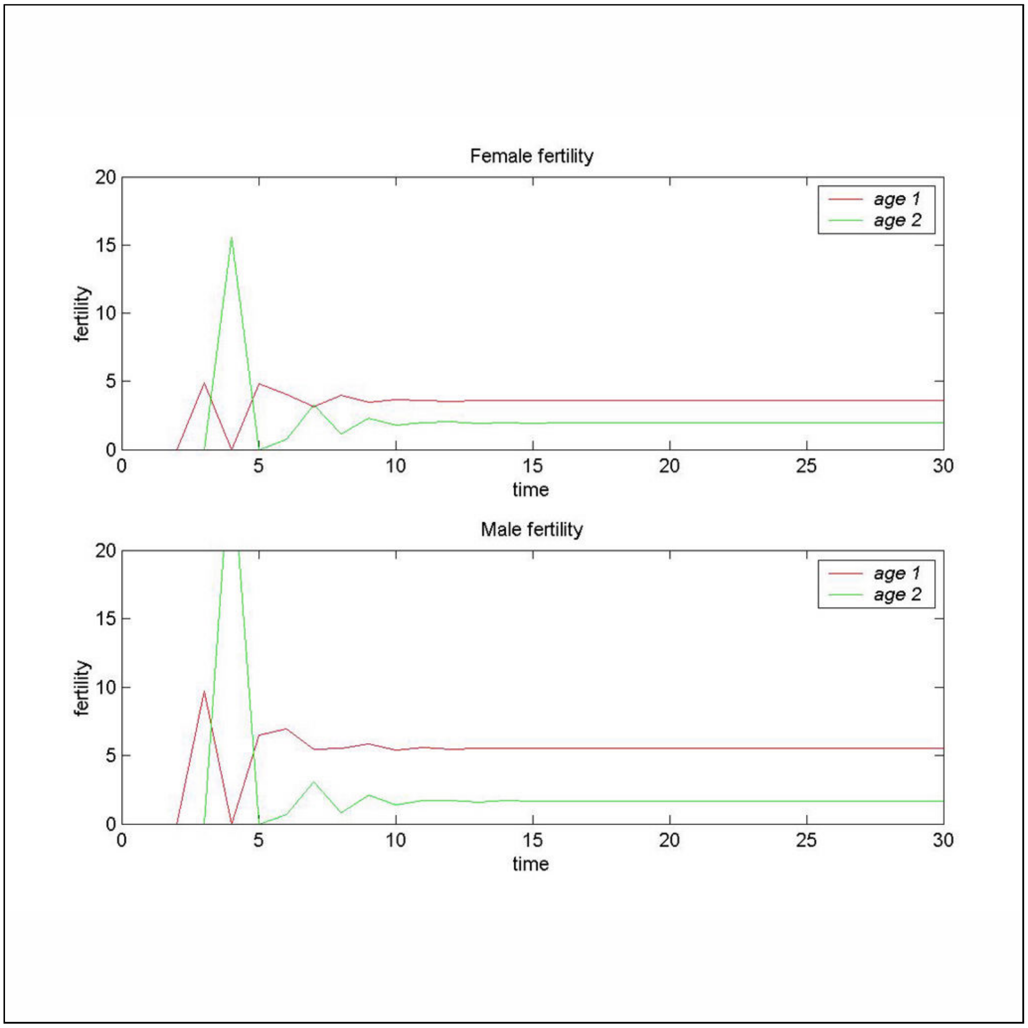

Figure 3.1: Birth rates

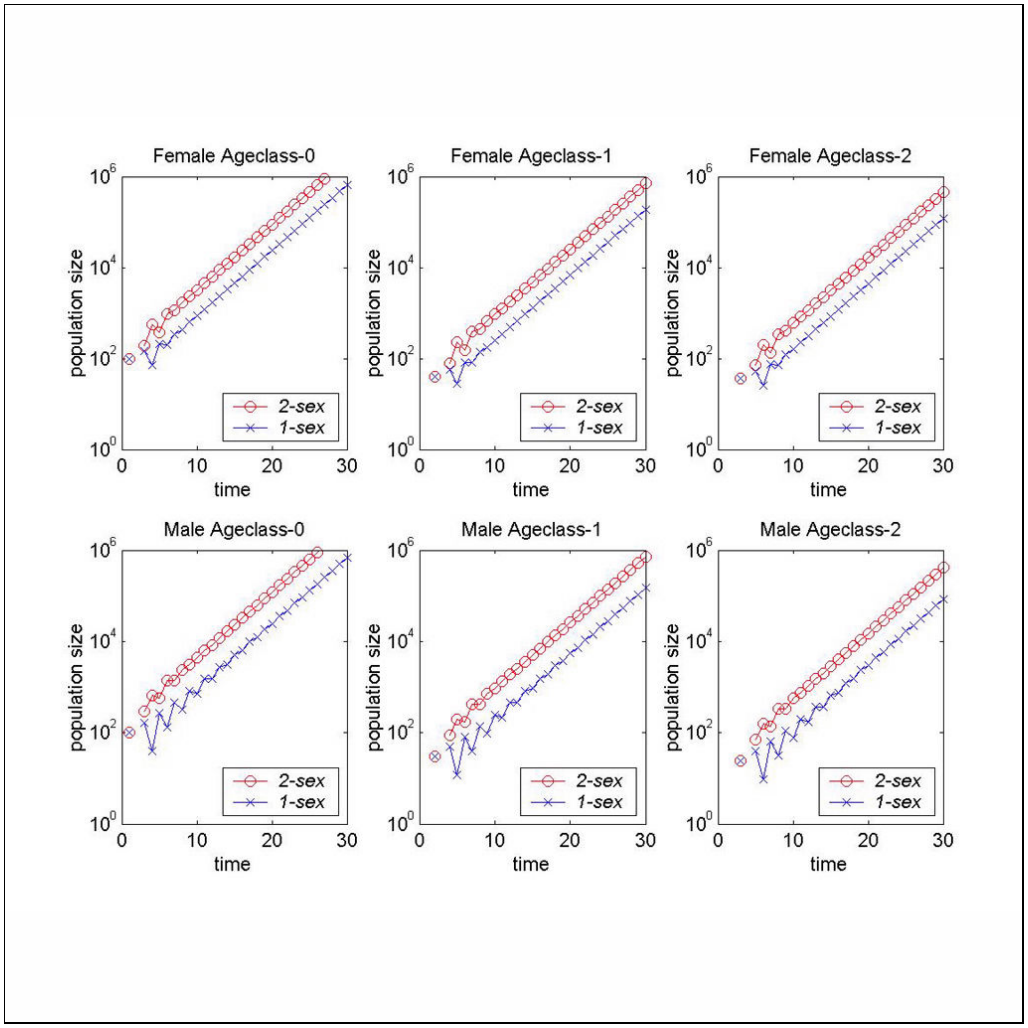

Figure 3.2: Population growth.

Chapter 4

Generalization of the Model

The population density is observed at the beginning of a specified time interval. This time interval is typically defined as the time between two consecutive breeding seasons; age classes will correspond to this interval. Other definitions are possible, for example insect population are frequently modeled along a "physiological" time scale (the product of ambient temperature and time measured in degree-days). Or we may wish to base our time unit on the length of some developmental stage or benchmark. In any event, here I will use the breeding season as our yardstick. I will number the first age class 0 (newborns) and these consist of all individuals born between the beginning of the breeding season up to the beginning of the next breeding season. Define the age parameters α, and $\tilde{\alpha}$ as the minimum reproductive age classes, and the ω and $\tilde{\omega}$ are the maximum reproductive ages of females and males respectively. The potential number of breeding season available to females and males are $\omega - \alpha + 1$ and $\tilde{\omega} - \tilde{\alpha} + 1$, and the maximum possible number of breeding seasons is $\min\{\omega - \alpha, \tilde{\omega} - \tilde{\alpha}\} + 1$. If i and j are the ages at which the couple is first paired then the actual number of breeding seasons available to females and males are $\omega - i + 1$ and $\tilde{\omega} - j + 1$ respectively so the maximum number of breeding seasons available to a given couple is $\min\{\omega - i, \tilde{\omega} - j\} + 1$, and that couple is currently $i + h$ and $j + h$ years old (female and male respectively). The maximum age for females is Ω and the maximum age for males is $\tilde{\Omega}$.

Let $F_i(t)$ be the total number or density of females in age class i at time t and $M_j(t)$ be the number or density of males in age class j at time t. Also let p_i and $\tilde{p}_j$ be the probabilities of survival for males and females from the current age classes, i and j, to the next, $i + 1$ and $j + 1$. We then have the following iterative relationships

$$F_{i+1}(t+1) = p_i F_i(t) \qquad i \geq 0 \tag{4.1}$$

$$M_{j+1}(t+1) = \tilde{p}_j M_j(t) \qquad j \geq 0 \tag{4.2}$$

I will denote the number of pairs of a particular age class in two ways. First let $C_h^{i,j}(t)$ be the number, at time t, of reproductive females (first mated at age i) that have been paired with males (first mated at age j) for h units of time, this will be equivalent to $C_{h,i+h,j+h}(t)$. Henceforth, for all variables and parameters involving couples, I will use the superscript position when I want to denote ages at which the couple first mated, and the subscript position for when I want to express the pair in terms of their current age (see Appendix I). Define the probability of a female that paired at age i with a male age j, remaining mated after h reproductive seasons as $\pi_h^{i,j}$ given that they have previously paired for $h-1$ seasons[1]. Note that this event conditions on the probability that they both survive to the next reproductive season, and that although the survival probabilities of mated males and females are usually different than the corresponding survivals of the un-mated cohort I will, for the sake of simplicity, assume that the variation has negligible impact on the mean overall survival rate. Then

$$C_{h+1}^{i,j}(t+1) = p_{i+h}\tilde{p}_{j+h}\pi_h^{i,j}C_h^{i,j}(t) \quad \text{if } h \geq 0, i \geq \alpha, \text{and } j \geq \tilde{\alpha} \tag{4.3}$$

Denoting single females as

$$\underline{F}_i^s = \begin{cases} \underline{F}_{\alpha-1} & \text{if } \ i = \alpha - 1 \\ \underline{F}_i \sum_{h=0}^{\min\{i-\alpha, \tilde{\omega}-\tilde{\alpha}\}} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}-h} \underline{C}_h^{i-h,j} & \text{if } \ \alpha \leq i \leq \omega \end{cases} \tag{4.4}$$

[1]The notation "$\pi_{h,i,j}$" will not be used in this paper.

and single males as

$$\underline{M}_j^s = \begin{cases} \underline{M}_{\tilde{\alpha}-1} & \text{if } j = \tilde{\alpha} - 1 \\ \underline{M}_j - \sum_{h=0}^{\min\{\omega-\alpha, j-\tilde{\alpha}\}} \sum_{i=\alpha}^{\omega-h} \underline{C}_h^{i,j-h} & \text{if } \tilde{\alpha} \le j \le \tilde{\omega} \end{cases} \tag{4.5}$$

Define the set of all adult single females at time t to be

$$\begin{aligned} \mathfrak{F}^s(t) &= \{F_i^s(t) : i \in (\alpha - 1, \omega - 1)\} \\ & \quad \mathfrak{F}^s \text{ is a subset of } \Re^{\omega-\alpha+1} \end{aligned}$$

the set of all adult single males

$$\begin{aligned} \mathfrak{M}^s(t) &= \left\{M_j^s(t) : j \in (\tilde{\alpha} - 1, \tilde{\omega} - 1)\right\} \\ & \quad \mathfrak{M}^s \text{ is a subset of } \Re^{\tilde{\omega}-\tilde{\alpha}+1} \end{aligned}$$

and the set of all couples

$$\begin{aligned} \mathfrak{C}(t) &= \left\{C_h^{i,j}(t) : j \in (\tilde{\alpha}, \tilde{\omega}), j \in (\tilde{\alpha}, \tilde{\omega}), h \in (0, \min\{\omega - \alpha, \tilde{\omega} - \tilde{\alpha}\})\right\} \\ & \quad \mathfrak{C}^s \text{ is a subset of } \Re^{(\omega-\alpha+1)\times(\tilde{\omega}-\tilde{\alpha}+1)\times(\min\{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}\}+1)} \end{aligned}$$

Let $\mathcal{N}^{i,j}(\mathfrak{F}^s(t), \mathfrak{M}^s(t), \mathfrak{C}(t))$ be a function determining the number of new matings between females of age i and males of age j at time t (this function will be discussed in detail later on.) I will consider the number of newly established couples at the beginning of time interval t as coming from those marriages that occurred during the previous time interval $t-1$. I also will calculate the rates associated with finding, courting and marrying a mate as a processes dependent on the state of the system in a single interval of time. Of course, in reality the factors effecting these rates can be extremely complex and the result of states integrated over either multiple (possible discontinuous) time intervals or fractions of a time interval or both. In any event we will consider

$$C_{0,i,j}(t) = C_0^{i,j}(t) = p_{i-1}\tilde{p}_{j-1}\mathcal{N}^{i-1,j-1}\left(\mathfrak{F}^s(t-1), \mathfrak{M}^s(t-1), \mathfrak{C}(t-1)\right) \tag{4.6}$$

The $p_{i-1}\tilde{p}_{j-1}$ term is because both individuals in the pair must survive for the pair to survive and we take $\pi_{-1}^{i-1,j-1} \equiv 1$ (the fraction of separations between the end of the $t-1$ interval and the t interval is negligible or is so minimal it can be absorbed into the other rate constants). Now if $i < \alpha$ or $j < \tilde{\alpha}$ then the following conditions hold,

$$C_h^{i,j}(t) \equiv 0\ ,\ \ \mathcal{N}^{i,j}\left(\mathfrak{F}^s(t), \mathfrak{M}^s(t), \mathfrak{C}(t)\right) \equiv 0\ ,\ \text{and}\ \pi_h^{i,j} \equiv 1 \tag{4.7}$$

That is, there are no couples in the previous season to carry over if at least one of the pair will be in their first reproductive season in that time interval - so all pairs are new. And if $i + h > \omega$ or $j + h > \tilde{\omega}$ then,

$$C_h^{i,j}(t) \equiv 0\ ,\ \text{and}\ \pi_{h-1}^{i,j} \equiv 0 \tag{4.8}$$

Here I am defining "couples" only as reproductive pairs, and we will assume that, even though couples may exist outside the reproductive span determined by their ages, for the purposes of the model I will count them as a couple only when they are within that span and "single" otherwise. I also assume that individuals outside this span have no influence on the pair formation process (such as competing for singles or otherwise interfering with or facilitating marriages). The initial and final reproductive ages are defined when fecundity of males and females are negligible (prior to mating and after senescence). The expected number of female births (fecundity) of a couple together for h seasons and mated at age (i,j) is $f_h^{i,j}$, and the expected number of male births is $\tilde{f}_h^{i,j}$. If $i < \alpha$ or $i + h > \omega$, and $j < \tilde{\alpha}$ or $j + h > \tilde{\omega}$ then the following conditions hold,

$$f_h^{i,j} \equiv 0 \text{ and } \tilde{f}_h^{i,j} \equiv 0 \tag{4.9}$$

The total number of female and male births resulting from reproduction during the time interval t are,

$$F_0(t+1) = \sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_{h,i,j}C_{h,i,j}(t) \tag{4.10a}$$

$$M_0(t+1) = \sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{h,i,j}C_{h,i,j}(t) \tag{4.10b}$$

And the age specific birthrates of females per female and males per male are (for $\alpha > i > \omega$, and $\tilde{\alpha} > j > \tilde{\omega}$),

$$\mathcal{B}_i(t) \equiv \begin{cases} \frac{1}{F_i(t)}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_{h,i,j}C_{h,i,j}(t) & \text{if } F_i(t) > 0 \\ 0 & \text{if } F_i(t) = 0 \end{cases} \tag{4.11a}$$

$$\tilde{\mathcal{B}}_j(t) \equiv \begin{cases} \frac{1}{M_j(t)}\sum_{i=\alpha}^{\omega}\sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{h,i,j}C_{h,i,j}(t) & \text{if } M_j(t) > 0 \\ 0 & \text{if } M_j(t) = 0 \end{cases} \tag{4.11b}$$

Rearranging and substituting these definitions in Equations 4.10a and 4.10b we have,

$$F_0(t+1) = \sum_{i=\alpha}^{\omega}\mathcal{B}_i(t)\,F_i(t) \tag{4.12a}$$

$$M_0(t+1) = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\tilde{\mathcal{B}}_j(t)\,M_j(t) \tag{4.12b}$$

The flows between the various subpopulations are illustrated (for males) by the compartment time-line in Figure 4.1.

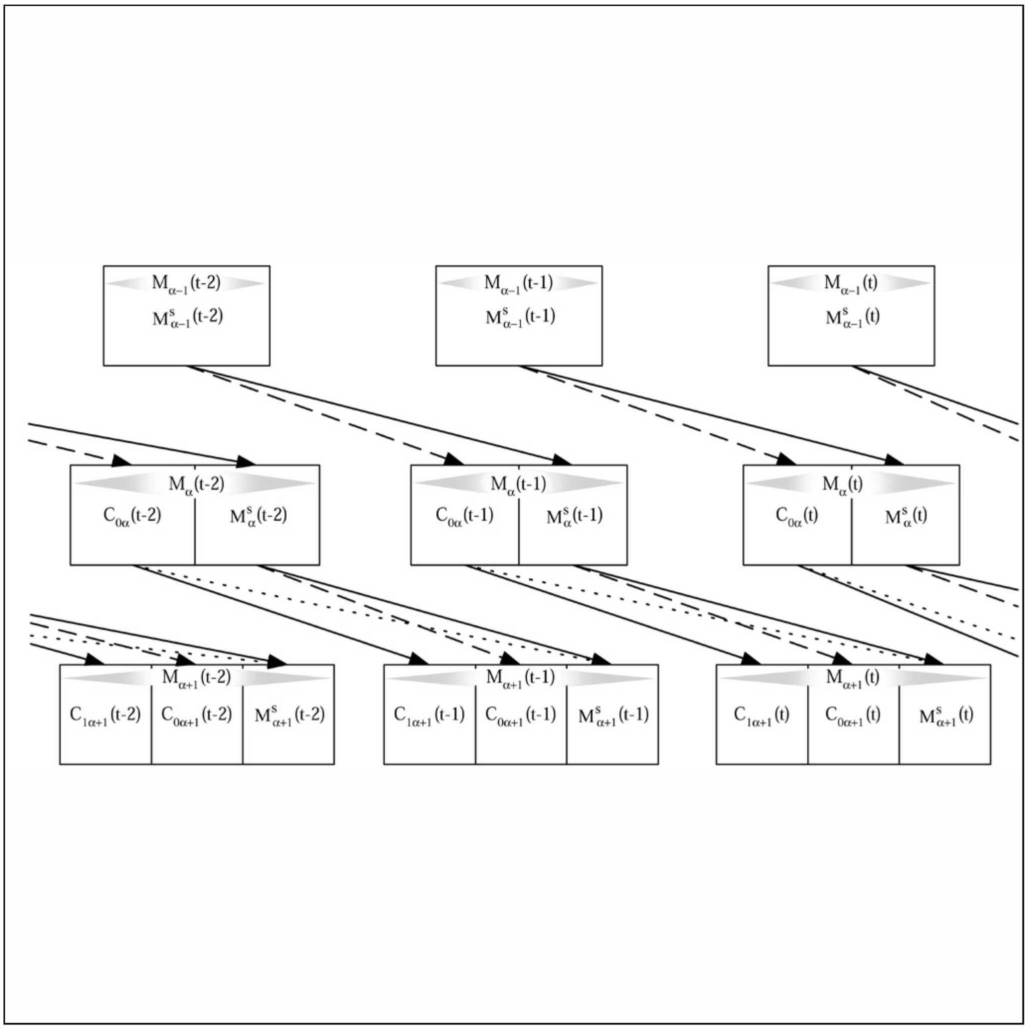

Figure 4.1: Compartment diagram.

The final step in the development of the model is to express the generation equations for the number of births at time $t+1$ in terms of the adult population at time t backtracked to the numbers at their birth (j time steps before). Let

$$\ell_i = \begin{cases} 1 & \text{if } i = 0 \\ \prod_{k=0}^{i-1} p_k & \text{if } i \geq 1 \end{cases} \tag{4.13a}$$

$$\tilde{\ell}_j = \begin{cases} 1 & \text{if } j = 0 \\ \prod_{k=0}^{j-1} \tilde{p}_k & \text{if } j \geq 1 \end{cases} \tag{4.13b}$$

these are probabilities of survivals from birth to the specified age. And

$$\mathcal{L}_h^{i,j} = \begin{cases} 1 & \text{if } h = 0 \\ \prod_{k=0}^{h-1} p_{i+k}\tilde{p}_{j+k}\pi_k^{i,j} & \text{if } h \geq 1 \end{cases} \tag{4.14}$$

this is probability of survival of a marriage for h mating seasons by a couple mated at the ages of i and j (female and male respectively). Note that if $i+h > \omega$ or $j+h > \tilde{\omega}$ then $\mathcal{L}_h^{i,j} = 0$ since $\pi_{h-1}^{i,j} = 0$ in this case. By iterating Equations 4.1, 4.2 and 4.3 and substituting 4.13a, 4.13b and 4.14 we can express the number of males and females of any age in terms of the number of births that produced them and the number of couples by the number of marriages that produced them (indices h, i and j now start at 1 rather than 0),

$$\begin{aligned} F_i(t) &= p_{i-1}F_{i-1}(t-1) \\ &= p_{i-1}p_{i-2}F_{i-2}(t-2) \\ &= p_{i-1}p_{i-2}\cdots p_0F_0(t-i) \\ &= \ell_i F_0(0, t-i) \end{aligned} \tag{4.15}$$

$$\begin{aligned} M_j(t) &= \tilde{p}_{j-1} M_{j-1}(t-1) \\ &= \tilde{p}_{j-1}\tilde{p}_{j-2} M_{j-2}(t-2) \\ &= \tilde{p}_{j-1}\tilde{p}_{j-2}\cdots\tilde{p}_0 M_0(t-j) \\ &= \tilde{\ell}_j M_0(t-j) \end{aligned} \tag{4.16}$$

$$\begin{aligned} C_h^{i,j}(t) &= p_{i+h-1}\tilde{p}_{j+h-1}\pi_{h-1}^{i,j} C_{h-1}^{i,j}(t-1) \\ &= p_{i+h-1}\tilde{p}_{j+h-1}\pi_{h-1}^{i,j} p_{i+h-2}\tilde{p}_{j+h-2}\pi_{h-2}^{i,j} C_{h-2}^{i,j}(t-2) \\ &= p_{i+h-1}\tilde{p}_{j+h-1}\pi_{h-1}^{i,j} p_{i+h-2}\tilde{p}_{j+h-2}\pi_{h-2}^{i,j}\cdots \\ &\quad \cdots p_i\tilde{p}_j\pi_0^{i,j} C_0^{i,j}(t-h) \\ &= \mathcal{L}_h^{i,j} C_0^{i,j}(t-h) \end{aligned} \tag{4.17}$$

The number of births at time $t+1$can now be expressed in terms of the number of births of their parents generation $i+1$ time units ago. Substituting 4.15 and 4.16 in Equations 4.12a and 4.12b we have,

$$F_0(t+1) = \sum_{i=\alpha}^{\omega} \mathcal{B}_i(t)\,\ell_i F_0(t-i) \tag{4.18a}$$

$$M_0(t+1) = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\mathcal{B}}_j(t)\,\tilde{\ell}_j M_0(t-j) \tag{4.18b}$$

The secondary sex ratio of males age j to females age i (primary sex ratio for male and female ages 0) at time t is

$$\mathcal{S}_{i,j}(t) = \frac{M_j(t)}{F_i(t)} \tag{4.19}$$

and the subjective primary sex ratio (this is the ratio of the expected number of male births for each female birth to individual parents that were mated at ages i & j and been mated for h units of time),

$$\sigma_h^{i,j} = \frac{\tilde{f}_h^{i,j}}{f_h^{i,j}}. \tag{4.20}$$

One would expect that for genetically determined sexes this should be close to one unless there is some type of gamete selection going on. For environmentally determined sexes this ratio can potentially be much more variable and differ quite a bit from one. However, there is strong evolutionary pressure for the sex ratios to be such as to produce equivalent growth rates in both sexes [45]. Whenever the numbers of one sex are under represented in the population, that sex will have a selective advantage unless there is some sort of environmental covariance that counter balances that advantage [9].

Chapter 5

Asymptotic growth-rate

I will now investigate the conditions necessary for the population to reach a time independent growth-rate, that is look for geometric solutions, that is solutions of the form λ^t :

$$F_i(t) = \lambda_F F_i(t-1) = \lambda_F^2 F_i(t-2) = \cdots = \lambda_F^t F_i(0), \tag{5.1a}$$

$$M_j(t) = \lambda_M M_j(t-1) = \lambda_M^2 M_j(t-2) = \cdots = \lambda_M^t M_j(0), \tag{5.1b}$$

$$C_h^{i,j}(t) = \lambda_C C_h^{i,j}(t-1) = \lambda_C^2 C_h^{i,j}(t-2) = \cdots = \lambda_C^t C_h^{i,j}(0), \tag{5.1c}$$

and show that all growth rates must be the same (i.e. $\lambda_F = \lambda_M = \lambda_C = \lambda$.)

Define the initial conditions for a geometrically growing population (denoted by an underscore) at some arbitrary time $t = 0$

$$\underline{F}_i \equiv F_i(0) \;\; ; \;\; \underline{M}_j \equiv M_j(0) \;\; ; \underline{C}_h^{i,j} \equiv C_h^{i,j}(0). \tag{5.2}$$

Thus,

$$F_i(t) = \lambda_F^t \underline{F}_i \;\; ; \;\; M_j(t) = \lambda_M^t \underline{M}_j \;\; ; \text{ and } \;\; C_h^{i.j}(t) = \lambda_C^t \underline{C}_h^{i.j}. \tag{5.3}$$

Substituting 5.3 in Equations 4.18a and 4.18b

$$\begin{aligned}
\lambda_F^{t+1} \underline{F}_0 &= \sum_{i=\alpha}^{\omega} \mathcal{B}_i(t)\, \ell_i \lambda_F^{t-i} \underline{F}_0, \\
\lambda_M^{t+1} \underline{M}_0 &= \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\mathcal{B}}_j(t)\, \tilde{\ell}_j \lambda_M^{t-i} \underline{M}_0.
\end{aligned}$$

we obtain after canceling like terms

$$
\begin{aligned}
1 &= \sum_{i=\alpha}^{\omega} \mathcal{B}_i\,(t)\,\ell_i \lambda_F^{-(i+1)}, && \text{(5.4a)}\\
1 &= \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\mathcal{B}}_j\,(t)\,\tilde{\ell}_j \lambda_M^{-(j+1)}. && \text{(5.4b)}
\end{aligned}
$$

In Equations 5.4a and 5.4b above the RHS's are functions of t but the LHS's are not. The only way for this to happen is for the fertilities ($\mathcal{B}$ and $\tilde{\mathcal{B}}$) to be constants with respect to time, that is $\mathcal{B}_i\,(t) = \underline{\mathcal{B}}_i$ and $\tilde{\mathcal{B}}_j\,(t) = \underline{\tilde{\mathcal{B}}}_j$ when there is geometric growth. The equations then become

$$
\begin{aligned}
1 &= \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i\ \ \ell_i\ \lambda_F^{-(i+1)}, && \text{(5.5a)}\\
1 &= \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \underline{\tilde{\mathcal{B}}}_j\ \ \tilde{\ell}_j\ \lambda_M^{-(j+1)}. && \text{(5.5b)}
\end{aligned}
$$

These are just the discrete Lotka-Euler equations expressed for each sex. They are similar to the characteristic equations of the associated Leslie matrices with λ's the eigenvalues.

5.1 Existence and uniqueness of eigenvalues

I will now demonstrate the existence of the eigenvalues, this is a reiteration of an argument made originally by Haldane [16] and later by Charlesworth [7] and Yodzis (whom we follow closely [48]). I am introducing nothing essential, but repeating the argument here to show it holds for each of the sexes (for the two sex case) when they are treated separately. I will then show that the λ found in both cases must be the same for the entire population (females, males and couples).

5.1.1 Existence of eigenvalues

Define the function $\Phi(\xi) = -1 + \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i \xi^{-(i+1)}$. The roots of this equation are then the solutions to the characteristic equation above (the λ's). Now as $\xi \to 0^+$ then $\Phi(\xi) \to \infty$ and as $\xi \to \infty$ then $\Phi(\xi) \to -1$ so by the intermediate value theorem there exists at least one real positive root. In addition the derivative of $\Phi(\xi)$ is $\Phi'(\xi) = -\sum_{i=\alpha}^{\omega} (i+1) \underline{\mathcal{B}}_i \ell_i \xi^{-i}$ which shows that $\Phi(\xi)$ is strictly decreasing for positive values of ξ. Thus there is *only one* real positive root of $\Phi(\xi)$ (that is $\Phi(\lambda_F) = 0$) which we will denote λ_{1F}. In general the roots of $\Phi(\xi)$ can be written $\lambda_{kF} = r_k e^{\mathrm{i}\phi_k} = r_k(\cos\phi_k + \mathrm{i}\sin\phi_k)$. So for $\Phi(\lambda_{kF})$ we have

$$\begin{aligned}
\Phi(\lambda_{kF}) &= -1 + \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_k^{-(i+1)} e^{-\mathrm{i}\phi_k(i+1)} = 0 &\quad (5.6a)\\
&= -1 + \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_k^{-(i+1)} e^{-\mathrm{i}\phi_k(i+1)} &\quad (5.6b)\\
&= -1 + \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_k^{-(i+1)} \left(\cos[-\phi_k(i+1)] + \mathrm{i}\sin[-\phi_k(i+1)]\right) &\quad (5.6c)\\
&= -1 + \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_k^{-(i+1)} \cos[-\phi_k(i+1)] &\\
&\quad + \mathrm{i}\sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_k^{-(i+1)} \sin[-\phi_k(i+1)] &\quad (5.6d)
\end{aligned}$$

Separating the real and imaginary parts we get

$$\begin{aligned}
\operatorname{Re}\Phi(\lambda_F) &= -1 + \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_k^{-(i+1)} \cos[-\phi_k(i+1)] = 0 &\quad (5.7a)\\
\operatorname{Im}\Phi(\lambda_F) &= \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_k^{-(i+1)} \sin[-\phi_k(i+1)] = 0 &\quad (5.7b)
\end{aligned}$$

Rearranging and simplifying

$$1 = \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_k^{-(i+1)} \cos\left[\phi_k (i+1)\right] \tag{5.8a}$$

$$0 = \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_k^{-(i+1)} \sin\left[\phi_k (i+1)\right] \tag{5.8b}$$

Now suppose that there is a λ_{kF} greater in modulus than λ_{1F} (i.e. $|\lambda_{*F}| > |\lambda_{1F}|$). But $|\lambda_{kF}| = r_k$ so $r_1 < r_*$ or $r_1^{-(i+1)} > r_*^{-(i+1)}$ for all i. This implies that

$$1 = \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_1^{-(i+1)} > \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_*^{-(i+1)} \geq \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_*^{-(i+1)} \cos\left[\phi_* (i+1)\right] \tag{5.9}$$

Which contradicts the requirement from the real part of $\Phi(\lambda_{*F})$ that $\sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i r_*^{-(i+1)} \cos\left[\phi_* (i+1)\right] = 1$. Therefore there is no eigenvalue larger in modulus than λ_{1F}.

What if there is a λ_{kF} equal in modulus to λ_{1F} (i.e. $|\lambda_{*F}| = |\lambda_{1F}|$)? This implies that $r_* = r_1$ and $\cos\left[\phi_* (i+1)\right] = 1$ for all $i \Longrightarrow \phi_* (i+1) = 2n_i\pi$ ($n_i = 0, 1, 2, \ldots$) or $\phi_* = \frac{2n_i\pi}{(i+1)}$. So for any two different ages $i = a$ and $i = b$, where $\underline{\mathcal{B}}_a$ and $\underline{\mathcal{B}}_b$ are greater than zero, we have $\frac{2n_a\pi}{(a+1)} = \frac{2n_b\pi}{(b+1)}$ or $n_b = \frac{b+1}{a+1} n_a$. Now if for these two ages $a+1$ and $b+1$ are relatively prime and since both n_a and n_b are integers then $n_a = m(a+1)$ where m is an integer so that $n_b = m(b+1)$ but then both $\phi_*(a+1) = 2n_a\pi = 2m(a+1)\pi$ and $\phi_*(b+1) = 2n_b\pi = 2m(b+1)\pi$ so that $\phi_* = 2m\pi$ in both cases. Thus $\cos\phi_* = 1$ and $\sin\phi_* = 0$ and so λ_{*F} is real and has the same modulus as λ_{1F}, therefore $\lambda_{*F} = \lambda_{1F}$. The effective fertilities ($\underline{\mathcal{B}}_i$) are called "honest" (see also Hoppensteadt [18]) whenever we have at least two ages where $\underline{\mathcal{B}}_a$ and $\underline{\mathcal{B}}_b > 0$ and $a+1$ and $b+1$ are relatively prime. It follows then that for honest fertilities that there is a unique real positive solution to the characteristic equation (λ_{1F}) that has the greatest modulus of all the eigenvalues. This eigenvalue is the dominant eigenvalue.

5.1.2 Sustained oscillations

Fertilities are "dishonest" when there is only a single age of reproduction other than age zero (semelparity) or reproduction is at two or more ages that all satisfy the common factor condition (for example ages 1 ($i+1=2$) and 3 ($i+1=4$). In these cases reproduction is periodic and gives rise to the phenomena of "population waves". In reality only cases where species are semelparous are common. A didactic example using three age classes was given by Bernardelli [1] which exhibits sustained oscillations in all three age classes.

5.1.3 Uniqueness of asymptotic growth rate (dominant eigenvalue)

A fixed ratio between age classes implies that the fertilities become time independent once a stable age distribution is achieved. As we noted before, the RHS's of Equations 5.4a and 5.4b are functions of t but the LHS's are not. From this we obtained 5.5a and 5.5b. This also implies that the growth rates of all the subpopulations must be the same. In order to show this we substitute 5.3 in Equations 4.11a and 4.11b and rearrange,

$$\underline{\mathcal{B}}_i = \left(\frac{\lambda_C}{\lambda_F}\right)^t \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_{h,i,j} \frac{\underline{C}_{h,i,j}}{\underline{F}_i} \tag{5.10a}$$

$$\underline{\tilde{\mathcal{B}}}_j = \left(\frac{\lambda_C}{\lambda_M}\right)^t \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{h,i,j} \frac{\underline{C}_{h,i,j}}{\underline{M}_j} \tag{5.10b}$$

Again the LHS's are constant with respect to time. Since the RHS's are functions the power of t, the ratios inside the brackets must be equal to 0 or 1. And since we are not interested in the trivial case, $\lambda_F = \lambda_C = \lambda_M = \lambda$. Now from 4.13a, 4.13b, 4.14

and 5.3 we have,

$$\underline{F}_i = \ell_i \lambda^{-i} \underline{F}_0 \tag{5.11a}$$

$$\underline{M}_j = \tilde{\ell}_j \lambda^{-j} \underline{M}_0 \tag{5.11b}$$

$$\underline{C}_h^{i,j} = \mathcal{L}_h^{i,j}\, \lambda^{-h} \underline{C}_0^{i,j} \tag{5.11c}$$

The Lotka-Euler equations, then are interchangeable for both sexes and provide the same eigenvalues as required. To see this note that

$$1 = \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i \lambda^{-(i+1)} \tag{5.12a}$$

$$= \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} f_{h,i,j} \frac{\underline{C}_{h,i,j}}{\underline{F}_i} \ell_i \lambda^{-(i+1)} \tag{5.12b}$$

$$= \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} f_{h,i,j} \frac{\underline{C}_{h,i,j}}{\underline{F}_0} \tag{5.12c}$$

$$\underline{F}_0 = \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} f_{h,i,j} \underline{C}_{h,i,j} \tag{5.12d}$$

But this is just the total number of female births at time 0 where $f_{h,i,j}$ is a fixed parameter defined as the number of female births per couple (of male age j, female age i and mated h years). Similarly $\tilde{f}_{h,i,j}$ is a fixed parameter defined as the number of male births per couple, so we can get the total number of male births at time 0 by replacing $f_{h,i,j}$ with $\tilde{f}_{h,i,j}$

$$\underline{F}_0 = \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} f_{h,i,j} \underline{C}_{h,i,j} \Longleftrightarrow \underline{M}_0 = \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} \tilde{f}_{h,i,j} \underline{C}_{h,i,j} \tag{5.13}$$

Then working backwards

$$\underline{M}_0 = \sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{h,i,j}\underline{C}_{h,i,j} \tag{5.14a}$$

$$1 = \sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{h,i,j}\frac{\underline{C}_{h,i,j}}{\underline{M}_0} \tag{5.14b}$$

$$1 = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{i=\alpha}^{\omega}\sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{h,i,j}\frac{\underline{C}_{h,i,j}}{\underline{M}_j}\tilde{\ell}_j\lambda^{-(j+1)} \tag{5.14c}$$

$$1 = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \underline{\tilde{\mathcal{B}}}_j\,\tilde{\ell}_j\lambda^{-(j+1)} \tag{5.14d}$$

5.1.4 Conditions on marriage function

I will have to admit to some slight of hand, since I assumed that $C_h^{i,j}(t) = \lambda^t\ \underline{C}_h^{i,j}$. But what I failed explore was the fact that the number of couples are themselves dependent on the number of males and females in the population by the relation $C_0^{i,j}(t) = p_{i-1}\tilde{p}_{j-1}\mathcal{N}^{i-1,j-1}(\mathfrak{F}^s(t-1), \mathfrak{M}^s(t-1), \mathfrak{C}(t-1))$. Now in general $C_h^{i,j}(t)$ will equal $\lambda^t\ \underline{C}_h^{i,j}$ only if $\underline{C}_0^{i,j} = \lambda^{-1}p_{i-1}\tilde{p}_{j-1}\mathcal{N}^{i-1,j-1}\left(\underline{\mathfrak{F}}^s, \underline{\mathfrak{M}}^s, \underline{\mathfrak{C}}\right)$ $= p_{i-1}\tilde{p}_{j-1}\mathcal{N}^{i-1,j-1}\left(\lambda^{-1}\underline{\mathfrak{F}}^s, \lambda^{-1}\underline{\mathfrak{M}}^s, \lambda^{-1}\underline{\mathfrak{C}}\right)$ that is $\mathcal{N}^{i-1,j-1}\left(\underline{\mathfrak{F}}^s, \underline{\mathfrak{M}}^s, \underline{\mathfrak{C}}\right)$ must be a homogeneous function. The proof is as follows. Assuming λ exists

$$C_0^{i,j}(t) = \lambda^t\underline{C}_0^{i,j} \tag{5.15}$$

By rewriting the left hand side we obtain

$$C_0^{i,j}(t) = p_{i-1}\tilde{p}_{j-1}\mathcal{N}^{i-1,j-1}(\mathfrak{F}^s(t-1), \mathfrak{M}^s(t-1), \mathfrak{C}(t-1)) \tag{5.16a}$$

$$= p_{i-1}\tilde{p}_{j-1}\mathcal{N}^{i-1,j-1}\left(\lambda^{t-1}\underline{\mathfrak{F}}^s,\ \lambda^{t-1}\underline{\mathfrak{M}}^s,\ \lambda^{t-1}\underline{\mathfrak{C}}\right) \tag{5.16b}$$

And by rewriting the right hand side we obtain

$$\begin{aligned}
\lambda^t \underline{C}_0^{i,j} &= \lambda^t C_0^{i,j}(0) && (5.17a)\\
&= \lambda^t p_{i-1}\tilde{p}_{j-1}\mathcal{N}^{i-1,j-1}\left(\mathfrak{F}^s(-1),\ \mathfrak{M}^s(-1), \mathfrak{C}(-1)\right) && (5.17b)\\
&= \lambda^t p_{i-1}\tilde{p}_{j-1}\mathcal{N}^{i-1,j-1}\left(\lambda^{-1}\ \underline{\mathfrak{F}}^s,\ \lambda^{-1}\underline{\mathfrak{M}}^s,\ \lambda^{-1}\underline{\mathfrak{C}}\right) && (5.17c)
\end{aligned}$$

So equating the last lines of each of these, canceling the $p_{i-1}\tilde{p}_{j-1}$ term and multiplying through by λ^{-t} we have

$$\lambda^{-t}\mathcal{N}^{i-1,j-1}\left(\lambda^{t-1}\underline{\mathfrak{F}}^s,\ \lambda^{t-1}\underline{\mathfrak{M}}^s,\ \lambda^{t-1}\underline{\mathfrak{C}}\right) = \mathcal{N}^{i-1,j-1}\left(\lambda^{-1}\ \underline{\mathfrak{F}}^s,\ \lambda^{-1}\underline{\mathfrak{M}}^s,\ \lambda^{-1}\underline{\mathfrak{C}}\right) \qquad (5.18)$$

for $t = 1$

$$\lambda^{-1}\mathcal{N}^{i-1,j-1}\left(\underline{\mathfrak{F}}^s, \underline{\mathfrak{M}}^s, \underline{\mathfrak{C}}\right) = N^{i-1,j-1}\left(\lambda^{-1}\ \underline{\mathfrak{F}}^s,\ \lambda^{-1}\underline{\mathfrak{M}}^s,\ \lambda^{-1}\underline{\mathfrak{C}}\right) \qquad (5.19)$$

If this is true we will have the existence and uniqueness of solutions to the characteristic equation given above and the population will asymptotically approach a stable (geometric) age distribution for honest fertilities and either stable or periodic geometric distributions for semelparous and dishonest (iteroparous) fertilities.

5.2 Sex ratios

Note also that the secondary sex ratios at each age become fixed over time,

$$\underline{\mathcal{S}}_{i,j} \equiv \mathcal{S}_{i,j}\left(0\right) = \frac{\underline{M}_j}{\underline{F}_i} = \frac{\tilde{\ell}_j \lambda^{-j} \underline{M}_0}{\ell_i \lambda^{-i} \underline{F}_0} = \frac{\tilde{\ell}_j \lambda^{-j}}{\ell_i \lambda^{-i}} \underline{\mathcal{S}}_{0,0} \tag{5.20}$$

and the (objective) primary sex ratio (the sex ratio at birth)

$$\underline{\mathcal{S}}_{0,0} = \frac{\underline{M}_0}{\underline{F}_0} \tag{5.21}$$

But

$$\underline{F}_0 = \lambda^{-1} \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} f_{h,i,j} \underline{C}_{h,i,j}$$

and

$$\underline{M}_0 = \lambda^{-1} \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h'=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} \tilde{f}_{h,i,j} \underline{C}_{h,i,j}$$

$$\begin{aligned}
\underline{\mathcal{S}}_{0,0} &= \frac{\lambda^{-1} \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} \tilde{f}_{h,i,j} \underline{C}_{h,i,j}}{\lambda^{-1} \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} f_{h,i,j} \underline{C}_{h,i,j}} && \text{(5.22a)} \\
&= \frac{\sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} \tilde{f}_h^{i-h,j-h} \underline{C}_h^{i-h,j-h}}{\sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} f_{h,i,j} \underline{C}_{h,i,j}} && \text{(5.22b)} \\
&= \frac{\sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i, \tilde{\omega}-j\}} f_h^{i,j} \underline{C}_h^{i,j} \sigma_h^{i,j}}{\sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i, \tilde{\omega}-j\}} f_h^{i,j} \underline{C}_h^{i,j}} && \text{(5.22c)}
\end{aligned}$$

We can see that the objective primary sex ratio (the primary sex ratio realized by the population) is a weighted average of the subjective primary sex ratios (the primary sex ratios at the individual level).

5.3 Recap

In summary (and for convenient reference) we write the crude birth rates and the Lotka type characteristic equations

$$\begin{aligned} \underline{\mathcal{B}}_i &= \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} f_{h,i,j} \, \frac{\underline{C}_{h,i,j}}{\underline{F}_i} && \text{(5.23a)} \\ \underline{\tilde{\mathcal{B}}}_j &= \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} \tilde{f}_{h,i,j} \, \frac{\underline{C}_{h,i,j}}{\underline{M}_j} && \text{(5.23b)} \end{aligned}$$

$$\begin{aligned} 1 &= \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \;\ell_i \;\lambda^{-(i+1)} && \text{(5.24a)} \\ 1 &= \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \underline{\tilde{\mathcal{B}}}_j \;\tilde{\ell}_j \;\lambda^{-(j+1)} && \text{(5.24b)} \end{aligned}$$

Chapter 6

Proportions

Assuming the existence of non-trivial (positive) solutions of the above stable age distribution ($\lambda > 0$) then we can make the following statements regarding proportions of individuals within each age class. Summing up total females (maximum longevity Ω), total males (maximum longevity $\tilde{\Omega}$), total mated couples, total newly mated females of age i, total newly mated males of age j, and total couples mated for h seasons (I will use dot notation to indicate sums over the entire range of particular index when other indices are not summed over).

6.1 Proportions derived from state variables

$$\underline{F} \equiv \sum_{i=0}^{\Omega} \underline{F}_i \ , \ \underline{M} \equiv \sum_{j=0}^{\tilde{\Omega}} \underline{M}_j \tag{6.1a}$$

$$\underline{F}_A \equiv \sum_{i=\alpha}^{\omega} \underline{F}_i \ , \ \ \underline{M}_A \equiv \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \underline{M}_j \tag{6.1b}$$

$$\underline{C}_{\bullet}^{i,j} \equiv \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \underline{C}_h^{i,j}, \ \underline{C}_{\bullet,i,j} \equiv \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \underline{C}_{h,i,j}, \tag{6.1c}$$

$$\underline{C}_h^{\bullet,\bullet} \equiv \sum_{i=\alpha}^{\omega-h} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}-h} \underline{C}_h^{i,j}, \tag{6.1d}$$

$$\begin{aligned} \underline{C} &\equiv \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \underline{C}_{h,i,j} \\ &= \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \underline{C}_h^{i,j}. \end{aligned} \tag{6.1e}$$

We can then express the proportions of individuals in each age group once a stable age structure is reached. Let

$$x_i \equiv \frac{\underline{F}_i}{\underline{F}}\ ,\ y_j \equiv \frac{\underline{M}_j}{\underline{M}}\ ,\ x_A \equiv \frac{\underline{F}_A}{\underline{F}}\ ,\text{ and }\ y_A \equiv \frac{\underline{M}_A}{\underline{M}} \tag{6.2}$$

$$z_h^{i,j} \equiv \frac{\underline{C}_h^{i,j}}{\underline{C}},\ z_\bullet^{i,j} \equiv \frac{\underline{C}_\bullet^{i,j}}{\underline{C}},\ z_{\bullet,i,j} \equiv \frac{\underline{C}_{\bullet,i,j}}{\underline{C}}\ ,\ \text{ and }\ z_h^{\bullet,\bullet} \equiv \frac{\underline{C}_h^{\bullet,\bullet}}{\underline{C}}. \tag{6.3}$$

The fraction of each age class that is single (by sex) is

$$\mathfrak{f}_i \equiv \frac{\underline{F}_i^s}{\underline{F}_i} \quad\text{and}\quad \mathfrak{m}_j \equiv \frac{\underline{M}_j^s}{\underline{M}_j}. \tag{6.4}$$

The proportion of all single female and male adults of reproductive age is

$$\langle\mathfrak{f}\rangle \equiv \frac{\underline{F}^s}{\underline{F}_A}\ ,\text{ and }\ \langle\mathfrak{m}\rangle \equiv \frac{\underline{M}^s}{\underline{M}_A}. \tag{6.5a}$$

Note also that for monogamous mating (the assumption here)

$$\langle\mathfrak{f}\rangle = \frac{\underline{F}^s}{\underline{F}_A} = 1 - \frac{\underline{C}}{\underline{F}_A}\ ,\text{ and} \tag{6.5b}$$

$$\langle\mathfrak{m}\rangle = \frac{\underline{M}^s}{\underline{M}_A} = 1 - \frac{\underline{C}}{\underline{M}_A}. \tag{6.5c}$$

Dividing Equations 5.11a, 5.11b and 5.11c by $\underline{F}$, $\underline{M}$ and $\underline{C}$ respectively we obtain

$$x_i = \ell_i \lambda^{-i} x_0, \tag{6.6a}$$

$$y_j = \tilde{\ell}_j \lambda^{-j} y_0, \tag{6.6b}$$

$$z_h^{i,j} = \mathcal{L}_h^{i,j} \lambda^{-h} z_0^{i,j}. \tag{6.6c}$$

Summing and rearranging

$$x_0 = \frac{1}{\sum_{i=0}^{\Omega} \ell_i \lambda^{-i}}, \tag{6.7a}$$

$$y_0 = \frac{1}{\sum_{j=0}^{\tilde{\Omega}} \tilde{\ell}_j \lambda^{-j}}. \tag{6.7b}$$

Define

$$\Lambda^{i,j} \equiv \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \mathcal{L}_h^{i,j} \lambda^{-h}, \tag{6.8}$$

(see footnote[1]) for couples mated at ages i and j, this is the expected number of couples mated for all lengths of time per new couple. Or $\left(\Lambda^{i,j}\right)^{-1}$ is the fraction of all couples mated at ages i and j, that are in their first season (time interval).

$$1 = \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \left(\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \mathcal{L}_h^{i,j} \lambda^{-h} \right) z_0^{i,j} = \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \Lambda^{i,j} z_0^{i,j} \tag{6.9}$$

and some more relationships

$$x_i = \frac{\ell_i \lambda^{-i}}{\sum_{k=0}^{\Omega} \ell_k \lambda^{-k}} \tag{6.10a}$$

$$y_j = \frac{\tilde{\ell}_j \lambda^{-j}}{\sum_{k=0}^{\tilde{\Omega}} \tilde{\ell}_k \lambda^{-k}} \tag{6.10b}$$

$$x_A = \frac{\underline{F}_A}{\underline{F}} = \frac{\sum_{i=\alpha}^{\omega} \underline{F}_i}{\underline{F}} = \sum_{i=\alpha}^{\omega} x_i = \frac{\sum_{i=\alpha}^{\omega} \ell_i \lambda^{-i}}{\sum_{k=0}^{\Omega} \ell_k \lambda^{-k}} \tag{6.10c}$$

$$y_A = \frac{\underline{M}_A}{\underline{M}} = \frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \underline{M}_i}{\underline{M}} = \sum_{j=\alpha}^{\tilde{\omega}} y_j = \frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_j \lambda^{-j}}{\sum_{k=0}^{\tilde{\Omega}} \tilde{\ell}_k \lambda^{-k}} \tag{6.10d}$$

$$\begin{aligned} \langle \mathfrak{f} \rangle &= \frac{\underline{F}^s}{\underline{F}_A} = \sum_{i=\alpha}^{\omega} \frac{\underline{F}_i^s}{\underline{F}_A} = \sum_{i=\alpha}^{\omega} \frac{\underline{F}_i}{\underline{F}} \frac{\underline{F}}{\underline{F}_A} \frac{\underline{F}_i^s}{\underline{F}_i} \\ &= \sum_{i=\alpha}^{\omega} \frac{x_i}{x_A} \mathfrak{f}_i = \frac{\sum_{i=\alpha}^{\omega} \ell_i \lambda^{-i} \mathfrak{f}_i}{\sum_{i=\alpha}^{\omega} \ell_i \lambda^{-i}}, \end{aligned} \tag{6.11}$$

[1]Since the notation "$\pi_{h,i,j}$" is undefined so is $\mathcal{L}_{h,i,j}$ and $\Lambda_{i,j}$.

and

$$\begin{aligned}\langle \mathfrak{m} \rangle &= \frac{\underline{M}^s}{\underline{M}_A} = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \frac{\underline{M}_j^s}{\underline{M}_A} = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \frac{\underline{M}_j}{\underline{M}} \frac{\underline{M}}{\underline{M}_A} \frac{\underline{M}_j^s}{\underline{M}_j} \\ &= \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \frac{y_j}{y_A} \mathfrak{m}_j = \frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_j \lambda^{-j} \mathfrak{m}_j}{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_j \lambda^{-j}} \end{aligned} \tag{6.12}$$

6.2 Sex ratio and birth rates

6.2.1 Primary sex ratio

The objective primary sex ratio is

$$\underline{\mathcal{S}}_{0,0} = \frac{\sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} f_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-h} z_0^{i,j} \sigma_h^{i,j}}{\sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} f_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-h} z_0^{i,j}} \tag{6.13}$$

6.2.2 Birth rates (fertilities)

I will here derive the crude birth rates in terms of proportions. The next few line will just show the algebraic manipulations necessary to arrive at the correct expressions for female and male fertilities. For female, expanding the ratio of couples aged i and j and together for h seasons (i.e. paired females) to total females of age i $(\underline{C}_{h,i,j}/\underline{F}_i)$ in terms of ratios ($\underline{C}_{h,i,j}/\underline{C}$ the fraction of a particular age classification out of all couples, $\underline{C}/\underline{F}_A$ the fraction all couples (i.e. paired females) out of all adult females, $\underline{F}_A/\underline{F}$ the fraction of all adult females out of all females and $\underline{F}_i/\underline{F}$ the fraction of all females age i out of all females) and then substituting parameter values we have

$$\underline{\mathcal{B}}_i = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_{h,i,j} \frac{\underline{C}_{h,i,j}}{\underline{C}} \frac{\underline{C}}{\underline{F}_A} \frac{\underline{F}_A}{\underline{F}} \frac{\underline{F}}{\underline{F}_i}$$

$$= \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_{h,i,j}\ z_{h,i,j}\,(1-\langle\mathfrak{f}\rangle)\,\frac{x_A}{x_i}$$

$$= (1-\langle\mathfrak{f}\rangle)\,\frac{x_A}{x_i} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_{h,i,j} z_{h,i,j}$$

$$= \left(1 - \frac{\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\mathfrak{f}_{i'}}{\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}}\right) \frac{\sum_{i=\alpha}^{\omega} \ell_i\lambda^{-i}}{\ell_i\lambda^{-i}} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_{h,i,j} z_{h,i,j}$$

$$= \frac{\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\,(1-\mathfrak{f}_{i'})}{\ell_i\lambda^{-i}} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_{h,i,j} z_{h,i,j}$$

$$= \frac{\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\,(1-\mathfrak{f}_{i'})}{\ell_i\lambda^{-i}} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_h^{i-h,j-h} z_h^{i-h,j-h}$$

$$= \frac{\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\,(1-\mathfrak{f}_{i'})}{\ell_i\lambda^{-i}} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_h^{i-h,j-h} \mathcal{L}_h^{i-h,j-h} \lambda^{-h} z_0^{i-h,j-h}. \tag{6.16}$$

And for males we go through a similar process

$$\underline{\tilde{\mathcal{B}}}_j = \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{\ h,i,j} \frac{\underline{C}_{h,i,j}}{\underline{C}} \frac{\underline{C}}{\underline{M}_A} \frac{\underline{M}_A}{\underline{M}} \frac{\underline{M}}{\underline{M}_j}$$

$$= \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{h,i,j}\ z_{h,i,j}\,(1-\langle\mathfrak{m}\rangle)\,\frac{y_A}{y_j}$$

$$= (1-\langle\mathfrak{m}\rangle)\,\frac{y_A}{y_j} \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{h,i,j} z_{h,i,j}$$

$$= \left(1 - \frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_j\lambda^{-j}\mathfrak{m}_j}{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_j\lambda^{-j}}\right) \frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_j\lambda^{-j}}{\tilde{\ell}_j\lambda^{-j}} \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{h,i,j} z_{h,i,j}$$

$$= \frac{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\,(1-\mathfrak{m}_{j'})}{\tilde{\ell}_j\lambda^{-j}} \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_{h,i,j} z_{h,i,j}$$

$$= \frac{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\,(1-\mathfrak{m}_{j'})}{\tilde{\ell}_j\lambda^{-j}} \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} \tilde{f}_h^{i-h,j-h} z_h^{i-h,j-h}$$

$$= \frac{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-j'} \left(1 - \mathfrak{m}_{j'}\right)}{\tilde{\ell}_j \lambda^{-j}} \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} \tilde{f}_h^{i-h,j-h} \mathcal{L}_h^{i-h,j-h} \lambda^{-h} z_0^{i-h,j-h}. \qquad (6.19)$$

The final expression is the ratio of all couples to males (for instance) of age j times the expected fertility of all males of age j (the double sum on the right) in a stable age structured population.

6.3 Reexpression of characteristic equations

By plugging in the above reformulation for the crude birth rates, we can express the characteristic equations in terms of proportions also. For females

$$1 = \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i \lambda^{-(i+1)}$$

$$= \left(\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'} \left(1 - \mathfrak{f}_{i'}\right) \right) \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} \lambda^{-1} f_h^{i-h,j-h} z_h^{i-h,j-h}$$

$$= \left(\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'} \left(1 - \mathfrak{f}_{i'}\right) \right) \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} f_h^{i-h,j-h} \mathcal{L}_h^{i-h,j-h} \lambda^{-(h+1)} z_0^{i-h,j-h}$$

$$= \left(\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'} \left(1 - \mathfrak{f}_{i'}\right) \right) \sum_{h=0}^{\min\{\omega-\alpha, \tilde{\omega}-\tilde{\alpha}\}} \sum_{\imath=\alpha+h}^{\omega} \sum_{j=\tilde{\alpha}+h}^{\tilde{\omega}} f_h^{i-h,j-h} \mathcal{L}_h^{i-h,j-h} \lambda^{-(h+1)} z_0^{i-h,j-h}$$

$$= \left(\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'} \left(1 - \mathfrak{f}_{i'}\right) \right) \sum_{h=0}^{\min\{\omega-\alpha, \tilde{\omega}-\tilde{\alpha}\}} \sum_{i=\alpha}^{\omega-h} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}-h} f_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-(h+1)} z_0^{i,j}$$

$$= \left(\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'} \left(1 - \mathfrak{f}_{i'}\right) \right) \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} z_0^{i,j} \left(\sum_{h=0}^{\min\{\omega-i, \tilde{\omega}-j\}} f_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-(h+1)} \right) \qquad (6.21)$$

And for males by analogy

$$1 = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \underline{\tilde{\mathcal{B}}}_j \ \tilde{\ell}_j \ \lambda^{-(j+1)}$$

$$= \left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-j'} \left(1 - \mathfrak{m}_{j'}\right) \right) \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{i=\alpha}^{\omega} z_0^{i,j} \left(\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \tilde{f}_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-(h+1)} \right) \tag{6.22}$$

6.3.1 Expected fecundity over the lifetime of a marriage

For a population at stable age distribution we define

$$\left\langle f^{i,j} \right\rangle \equiv \frac{\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} f_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-h}}{\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \mathcal{L}_h^{i,j} \lambda^{-h}} = \frac{\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} f_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-h}}{\Lambda^{i,j}} \tag{6.23a}$$

$$\left\langle \tilde{f}^{i,j} \right\rangle \equiv \frac{\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \tilde{f}_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-h}}{\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \mathcal{L}_h^{i,j} \lambda^{-h}} = \frac{\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \tilde{f}_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-h}}{\Lambda^{i,j}} \tag{6.23b}$$

These are the expected fecundities of a couple that were mated at ages i and j averaged over the lifetime of the marriage in a stable age structured population. And

$$\left\langle \sigma^{i,j} \right\rangle \equiv \frac{\left\langle \tilde{f}^{i,j} \right\rangle}{\left\langle f^{i,j} \right\rangle} = \frac{\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \sigma_h^{i,j} f_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-h}}{\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} f_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-h}} \tag{6.24}$$

is the averaged subjective primary sex ratio for a couples that were mated at ages i and j (averaged over the lifetime of the marriage in a stable age structured population).

6.3.2 Characteristic equations using expected fecundity

$$1 = \left(\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-(i'+1)} \left(1 - \mathfrak{f}_{i'}\right) \right) \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \left\langle f^{i,j} \right\rangle \Lambda^{i,j} z_0^{i,j} \tag{6.25}$$

and

$$1 = \left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-(j'+1)} \left(1 - \mathfrak{m}_{j'}\right) \right) \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \left\langle \tilde{f}^{i,j} \right\rangle \Lambda^{i,j} z_0^{i,j} \tag{6.26}$$

All the above expressions of the characteristic equations are the expected fraction of the population paired times the expected population produced per couple (the double sum) in a stable age structured population for example rearranging Equation 6.25

$$\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-(i'+1)} \left(1 - \mathfrak{f}_{i'}\right) = \frac{1}{\sum\limits_{i=\alpha}^{\omega} \sum\limits_{j=\tilde{\alpha}}^{\tilde{\omega}} \left\langle f^{i,j} \right\rangle \Lambda^{i,j} z_0^{i,j}}. \tag{6.27}$$

6.4 Fisher's reproductive value.

The concept of reproductive value has it's analogy in finance. As Fisher [9] puts it

> "The analogy with money does, however, make clear the argument for another simple application of the combined death and reproduction rates. We may ask, not only about the newly born, but about persons of any chosen age, what is the present value of their future offspring; and if the present value is calculated at the rate determined as before, the question has the definite meaning – To what extent will persons of this age, on average, contribute to the ancestry of future generations? The question is one of some interest, since the direct action of Natural Selection must be proportional to this contribution."

Another way of interpreting these is at the present time one girl age i will contribute to future generations (on average), at some specified point in time, as much as V_i newborn girls now. These values typically increase up until the age of first reproduction and then start to decline again. The reason for this is that the reproductive value takes into account both the delay in time till reproductive ages and the probability of surviving to those ages. The reproductive values for newborns (when i or $j = 0$) are just the original characteristic equations in the previous section.

If V_i is the reproductive value for a female at age i and $\tilde{V}_j$ is the reproductive value for a male age j.

$$V_i = \frac{\lambda^i}{\ell_i} \sum_{k=\max\{i,\alpha\}}^{\omega} \underline{\mathcal{B}}_k \ell_k \lambda^{-(k+1)} = \frac{\lambda^i}{\ell_i} \sum_{k=i}^{\omega} \underline{\mathcal{B}}_k \ell_k \lambda^{-(k+1)} \tag{6.28a}$$

$$= \begin{cases} \frac{\lambda^i}{\ell_i} & \text{if } i \le \alpha \\ \frac{\lambda^i}{\ell_i} \sum_{k=i}^{\omega} \underline{\mathcal{B}}_k \ell_k \lambda^{-(k+1)} & \text{if } i > \alpha \end{cases} \tag{6.28b}$$

$$\tilde{V}_j = \frac{\lambda^j}{\tilde{\ell}_j} \sum_{k=\max\{\tilde{\alpha},j\}}^{\tilde{\omega}} \underline{\tilde{\mathcal{B}}}_k \tilde{\ell}_k \lambda^{-(k+1)} = \frac{\lambda^j}{\tilde{\ell}_j} \sum_{k=j}^{\tilde{\omega}} \underline{\tilde{\mathcal{B}}}_k \tilde{\ell}_k \lambda^{-(k+1)} \tag{6.29a}$$

$$= \begin{cases} \frac{\lambda^j}{\tilde{\ell}_j} & \text{if } j \le \tilde{\alpha} \\ \frac{\lambda^j}{\tilde{\ell}_j} \sum_{k=j}^{\tilde{\omega}} \underline{\tilde{\mathcal{B}}}_k \tilde{\ell}_k \lambda^{-(k+1)} & \text{if } j > \tilde{\alpha} \end{cases} \tag{6.29b}$$

Rewriting in terms of proportions we have

$$V_i = \frac{\lambda^i}{\ell_i} \left(\sum_{k=i}^{\omega} \ell_k \lambda^{-(k+1)} \left(1 - \mathfrak{f}_k\right) \right) \sum_{i'=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} f_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-h} z_0^{i',j} \tag{6.30}$$

$$\tilde{V}_j = \frac{\lambda^j}{\tilde{\ell}_j} \left(\sum_{k=j}^{\tilde{\omega}} \tilde{\ell}_k \lambda^{-(k+1)} \left(1 - \mathfrak{m}_k\right) \right) \sum_{i=\alpha}^{\omega} \sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \tilde{f}_h^{i,j} \mathcal{L}_h^{i,j} \lambda^{-h} z_0^{i,j'} \tag{6.31}$$

6.5 Gross and Net reproductive rates

The gross reproductive rate is the expected number of offspring that a newborn will have over its lifetime if it survives from birth to the end of the reproductive span.

$$\underline{GRR} = \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \tag{6.32a}$$

$$= \left(\sum_{i'=\alpha}^{\omega} (1 - \mathfrak{f}_{i'}) \right) \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha,j-\tilde{\alpha}\}} f_h^{i-h,j-h} z_h^{i-h,j-h} \tag{6.32b}$$

for females. And

$$\underset{\sim}{\widetilde{GRR}} = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \underset{\sim}{\tilde{\mathcal{B}}}_j \tag{6.33a}$$

$$= \left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} (1 - \mathfrak{m}_{j'})\right) \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} \tilde{f}_h^{i-h,j-h} z_h^{i-h,j-h} \tag{6.33b}$$

for males.

The net reproductive rate is the expected number of offspring that newborns have from birth to the end of the reproductive span (subject to survival). In other words the factor by which the population will increase in one generation. For a population with a stable age distribution it is

$$\underset{\sim}{R}_0 = \sum_{i=\alpha}^{\omega} \underset{\sim}{\mathcal{B}}_i \ell_i \tag{6.34a}$$

$$= \left(\sum_{i'=\alpha}^{\omega} \ell_{i'} (1 - \mathfrak{f}_{i'})\right) \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} f_h^{i-h,j-h} z_h^{i-h,j-h} \tag{6.34b}$$

for females. And

$$\underset{\sim}{\tilde{R}}_0 = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \underset{\sim}{\tilde{\mathcal{B}}}_j \tilde{\ell}_j \tag{6.35a}$$

$$= \left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} (1 - \mathfrak{m}_{j'})\right) \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{i-\alpha, j-\tilde{\alpha}\}} \tilde{f}_h^{i-h,j-h} z_h^{i-h,j-h} \tag{6.35b}$$

for males.

Since λ, ℓ_i,and $\tilde{\ell}_j$ are all non negative and for $\underline{\mathcal{B}}_i, \underline{\tilde{\mathcal{B}}}_j$,there is at least one value of each which is positive on the intervals $[\alpha, \omega]$ and $[\tilde{\alpha}, \tilde{\omega}]$ respectively then

$$\underline{R}_0 < 1 \Leftrightarrow \lambda < 1 \Leftrightarrow \underline{\tilde{R}}_0 < 1 \tag{6.36}$$

$$\underline{R}_0 = 1 \Leftrightarrow \lambda = 1 \Leftrightarrow \underline{\tilde{R}}_0 = 1 \tag{6.37}$$

$$\underline{R}_0 > 1 \Leftrightarrow \lambda > 1 \Leftrightarrow \underline{\tilde{R}}_0 > 1 \tag{6.38}$$

This can easily be shown by a Taylor expansion of the characteristic equations. For example for females,

$$\begin{aligned} 1 &= \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i \ \lambda^{-(i+1)} \\ &= \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i + \sum_{k=1}^{\infty} \sum_{i=\alpha}^{\omega} (-1)^k \binom{i+k}{k} (\lambda - 1)^k \underline{\mathcal{B}}_i \ell_i \\ &= \underline{R}_0 + \sum_{k=1}^{\infty} \sum_{i=\alpha}^{\omega} (-1)^k \binom{i+k}{k} (\lambda - 1)^k \underline{\mathcal{B}}_i \ell_i \end{aligned} \tag{6.39}$$

Hence

$$\underline{R}_0 = 1 + (\lambda - 1) \sum_{i=\alpha}^{\omega} (i+1) \underline{\mathcal{B}}_i \ell_i - O\left[(\lambda - 1)^2\right] \tag{6.40}$$

When $\lambda = 1$ each of the higher degree terms of the Taylor expansion are zero, so $\underline{R}_0 = 1$. Conversely when $\underline{R}_0 = 1$ the higher degree terms of the Taylor expansion must sum to zero, and the only way for this to happen is if $\lambda = 1$ due to the positivity of the $\underline{\mathcal{B}}_i \ell_i$ terms. When $\lambda > 1$ the sign of the 1$^{\text{st}}$ degree term is positive so $\underline{R}_0 > 1$. When $\lambda < 1$ the sign of the 1$^{\text{st}}$ degree term is negative so $\underline{R}_0 < 1$. Again the converse arguments hold true due to the positivity of the $\underline{\mathcal{B}}_i \ell_i$ terms.

6.6 Generation time

Keyfitz [26] states

> "The net reproductive rate R_0 is the number of (her own) girl children by which it is expected, under the current regime of mortality and fertility, that a newly born girl child will be replaced. A reasonable definition of T, the length of generation, is that it is the time in which this replacement occurs".

For the two sex model there will typically be two different generation times one for females and one for males. By this definition we have for females

$$R_0(t) = \frac{F_0(t)}{F_0(t-T)} \tag{6.41a}$$

$$= \frac{\sum_{i=\alpha}^{\omega} \mathcal{B}_i(t-1)\,\ell_i F_0(t-1-i)}{\sum_{i=\alpha}^{\omega} \mathcal{B}_i(t-1-T_G)\,\ell_i F_0(t-1-T_G-i)} \tag{6.41b}$$

And for a population with stable age structure

$$\underline{R}_0 = \frac{\sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i\ \lambda^{t-1-i} \underline{F}_0}{\sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i\ \lambda^{t-1-\underline{T}_G-i} \underline{F}_0} \tag{6.42a}$$

$$= \frac{\lambda^{t-1} \underline{F}_0 \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i \lambda^{-i}}{\lambda^{t-1-\underline{T}_G} \underline{F}_0 \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i \lambda^{-i}} \tag{6.42b}$$

$$= \lambda^{\underline{T}_G} \tag{6.42c}$$

So for females and males,

$$\lambda^{\underline{T}_G} = \underline{R}_0 \quad \text{and} \quad \lambda^{\underline{\tilde{T}}_G} = \underline{\tilde{R}}_0 \tag{6.43}$$

Solving for $\underline{T}_G$ and $\underline{\tilde{T}}_G$ (for a non-stationary population, $\lambda \neq 1$)

$$\underline{T}_G = \frac{\ln \underline{R}_0}{\ln \lambda} \quad \text{and} \quad \underline{\tilde{T}}_G = \frac{\ln \underline{\tilde{R}}_0}{\ln \lambda} \tag{6.44}$$

6.6.1 Mean age of parentage in a cohort.

The mean ages of parentage (e.g. childbearing for females) in a cohort are

$$\mu_1(t) = \frac{\sum_{i=\alpha}^{\omega} i\mathcal{B}_i(t)\,\ell_i}{\sum_{i=\alpha}^{\omega} \mathcal{B}_i(t)\,\ell_i}, \text{ and } \tilde{\mu}_1(t) = \frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} j\tilde{\mathcal{B}}_j(t)\,\tilde{\ell}_j}{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\mathcal{B}}_j(t)\,\tilde{\ell}_j}. \tag{6.45}$$

Moments of the maternity (paternity) function

The moments of the maternity function (or paternity as the case may be) can be written

$$\frac{R_n(t)}{R_0(t)} = \frac{\sum_{i=\alpha}^{\omega} i^n\mathcal{B}_i(t)\,\ell_i}{\sum_{i=\alpha}^{\omega} \mathcal{B}_i(t)\,\ell_i} \tag{6.46}$$

$$\frac{\tilde{R}_n(t)}{\tilde{R}_0(t)} = \frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} j^n\tilde{\mathcal{B}}_j(t)\,\tilde{\ell}_j}{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\mathcal{B}}_j(t)\,\tilde{\ell}_j} \tag{6.47}$$

And the central moments of the maternity (paternity) function can be written ($n > 1$)

$$\mu_n(t) = \frac{\sum_{i=\alpha}^{\omega} (i - \mu_1(t))^n\,\mathcal{B}_i(t)\,\ell_i}{\sum_{i=\alpha}^{\omega} \mathcal{B}_i(t)\,\ell_i} \tag{6.48}$$

$$\tilde{\mu}_n(t) = \frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} (j - \tilde{\mu}_1(t))^n\,\tilde{\mathcal{B}}_j(t)\,\tilde{\ell}_j}{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\mathcal{B}}_j(t)\,\tilde{\ell}_j} \tag{6.49}$$

These are parametric discriptions of the distribution of the crude birth rate over the age of the females or males. For example μ_1 is the mean age of parentage as I've already stated, μ_2 is the variance of age of parentage, μ_3 is the skewedness of age of parentage, etc. I'll use these moments later on to compare the different measures for the time between generations.

6.6.2 Mean age of parentage in a population with a stable age distribution

The mean age of parentage in a population with a stable age distribution for females and males respectively are

$$A = \frac{\sum_{i=\alpha}^{\omega} i\underline{\mathcal{B}}_i \ell_i \lambda^{-(i+1)}}{\sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i \lambda^{-(i+1)}} \text{ and } \tilde{A} = \frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} j\underline{\tilde{\mathcal{B}}}_j \tilde{\ell}_j \lambda^{-(j+1)}}{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \underline{\tilde{\mathcal{B}}}_j \tilde{\ell}_j \lambda^{-(j+1)}} \tag{6.50}$$

But $\sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i \lambda^{-(i+1)} = 1 = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \underline{\tilde{\mathcal{B}}}_j \tilde{\ell}_j \lambda^{-(j+1)}$

$$A = \sum_{i=\alpha}^{\omega} i\underline{\mathcal{B}}_i \ell_i \lambda^{-(i+1)} \text{and } \tilde{A} = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} j\underline{\tilde{\mathcal{B}}}_j \tilde{\ell}_j \lambda^{-(j+1)} \tag{6.51}$$

6.6.3 Moment-generating function and cumulant-generating function for the net maternity function

Define (for females)

$$\psi(\xi) = \sum_{i=\alpha}^{\omega} e^{i\xi} \underline{\mathcal{B}}_i \ell_i \tag{6.52}$$

Writing successive derivatives

$$\frac{d}{d\xi}\psi(\xi) = \sum_{i=\alpha}^{\omega} i\underline{\mathcal{B}}_i \ell_i e^{i\xi} \tag{6.53a}$$

$$\vdots$$

$$\frac{d^k}{d\xi^k}\psi(\xi) = \sum_{i=\alpha}^{\omega} i^k \underline{\mathcal{B}}_i \ell_i e^{i\xi} \tag{6.53b}$$

Evaluated at $\xi = 0$

$$\begin{aligned}
\left.\psi(\xi)\right|_{\xi=0} &= \sum_{i=\alpha}^{\omega} \underline{\mathcal{B}}_i \ell_i = \underline{R}_0 && \text{(6.54a)}\\
\left.\frac{d}{d\xi}\psi(\xi)\right|_{\xi=0} &= \sum_{i=\alpha}^{\omega} i\underline{\mathcal{B}}_i \ell_i = \underline{R}_1 && \text{(6.54b)}\\
\left.\frac{d^2}{d\xi^2}\psi(\xi)\right|_{\xi=0} &= \sum_{i=\alpha}^{\omega} i^2\underline{\mathcal{B}}_i \ell_i = \underline{R}_2 && \text{(6.54c)}\\
&\vdots\\
\left.\frac{d^n}{d\xi^n}\psi(\xi)\right|_{\xi=0} &= \sum_{i=\alpha}^{\omega} i^n\underline{\mathcal{B}}_i \ell_i = \underline{R}_n && \text{(6.54d)}
\end{aligned}$$

and

$$\psi(\xi) = \sum_{n=0}^{\infty} R_n \frac{\xi^n}{n!}$$

Then $\frac{\psi(\xi)}{\underline{R}_0}$ is the moment generating function for net maternity function and $\ln\left[\frac{\psi(\xi)}{\underline{R}_0}\right]$ is the cumulant generating function

$$\frac{1}{\underline{R}_0}\left.\frac{d^n}{d\xi^n}\psi(\xi)\right|_{\xi=0} = \frac{\underline{R}_n}{\underline{R}_0} \tag{6.55}$$

$$\ln\left[\frac{\psi(\xi)}{\underline{R}_0}\right] = \sum_{n=1}^{\infty} \kappa_n \frac{\xi^n}{n!} \tag{6.56}$$

To relate the cumulants to the moments of the maternity function

$$\begin{aligned}
\frac{d}{d\xi}\ln\left[\frac{\psi(\xi)}{\underline{R}_0}\right] &= \frac{\sum_{n=0}^{\infty} R_{n+1}\frac{\xi^n}{n!}}{\sum_{n=0}^{\infty} R_n\frac{\xi^n}{n!}} && \text{(6.57a)}\\
\frac{d^2}{d\xi^2}\ln\left[\frac{\psi(\xi)}{\underline{R}_0}\right] &= \frac{\sum_{n=0}^{\infty} R_{n+2}\frac{\xi^n}{n!}}{\sum_{n=0}^{\infty} R_{n+1}\frac{\xi^n}{n!}} - \left(\frac{\sum_{n=0}^{\infty} R_{n+1}\frac{\xi^n}{n!}}{\sum_{n=0}^{\infty} R_n\frac{\xi^n}{n!}}\right)^2 && \text{(6.57b)}\\
&\vdots
\end{aligned}$$

Evaluating at $\xi = 0$

$$\ln\left[\frac{\psi(\xi)}{\underline{R}_0}\right]\Bigg|_{\xi=0} = 0 \tag{6.58a}$$

$$\frac{d}{d\xi}\ln\left[\frac{\psi(\xi)}{\underline{R}_0}\right]\Bigg|_{\xi=0} = \frac{R_1}{R_0} \tag{6.58b}$$

$$\frac{d^2}{d\xi^2}\ln\left[\frac{\psi(\xi)}{\underline{R}_0}\right]\Bigg|_{\xi=0} = \frac{R_2}{R_1} - \left(\frac{R_1}{R_0}\right)^2 \tag{6.58c}$$

$$\vdots$$

The Taylor expansion is

$$\ln\left[\frac{\psi(\xi)}{\underline{R}_0}\right] = \frac{R_1}{R_0}\xi + \left(\frac{R_2}{R_1} - \left(\frac{R_1}{R_0}\right)^2\right)\frac{\xi^2}{2} + \cdots = \kappa_1\xi + \kappa_2\frac{\xi^2}{2} + \cdots \tag{6.59}$$

So the cumulants can be related to the central moments as $\kappa_1 = \frac{R_1}{R_0} = \underline{\mu}_1, \kappa_2 = \left(\frac{R_2}{R_1} - \left(\frac{R_1}{R_0}\right)^2\right) = \underline{\mu}_2, \kappa_3 = \underline{\mu}_3, \kappa_4 = \underline{\mu}_4 - 3\underline{\mu}_2^2, \ldots$

Note that analogous expressions can be written for the paternity functions

6.6.4 Relation between the mean age of parentage in a cohort, the mean age of parentage in a population with a stable age distribution, and the generation time.

If we let $\xi = -\ln\lambda$ then we can write the expression for generation time (for females) as

$$\underline{T}_G = \frac{\ln\underline{R}_0}{\ln\lambda} = -\frac{1}{\ln\lambda}\ln\left(\frac{1}{\underline{R}_0}\right) = -\frac{1}{\ln\lambda}\ln\left[\frac{\psi\left(-\ln\lambda\right)}{\lambda\underline{R}_0}\right] \tag{6.60}$$

since $\frac{1}{\lambda}\psi\left(-\ln\lambda\right) = \sum_{i=\alpha}^{\omega}\underline{\mathcal{B}}_i\ell_i\lambda^{-(i+1)}$ is the characteristic equation (equals 1)

$$
\begin{aligned}
\underline{T}_G &= -\frac{1}{\ln\lambda}\ln\left(\frac{\psi\left(-\ln\lambda\right)}{\lambda\underline{R}_0}\right) = 1 - \frac{1}{\ln\lambda}\ln\left(\frac{\psi\left(-\ln\lambda\right)}{\underline{R}_0}\right) && \text{(6.61a)}\\
&= 1 - \frac{1}{\ln\lambda}\sum_{n=1}^{\infty}\left(-1\right)^n\frac{\left(\ln\lambda\right)^n}{n!}\kappa_n && \text{(6.61b)}\\
&= 1 + \kappa_1 - \frac{\ln\lambda}{2!}\kappa_2 + \frac{\left(\ln\lambda\right)^2}{3!}\kappa_3 - \sum_{n=4}^{\infty}\left(-1\right)^n\frac{\left(\ln\lambda\right)^{n-1}}{n!}\kappa_n && \text{(6.61c)}\\
&= 1 + \underline{\mu}_1 - \frac{\ln\lambda}{2}\underline{\mu}_2 + \frac{\left(\ln\lambda\right)^2}{6}\underline{\mu}_3 - \cdots && \text{(6.61d)}
\end{aligned}
$$

Now assuming $\underline{\mathcal{B}}_i \sim$ constant with respect to λ

$$
\begin{aligned}
\frac{d}{d\lambda}\psi\left(-\ln\lambda\right) &= \frac{d}{d\lambda}\sum_{i=\alpha}^{\omega}\underline{\mathcal{B}}_i\ell_i\lambda^{-i} && \text{(6.62a)}\\
&= -\sum_{i=\alpha}^{\omega} i\underline{\mathcal{B}}_i\ell_i\lambda^{-(i+1)} && \text{(6.62b)}\\
&= -A && \text{(6.62c)}
\end{aligned}
$$

Relating A to the cumulants

$$
\begin{aligned}
A &= \frac{-\frac{d}{d\lambda}\psi\left(-\ln\lambda\right)}{\lambda^{-1}\psi\left(-\ln\lambda\right)} \qquad [\text{denominator } = 1] && \text{(6.63a)}\\
&= \frac{-\lambda}{\psi\left(\xi\right)}\frac{d\xi}{d\lambda}\frac{d}{d\xi}\psi\left(\xi\right) = \left(-\lambda\frac{d}{d\lambda}\left(-\ln\lambda\right)\right)\left(\frac{1}{\psi\left(\xi\right)}\frac{d}{d\xi}\psi\left(\xi\right)\right) && \text{(6.63b)}\\
&= \frac{1}{\psi\left(\xi\right)}\frac{d}{d\xi}\psi\left(\xi\right) = \frac{d}{d\xi}\left[\ln\left(\psi\left(\xi\right)\right)\right] && \text{(6.63c)}\\
&= \frac{d}{d\xi}\left[\ln\left(\frac{\psi\left(\xi\right)}{\underline{R}_0}\right) + \ln\left(\underline{R}_0\right)\right] && \text{(6.63d)}
\end{aligned}
$$

$$= \frac{d}{d\xi}\left[\ln\left(\frac{\psi(\xi)}{\underline{R}_0}\right)\right] \qquad [\underline{R}_0 \text{ is constant with respect to } \xi] \tag{6.63e}$$

$$= \frac{d}{d\xi}\sum_{n=1}^{\infty}\kappa_n\frac{\xi^n}{n!} \tag{6.63f}$$

$$= \sum_{n=1}^{\infty}\kappa_n\frac{\xi^{n-1}}{n-1!} \tag{6.63g}$$

$$= \sum_{n=1}^{\infty}(-1)^{n-1}\kappa_n\frac{(\ln\lambda)^{n-1}}{n-1!} \tag{6.63h}$$

Then A in terms of the moments is

$$A = \sum_{n=1}^{\infty}(-1)^{n-1}\kappa_n\frac{(\ln\lambda)^{n-1}}{n-1!} \tag{6.64a}$$

$$= \kappa_1 - \frac{\ln\lambda}{1!}\kappa_2 + \frac{(\ln\lambda)^2}{2!}\kappa_3 - \cdots \tag{6.64b}$$

$$= \underline{\mu}_1 - (\ln\lambda)\,\underline{\mu}_2 + \frac{(\ln\lambda)^2}{2}\underline{\mu}_3 - \cdots \tag{6.64c}$$

Twice the generation time minus A gives

$$\begin{array}{rcl} 2\underline{T}_G & = & 2 + 2\underline{\mu}_1 - (\ln\lambda)\,\underline{\mu}_2 + \frac{(\ln\lambda)^2}{3}\underline{\mu}_3 - \cdots \\ -A & = & -\left[\underline{\mu}_1 - (\ln\lambda)\,\underline{\mu}_2 + \frac{(\ln\lambda)^2}{2}\underline{\mu}_3 - \cdots\right] \\ \hline 2\underline{T}_G - A & = & 2 + \underline{\mu}_1 - \frac{(\ln\lambda)^2}{6}\underline{\mu}_3 - \cdots \end{array} \tag{6.65}$$

Solving for T_G to a second degree approximation we have

$$\underline{T}_G \approx 1 + \frac{\left(A + \underline{\mu}_1\right)}{2} \tag{6.66}$$

A slight over estimate with error on the order of $\frac{(\ln\lambda)^2}{12}\underline{\mu}_3$. This is different than reported in Caswell [5] $\left[\underline{T}_G \approx \frac{(A+\underline{\mu}_1)}{2}\right]$ which is due to my starting count of age at 0 whereas he starts at 1 (see also Coale, [6] for the continuous time derivation). A similar result holds for the male generation time $\underline{\tilde{T}}_G \approx 1 + \frac{(\tilde{A}+\underline{\tilde{\mu}}_1)}{2}$. For a stationary population the time between generations is exactly the mean age of reproduction (starting counting at 0) plus one.

$$\underline{T}_G = 1 + \underline{\mu}_1 = 1 + \sum_{i=\alpha}^{\omega} i\underline{\mathcal{B}}_i \ell_i \tag{6.67a}$$

$$\underline{\tilde{T}}_G = 1 + \underline{\tilde{\mu}}_1 = 1 + \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} j\underline{\tilde{\mathcal{B}}}_j \tilde{\ell}_j \tag{6.67b}$$

since $\lambda = 1$ implies R_0 and $\tilde{R}_0 = 1$.

Chapter 7

Marriage function

7.1 Conceptualizing the marriage function

7.1.1 Properties for a "nice" marriage function

The marriage function $\mathcal{N}^{i,j}\left(\mathfrak{F}^s\left(t\right), \mathfrak{M}^s\left(t\right), \mathfrak{C}\left(t\right)\right)$ is a function determining the number of new pair bondings between females of age i and males of age j at time t. There are seven mathematical constrants (conditions) expressing the behavior a "nice" function should have. The first six of these conditions are somewhat intuitive. Conditions (i)-(v) and (vii) have been stated in one form or another by many authors, see for example McFarland [31] and Fredrickson [11]:

(i) the marriage rate is always non-negative,

$$\mathcal{N}^{i,j}\left(\mathfrak{F}^s, \mathfrak{M}^s, \mathfrak{C}\right) \geq 0 \tag{7.1}$$

(ii) if there are no singles of either sex of any age class then there are no marriages in the corresponding age class,

$$\mathcal{N}^{i,j}\left(\mathfrak{F}^s, \mathfrak{M}^s, \mathfrak{C}\right) = 0 \quad \text{if either } F_i^s = 0\ , \ \text{ or } \ M_j^s = 0 \tag{7.2}$$

(iii) the number of marriages of particular age couples cannot be larger than the minimum number of singles of either sex available to marry,

$$\sum_j \mathcal{N}^{i,j}\left(\mathfrak{F}^s, \mathfrak{M}^s, \mathfrak{C}\right) \ \leq \ F_i^s \tag{7.3a}$$

$$\text{and} \quad \sum_i \mathcal{N}^{i,j}\left(\mathfrak{F}^s, \mathfrak{M}^s, \mathfrak{C}\right) \ \leq \ M_j^s \tag{7.3b}$$

(iv) increasing or decreasing the number of singles in the age classes marrying, changes the rate of marriage between those age classes in the same direction,

$$\left.\begin{aligned} \tfrac{\partial}{\partial F_i^s}\mathcal{N}^{i,j}\left(\mathfrak{F}^s, \mathfrak{M}^s, \mathfrak{C}\right) \geq 0 \\ \tfrac{\partial}{\partial M_j^s}\mathcal{N}^{i,j}\left(\mathfrak{F}^s, \mathfrak{M}^s, \mathfrak{C}\right) \geq 0 \end{aligned}\right\} \text{ for } F_i^s > 0 \text{ , and } M_j^s > 0 \tag{7.4}$$

(v) increasing or decreasing the number of singles in the age classes other than those marrying, changes the rate of marriage in the opposite direction (competition),

$$\left.\begin{aligned} \tfrac{\partial}{\partial F_{i'}^s}\mathcal{N}^{i,j}\left(\mathfrak{F}^s, \mathfrak{M}^s, \mathfrak{C}\right) \leq 0 \\ \tfrac{\partial}{\partial M_{j'}^s}\mathcal{N}^{i,j}\left(\mathfrak{F}^s, \mathfrak{M}^s, \mathfrak{C}\right) \leq 0 \end{aligned}\right\} \text{ for } \ F_i^s \ \& \ F_{i'\neq i}^s > 0 \text{ , and } \ M_j^s \ \& \ M_{j'\neq j}^s > 0 \tag{7.5}$$

(vi) increasing or decreasing the number of already mated couples of any age classes, changes the rate of marriage in the opposite direction (interference)

$$\frac{\partial}{\partial C_h^{i',j'}}\mathcal{N}^{i,j}\left(\mathfrak{F}^s, \mathfrak{M}^s, \mathfrak{C}\right) \leq 0 \quad \text{for } F_i^s > 0 \text{ , } \ M_j^s > 0 \text{ , and } C_h^{i',j'} > 0 \tag{7.6}$$

(vii) scaling all components by a constant (positive) factor scales the rate by the same factor (homogeneity),

$$\mathcal{N}^{i,j}\left(k\mathfrak{F}^s, k\mathfrak{M}^s, k\mathfrak{C}\right) = k\mathcal{N}^{i,j}\left(\mathfrak{F}^s, \mathfrak{M}^s, \mathfrak{C}\right) \quad \text{for } k \geq 0 \tag{7.7}$$

7.2 Proposal of a marriage function

7.2.1 Marriage rates and the type II functional response

There are various possibilities for the specific form of the marriage function. The most common approach is to base the rate of contact between sex-age classes on some partition of a generalized (power) mean of the interacting classes (Keyfitz,1972 [24], and Schoen, 1981 [43]), with a generalized form of the harmonic mean usually the function of choice since it meets all of the criteria listed above. However, rather than just using a function chosen for it's mathematical properties I will develop a model here based on a process of encounters and sequential courtships. The approach I take is analogous to the extention of predator-prey interaction in Holling's disk equation (a type II functional response; Holling, 1959 [20]) that is further developed into a prey-based optimal diet model of foraging behavior by Stephens and Krebs (1986 [46]). Following these developments define T as the average length of time to successfully find a mate, T_s as the time within that interval that an un-mated individual - the "searcher"(sounds better than predator in this context) - devotes to searching for a mate, and T_c as courting time (equivalent to "handling time" in the foraging theory jargon) . In this case I include pre-reproductive mating related behaviors in the definition of courting (such as nest building) though the courtship time includes all unsuccessful courtships as well as the successful ones. I will also specify a fixed amount of time devoted to non-mating activities T_o. So $T = T_s + T_c + T_o$. If the average number of marriages per male in this time interval is $\tilde{N}$ then marriage rate per single male is $\widetilde{\mathfrak{n}}$

$$\widetilde{\mathfrak{n}} = \frac{\tilde{N}}{T_s + T_c + T_o} \tag{7.8}$$

The time spent doing non-mating related activities is a constant fraction $(1-\tilde{c})$ of the total time $T_o = (1-\tilde{c})\,T$ but $T = T_s{+}T_c{+}T_o$ so $T_o = (1-\tilde{c})\,T_s{+}(1-\tilde{c})\,T_c{+}(1-\tilde{c})\,T_o$. Solving for T_o explicitly $T_o = \frac{1-\tilde{c}}{\tilde{c}}T_s + \frac{1-\tilde{c}}{\tilde{c}}T_c$

$$\begin{aligned} \tilde{\mathfrak{n}} &= \frac{\tilde{N}}{T_s + T_c + \left(\frac{1-\tilde{c}}{\tilde{c}}T_s + \frac{1-\tilde{c}}{\tilde{c}}T_c\right)} \\ &= \frac{\tilde{c}\tilde{N}}{T_s + T_c} \end{aligned} \tag{7.9}$$

Probability of initiating a courtship

I will also assume that the encounters between males and females can be partitioned into courtships initiated by the males and those initiated by females. When courtships are initiated by males we will say that the males are the searchers, and when initiated by females we will say that females are the searchers. Define η and $1-\eta$ as the probabilities that a given courtship was initiated by a male or a female respectively. The initiation will be viewed as an instantaneous event so that the probability of simultaneous initiation by both parties is negligible. There is a fair amount of research that has been done on who and how initiation of courtship takes place in humans (see for example [47] , [42], [12]). Monica Moore for example provides a list of 52 different non-verbal signals that females use to initiate courtships and their frequency of use in approximately 200 subjects [34] and in a separate study the nonverbal signals used to discourage courtship [35]. T. Perper estimates that women are responsible for initiating courtships about 2/3 of the time [36]. I am unaware of any studies that breaks down initiation by age though. In many organisms it will no doubt be the case that these parameters will be rather nebulous quantities and difficult to measure. There are many factors that could come into play such as pheromones, sounds out of range of human hearing, subtle display patterns, or other signals which are not recognized by human investigators. Indeed it would not be surprising that the frequency of initiation also turns out to be confounded by the the age predispositions (see below) and relative density of the sexes of those age classes. Of course this is not necessarily the case for all organisms though, and in many cases, particularly when one sex or the other exclusively initiates, the situation is more clear cut.

Now if $\tilde{\mathcal{E}}$ is the rate of encounters that a male makes with single females per unit time searched (units: $\frac{\text{[encounters]}}{\text{[time searched][male]}}$), q is the fraction of courtships that result in a marriage (units: $\frac{\text{[marriages]}}{\text{[courtships]}}$), and $\tilde{\rho}$ is the fraction of encounters that result in courtships (units: $\frac{\text{[courtships]}}{\text{[encounters]}}$, an encounter is considered a potential courtship) then $\widetilde{N} = \eta q \rho \tilde{\mathcal{E}} T_s$ is the average number of marriages per male that occur in length of time T_s. If the "individual-hours" spent courting per courtship is h (units: $\frac{\text{[time courting][males]}}{\text{[courtships]}}$) then the overall time spent courting is $T_c = h\rho\tilde{\mathcal{E}}T_s$. Hence the marriage rate per single male is

$$\widetilde{\mathfrak{n}} = \frac{\eta q \tilde{c} \rho \tilde{\mathcal{E}} T_s}{T_s + h\tilde{\rho}\tilde{\mathcal{E}}T_s} = \frac{\eta q \tilde{c} \rho \tilde{\mathcal{E}}}{1 + h\rho\tilde{\mathcal{E}}}. \tag{7.10}$$

An analogous expression can be formulated in the same way for the marriage rate per single female.

7.2.2 Age specific marriage rates

Now let $\left[\tilde{\mathcal{E}}\left(\mathfrak{F}^s\right)\right]_{i,j}$ (or just $\tilde{\mathcal{E}}_{i,j}$ for short) equal the rate of encounter that single males age j have with single females age i per unit time searched per single male age j, The constant $\tilde{c}_j$ is the average fraction of total time that a single male spends pursuing mating activities, $q_{i,j}$ is the proportion of courting couples that marry, and $h_{i,j}$ is the average "individual-hours" it takes for a courtship between a male age j and a female age i (we assume that this is the same whether male or females initiate). The probabilities that single males (j) or single females (i) will initiate an encounter with the opposite sex of indicated age are $\eta_{i,j}$ and $\left(1 - \eta_{i,j}\right)$ respectively.

Age predispositions and joint age predispositions

Define $\tilde{a}_{i,j}$ as the probability that a male age j will want to court a female age i upon encountering her (units: $\frac{\text{[courtships between } i \text{ \& } j \text{ (acceptable to males)]}}{\text{[encounters between } i \text{ \& } j\text{]}}$). And $a_{i,j}$ is the probability that a female age i will want to court a male age j upon encountering him. I will call these the age predispositions. The joint predisposition is $\tilde{a}_{i,j}a_{i,j} = \rho_{i,j}$ (probability that a male age j and female age i will want to court each other). Then the rate at which male searchers age j marry females age i is (at time t)

$$\widetilde{\mathfrak{n}}_{i,j}(t) = \frac{\eta_{i,j}\tilde{c}_j q_{i,j}\rho_{i,j}\tilde{\mathcal{E}}_{i,j}(t)}{1+\sum_{i'=\alpha-1}^{\omega-1}\rho_{i',j}h_{i',j}\tilde{\mathcal{E}}_{i',j}(t)} \tag{7.11}$$

7.2.3 Explicit encounter rates

Assume that mixing is proportional to the fraction of single females that are age i so that the encounter rate is

$$\tilde{\mathcal{E}}_{i,j}(t) = \tilde{k}_{i,j}\frac{F_i^s(t)}{\sum_{i'=\alpha-1}^{\omega-1}F_{i'}^s(t)}. \tag{7.12a}$$

When females age i search the encounter rate is

$$\mathcal{E}_{i,j}(t) = k_{i,j}\frac{M_j^s(t)}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}M_{j'}^s(t)}. \tag{7.12b}$$

Where $\tilde{k}_{i,j}$ is the rate of encounter that single males age j have with single females age i per unit time searched per single males age j per fraction of single females that are age i (units: $\frac{\text{[encounters between } i \text{ \& } j \text{ (resulting from males searching)]}}{\text{[time searched][single males age } j\text{][fraction of single females that are age } i\text{]}}$). Noting that [fraction of single females that are age i] $\times$ [search time] is the average search time wherein females of age i are encountered [search time attributable to females age i] we can re-express the units as $\left(\frac{\text{[encounters between } i \text{ \& } j \text{ (resulting from males searching)]}}{\text{[search time attributable to females age } i \text{][single males age } j\text{]}}\right)$

$$\widetilde{\mathfrak{n}}_{i,j}(t) = \frac{\eta_{i,j}\tilde{c}_j\rho_{i,j}\tilde{k}_{i,j}q_{i,j}\frac{F_i^s(t)}{\sum_{i''=\alpha-1}^{\omega-1}F_{i''}^s(t)}}{1+\sum_{i'=\alpha-1}^{\omega-1}\rho_{i',j}\tilde{k}_{i',j}h_{i',j}\frac{F_{i'}^s(t)}{\sum_{i''=\alpha-1}^{\omega-1}F_{i''}^s(t)}} \tag{7.13a}$$

$$= \frac{\eta_{i,j}\tilde{c}_j\rho_{i,j}\tilde{k}_{i,j}q_{i,j}F_i^s(t)}{\sum_{i''=\alpha-1}^{\omega-1}\underline{F}_{i''}^s(t)+\sum_{i'=\alpha-1}^{\omega-1}\rho_{i',j}\tilde{k}_{i',j}h_{i',j}F_{i'}^s(t)}. \tag{7.13b}$$

The average marriage rate between males age j and females age i when males age j are initiating the encounters

$$M_j^s(t)\,\widetilde{\mathfrak{n}}_{i,j}(t) = \frac{\eta_{i,j}\tilde{c}_j\rho_{i,j}\tilde{k}_{i,j}q_{i,j}F_i^s(t)\,M_j^s(t)}{\sum_{i'=\alpha-1}^{\omega-1}\left(1+\rho_{i',j}\tilde{k}_{i',j}h_{i',j}\right)F_{i'}^s(t)} \tag{7.14a}$$

Similarly for females age i initiating with males age j

$$F_i^s(t)\,\mathfrak{n}_{i,j}(t) = \frac{\left(1-\eta_{i,j}\right)c_i\rho_{i,j}k_{i,j}q_{i,j}M_j^s(t)\,F_i^s(t)}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}\left(1+\rho_{i,j'}h_{i,j'}k_{i,j'}\right)M_{j'}^s(t)} \tag{7.14b}$$

7.2.4 Preferences

Preference coefficient

Let

$$\tilde{w}_{i,j} = 1+\rho_{i,j}h_{i,j}\tilde{k}_{i,j} \tag{7.15}$$

(units: $1+\frac{\text{[time courting between female } i \text{ \& male } j\text{]}}{\text{[search time attributable to females age } i\text{]}}$
$=\frac{\text{[time spent in mating activities between female } i \text{ \& male } j\text{]}}{\text{[search time attributable to females age } i\text{]}}$). Call this the preference coefficient of male age j for female age i. And, of course $w_{i,j} = 1+\rho_{i,j}h_{i,j}k_{i,j}$.

Preference probability

Rather than dealing with the preference coefficient it may be more intuitive and probably easier to estimate a preference probability i.e.

$$\tilde{v}_{i,j} = \frac{\tilde{w}_{i,j}}{\sum_{i'} \tilde{w}_{i',j}} \tag{7.16}$$

This is the standardized fraction of time that initiating males age j spend in mating activities with female of age i (it is the fraction of time that initiating males age j would spend in mating activities with female of age i given equal numbers of all age females[1]). Let

$$\tilde{u}_{i,j} = \frac{\eta_{i,j}\tilde{c}_j\tilde{k}_{i,j}\rho_{i,j}q_{i,j}}{1+\rho_{i,j}h_{i,j}\tilde{k}_{i,j}} = \frac{\eta_{i,j}\tilde{c}_j\tilde{k}_{i,j}\rho_{i,j}q_{i,j}}{\tilde{w}_{i,j}} \tag{7.17}$$

(units: $\frac{\text{[marriages between } i \text{ \& } j \text{ (resulting from males initiating)]}}{\text{[single males age } j\text{][search time attributable to females age } i\text{]}} \div$
$\frac{\text{[time spent in mating activities between female } i \text{ \& male } j\text{]}}{\text{[search time attributable to females age } i\text{]}}$
$= \frac{\text{[marriages between } i \text{ \& } j \text{ (resulting from males initiating)]}}{\text{[single males age } j\text{][time spent in mating activities between female } i \text{ \& male } j\text{]}}$),
and $u_{i,j} = \left(1-\eta_{i,j}\right) c_i k_{i,j}\rho_{i,j}q_{i,j}/w_{i,j}$. I will express the rate $\tilde{c}_j\tilde{k}_{i,j}\rho_{i,j}$ as "existent courtships" per unit time, this means that because courtships resulting from males initiating is calculated from the rate $\tilde{k}_{i,j}\rho_{i,j}$ as if this were a continual process without break for non-mating activities, and mating activities are only occurring for a $\tilde{c}_j$ fraction of the time, then to get the number of courtships that "exist" in the time that is actually available we adjust by this factor ($\tilde{c}_j$). Note that $u_{i,j}$ and $\tilde{u}_{i,j}$ are the maximal rates of marriage between female i & male j for female initiating and males initiating respectively. By maximal we mean that (for $\tilde{u}_{i,j}$ for example) this would be the rate per male age j if the adult female population consisted entirely of females age i or if

[1] There is an assumption here that the preferences also do not effect the time spent on non-mating activities.

males age j had a sole preference for females age i. We can then write

$$M_j^s(t)\,\tilde{\mathfrak{n}}_{i,j}(t) = \frac{\tilde{v}_{i,j}F_i^s(t)}{\sum_{i'=\alpha-1}^{\omega-1}\tilde{v}_{i',j}F_{i'}^s(t)}\tilde{u}_{i,j}M_j^s(t) \tag{7.18a}$$

And for females initiating

$$F_i^s(t)\,\mathfrak{n}_{i,j}(t) = \frac{v_{i,j}M_j^s(t)}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}v_{i,j'}M_{j'}^s(t)}u_{i,j}F_i^s(t) \tag{7.18b}$$

In 7.18a above, the expression $\frac{\tilde{v}_{i,j}F_i^s(t)}{\sum_{i'=\alpha-1}^{\omega-1}\tilde{v}_{i',j}F_{i'}^s(t)}$ represents the actual fraction of time that initiating males age j spend in mating activities with female of age i, and a similar interpretation for the females initiating.

7.2.5 The overall marriage rate

To obtain the overall rate we sum the two rates.

$$\mathcal{N}^{i,j}(t) = \frac{\tilde{v}_{i,j}F_i^s(t)}{\sum_{i'=\alpha-1}^{\omega-1}\tilde{v}_{i',j}F_{i'}^s(t)}\tilde{u}_{i,j}M_j^s(t) + \frac{v_{i,j}M_j^s(t)}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}v_{i,j'}M_{j'}^s(t)}u_{i,j}F_i^s(t)$$

$$= \left(\frac{\tilde{u}_{i,j}\tilde{v}_{i,j}}{\sum_{i'=\alpha-1}^{\omega-1}\tilde{v}_{i',j}F_{i'}^s(t)} + \frac{u_{i,j}v_{i,j}}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}v_{i,j'}M_{j'}^s(t)}\right)F_i^s(t)\,M_j^s(t), \tag{7.19}$$

or

$$\mathcal{N}^{i,j}(t) = Q_{i,j}\left(\mathfrak{F}^s(t), \mathfrak{M}^s(t)\right)\;F_i^s(t)\,M_j^s(t) \tag{7.20}$$

where

$$Q_{i,j}\left(\mathfrak{F}^s(t), \mathfrak{M}^s(t)\right) \equiv \left(\frac{\tilde{u}_{i,j}\tilde{v}_{i,j}}{\sum_{i'=\alpha-1}^{\omega-1}\tilde{v}_{i',j}F_{i'}^s(t)} + \frac{u_{i,j}v_{i,j}}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}v_{i,j'}M_{j'}^s(t)}\right) \tag{7.21}$$

(or just $Q_{ij}(t)$ for short). The average marriage rate between males age j and females age i once a stable age distribution is obtained is

$$\underline{\mathcal{N}}^{i,j} = \left(\frac{\tilde{u}_{i,j}\tilde{v}_{i,j}}{\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j}\underline{F}_{i'}^{s}} + \frac{u_{i,j}v_{i,j}}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'}\underline{M}_{j'}^{s}} \right) \underline{F}_i^s \underline{M}_j^s \tag{7.22a}$$

$$= \underline{Q}_{i,j}\underline{F}_i^s \underline{M}_j^s \tag{7.22b}$$

7.2.6 Competition, interference, and facilitation

I note in passing that we can also include terms for competition, interference, and facilitation in the denominator. If, for example, the rate of mixing with singles of a particular age is reduced by competition from others of the same sex and/or interference from already mated individuals the rate (for males) might look like

$$\frac{\tilde{u}_{i,j}\tilde{v}_{i,j}F_i^s(t)}{\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} \tilde{\varsigma}_j M_j^s(t) + \sum_{i'=\alpha}^{\omega} \sum_{h=0}^{\min\{i'-\alpha, j-\tilde{\alpha}\}} \tilde{\vartheta}_{h,i'} C_{h,i',j}(t) + \sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j} F_{i'}^s(t)} \tag{7.23a}$$

and for females

$$\frac{u_{i,j}v_{i,j}M_j^s(t)}{\sum_{i'=\alpha-1}^{\omega-1} \varsigma_{i'} F_{i'}^s(t) + \sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{i-\alpha, j'-\tilde{\alpha}\}} \vartheta_{h,j'} C_{h,i,j'}(t) + \sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'} M_{j'}^s(t)} \tag{7.23b}$$

Rather than expand this mess I will just note that we can easily see that the numerator of $\mathcal{N}^{i,j}(t)$ stays the same while the denominator re-scales in terms of $F_i^s(t)$ and $M_j^s(t)$ and gains terms $C_{h,i,j'}(t)$ summed over i and h, and j and h separately. One would expect that the values of the v's are large in comparison to the ς's and ϑ's and that therefore the overall rates are reduced but the relative rates are affected less so, since the individual effects tend to average out. In further developments I will not here consider these explicit types of competition or interference from (potentially) non-mating interactions. Even so there are still indirect effects due to the reduction of numbers of available mates from marriages that do occur. And finally I also note, in passing, that the actual mating behavior often violates some of the seven conditions for a "desirable" mathematical function. For instance the mere occurrence of a marriage may induce social facilitation (copying) among peers (violation of condition vi.), or increasing the number of competing males (for instance) for a limited number of females may cause non-linear increase in the number of marriages (violation of conditions v and/or vii), or mating may be non- monogamous (violation of conditions iii and vii). For monogamous systems though condition iii must be met (particularly in the case of discrete time to avoid the embarrassment of negative quantities!)

7.2.7 A quick fix for excessive rates

If the total number of marriages of singles predicted is greater than the number available, that is $\sum_{i=\alpha-1}^{\omega-1} F_i^s(t) M_j^s(t) Q_{i,j}(t) > M_j^s(t)$ or $\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} F_i^s(t) M_j^s(t) Q_{i,j}(t) > F_i^s(t)$ then distribute the marriages among singles in proportion to the *relative* rates of marriage. The rationale for this is that the time until all the available singles of a particular age are mated is proportional to the reciprocal of the total marriage rate for that age class. For example, in the case of female age i marriages, if the total number of marriages of females predicted is greater than the number available: $F_i^s(t) \sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} M_j^s(t) Q_{i,j}(t) > F_i^s(t)$ or $\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} M_j^s(t) Q_{i,j}(t) > 1$. Now in general the number of female mates age i that are desired in a single time interval is $F_i^d(t) = F_i^s(t) \sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j}(t) M_j^s(t)$ ("d" for desired female mates). But if the RHS is large enough then all single females age i are mated before the end of the time interval. They are all mated in some fraction of the time interval τ $(0 < \tau \leq 1)$, such that

$\tau F_i^d(t) = F_i^s(t)$. Then

$$\tau F_i^d(t) = F_i^s(t) = \tau F_i^s(t) \sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j}(t) M_j^s(t) \tag{7.24}$$

and

$$\tau = \frac{1}{\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j}(t) M_j^s(t)} \tag{7.25}$$

The right hand side of Equation 7.24 can then be rewritten as

$$\begin{aligned} \tau F_i^d(t) &= F_i^s(t) \\ &= \underbrace{\frac{Q_{i,\tilde{\alpha}-1}(t) M_{\tilde{\alpha}-1}^s(t) F_i^s(t)}{\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j}(t) M_j^s(t)}}_{\text{marriages between } F_i^s \& M_{\tilde{\alpha}-1}^s} + \underbrace{\frac{Q_{i,\tilde{\alpha}}(t) M_{\tilde{\alpha}}^s(t) F_i^s(t)}{\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j}(t) M_j^s(t)}}_{\text{marriages between } F_i^s \& M_{\tilde{\alpha}}^s} + \cdots \\ &\quad + \underbrace{\frac{Q_{i,\tilde{\omega}-1}(t) M_{\tilde{\omega}-1}^s(t) F_i^s(t)}{\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j}(t) M_j^s(t)}}_{\text{marriages between } F_i^s \& M_{\tilde{\omega}-1}^s} \end{aligned} \tag{7.26}$$

Thus we see that the distribution of the marriages of females age i to males age j is $\frac{Q_{i,j}(t)M_j^s(t)}{\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j}(t)M_j^s(t)} F_i^s(t)$. Similarly if the total number of marriages of males predicted is too high: $\sum_{i=\alpha-1}^{\omega-1} Q_{i,j}(t) F_i^s(t) > 1$, then we the distribute the marriages of males age j to females age i as $\frac{Q_{i,j}(t)F_i^s(t)}{\sum_{i=\alpha-1}^{\omega-1} Q_{i,j}(t)F_i^s(t)} M_j^s(t)$, and if both $\sum_{i=\alpha-1}^{\omega-1} Q_{i,j}(t) F_i^s(t) > 1$, and $\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j}(t) M_j^s(t) > 1$, are true then we take the minimum distributed number of marriages.

Thus the natality function looks like

$$\mathcal{N}^{i,j}(t) = \tau_{i,j}(t) Q_{i,j}(t) F_i^s(t) M_j^s(t) \tag{7.27}$$

where $Q_{i,j}(t)$ is defined in 7.21, and

$$\tau_{i,j}(t) = \min\left\{1, \frac{1}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} Q_{i,j'}(t) M_{j'}^s(t)}, \frac{1}{\sum_{i'=\alpha-1}^{\omega-1} Q_{i'j}(t) F_{i'}^s(t)}\right\} \tag{7.28}$$

For the number of couples

$$C_0^{i+1,j+1}(t+1) = p_i \tilde{p}_j \tau_{i,j}(t)\, Q_{i,j}(t)\, F_i^s(t)\, M_j^s(t) \tag{7.29}$$

For the stable age distribution we have $\underline{\mathcal{N}}^{i,j} = \underline{\tau}_{i,j}\underline{Q}_{i,j}\underline{F}_i^s\underline{M}_j^s$. And from Equations 4.6 and 5.1c we have $\underline{C}_0^{i,j} = \lambda^{-1}p_{i-1}\tilde{p}_{j-1}\underline{\mathcal{N}}^{i-1,j-1}$ so that

$$\underline{C}_0^{i+1,j+1} = \underline{\tau}_{i,j}\frac{p_i\tilde{p}_j}{\lambda}\underline{Q}_{i,j}\underline{F}_i^s\underline{M}_j^s \tag{7.30}$$

7.2.8 More on proportions

Age distribution of new couples

Dividing through Equation 7.30 by $\underline{C}$ we obtain

$$z_0^{i+1,j+1} = \underline{\tau}_{i,j}\frac{p_i\tilde{p}_j}{\lambda}\underline{C}\underline{Q}_{i,j}\frac{\underline{F}_i^s}{\underline{C}}\frac{\underline{M}_j^s}{\underline{C}} \tag{7.31}$$

Expanding using stable age solutions for the proportions (6.2, 6.4, 6.5a, 6.11, and 6.12)

$$z_0^{i+1,j+1} = \underline{\tau}_{i,j}\frac{p_i\tilde{p}_j}{\lambda}\underline{C}\underline{Q}_{i,j}\left(\frac{\underline{F}_{i'}^s}{\underline{F}_{i'}}\frac{\underline{F}_{i'}}{\underline{F}}\frac{\underline{F}}{\underline{F}_A}\frac{\underline{F}_A}{\underline{C}}\right)\left(\frac{\underline{M}_{j'}^s}{\underline{M}_{j'}}\frac{\underline{M}_{j'}}{\underline{M}}\frac{\underline{M}}{\underline{M}_A}\frac{\underline{M}_A}{\underline{C}}\right)$$

$$= \underline{\tau}_{i,j}\frac{p_i\tilde{p}_j}{\lambda}\underline{C}\underline{Q}_{i,j}\left(\mathfrak{f}_{i'}x_{i'}x_A^{-1}\left(1-\langle\mathfrak{f}\rangle\right)^{-1}\right)\left(\mathfrak{m}_{j'}y_{j'}y_A^{-1}\left(1-\langle\mathfrak{m}\rangle\right)^{-1}\right)$$

$$= \underline{\tau}_{i,j}\frac{p_i\tilde{p}_j}{\lambda}\underline{C}\underline{Q}_{i,j}\left(\mathfrak{f}_{i'}\frac{\ell_{i'}\lambda^{-i'}}{\sum_{i'=\alpha}^{\omega}\ell_{i'}\lambda^{-i'}}\left(1-\frac{\sum_{i'=\alpha}^{\omega}\ell_{i'}\lambda^{-i'}\mathfrak{f}_{i'}}{\sum_{i'=\alpha}^{\omega}\ell_{i'}\lambda^{-i'}}\right)^{-1}\right)$$
$$\times\left(\mathfrak{m}_{j'}\frac{\tilde{\ell}_{j'}\lambda^{-j'}}{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\tilde{\ell}_{j'}\lambda^{-j'}}\left(1-\frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\tilde{\ell}_{j'}\lambda^{-j'}\mathfrak{m}_{j'}}{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\tilde{\ell}_{j'}\lambda^{-j'}}\right)^{-1}\right)$$

$$= \underline{T}_{i,j} \frac{p_i \tilde{p}_j}{\lambda} \underline{CQ}_{i,j} \left(\frac{\ell_i \lambda^{-i} \mathfrak{f}_i}{\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'} (1 - \mathfrak{f}_{i'})} \right) \left(\frac{\tilde{\ell}_j \lambda^{-j} \mathfrak{m}_j}{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-j'} (1 - \mathfrak{m}_{j'})} \right) \tag{7.32}$$

This can be simplified as

$$\begin{aligned} z_0^{i+1,j+1} &= \frac{p_i \tilde{p}_j}{\lambda} \ell_i \tilde{\ell}_j \lambda^{-(i+j)} \underline{T}_{i,j} U_{i,j} \mathfrak{f}_i \mathfrak{m}_j \\ &= \ell_{i+1} \tilde{\ell}_{j+1} \lambda^{-(i+j+1)} \underline{T}_{i,j} U_{i,j} \mathfrak{f}_i \mathfrak{m}_j \end{aligned} \tag{7.33}$$

where the potential marriage rate with respect to fraction of single males and females within each age class is

$$U_{i,j} \equiv \frac{\underline{CQ}_{i,j}}{\left[\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'} (1 - \mathfrak{f}_{i'})\right] \left[\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-j'} (1 - \mathfrak{m}_{j'})\right]} \tag{7.34}$$

Now

$$\underline{CQ}_{i,j} = \frac{\tilde{u}_{i,j} \tilde{v}_{i,j}}{\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j} \left(\underline{F}_{i'}^s / \underline{C}\right)} + \frac{u_{i,j} v_{i,j}}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'} \left(\underline{M}_{j'}^s / \underline{C}\right)}$$

$$= \frac{\tilde{u}_{i,j} \tilde{v}_{i,j}}{\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j} \frac{\underline{F}_{i'}^s}{\underline{F}_{i'}} \frac{\underline{F}_{i'}}{\underline{F}} \frac{\underline{F}}{\underline{F}_A} \frac{\underline{F}_A}{\underline{C}}} + \frac{u_{i,j} v_{i,j}}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'} \frac{\underline{M}_{j'}^s}{\underline{M}_{j'}} \frac{\underline{M}_{j'}}{\underline{M}} \frac{\underline{M}}{\underline{M}_A} \frac{\underline{M}_A}{\underline{C}}}$$

$$= \frac{\tilde{u}_{i,j} \tilde{v}_{i,j}}{\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j} \mathfrak{f}_{i'} x_{i'} x_A^{-1} (1 - \langle \mathfrak{f} \rangle)^{-1}} + \frac{u_{i,j} v_{i,j}}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'} \mathfrak{m}_{j'} y_{j'} y_A^{-1} (1 - \langle \mathfrak{m} \rangle)^{-1}}$$

$$= \frac{\tilde{u}_{i,j} \tilde{v}_{i,j} x_A (1 - \langle \mathfrak{f} \rangle)}{\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j} \mathfrak{f}_{i'} x_{i'}} + \frac{u_{i,j} v_{i,j} y_A (1 - \langle \mathfrak{m} \rangle)}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'} \mathfrak{m}_{j'} y_{j'}}$$

$$\begin{aligned} = \; & \frac{\tilde{u}_{i,j} \tilde{v}_{i,j} \sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'}}{\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j} \mathfrak{f}_{i'} \ell_{i'} \lambda^{-i'}} \left(1 - \frac{\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'} \mathfrak{f}_{i'}}{\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'}} \right) + \cdots \\ & \frac{u_{i,j} v_{i,j} \sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-j'}}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'} \mathfrak{m}_{j'} \tilde{\ell}_{j'} \lambda^{-j'}} \left(1 - \frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-j'} \mathfrak{m}_{j'}}{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-j'}} \right) \end{aligned}$$

$$= \frac{\tilde{u}_{i,j} \tilde{v}_{i,j} \sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'} (1 - \mathfrak{f}_{i'})}{\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j} \ell_{i'} \lambda^{-i'} \mathfrak{f}_{i'}} + \frac{u_{i,j} v_{i,j} \sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-j'} (1 - \mathfrak{m}_{j'})}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'} \tilde{\ell}_{j'} \lambda^{-j'} \mathfrak{m}_{j'}} \tag{7.35}$$

Substituting line 7.35 for $\underline{CQ}_{i,j}$ in definition 7.34

$$U_{i,j} = \frac{\tilde{u}_{i,j}\tilde{v}_{i,j}}{\left(\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j}\ell_{i'}\lambda^{-i'}\mathfrak{f}_{i'}\right)\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\left(1-\mathfrak{m}_{j'}\right)\right)} + \frac{u_{i,j}v_{i,j}}{\left(\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'}\tilde{\ell}_{j'}\lambda^{-j'}\mathfrak{m}_{j'}\right)\left(\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\left(1-\mathfrak{f}_{i'}\right)\right)} \tag{7.36}$$

Factoring out the ratio of singles of a particular age class to total number of couples in the denominator of the time interval fraction, $\underline{\tau}_{i,j}$ can be rewritten

$$\underline{\tau}_{i,j} = \min\left\{1, \frac{1}{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} \underline{CQ}_{i,j'}\left(\underline{M}_{j'}^{s}/\underline{C}\right)}, \frac{1}{\sum_{i'=\alpha-1}^{\omega-1} \underline{CQ}_{i',j}\left(\underline{F}_{i'}^{s}/\underline{C}\right)}\right\} \tag{7.37}$$

Furthur expanding and substituting the relevant expressions in the denominator of the second term of the time interval fraction above,

$$\begin{aligned}
\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} \underline{CQ}_{i,j'}\left(\underline{M}_{j'}^{s}/\underline{C}\right) &= \sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} \underline{CQ}_{i,j'}\frac{\underline{M}_{j'}^{s}}{\underline{M}_{j'}}\frac{\underline{M}_{j'}}{\underline{M}}\frac{\underline{M}}{\underline{M}_{A}}\frac{\underline{M}_{A}}{\underline{C}} \\
&= \sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} \underline{CQ}_{i,j'}\mathfrak{m}_{j'}y_{j'}y_{A}^{-1}\left(1-\langle\mathfrak{m}\rangle\right)^{-1} \\
&= \frac{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} \underline{CQ}_{i,j'}\mathfrak{m}_{j'}y_{j'}}{y_{A}\left(1-\langle\mathfrak{m}\rangle\right)} \\
&= \frac{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} \underline{CQ}_{i,j'}\mathfrak{m}_{j'}y_{j'}}{y_{A}}\left(1-\langle\mathfrak{m}\rangle\right)^{-1} \\
&= \frac{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} \underline{CQ}_{i,j'}\mathfrak{m}_{j'}\tilde{\ell}_{j'}\lambda^{-j'}}{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}}\left(1-\frac{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\mathfrak{m}_{j'}}{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}}\right)^{-1} \\
&= \frac{\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} \underline{CQ}_{i,j'}\mathfrak{m}_{j'}\tilde{\ell}_{j'}\lambda^{-j'}}{\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\left(1-\mathfrak{m}_{j'}\right)} \\
&= \left(\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\left(1-\mathfrak{f}_{i'}\right)\right)\left(\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} U_{i,j'}\tilde{\ell}_{j'}\lambda^{-j'}\mathfrak{m}_{j'}\right) \qquad (7.39)
\end{aligned}$$

Similarly

$$\sum_{i'=\alpha-1}^{\omega-1} \underline{CQ}_{i',j} \left(\underline{F}^s_{i'}/\underline{C}\right) = \left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-j'} \left(1-\mathfrak{m}_{j'}\right)\right) \left(\sum_{j'=\alpha-1}^{\omega-1} U_{i',j} \ell_{i'} \lambda^{-i'} \mathfrak{f}_{i'}\right) \tag{7.40}$$

So

$$\underline{\mathcal{T}}_{i,j} = \min \left\{ \begin{array}{c} 1, \\ \frac{1}{\sum_{i'=\alpha}^{\omega} \ell_{i'} \lambda^{-i'} (1-\mathfrak{f}_{i'}) \sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} U_{i,j'} \tilde{\ell}_{j'} \lambda^{-j'} \mathfrak{m}_{j'}}, \\ \frac{1}{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'} \lambda^{-j'} \left(1-\mathfrak{m}_{j'}\right) \sum_{j'=\alpha-1}^{\omega-1} U_{i',j} \ell_{i'} \lambda^{-i'} \mathfrak{f}_{i'}} \end{array} \right\} \tag{7.41}$$

Finally define the realized marriage rate with respect to fraction of single males and females within each age class

$$\mathcal{U}_{i,j} \equiv \underline{\mathcal{T}}_{i,j} U_{i,j} \tag{7.42}$$

Then the number of new couples from 7.33 is

$$z_0^{i+1,j+1} = \mathcal{U}_{i,j} \ell_{i+1} \tilde{\ell}_{j+1} \lambda^{-(i+j+1)} \mathfrak{f}_i \mathfrak{m}_j \tag{7.43}$$

So summing over all indices for $z_h^{i,j}$ and substituting Equations 6.6c

$$1 = \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} z_h^{i,j} \tag{7.44a}$$

$$= \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \left(\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \mathcal{L}_h^{i,j} \lambda^{-h} \right) z_0^{i,j} \tag{7.44b}$$

$$= \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \Lambda^{i,j} z_0^{i,j} \tag{7.44c}$$

Substituting the RHS of Equation 7.43 for $z_0^{i,j}$ then

$$1 = \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \Lambda^{i,j} \ell_i \tilde{\ell}_j \lambda^{-(i+j-1)} \mathcal{U}_{i-1,j-1} \mathfrak{f}_{i-1} \mathfrak{m}_{j-1} \tag{7.44d}$$

Shifting indices

$$1 = \sum_{i=\alpha-1}^{\omega-1} \sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} \Lambda^{i+1,j+1} \ell_{i+1} \tilde{\ell}_{j+1} \lambda^{-(i+j+1)} \mathcal{U}_{i,j} \mathfrak{f}_i \mathfrak{m}_j \tag{7.44e}$$

Expanding the $\alpha - 1$ and $\tilde{\alpha} - 1$ terms,

$$\begin{aligned} 1 \;=\; & \sum_{j=\tilde{\alpha}}^{\tilde{\omega}-1} \sum_{i=\alpha}^{\omega-1} \Lambda^{i+1,j+1} \ell_{i+1} \tilde{\ell}_{j+1} \lambda^{-(i+j+1)} \mathcal{U}_{i,j} \mathfrak{f}_i \mathfrak{m}_j + \sum_{i=\alpha}^{\omega-1} \Lambda^{i+1,\tilde{\alpha}} \ell_{i+1} \tilde{\ell}_{\tilde{\alpha}} \lambda^{-(i+\tilde{\alpha})} \mathcal{U}_{i,\tilde{\alpha}-1} \mathfrak{f}_i \\ & + \sum_{j=\tilde{\alpha}}^{\tilde{\omega}-1} \Lambda^{\alpha,j+1} \ell_{\alpha} \tilde{\ell}_{j+1} \lambda^{-(\alpha+j)} \mathcal{U}_{\alpha-1,j} \mathfrak{m}_j + \Lambda^{\alpha,\tilde{\alpha}} \ell_{\alpha} \tilde{\ell}_{\tilde{\alpha}} \lambda^{-(\alpha+\tilde{\alpha}-1)} \mathcal{U}_{\alpha-1,\tilde{\alpha}-1} \end{aligned} \tag{7.44f}$$

Proportion of singles in each age class

Now looking at the proportion of single males in each age class a little more closely

$$\underline{M}_j^s = \begin{cases} \underline{M}_{\tilde{\alpha}-1} & \text{if } \; j = \tilde{\alpha} - 1 \\ \underline{M}_j - \sum_{h=0}^{\min\{\omega-\alpha,j-\tilde{\alpha}\}} \sum_{i=\alpha}^{\omega-h} \underline{C}_h^{i,j-h} & \text{if } \; \tilde{\alpha} \leq j \leq \tilde{\omega} \end{cases}$$

So if $\tilde{\alpha} \leq j \leq \tilde{\omega}$ we re-express the identity above in terms of proportions

$$\begin{aligned} \underline{M}_j - \underline{M}_j^s &= \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{\omega-i,j-\tilde{\alpha}\}} \underline{C}_h^{i,j-h} && (7.45a) \\ \left(1 - \frac{\underline{M}_j^s}{\underline{M}_j}\right) \frac{\underline{M}_j}{\underline{M}} &= \frac{\underline{M}_A}{\underline{M}} \frac{\underline{C}}{\underline{M}_A} \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{\omega-i,j-\tilde{\alpha}\}} \frac{\underline{C}_h^{i,j-h}}{\underline{C}} && (7.45b) \\ (1 - \mathfrak{m}_j)\, y_j &= y_A \,(1 - \langle \mathfrak{m} \rangle) \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{\omega-i,j-\tilde{\alpha}\}} z_h^{i,j-h} && (7.45c) \\ (1 - \mathfrak{m}_j) &= \frac{y_A}{y_j} \,(1 - \langle \mathfrak{m} \rangle) \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{\omega-i,j-\tilde{\alpha}\}} z_h^{i,j-h}. && (7.45d) \end{aligned}$$

Expanding the proportion of couples in terms of new pairs and then those in terms of the marriage rate

$$\mathfrak{m}_j = 1 - \frac{y_A}{y_j}\left(1 - \sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \frac{y_{j'}}{y_A}\mathfrak{m}_{j'}\right)\sum_{i=\alpha}^{\omega}\sum_{h=0}^{\min\{\omega-i,j-\tilde{\alpha}\}} z_h^{i,j-h} \tag{7.46a}$$

$$= 1 - \left(\tilde{\ell}_j^{-1}\lambda^j \sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\left(1 - \mathfrak{m}_{j'}\right)\right)\sum_{i=\alpha}^{\omega}\Lambda^{i,j} z_0^{i,j} \tag{7.46b}$$

$$= 1 - \left(\tilde{\ell}_j^{-1}\lambda^j \sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\left(1 - \mathfrak{m}_{j'}\right)\right)\sum_{i=\alpha-1}^{\omega-1}\Lambda^{i+1,j}\ell_{i+1}\tilde{\ell}_j\lambda^{-(i+j)}\mathcal{U}_{i,j-1}\mathfrak{f}_i\mathfrak{m}_{j-1} \tag{7.46c}$$

Factoring out the terms dependent on j on the RHS (j' is a dummy variable) we have

$$\mathfrak{m}_j = 1 - \left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\left(1 - \mathfrak{m}_{j'}\right)\right)\left(\sum_{i=\alpha-1}^{\omega-1}\Lambda^{i+1,j}\mathcal{U}_{i,j-1}\ell_{i+1}\lambda^{-i}\mathfrak{f}_i\right)\mathfrak{m}_{j-1} \tag{7.47}$$

And similarly for the females

$$\mathfrak{f}_i = 1 - \left(\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\left(1 - \mathfrak{f}_{i'}\right)\right)\left(\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1}\Lambda^{i,j+1}\mathcal{U}_{i-1,j}\tilde{\ell}_{j+1}\lambda^{-j}\mathfrak{m}_j\right)\mathfrak{f}_{i-1} \tag{7.48}$$

Note that the terms in parenthesis on the RHS of 7.47 and 7.48 are constants with respective to age class. In order to simplify the following manipulations I'll define the following two constants

$$\tilde{K}_j \equiv \left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\left(1 - \mathfrak{m}_{j'}\right)\right)\left(\sum_{i=\alpha-1}^{\omega-1}\Lambda^{i+1,j}\mathcal{U}_{i,j-1}\ell_{i+1}\lambda^{-i}\mathfrak{f}_i\right) \tag{7.49a}$$

$$K_i \equiv \left(\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\left(1 - \mathfrak{f}_{i'}\right)\right)\left(\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1}\Lambda^{i,j+1}\mathcal{U}_{i-1,j}\tilde{\ell}_{j+1}\lambda^{-j}\mathfrak{m}_j\right) \tag{7.49b}$$

The individual terms of Equation 7.47 can be written as a function of these constants

$$\mathfrak{m}_j = 1 - \tilde{K}_j \mathfrak{m}_{j-1} \tag{7.50a}$$

$$\mathfrak{m}_{\tilde{\alpha}} = 1 - \tilde{K}_{\tilde{\alpha}} \tag{7.50b}$$

$$\mathfrak{m}_{\tilde{\alpha}+1} = 1 - \tilde{K}_{\tilde{\alpha}+1} + \tilde{K}_{\tilde{\alpha}+1}\tilde{K}_{\tilde{\alpha}} \tag{7.50c}$$

$$\mathfrak{m}_{\tilde{\alpha}+2} = 1 - \tilde{K}_{\tilde{\alpha}+2} + \tilde{K}_{\tilde{\alpha}+2}\tilde{K}_{\tilde{\alpha}+1} - \tilde{K}_{\tilde{\alpha}+2}\tilde{K}_{\tilde{\alpha}+1}\tilde{K}_{\tilde{\alpha}} \tag{7.50d}$$

$$\vdots$$

$$\mathfrak{m}_j = 1 - \sum_{n=\tilde{\alpha}}^{j} (-1)^{n-\tilde{\alpha}} \prod_{m=\tilde{\alpha}}^{n} \tilde{K}_{j+\tilde{\alpha}-m} \tag{7.50e}$$

$$\mathfrak{m}_j = 1 - \sum_{n=0}^{j-\tilde{\alpha}} (-1)^{n} \prod_{m=0}^{n} \tilde{K}_{j-m} \tag{7.50f}$$

And simarlarly for the individual terms of Equation 7.48

$$\mathfrak{f}_i = 1 - K_i \mathfrak{f}_{i-1} \tag{7.51a}$$

$$\mathfrak{f}_{\alpha} = 1 - K_{\alpha} \tag{7.51b}$$

$$\mathfrak{f}_{\alpha+1} = 1 - K_{\alpha+1} + K_{\alpha+1}K_{\alpha} \tag{7.51c}$$

$$\mathfrak{f}_{\alpha+2} = 1 - K_{\alpha+2} + K_{\alpha+2}K_{\alpha+1} - K_{\alpha+2}K_{\alpha+1}K_{\alpha} \tag{7.51d}$$

$$\vdots$$

$$\mathfrak{f}_i = 1 - \sum_{n=\alpha}^{i} (-1)^{n-\alpha} \prod_{m=\alpha}^{n} K_{i+\alpha-m} \tag{7.51e}$$

$$\mathfrak{f}_i = 1 - \sum_{n=0}^{i-\alpha} (-1)^{n} \prod_{m=0}^{n} K_{i-m} \tag{7.51f}$$

Note that

$$K_i = (1 - \mathfrak{f}_i) / \mathfrak{f}_{i-1} \tag{7.52a}$$

$$\text{and} \quad \tilde{K}_j = (1 - \mathfrak{m}_j) / \mathfrak{m}_{j-1} \tag{7.52b}$$

that is K_i and $\tilde{K}_j$ are the ratio of fraction mated in a given age class to the fraction single in the prior age class for females or males.

Sex ratios

The final elements needed for a complete solution to our system comes from the sex ratios. Manipulations of Equations 5.20, 6.3, 6.4, 6.6c and 6.8 yield the following

$$\underline{\mathcal{S}}_{\alpha,\tilde{\alpha}} = \frac{\underline{M}_{\tilde{\alpha}}}{\underline{F}_{\alpha}} = \frac{\frac{\underline{M}_{\tilde{\alpha}}}{\underline{C}_{\bullet}^{\bullet\tilde{\alpha}}}\frac{\underline{C}_{\bullet}^{\bullet\tilde{\alpha}}}{\underline{C}}}{\frac{\underline{F}_{\alpha}}{\underline{C}_{\bullet}^{\alpha\bullet}}\frac{\underline{C}_{\bullet}^{\alpha\bullet}}{\underline{C}}} = \frac{\frac{\underline{M}_{\tilde{\alpha}}}{\underline{M}_{\tilde{\alpha}}-\underline{M}_{\tilde{\alpha}}^{s}}\frac{\underline{C}_{\bullet}^{\bullet\tilde{\alpha}}}{\underline{C}}}{\frac{\underline{F}_{\alpha}}{\underline{F}_{\alpha}-\underline{F}_{\alpha}^{s}}\frac{\underline{C}_{\bullet}^{\alpha\bullet}}{\underline{C}}} \tag{7.53a}$$

$$= \frac{\frac{1}{1-\mathfrak{m}_{\tilde{\alpha}}} z_{\bullet}^{\bullet\tilde{\alpha}}}{\frac{1}{1-\mathfrak{f}_{\alpha}} z_{\bullet}^{\alpha\bullet}} = \frac{(1-\mathfrak{f}_{\alpha})\, z_{\bullet}^{\bullet\tilde{\alpha}}}{(1-\mathfrak{m}_{\tilde{\alpha}})\, z_{\bullet}^{\alpha\bullet}} \tag{7.53b}$$

$$= \frac{(1-\mathfrak{f}_{\alpha}) \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-\tilde{\alpha}\}} z_h^{i\tilde{\alpha}}}{(1-\mathfrak{m}_{\tilde{\alpha}}) \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-\alpha,\tilde{\omega}-j\}} z_h^{\alpha j}} \tag{7.53c}$$

$$= \frac{(1-\mathfrak{f}_{\alpha}) \sum_{i=\alpha}^{\omega} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-\tilde{\alpha}\}} \mathcal{L}_h^{i,\tilde{\alpha}}\, \lambda^{-h} z_0^{i,\tilde{\alpha}}}{(1-\mathfrak{m}_{\tilde{\alpha}}) \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-\alpha,\tilde{\omega}-j\}} \mathcal{L}_h^{\alpha,j}\, \lambda^{-h} z_0^{\alpha j}} \tag{7.53d}$$

$$= \frac{(1-\mathfrak{f}_{\alpha}) \sum_{i=\alpha}^{\omega} \Lambda^{i,\tilde{\alpha}} z_0^{i,\tilde{\alpha}}}{(1-\mathfrak{m}_{\tilde{\alpha}}) \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \Lambda^{\alpha,j} z_0^{\alpha j}} \tag{7.53e}$$

$$= \frac{(1-\mathfrak{f}_{\alpha}) \sum_{i=\alpha-1}^{\omega-1} \Lambda^{i+1,\tilde{\alpha}} \ell_{i+1} \tilde{\ell}_{\tilde{\alpha}} \lambda^{-(i+\tilde{\alpha})} \mathcal{U}_{i,\tilde{\alpha}-1} \mathfrak{f}_i}{(1-\mathfrak{m}_{\tilde{\alpha}}) \sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} \Lambda^{\alpha,j+1} \ell_{\alpha} \tilde{\ell}_{j+1} \lambda^{-(\alpha+j)} \mathcal{U}_{\alpha-1,j} \mathfrak{m}_j} \tag{7.53f}$$

But from Equations 5.20, 6.13, 4.20 and 7.43

$$\underline{\mathcal{S}}_{\alpha,\tilde{\alpha}} = \frac{\tilde{\ell}_{\tilde{\alpha}} \lambda^{-\tilde{\alpha}}}{\ell_{\alpha} \lambda^{-\alpha}} \underline{\mathcal{S}}_{0,0} = \frac{\tilde{\ell}_{\tilde{\alpha}} \lambda^{-\tilde{\alpha}} \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \tilde{f}_h^{i,j} \mathcal{L}_h^{i,j}\, \lambda^{-h} z_0^{i,j}}{\ell_{\alpha} \lambda^{-\alpha} \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} f_h^{i,j} \mathcal{L}_h^{i,j}\, \lambda^{-h} z_0^{i,j}} \tag{7.54a}$$

$$= \frac{\tilde{\ell}_{\tilde{\alpha}} \lambda^{-\tilde{\alpha}} \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} \tilde{f}_h^{i,j} \mathcal{L}_h^{i,j} \mathcal{U}_{i-1,j-1} \ell_i \tilde{\ell}_j \lambda^{-(i+j+h)} \mathfrak{f}_{i-1} \mathfrak{m}_{j-1}}{\ell_{\alpha} \lambda^{-\alpha} \sum_{i=\alpha}^{\omega} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}} f_h^{i,j} \mathcal{L}_h^{i,j} \mathcal{U}_{i-1,j-1} \ell_i \tilde{\ell}_j \lambda^{-(i+j+h)} \mathfrak{f}_{i-1} \mathfrak{m}_{j-1}} \tag{7.54b}$$

Hence equating the two RHS's of 7.53f and 7.54b

$$\frac{(1-\mathfrak{f}_\alpha)\sum_{i=\alpha-1}^{\omega-1}\Lambda^{i+1,\tilde{\alpha}}\ell_{i+1}\tilde{\ell}_{\tilde{\alpha}}\lambda^{-(i+\tilde{\alpha})}\mathcal{U}_{i,\tilde{\alpha}-1}\mathfrak{f}_i}{(1-\mathfrak{m}_{\tilde{\alpha}})\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1}\Lambda^{\alpha,j+1}\ell_\alpha\tilde{\ell}_{j+1}\lambda^{-(\alpha+j)}\mathcal{U}_{\alpha-1,j}\mathfrak{m}_j}$$

$$=\frac{\tilde{\ell}_{\tilde{\alpha}}\lambda^{-\tilde{\alpha}}\sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}}f_h^{i,j}\mathcal{L}_h^{i,j}\mathcal{U}_{i-1,j-1}\ell_i\tilde{\ell}_j\lambda^{-(i+j+h)}\mathfrak{f}_{i-1}\mathfrak{m}_{j-1}}{\ell_\alpha\lambda^{-\alpha}\sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}}f_h^{i,j}\mathcal{L}_h^{i,j}\mathcal{U}_{i-1,j-1}\ell_i\tilde{\ell}_j\lambda^{-(i+j+h)}\mathfrak{f}_{i-1}\mathfrak{m}_{j-1}} \tag{7.55}$$

But from 6.21, 6.22, and 7.43 we have

$$1=\left(\sum_{i'=\alpha}^{\omega}\ell_{i'}\lambda^{-i'}\left(1-\mathfrak{f}_{i'}\right)\right)\sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}}f_h^{i,j}\mathcal{L}_h^{i,j}\mathcal{U}_{i-1,j-1}\ell_i\tilde{\ell}_j\lambda^{-(i+j+h)}\mathfrak{f}_{i-1}\mathfrak{m}_{j-1} \tag{7.56}$$

$$1=\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\tilde{\ell}_{j'}\lambda^{-j'}\left(1-\mathfrak{m}_{j'}\right)\right)\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{i=\alpha}^{\omega}\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}}\tilde{f}_h^{i,j}\mathcal{L}_h^{i,j}\mathcal{U}_{i-1,j-1}\ell_i\tilde{\ell}_j\lambda^{-(i+j+h)}\mathfrak{f}_{i-1}\mathfrak{m}_{j-1} \tag{7.57}$$

So the RHS of 7.55 is

$$\frac{\tilde{\ell}_{\tilde{\alpha}}\lambda^{-\tilde{\alpha}}\left(\sum_{i'=\alpha}^{\omega}\ell_{i'}\lambda^{-i'}\left(1-\mathfrak{f}_{i'}\right)\right)}{\ell_\alpha\lambda^{-\alpha}\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\tilde{\ell}_{j'}\lambda^{-j'}\left(1-\mathfrak{m}_{j'}\right)\right)} \tag{7.58}$$

Then

$$\frac{(1-\mathfrak{f}_\alpha)\sum_{i=\alpha-1}^{\omega-1}\Lambda^{i+1,\tilde{\alpha}}\ell_{i+1}\lambda^{-(i+\tilde{\alpha})}\mathcal{U}_{i,\tilde{\alpha}-1}\mathfrak{f}_i}{(1-\mathfrak{m}_{\tilde{\alpha}})\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1}\Lambda^{\alpha,j+1}\tilde{\ell}_{j+1}\lambda^{-(\alpha+j)}\mathcal{U}_{\alpha-1,j}\mathfrak{m}_j}=\frac{\tilde{\ell}_{\tilde{\alpha}}\lambda^{-\tilde{\alpha}}\left(\sum_{i'=\alpha}^{\omega}\ell_{i'}\lambda^{-i'}\left(1-\mathfrak{f}_{i'}\right)\right)}{\ell_\alpha\lambda^{-\alpha}\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\tilde{\ell}_{j'}\lambda^{-j'}\left(1-\mathfrak{m}_{j'}\right)\right)} \tag{7.59}$$

or the fraction females mated in the first reproductive age class is directly proportional to the fraction males mated in the first reproductive age class

$$(1-\mathfrak{f}_\alpha)=\frac{\tilde{\ell}_{\tilde{\alpha}}\lambda^{-\tilde{\alpha}}\left(\sum_{i'=\alpha}^{\omega}\ell_{i'}\lambda^{-i'}\left(1-\mathfrak{f}_{i'}\right)\right)\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1}\Lambda^{\alpha,j+1}\tilde{\ell}_{j+1}\lambda^{-(j+\alpha)}\mathcal{U}_{\alpha-1,j}\mathfrak{m}_j}{\ell_\alpha\lambda^{-\alpha}\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\tilde{\ell}_{j'}\lambda^{-j'}\left(1-\mathfrak{m}_{j'}\right)\right)\sum_{i=\alpha-1}^{\omega-1}\Lambda^{i+1,\tilde{\alpha}}\ell_{i+1}\lambda^{-(i+\tilde{\alpha})}\mathcal{U}_{i,\tilde{\alpha}-1}\mathfrak{f}_i}(1-\mathfrak{m}_{\tilde{\alpha}}) \tag{7.60}$$

Chapter 8

Solutions with age-invariant parameters

In the following section I will develop the relationships between the fraction of individuals that are single in the first reproductive age class and all the other age classes for each sex when the life history parameters are assumed constant for all age classes and reproductive parameters are constant for all reproductive adult age classes. I will also flesh out a relationship between the fraction single males and the fraction single females in the first reproductive age classes. In part 2 I will derive another relationship between fraction singles male and female in the first reproductive age classes. Then in part 3 I will put these together so that we will have the fraction singles in all age classes for both sexes. Finally in Part 4. I will determine the growth rate (λ) of the population, completing all the elements needed for a complete solution of our system. The point of all this is to examine, in a sense, the "average" behavior of the model so that we can have at least some frame of reference for when things get more complicated.

8.1 Part 1. Relating singles of all age classes to the first reproductive age class.

Assume the single season survival probabilities are the same with regards to age, that is $p_i = p$, and $\tilde{p}_j = \tilde{p}$. And also suppose that the probability that a marriage will survive (given that neither partner dies) from any season to the next is independent of the ages of the individuals and the length of time that they have been mated (i.e. $\pi_h^{i,j} = \pi$). Then $\ell_i = p^i$, $\tilde{\ell}_j = \tilde{p}^j$, $\mathcal{L}_h^{i,j} = (p\tilde{p}\pi)^h$. Summarizing

$$
\begin{aligned}
p_i &= p, \;\; \tilde{p}_j = \tilde{p}, \;\; \text{and } \pi_h^{i,j} = \pi && \text{(8.1a)}\\
\ell_i &= p^i, \; \tilde{\ell}_j = \tilde{p}^j, \;\; \text{and } \mathcal{L}_h^{i,j} = (p\tilde{p}\pi)^h && \text{(8.1b)}\\
\Lambda^{i,j} &= \left(1 - \frac{p\tilde{p}\pi}{\lambda}\right)^{-1}\left(1 - \left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\min\{\omega-i,\tilde{\omega}-j\}}\right) && \text{(8.1c)}
\end{aligned}
$$

The age class variables become

$$
\begin{aligned}
x_i &= \frac{(p/\lambda)^i}{\sum_{k=0}^{\infty}(p/\lambda)^k} = \left(\frac{p}{\lambda}\right)^i\left(1 - \frac{p}{\lambda}\right) && \text{(8.2a)}\\
y_j &= \frac{(\tilde{p}/\lambda)^j}{\sum_{k=0}^{\infty}(\tilde{p}/\lambda)^k} = \left(\frac{\tilde{p}}{\lambda}\right)^j\left(1 - \frac{\tilde{p}}{\lambda}\right) && \text{(8.2b)}
\end{aligned}
$$

$$
\begin{aligned}
x_A &= \frac{\sum_{i=\alpha}^{\infty}(p/\lambda)^i}{\sum_{k=0}^{\infty}(p/\lambda)^k} = \left(\frac{p}{\lambda}\right)^{\alpha} && \text{(8.3a)}\\
y_A &= \frac{\sum_{j=\tilde{\alpha}}^{\infty}(\tilde{p}/\lambda)^j}{\sum_{k=0}^{\infty}(\tilde{p}/\lambda)^k} = \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} && \text{(8.3b)}
\end{aligned}
$$

For the fraction of adult males and females that are single

$$
\begin{aligned}
\frac{\underline{F}^s}{\underline{F}_A} &= \langle \mathfrak{f} \rangle = \sum_{i=\alpha}^{\omega} \frac{x_i}{x_A}\mathfrak{f}_i \\
&= \left(\sum_{i=\alpha}^{\omega} \ell_i \lambda^{-i}\right)^{-1} \sum_{i=\alpha}^{\omega} \ell_i \lambda^{-i}\mathfrak{f}_i \\
&= \left(\frac{1 - \frac{p}{\lambda}}{1 - \left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}}\right) \sum_{i=\alpha}^{\omega} \left(\frac{p}{\lambda}\right)^{i-\alpha} \mathfrak{f}_i && \text{(8.4)}
\end{aligned}
$$

$$
\begin{aligned}
\frac{\underline{M}^s}{\underline{M}_A} &= \langle \mathfrak{m} \rangle = \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \frac{y_j}{y_A}\mathfrak{m}_j \\
&= \left(\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_j \lambda^{-j}\right)^{-1} \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_j \lambda^{-j}\mathfrak{m}_j \\
&= \left(\frac{1 - \frac{\tilde{p}}{\lambda}}{1 - \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}}\right) \sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \left(\frac{\tilde{p}}{\lambda}\right)^{j-\tilde{\alpha}} \mathfrak{m}_j && \text{(8.5)}
\end{aligned}
$$

I will also assume there is no age distinction for search rates, fraction of time devoted to reproductive activity, courtship time, or courtship preferences. So $\tilde{u}_{i,j} = \tilde{u}$ and $u_{i,j} = u$ (courtships per single male or female respectively per unit time are the same for all ages). Also $\tilde{\nu}_{i,j} = \tilde{\nu}$, and $\nu_{i,j} = \nu$ (time that males and females respectively spend in reproductive activity per time searched is the same for all ages). And I will also assume that the fraction of marriages between females and males that occur due to male searching is the same regardless of age $\eta_{i,j} = \eta$. Finally the fraction of courtships that result in marriage is independent of age so that from 7.36 and 7.42

$$\mathcal{U}_{i,j} = \underline{\mathcal{T}}_{i,j} U_{i,j}$$

$$\begin{aligned} U_{i,j} \quad = \quad & \frac{\tilde{u}_{i,j}\tilde{v}_{i,j}}{\left(\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}_{i',j}\ell_{i'}\lambda^{-i'}\mathfrak{f}_{i'}\right)\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\left(1-\mathfrak{m}_{j'}\right)\right)} \\ & + \frac{u_{i,j}v_{i,j}}{\left(\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v_{i,j'}\tilde{\ell}_{j'}\lambda^{-j'}\mathfrak{m}_{j'}\right)\left(\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\left(1-\mathfrak{f}_{i'}\right)\right)} \end{aligned}$$

$$\underline{\mathcal{T}}_{i,j} = \min\left\{\begin{array}{c} 1, \\ \left[\left(\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} U_{i,j'}\tilde{\ell}_{j'}\lambda^{-j'}\mathfrak{m}_{j'}\right)\left(\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\left(1-\mathfrak{f}_{i'}\right)\right)\right]^{-1}, \\ \left[\left(\sum_{j'=\alpha-1}^{\omega-1} U_{i',j}\ell_{i'}\lambda^{-i'}\mathfrak{f}_{i'}\right)\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\left(1-\mathfrak{m}_{j'}\right)\right)\right]^{-1} \end{array}\right\}$$

$$\mathcal{U} = \underline{\mathcal{T}} U \tag{8.6}$$

$$\begin{aligned} U \quad = \quad & \frac{\tilde{u}\tilde{v}}{\left(\sum_{i'=\alpha-1}^{\omega-1} \tilde{v}\left(\frac{p}{\lambda}\right)^{i'}\mathfrak{f}_{i'}\right)\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \left(\frac{\tilde{p}}{\lambda}\right)^{j'}\left(1-\mathfrak{m}_{j'}\right)\right)} \\ & + \frac{uv}{\left(\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1} v\left(\frac{\tilde{p}}{\lambda}\right)^{j'}\mathfrak{m}_{j'}\right)\left(\sum_{i'=\alpha}^{\omega} \left(\frac{p}{\lambda}\right)^{i'}\left(1-\mathfrak{f}_{i'}\right)\right)} \end{aligned} \tag{8.7a}$$

canceling the v's and $\tilde{v}$'s

$$U = \frac{\tilde{u}}{\left(\sum_{i'=\alpha-1}^{\omega-1}\left(\frac{p}{\lambda}\right)^{i'}\mathfrak{f}_{i'}\right)\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\left(\frac{\tilde{p}}{\lambda}\right)^{j'}(1-\mathfrak{m}_{j'})\right)} + \frac{u}{\left(\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}\left(\frac{\tilde{p}}{\lambda}\right)^{j'}\mathfrak{m}_{j'}\right)\left(\sum_{i'=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^{i'}(1-\mathfrak{f}_{i'})\right)} \tag{8.7b}$$

$$\underline{\tau} = \min\left\{\begin{array}{c} 1, \\ \left[U\left(\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}\left(\frac{\tilde{p}}{\lambda}\right)^{j'}\mathfrak{m}_{j'}\right)\left(\sum_{i'=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^{i'}(1-\mathfrak{f}_{i'})\right)\right]^{-1}, \\ \left[U\left(\sum_{j'=\alpha-1}^{\omega-1}\left(\frac{p}{\lambda}\right)^{i'}\mathfrak{f}_{i'}\right)\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\left(\frac{\tilde{p}}{\lambda}\right)^{j'}(1-\mathfrak{m}_{j'})\right)\right]^{-1} \end{array}\right\} \tag{8.8}$$

Substituting for τ and canceling terms

$$\mathcal{U} = \min\left\{\begin{array}{c} U, \\ \left[\left(\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}\left(\frac{\tilde{p}}{\lambda}\right)^{j'}\mathfrak{m}_{j'}\right)\left(\sum_{i'=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^{i'}(1-\mathfrak{f}_{i'})\right)\right]^{-1}, \\ \left[\left(\sum_{j'=\alpha-1}^{\omega-1}\left(\frac{p}{\lambda}\right)^{i'}\mathfrak{f}_{i'}\right)\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\left(\frac{\tilde{p}}{\lambda}\right)^{j'}(1-\mathfrak{m}_{j'})\right)\right]^{-1} \end{array}\right\} \tag{8.9}$$

8.1.1 The expected number of couples mated for all lengths of time per new couple with age invariant parameters.

In order to simplify things considerably I will make the following approximation for Equation 8.1c. Noting that

$$1 \le \Lambda^{i,j} \le \left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\min\{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}\}}\right) < \left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1} \tag{8.10}$$

Then for $\lambda > p\tilde{p}\pi$ there exists an ξ such that

$$\Lambda^{i,j} \approx \Lambda = \left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1} \tag{8.11}$$

where $0 \le \xi \le \min\{\omega-\alpha, \tilde{\omega}-\tilde{\alpha}\}$

This is essentially saying that newl couples comprise a constant fraction of all couples mated at the same ages. It is a rather rough approximation but a very useful one.

8.1.2 Ratios of fraction mated to fraction single one age step younger

Making the appropriate substitutions for age invariant parameters the definition 7.49a becomes

$$\tilde{K}_j \equiv \left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \tilde{\ell}_{j'}\lambda^{-j'}\left(1-\mathfrak{m}_{j'}\right)\right)\left(\sum_{i=\alpha-1}^{\omega-1} \Lambda^{i+1,j}\mathcal{U}_{i,j-1}\ell_{i+1}\lambda^{-i}\mathfrak{f}_i\right) \tag{8.12a}$$

$$= \lambda\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \left(\frac{\tilde{p}}{\lambda}\right)^{j'}\left(1-\mathfrak{m}_{j'}\right)\right)\left(\sum_{i=\alpha-1}^{\omega-1} \Lambda^{i+1,j}\mathcal{U}_{i,j-1}\left(\frac{p}{\lambda}\right)^{i+1}\mathfrak{f}_i\right) \tag{8.12b}$$

$$= \mathcal{U}p\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \left(\frac{\tilde{p}}{\lambda}\right)^{j'}\left(1-\mathfrak{m}_{j'}\right)\right)\left(\sum_{i=\alpha-1}^{\omega-1} \Lambda^{i+1,j}\left(\frac{p}{\lambda}\right)^{i}\mathfrak{f}_i\right) \tag{8.12c}$$

$$= \mathcal{U}p\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}} \left(\frac{\tilde{p}}{\lambda}\right)^{j'}\left(1-\mathfrak{m}_{j'}\right)\right)\left(\sum_{i=\alpha-1}^{\omega-1} \left(\frac{p}{\lambda}\right)^{i}\mathfrak{f}_i\right) \tag{8.12d}$$

And after substitution of age invariant parameters definition 7.49b similarly becomes

$$K_i \equiv \left(\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\left(1-\mathfrak{f}_{i'}\right)\right)\left(\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} \Lambda^{i,j+1}\mathcal{U}_{i-1,j}\tilde{\ell}_j\lambda^{-j}\mathfrak{m}_j\right)\frac{\ell_{i-1}\lambda}{\ell_i} \tag{8.13a}$$

$$= \lambda\left(\sum_{i'=\alpha}^{\omega} \left(\frac{p}{\lambda}\right)^{i'}\left(1-\mathfrak{f}_{i'}\right)\right)\left(\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} \Lambda^{i,j+1}\mathcal{U}_{i-1,j}\left(\frac{\tilde{p}}{\lambda}\right)^{j+1}\mathfrak{m}_j\right) \tag{8.13b}$$

$$= \mathcal{U}\tilde{p}\left(1+\frac{p\tilde{p}\pi}{\lambda}\right)\left(\sum_{i'=\alpha}^{\omega} \left(\frac{p}{\lambda}\right)^{i'}\left(1-\mathfrak{f}_{i'}\right)\right)\left(\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} \Lambda^{i,j+1}\left(\frac{\tilde{p}}{\lambda}\right)^{j}\mathfrak{m}_j\right) \tag{8.13c}$$

$$= \mathcal{U}\tilde{p}\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)\left(\sum_{i'=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^{i'}(1-\mathfrak{f}_{i'})\right)\left(\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1}\left(\frac{\tilde{p}}{\lambda}\right)^{j}\mathfrak{m}_j\right) \tag{8.13d}$$

But then K_i and $\tilde{K}_j$ is the same for all values of i and j for which 8.12d and 8.13d are valid. So $K_i = K$ for $\alpha \leq i \leq \omega$ and $\tilde{K}_j = \tilde{K}$ for $\tilde{\alpha} \leq j \leq \tilde{\omega}$.

8.1.3 Fractions single

$$\begin{aligned}
\mathfrak{m}_j &= 1-\sum_{n=\tilde{\alpha}}^{j}(-1)^{n-\tilde{\alpha}}\prod_{m=\tilde{\alpha}}^{n}\tilde{K} \\
&= \sum_{n=\tilde{\alpha}}^{j+1}\left(-\tilde{K}\right)^{n-\tilde{\alpha}} = \sum_{n=0}^{j-\tilde{\alpha}+1}\left(-\tilde{K}\right)^{n} \\
&= \frac{1-\left(-\tilde{K}\right)^{j-\tilde{\alpha}+2}}{1+\tilde{K}}
\end{aligned} \tag{8.14}$$

$$\begin{aligned}
\mathfrak{f}_i &= 1-\sum_{n=\alpha}^{i}(-1)^{n-\alpha}\prod_{m=\alpha}^{n}K \\
&= \sum_{n=\alpha}^{i+1}(-K)^{n-\alpha} = \sum_{n=0}^{i-\alpha+1}(-K)^{n} \\
&= \frac{1-(-K)^{i-\alpha+2}}{1+K}
\end{aligned} \tag{8.15}$$

But

$$\mathfrak{m}_{\tilde{\alpha}} = 1-\tilde{K} \Longrightarrow \tilde{K} = 1-\mathfrak{m}_{\tilde{\alpha}} \tag{8.16a}$$

$$\mathfrak{f}_{\alpha} = 1-K \Longrightarrow K = 1-\mathfrak{f}_{\alpha} \tag{8.16b}$$

Substituting in 8.14 and 8.15

$$\mathfrak{m}_j = \frac{1-\left(-\tilde{K}\right)^{j-\tilde{\alpha}+2}}{1+\tilde{K}} = \frac{1-\left(\mathfrak{m}_{\tilde{\alpha}}-1\right)^{j-\tilde{\alpha}+2}}{2-\mathfrak{m}_{\tilde{\alpha}}} \tag{8.17a}$$

$$\mathfrak{f}_i = \frac{1-\left(-K\right)^{i-\alpha+2}}{1+K} = \frac{1-\left(\mathfrak{f}_{\alpha}-1\right)^{i-\alpha+2}}{2-\mathfrak{f}_{\alpha}} \tag{8.17b}$$

Recall that K_i and $\tilde{K}_j$ are the ratios of fraction mated in a given age class to the fraction single in the prior age class for females or males respectively. Or in other words the fraction mated in a given age class is proportional to the fraction single in the prior age class for females or males respectively $1-\mathfrak{f}_i = \mathfrak{f}_{i-1}K$ and $1-\mathfrak{m}_j = \mathfrak{m}_{j-1}\tilde{K}$. This of course makes sense – if there is a larger fraction of singles available to mate at a given age then its not surprising that a larger fraction of the next age class is mated. In this case the ratio of the fraction mated to the fraction single in the prior age class is the same for all age classes. Since the first age classes that are eligible to mate are $\alpha - 1$ and $\tilde{\alpha} - 1$ and all individuals are single in those age classes we have $1-\mathfrak{f}_i = \mathfrak{f}_{i-1}\left(1-\mathfrak{f}_{\alpha}\right)$ and $1-\mathfrak{m}_j = \mathfrak{m}_{j-1}\left(1-\mathfrak{m}_{\tilde{\alpha}}\right)$, This rather simple observation has some remarkable consequences. For example expanding $\mathfrak{f}_i$ in terms of $\mathfrak{f}_{\alpha}$ for the sequence of i's

$$\mathfrak{f}_{\alpha+1} = 1-\mathfrak{f}_{\alpha}+\mathfrak{f}_{\alpha}^2 \tag{8.18a}$$

$$\mathfrak{f}_{\alpha+2} = 0+2\mathfrak{f}_{\alpha}-2\mathfrak{f}_{\alpha}^2+\mathfrak{f}_{\alpha}^3 \tag{8.18b}$$

$$\mathfrak{f}_{\alpha+3} = 1-2\mathfrak{f}_{\alpha}+4\mathfrak{f}_{\alpha}^2-3\mathfrak{f}_{\alpha}^3+\mathfrak{f}_{\alpha}^4 \tag{8.18c}$$

$$\mathfrak{f}_{\alpha+4} = 0+3\mathfrak{f}_{\alpha}-6\mathfrak{f}_{\alpha}^2+7\mathfrak{f}_{\alpha}^3-4\mathfrak{f}_{\alpha}^4+\mathfrak{f}_{\alpha}^5 \tag{8.18d}$$

$$\mathfrak{f}_{\alpha+5} = 1-3\mathfrak{f}_{\alpha}+9\mathfrak{f}_{\alpha}^2-13\mathfrak{f}_{\alpha}^3+11\mathfrak{f}_{\alpha}^4-5\mathfrak{f}_{\alpha}^5+\mathfrak{f}_{\alpha}^6 \tag{8.18e}$$

$$\mathfrak{f}_{\alpha+n} = \sum_{m=0}^{n+1}\left(\sum_{k=m}^{n+1}\left(-1\right)^{k+m}\binom{k}{m}\right)\mathfrak{f}_{\alpha}^m \tag{8.18f}$$

Let's look at a plot of these first as a function of $\mathfrak{f}_\alpha$ for a few values of i and then as a function of i for few values of $\mathfrak{f}_\alpha$.

Figure 8.1 shows that for $\mathfrak{f}_\alpha$ ranging from 0 to 1 the values of $\mathfrak{f}_i$ (for $i = \alpha, \alpha + 1, \alpha + 2, \alpha + 7, \alpha + 8, \alpha + 19, \alpha + 20$,and ∞) alternate from high to low, or low to high in successive age classes, and the amplitude of the alternation can be related to the initial fraction remaining single (or fraction marrying). These alternate between greater than $\mathfrak{f}_\infty$ $(= 1/(2 - \mathfrak{f}_\alpha))$ and less than $\mathfrak{f}_\infty$ (but greater than $\mathfrak{f}_\alpha$). For example when $\mathfrak{f}_\alpha = 0.2$ (20% of the females age α are single) then 84% of the females in next age class ($i = \alpha + 1$) are single and 32.8% of the females age $\alpha + 2$ are single, etc. ($\mathfrak{f}_\infty$ =55.55%)

Each line in Figure 8.2 shows the sequence of $\mathfrak{f}_i$'s for particular initial values of $\mathfrak{f}_\alpha$. For example the line with the square symbols start out with $\mathfrak{f}_\alpha = 0.5$ at the y-intercept ($\kappa = 0$), the next value ($\kappa = 1$) is $\mathfrak{f}_{\alpha+1} = 0.75$ and so on progressing with dampning "oscillations" toward it's asmototic value of $\mathfrak{f}_\infty = 2/3$

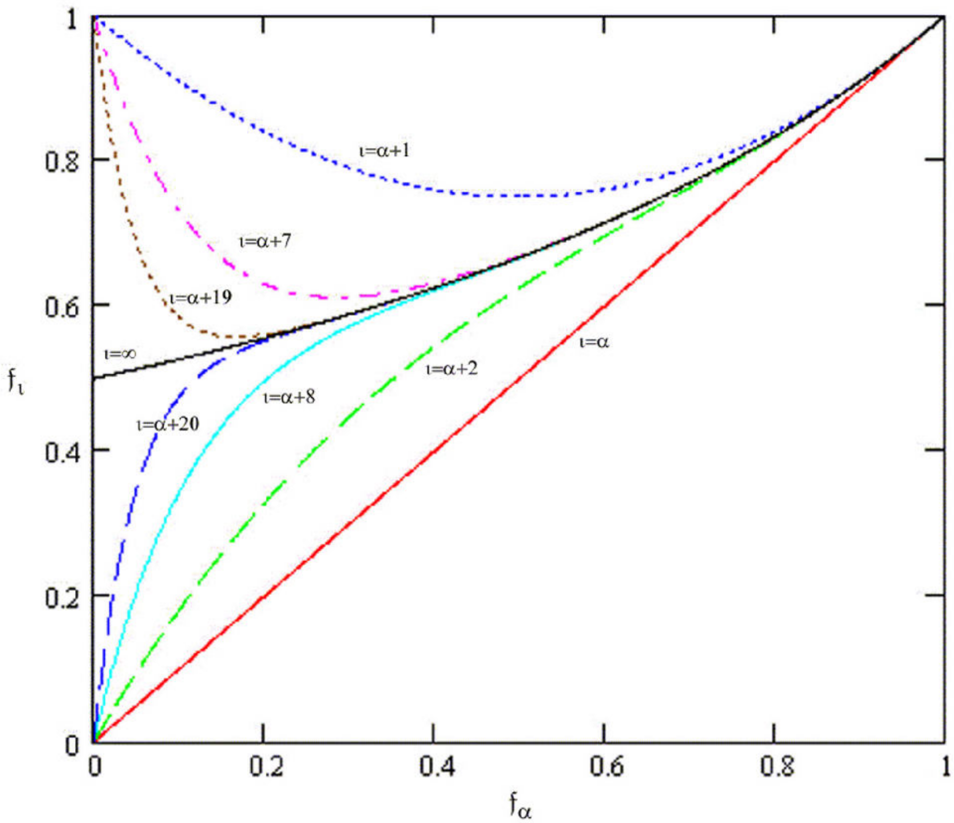

Figure 8.1: $\mathfrak{f}_i$ as a function of $\mathfrak{f}_\alpha$

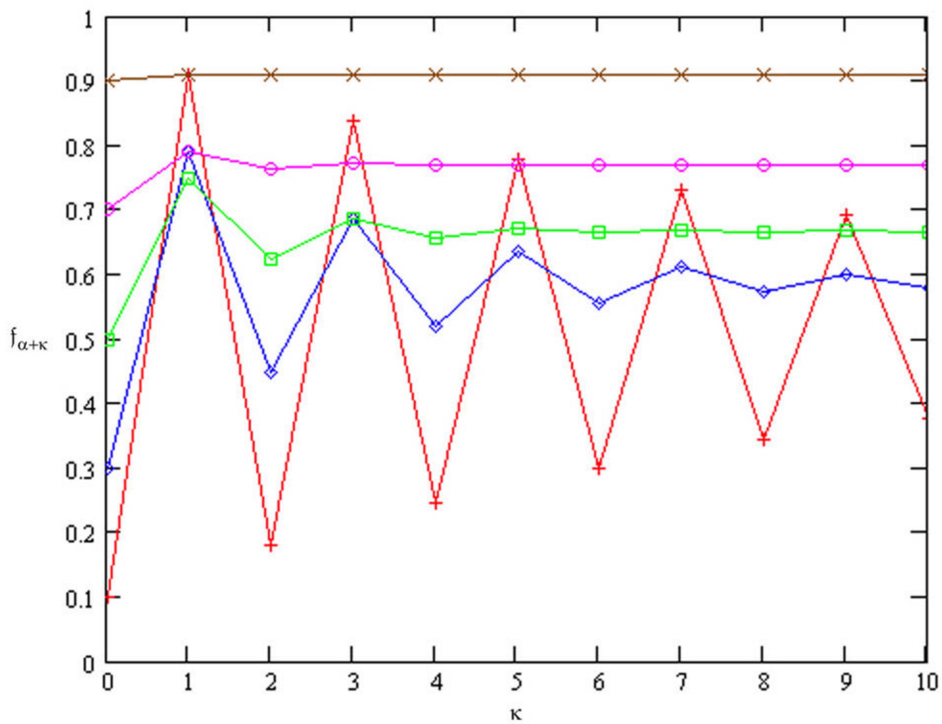

Figure 8.2: $\mathfrak{f}_{\alpha+\kappa}$ as a function of κ

8.1.4 Marriage rate

Rewriting $\mathcal{U}$ in terms of $\mathfrak{m}_{\tilde{\alpha}}$ and $\mathfrak{f}_\alpha$ we start with 8.7b and 8.9

$$
\begin{aligned}
U &= \frac{\tilde{u}}{\left(\sum_{i'=\alpha-1}^{\omega-1}\left(\frac{p}{\lambda}\right)^{i'}\mathfrak{f}_{i'}\right)\left(\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\left(\frac{\tilde{p}}{\lambda}\right)^{j'}(1-\mathfrak{m}_{j'})\right)} \\
&\quad + \frac{u}{\left(\sum_{i'=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^{i'}(1-\mathfrak{f}_{i'})\right)\left(\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}\left(\frac{\tilde{p}}{\lambda}\right)^{j'}\mathfrak{m}_{j'}\right)} \\
\mathcal{U} &= \min\left\{\begin{array}{c} U, \\ \frac{1}{\sum_{i'=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^{i'}(1-\mathfrak{f}_{i'})\sum_{j'=\tilde{\alpha}-1}^{\tilde{\omega}-1}\left(\frac{\tilde{p}}{\lambda}\right)^{j'}\mathfrak{m}_{j'}}, \\ \frac{1}{\sum_{j'=\tilde{\alpha}}^{\tilde{\omega}}\left(\frac{\tilde{p}}{\lambda}\right)^{j'}(1-\mathfrak{m}_{j'})\sum_{j'=\alpha-1}^{\omega-1}\left(\frac{p}{\lambda}\right)^{i'}\mathfrak{f}_{i'}} \end{array}\right\}
\end{aligned}
$$

Substituting and expanding the sums in the denominators above using 8.17a and 8.17b

$$\sum_{i=\alpha-k}^{\omega-k}\left(\frac{p}{\lambda}\right)^i\mathfrak{f}_i = \frac{1}{2-\mathfrak{f}_\alpha}\left(\sum_{i=\alpha-k}^{\omega-k}\left(\frac{p}{\lambda}\right)^i - \frac{1}{(\mathfrak{f}_\alpha-1)^{\alpha-2}}\sum_{i=\alpha-k}^{\omega-k}\left(\frac{p(\mathfrak{f}_\alpha-1)}{\lambda}\right)^i\right) \tag{8.19a}$$

$$= \left(\frac{1}{2-\mathfrak{f}_\alpha}\right)\left(\frac{p}{\lambda}\right)^{\alpha-k}\left(\frac{1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}}{1-\frac{p}{\lambda}} - (\mathfrak{f}_\alpha-1)^{2-k}\frac{1-\left(\frac{p}{\lambda}(\mathfrak{f}_\alpha-1)\right)^{\omega-\alpha+1}}{1-\frac{p}{\lambda}(\mathfrak{f}_\alpha-1)}\right) \tag{8.19b}$$

$$\sum_{i=\alpha-k}^{\omega-k}\left(\frac{p}{\lambda}\right)^i(1-\mathfrak{f}_i) = \sum_{i=\alpha-k}^{\omega-k}\left(\frac{p}{\lambda}\right)^i - \sum_{i=\alpha-k}^{\omega-k}\left(\frac{p}{\lambda}\right)^i\mathfrak{f}_i \tag{8.20a}$$

$$= \sum_{i=\alpha-k}^{\omega-k}\left(\frac{p}{\lambda}\right)^i - \frac{1}{2-\mathfrak{f}_\alpha}\left(\sum_{i=\alpha-k}^{\omega-k}\left(\frac{p}{\lambda}\right)^i - \frac{1}{(\mathfrak{f}_\alpha-1)^{\alpha-2}}\sum_{i=\alpha-k}^{\omega-k}\left(\frac{p(\mathfrak{f}_\alpha-1)}{\lambda}\right)^i\right) \tag{8.20b}$$

$$= \left(\frac{1-\mathfrak{f}_\alpha}{2-\mathfrak{f}_\alpha}\right)\left(\sum_{i=\alpha-k}^{\omega-k}\left(\frac{p}{\lambda}\right)^i - \frac{1}{(\mathfrak{f}_\alpha-1)^{\alpha-1}}\sum_{i=\alpha-k}^{\omega-k}\left(\frac{p(\mathfrak{f}_\alpha-1)}{\lambda}\right)^i\right) \tag{8.20c}$$

$$= \left(\frac{1-\mathfrak{f}_\alpha}{2-\mathfrak{f}_\alpha}\right)\left(\frac{p}{\lambda}\right)^{\alpha-k}\left[\frac{\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)}{\left(1-\frac{p}{\lambda}\right)} - (\mathfrak{f}_\alpha-1)^{1-k}\frac{\left(1-\left[\left(\frac{p}{\lambda}\right)(\mathfrak{f}_\alpha-1)\right]^{\omega-\alpha+1}\right)}{\left(1+\frac{p}{\lambda}(1-\mathfrak{f}_\alpha)\right)}\right] \tag{8.20d}$$

For males

$$\sum_{j=\tilde{\alpha}-k}^{\tilde{\omega}-k} \left(\frac{\tilde{p}}{\lambda}\right)^{j} \mathfrak{m}_j$$

$$= \frac{\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}-k}}{2-\mathfrak{m}_{\tilde{\alpha}}} \left[\frac{\left(1-\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{\tilde{p}}{\lambda}\right)} - \frac{(\mathfrak{m}_{\tilde{\alpha}}-1)^{2-k}\left(1-\left[\left(\frac{\tilde{p}}{\lambda}\right)(\mathfrak{m}_{\tilde{\alpha}}-1)\right]^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1+\frac{\tilde{p}}{\lambda}(1-\mathfrak{m}_{\tilde{\alpha}})\right)} \right] \tag{8.21}$$

and

$$\sum_{j=\tilde{\alpha}-k}^{\tilde{\omega}-k} \left(\frac{\tilde{p}}{\lambda}\right)^{j} (1-\mathfrak{m}_j)$$

$$= \left(\frac{1-\mathfrak{m}_{\tilde{\alpha}}}{2-\mathfrak{m}_{\tilde{\alpha}}}\right)\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}-k} \left[\frac{\left(1-\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{\tilde{p}}{\lambda}\right)} - \frac{(\mathfrak{m}_{\tilde{\alpha}}-1)^{1-k}\left(1-\left[\left(\frac{\tilde{p}}{\lambda}\right)(\mathfrak{m}_{\tilde{\alpha}}-1)\right]^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1+\frac{\tilde{p}}{\lambda}(1-\mathfrak{m}_{\tilde{\alpha}})\right)} \right] \tag{8.22}$$

Define

$$\tilde{G} = \sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} \left(\frac{\tilde{p}}{\lambda}\right)^{j} \mathfrak{m}_j$$

$$= \frac{\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}-1}}{2-\mathfrak{m}_{\tilde{\alpha}}} \left[\frac{\left(1-\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{\tilde{p}}{\lambda}\right)} + \frac{(1-\mathfrak{m}_{\tilde{\alpha}})\left(1-\left[\left(\frac{\tilde{p}}{\lambda}\right)(\mathfrak{m}_{\tilde{\alpha}}-1)\right]^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1+\frac{\tilde{p}}{\lambda}(1-\mathfrak{m}_{\tilde{\alpha}})\right)} \right] \tag{8.23}$$

$$G = \sum_{i=\alpha-1}^{\omega-1} \left(\frac{p}{\lambda}\right)^{i} \mathfrak{f}_i$$

$$= \frac{\left(\frac{p}{\lambda}\right)^{\alpha-1}}{2-\mathfrak{f}_{\alpha}} \left[\frac{\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)}{\left(1-\frac{p}{\lambda}\right)} + \frac{(1-\mathfrak{f}_{\alpha})\left(1-\left[\left(\frac{p}{\lambda}\right)(\mathfrak{f}_{\alpha}-1)\right]^{\omega-\alpha+1}\right)}{\left(1+\frac{p}{\lambda}(1-\mathfrak{f}_{\alpha})\right)} \right] \tag{8.24}$$

Note that

$$\begin{aligned}
\sum_{j=\tilde{\alpha}}^{\tilde{\omega}} \left(\frac{\tilde{p}}{\lambda}\right)^{j} (1-\mathfrak{m}_j) &= (1-\mathfrak{m}_{\tilde{\alpha}})\left(\frac{\tilde{p}}{\lambda}\right) \sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1} \left(\frac{\tilde{p}}{\lambda}\right)^{j} \mathfrak{m}_j \\
&= (1-\mathfrak{m}_{\tilde{\alpha}})\left(\frac{\tilde{p}}{\lambda}\right) \tilde{G}
\end{aligned} \tag{8.25}$$

and

$$\sum_{i=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^{i}(1-\mathfrak{f}_i) = (1-\mathfrak{f}_\alpha)\left(\frac{p}{\lambda}\right)\sum_{i=\alpha-1}^{\omega-1}\left(\frac{p}{\lambda}\right)^{i}\mathfrak{f}_i$$
$$= (1-\mathfrak{f}_\alpha)\left(\frac{p}{\lambda}\right)G \tag{8.26}$$

Then

$$U = \frac{\tilde{u}}{(1-\mathfrak{m}_{\tilde{\alpha}})\left(\frac{\tilde{p}}{\lambda}\right)\tilde{G}G} + \frac{u}{(1-\mathfrak{f}_\alpha)\left(\frac{p}{\lambda}\right)G\tilde{G}} \tag{8.27a}$$

$$\mathcal{U} = \min\left\{U, \frac{1}{(1-\mathfrak{f}_\alpha)\left(\frac{p}{\lambda}\right)G\tilde{G}}, \frac{1}{(1-\mathfrak{m}_{\tilde{\alpha}})\left(\frac{\tilde{p}}{\lambda}\right)\tilde{G}G}\right\} \tag{8.27b}$$

Now substituting 8.24 and 8.25 into 8.12d; and 8.23 and 8.26 into 8.13d yields

$$\tilde{K} = \mathcal{U}\tilde{G}G\left(\frac{\tilde{p}p}{\lambda}\right)\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)(1-\mathfrak{m}_{\tilde{\alpha}}) \tag{8.28a}$$

$$K = \mathcal{U}\tilde{G}G\left(\frac{\tilde{p}p}{\lambda}\right)\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)(1-\mathfrak{f}_\alpha) \tag{8.28b}$$

But these and 8.16a and 8.16b imply that

$$\mathcal{U}\tilde{G}G\left(\frac{\tilde{p}p}{\lambda}\right)\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right) = 1 \tag{8.29}$$

or

$$\mathcal{U} = \frac{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}{\tilde{G}G\left(\frac{\tilde{p}p}{\lambda}\right)\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)} \tag{8.30}$$

8.1.5 Fraction new couples relative to couples mated for all lengths of time

And then this with 8.27 yields

$$\frac{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}{\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)} = \min\left\{\frac{\tilde{u}p}{(1-\mathfrak{m}_{\tilde{\alpha}})} + \frac{u\tilde{p}}{(1-\mathfrak{f}_{\alpha})}, \frac{\tilde{p}}{(1-\mathfrak{f}_{\alpha})}, \frac{p}{(1-\mathfrak{m}_{\tilde{\alpha}})}\right\} \tag{8.31}$$

Solving for $\mathfrak{m}_{\tilde{\alpha}}$ the first term of the minimum function yields:

$$\mathfrak{m}_{\tilde{\alpha}} = 1 - \frac{\tilde{u}p\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)(1-\mathfrak{f}_{\alpha})}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)(1-\mathfrak{f}_{\alpha}) - u\tilde{p}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)} \tag{8.32}$$

The second term (single females limiting) yields $\mathfrak{f}_{\alpha}$:

$$\mathfrak{f}_{\alpha} = 1 - \frac{\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}\tilde{p} \tag{8.33}$$

And the third term (single males limiting) yields $\mathfrak{m}_{\tilde{\alpha}}$:

$$\mathfrak{m}_{\tilde{\alpha}} = 1 - \frac{\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}p \tag{8.34}$$

8.2 Part 2. Sex ratios in the first reproductive age classes

To determine the complimentary values of $\mathfrak{m}_{\tilde{\alpha}}$ or $\mathfrak{f}_{\alpha}$ we expand the secondary sex ratio for ages $\tilde{\alpha}$ and α. From Equation 7.53f with age-invariant parameters $\left(z_0^{i,j} = \mathcal{U}_{i-1,j-1}\ell_i\tilde{\ell}_j\lambda^{-(i+j+1)}\mathfrak{f}_{i-1}\mathfrak{m}_{j-1} \rightarrow \mathcal{U}\left(\frac{p}{\lambda}\right)^i\left(\frac{\tilde{p}}{\lambda}\right)^j\lambda^{-1}\mathfrak{f}_{i-1}\mathfrak{m}_{j-1}\right)$

$$\underline{\mathcal{S}}_{\alpha,\tilde{\alpha}} = \frac{(1-\mathfrak{f}_\alpha)\sum_{i=\alpha-1}^{\omega-1}\Lambda^{i+1,\tilde{\alpha}}\ell_{i+1}\tilde{\ell}_{\tilde{\alpha}}\lambda^{-(i+\tilde{\alpha})}\mathcal{U}_{i,\tilde{\alpha}-1}\mathfrak{f}_i}{(1-\mathfrak{m}_{\tilde{\alpha}})\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1}\Lambda^{\alpha,j+1}\ell_\alpha\tilde{\ell}_{j+1}\lambda^{-(\alpha+j)}\mathcal{U}_{\alpha-1,j}\mathfrak{m}_j} \tag{8.35a}$$

$$= \frac{(1-\mathfrak{f}_\alpha)\sum_{i=\alpha}^{\omega}\Lambda\mathcal{U}\lambda^{-1}\left(\frac{p}{\lambda}\right)^i\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\mathfrak{f}_{i-1}}{(1-\mathfrak{m}_{\tilde{\alpha}})\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\Lambda\mathcal{U}\lambda^{-1}\left(\frac{p}{\lambda}\right)^\alpha\left(\frac{\tilde{p}}{\lambda}\right)^j\mathfrak{m}_{j-1}} \tag{8.35b}$$

$$= \frac{(1-\mathfrak{f}_\alpha)\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}-1}\sum_{i=\alpha-1}^{\omega-1}\left(\frac{p}{\lambda}\right)^i\mathfrak{f}_i}{(1-\mathfrak{m}_{\tilde{\alpha}})\left(\frac{p}{\lambda}\right)^{\alpha-1}\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1}\left(\frac{\tilde{p}}{\lambda}\right)^j\mathfrak{m}_j} \tag{8.35c}$$

And 7.54b with age-invariant parameters becomes,

$$\underline{\mathcal{S}}_{\alpha,\tilde{\alpha}} = \frac{\tilde{\ell}_{\tilde{\alpha}}}{\ell_\alpha}\underline{\mathcal{S}}_{0,0} = \frac{\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}}\tilde{f}\mathcal{L}_h\lambda^{-h}z_0^{i,j}}{\left(\frac{p}{\lambda}\right)^{\alpha}\sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}}f\mathcal{L}_h\lambda^{-h}z_0^{i,j}} \tag{8.36a}$$

$$= \frac{\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\tilde{f}\sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\left(\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}}\mathcal{L}_h\lambda^{-h}\right)z_0^{i,j}}{\left(\frac{p}{\lambda}\right)^{\alpha}f\sum_{i=\alpha}^{\omega}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}}\left(\sum_{h=0}^{\min\{\omega-i,\tilde{\omega}-j\}}\mathcal{L}_h\lambda^{-h}\right)z_0^{i,j}} \tag{8.36b}$$

$$= \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{-\alpha}\sigma \tag{8.36c}$$

So equating the RHS's of 8.35c and 8.36c

$$\frac{(1-\mathfrak{f}_\alpha)\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}-1}\sum_{i=\alpha-1}^{\omega-1}\left(\frac{p}{\lambda}\right)^i\mathfrak{f}_i}{(1-\mathfrak{m}_{\tilde{\alpha}})\left(\frac{p}{\lambda}\right)^{\alpha-1}\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1}\left(\frac{\tilde{p}}{\lambda}\right)^j\mathfrak{m}_j} = \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{-\alpha}\sigma \tag{8.37}$$

Rearranging

$$1-\mathfrak{f}_\alpha = \frac{\left(\frac{\tilde{p}}{\lambda}\right)\sum_{j=\tilde{\alpha}-1}^{\tilde{\omega}-1}\left(\frac{\tilde{p}}{\lambda}\right)^j\mathfrak{m}_j}{\left(\frac{p}{\lambda}\right)\sum_{i=\alpha-1}^{\omega-1}\left(\frac{p}{\lambda}\right)^i\mathfrak{f}_i}\sigma\left(1-\mathfrak{m}_{\tilde{\alpha}}\right) \tag{8.38a}$$

$$= \frac{\left(\frac{\tilde{p}}{\lambda}\right)\tilde{G}}{\left(\frac{p}{\lambda}\right)G}\sigma\left(1-\mathfrak{m}_{\tilde{\alpha}}\right) \tag{8.38b}$$

Now substituting the definitions of $\tilde{G}$ and G (Equations 8.25 and 8.26)

$$\left(\frac{1-\mathfrak{f}_\alpha}{2-\mathfrak{f}_\alpha}\right)\left(\frac{\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)}{\left(1-\frac{p}{\lambda}\right)}+\frac{(1-\mathfrak{f}_\alpha)\left(1-\left[\left(\frac{p}{\lambda}\right)(\mathfrak{f}_\alpha-1)\right]^{\omega-\alpha+1}\right)}{\left(1+\frac{p}{\lambda}(1-\mathfrak{f}_\alpha)\right)}\right)$$

$$= \sigma \frac{\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}}{\left(\frac{p}{\lambda}\right)^{\alpha}} \left(\frac{1-\mathfrak{m}_{\tilde{\alpha}}}{2-\mathfrak{m}_{\tilde{\alpha}}}\right) \left(\frac{\left(1-\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{\tilde{p}}{\lambda}\right)} + \frac{\left(1-\mathfrak{m}_{\tilde{\alpha}}\right)\left(1-\left[\left(\frac{\tilde{p}}{\lambda}\right)\left(\mathfrak{m}_{\tilde{\alpha}}-1\right)\right]^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1+\frac{\tilde{p}}{\lambda}\left(1-\mathfrak{m}_{\tilde{\alpha}}\right)\right)} \right) \tag{8.39}$$

8.2.1 Number of reproductive age classes less than 3

For $\omega - \alpha$ and $\tilde{\omega} - \tilde{\alpha}$ less than 2, Equation 8.39 becomes

	$\tilde{\omega} = \tilde{\alpha}$
$\omega = \alpha$	$(1-\mathfrak{f}_\alpha) = \sigma \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} \left(\frac{p}{\lambda}\right)^{-\alpha} (1-\mathfrak{m}_{\tilde{\alpha}})$
$\omega = \alpha + 1$	$\left(1+\frac{p}{\lambda}\mathfrak{f}_\alpha\right)(1-\mathfrak{f}_\alpha) = \sigma \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} \left(\frac{p}{\lambda}\right)^{-\alpha} (1-\mathfrak{m}_{\tilde{\alpha}})$

(8.40a)

	$\tilde{\omega} = \tilde{\alpha} + 1$
$\omega = \alpha$	$(1-\mathfrak{f}_\alpha) = \sigma \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} \left(\frac{p}{\lambda}\right)^{-\alpha} \left(1+\frac{\tilde{p}}{\lambda}\mathfrak{m}_{\tilde{\alpha}}\right)(1-\mathfrak{m}_{\tilde{\alpha}})$
$\omega = \alpha + 1$	$\left(1+\frac{p}{\lambda}\mathfrak{f}_\alpha\right)(1-\mathfrak{f}_\alpha) = \sigma \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} \left(\frac{p}{\lambda}\right)^{-\alpha} \left(1+\frac{\tilde{p}}{\lambda}\mathfrak{m}_{\tilde{\alpha}}\right)(1-\mathfrak{m}_{\tilde{\alpha}})$

(8.40b)

For $\omega = \alpha+1$ and $\tilde{\omega} = \tilde{\alpha}+1$, and $2\sigma < \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}-1} \left(\frac{p}{\lambda}\right)^{1-\alpha} \left(\frac{\lambda+p}{\lambda+\tilde{p}}\right)^2$ or $\mathfrak{f}_\alpha$ close to 1, Equation 8.39 is approximately

$$(1-\mathfrak{f}_\alpha) = \frac{\left(1+\frac{p}{\lambda}\right)}{2\frac{p}{\lambda}} \left(1 - \sqrt{\left(1 - \frac{4\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{-\alpha}\frac{p}{\lambda}\left(1+\frac{\tilde{p}}{\lambda}\mathfrak{m}_{\tilde{\alpha}}\right)(1-\mathfrak{m}_{\tilde{\alpha}})}{\left(1+\frac{p}{\lambda}\right)^2}\right)}\right) \tag{8.41a}$$

$$\approx \left(\frac{\left(1+\frac{\tilde{p}}{\lambda}\mathfrak{m}_{\tilde{\alpha}}\right)}{\left(1+\frac{p}{\lambda}\right)}\right) \sigma \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} \left(\frac{p}{\lambda}\right)^{-\alpha} (1-\mathfrak{m}_{\tilde{\alpha}}) \tag{8.41b}$$

For $\omega = \alpha + 1$ and $\tilde{\omega} = \tilde{\alpha} + 1$, and $2\sigma > \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}-1} \left(\frac{p}{\lambda}\right)^{1-\alpha} \left(\frac{\lambda+p}{\lambda+\tilde{p}}\right)^2$ or $\mathfrak{m}_{\tilde{\alpha}}$ close to 1, Equation 8.39 is approximately

$$(1 - \mathfrak{m}_{\tilde{\alpha}}) = \frac{\left(1 + \frac{\tilde{p}}{\lambda}\right)}{2\frac{\tilde{p}}{\lambda}} \left(1 - \sqrt{\left(1 - \frac{4\left(\frac{p}{\lambda}\right)^{\alpha} \left(1 + \frac{p}{\lambda}\mathfrak{f}_{\alpha}\right)(1 - \mathfrak{f}_{\alpha})}{\sigma \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}-1} \left(1 + \frac{\tilde{p}}{\lambda}\right)^2}\right)}\right) \tag{8.42a}$$

$$\approx \frac{\left(1 + \frac{p}{\lambda}\mathfrak{f}_{\alpha}\right)\left(\frac{p}{\lambda}\right)^{\alpha}}{\sigma\left(1 + \frac{\tilde{p}}{\lambda}\right)\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}} (1 - \mathfrak{f}_{\alpha}) \tag{8.42b}$$

8.2.2 Number of reproductive age classes 3 or greater.

If we expect $\mathfrak{f}_{\alpha} > \mathfrak{m}_{\tilde{\alpha}}$ then make the following approximations. For the case when $\mathfrak{m}_{\tilde{\alpha}} = 0$ then denote $\tilde{G}$ by "$\tilde{G}_0$" and Equation 8.23 becomes

$$\tilde{G}_0 = \left(\frac{\left(1 - \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1+k}\right)}{\left(\frac{\tilde{p}}{\lambda}\right)^{1-\tilde{\alpha}} \left(1 - \left(\frac{\tilde{p}}{\lambda}\right)^2\right)}\right) \qquad k = \begin{cases} 0 & \text{if } \tilde{\omega} - \tilde{\alpha} + 1 \text{ is even} \\ 1 & \text{if } \tilde{\omega} - \tilde{\alpha} + 1 \text{ is odd} \end{cases} \tag{8.43}$$

Letting $1 - A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}$ be the $\mathfrak{m}_{\tilde{\alpha}}$ intercept of Equation 8.39 , that is $A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}} = (1 - \mathfrak{f}_{\alpha})|_{\mathfrak{m}_{\tilde{\alpha}}=0}$, then we have

$$\begin{aligned} 0 \;=\; & \Bigg[\left(\frac{A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}}{1 + A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}}\right) \\ & \times \left(\frac{\left(1 - \left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)}{\left(1 - \frac{p}{\lambda}\right)} + \frac{A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}\left(1 - \left(-\frac{p}{\lambda}A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}\right)^{\omega-\alpha+1}\right)}{\left(1 + \frac{p}{\lambda}A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}\right)}\right)\Bigg] \\ & -\sigma\left(\frac{p}{\lambda}\right)^{-\alpha}\left(\frac{\tilde{p}}{\lambda}\right)\tilde{G}_0 \end{aligned} \tag{8.44}$$

Thus the term $A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}$ is defined implicitly and must be obtained numerically. The fraction of mated females in the first reproductive age class $(1 - \mathfrak{f}_{\alpha})$ can be approximated as

$$(1 - \mathfrak{f}_{\alpha}) \approx A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}} \left(\frac{1 - \mathfrak{m}_{\tilde{\alpha}}}{2 - \mathfrak{m}_{\tilde{\alpha}}}\right), \quad \text{for } \omega - \alpha, \text{ and } \tilde{\omega} - \tilde{\alpha} \geq 1 \tag{8.45}$$

Similarly if $\mathfrak{m}_{\tilde{\alpha}} > \mathfrak{f}_\alpha$ then $\tilde{A}_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}} = (1-\mathfrak{m}_{\tilde{\alpha}})|_{\mathfrak{f}_\alpha=0}$ and

$$(1-\mathfrak{m}_{\tilde{\alpha}}) \approx \tilde{A}_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}} \left(\frac{1-\mathfrak{f}_\alpha}{2-\mathfrak{f}_\alpha}\right) \tag{8.46}$$

The term $\tilde{A}_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}$ is also defined implicitly by

$$\begin{aligned} 0 \;=\; & \left[\left(\frac{\tilde{A}_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}}{1+\tilde{A}_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}}\right)\right. \\ & \left.\times\left(\frac{\left(1-\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{\tilde{p}}{\lambda}\right)} + \frac{\tilde{A}_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}\left(1-\left(-\frac{\tilde{p}}{\lambda}\tilde{A}_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1+\frac{\tilde{p}}{\lambda}\tilde{A}_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}\right)}\right)\right] \\ & -\sigma^{-1}\left(\frac{\tilde{p}}{\lambda}\right)^{-\tilde{\alpha}}\left(\frac{p}{\lambda}\right) G_0 \end{aligned} \tag{8.47}$$

and

$$G_0 = \left(\frac{\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1+k}\right)}{\left(\frac{p}{\lambda}\right)^{1-\alpha}\left(1-\left(\frac{p}{\lambda}\right)^2\right)}\right) \qquad k = \begin{cases} 0 & \text{if } \omega-\alpha+1 \text{ is even} \\ 1 & \text{if } \omega-\alpha+1 \text{ is odd} \end{cases} \tag{8.48}$$

For $\mathfrak{f}_\alpha > \mathfrak{m}_{\tilde{\alpha}}$ when $\omega-\alpha$ is large we have

$$\left(\frac{1-\mathfrak{f}_\alpha}{2-\mathfrak{f}_\alpha}\right)\left(\frac{\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)}{\left(1-\frac{p}{\lambda}\right)} + \frac{(1-\mathfrak{f}_\alpha)}{\left(1+\frac{p}{\lambda}(1-\mathfrak{f}_\alpha)\right)}\right) \approx \sigma\left(\frac{p}{\lambda}\right)^{-\alpha}\left(\frac{\tilde{p}}{\lambda}\right)\tilde{G}_0 \tag{8.49}$$

rearranging

$$\begin{aligned} 0 \;\approx\; & -\sigma\left(1-\frac{p}{\lambda}\right)\left(\frac{p}{\lambda}\right)^{-\alpha}\left(\frac{\tilde{p}}{\lambda}\right)\tilde{G}_0 \qquad (8.50) \\ & +\left(\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right) - \sigma\left(\frac{p}{\lambda}\right)^{-\alpha}\left(\frac{\tilde{p}}{\lambda}\right)\left(1-\left(\frac{p}{\lambda}\right)^2\right)\tilde{G}_0\right)(1-\mathfrak{f}_\alpha) \\ & +\left(\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)\left(\frac{p}{\lambda}\right) + \left(1-\frac{p}{\lambda}\right)\left(1-\sigma\left(\frac{p}{\lambda}\right)^{-\alpha}\left(\frac{\tilde{p}}{\lambda}\right)\left(\frac{p}{\lambda}\right)\tilde{G}_0\right)\right)(1-\mathfrak{f}_\alpha)^2 \end{aligned}$$

solving for the relevant root we have the $\mathfrak{m}_{\tilde{\alpha}}$ intercept as

$$A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}} = (1-\mathfrak{f}_\alpha)\big|_{\mathfrak{m}_{\tilde{\alpha}}=0}$$

$$\approx \frac{\left(\frac{p}{\lambda}\right)^\alpha\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)-\sigma\left(1-\left(\frac{p}{\lambda}\right)^2\right)\left(\frac{\tilde{p}}{\lambda}\right)\tilde{G}_0}{2\left(\left(\frac{p}{\lambda}\right)^\alpha\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+2}\right)-\sigma\left(\frac{p}{\lambda}\right)\left(1-\frac{p}{\lambda}\right)\left(\frac{\tilde{p}}{\lambda}\right)\tilde{G}_0\right)}$$
$$\times\left(-1+\sqrt{1+\frac{4\sigma\left(\frac{\tilde{p}}{\lambda}\right)\left(1-\frac{p}{\lambda}\right)\left(\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+2}\right)-\sigma\left(\frac{p}{\lambda}\right)\left(1-\frac{p}{\lambda}\right)\left(\frac{\tilde{p}}{\lambda}\right)\tilde{G}_0\right)\tilde{G}_0}{\left(\left(\frac{p}{\lambda}\right)^\alpha\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)-\sigma\left(\frac{\tilde{p}}{\lambda}\right)\left(1-\left(\frac{p}{\lambda}\right)^2\right)\tilde{G}_0\right)^2}}\right)$$

$$\approx \frac{\sigma\left(\frac{\tilde{p}}{\lambda}\right)\left(1-\frac{p}{\lambda}\right)\tilde{G}_0}{\left(\left(\frac{p}{\lambda}\right)^\alpha\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)-\sigma\left(\frac{\tilde{p}}{\lambda}\right)\left(1-\left(\frac{p}{\lambda}\right)^2\right)\tilde{G}_0\right)} \tag{8.51}$$

A better approximation for the conditions $\omega-\alpha, \tilde{\omega}-\tilde{\alpha} > 1$ and $p > \tilde{p}$ is given by

$$A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}} \approx \frac{\sigma\left(\frac{\tilde{p}}{\lambda}\right)\left(1-\frac{p}{\lambda}\right)\tilde{G}_0}{\left(\left(\frac{p}{\lambda}\right)^\alpha\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)-\left(\frac{\omega-\alpha+1}{2(\omega-\alpha+2)}\right)\sigma\left(\frac{\tilde{p}}{\lambda}\right)\left(1-\left(\frac{p}{\lambda}\right)^2\right)\tilde{G}_0\right)} \tag{8.52}$$

and again we approximate $1-\mathfrak{f}_\alpha$ as

$$(1-\mathfrak{f}_\alpha) \approx A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}\left(\frac{1-\mathfrak{m}_{\tilde{\alpha}}}{2-\mathfrak{m}_{\tilde{\alpha}}}\right) \tag{8.53}$$

And for $\mathfrak{m}_{\tilde{\alpha}} > \mathfrak{f}_\alpha$ when $\tilde{\omega}-\tilde{\alpha}$ is large we have

$$\tilde{A}_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}} \approx \frac{\left(\frac{p}{\lambda}\right)\left(1-\frac{\tilde{p}}{\lambda}\right)G_0}{\left(\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(1-\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)-\left(\frac{\tilde{\omega}-\tilde{\alpha}+1}{2(\tilde{\omega}-\tilde{\alpha}+2)}\right)\left(\frac{p}{\lambda}\right)\left(1-\left(\frac{\tilde{p}}{\lambda}\right)^2\right)G_0\right)} \tag{8.54}$$

and again we approximate $1-\mathfrak{f}_\alpha$ as

$$(1-\mathfrak{m}_{\tilde{\alpha}}) \approx \tilde{A}_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}\left(\frac{1-\mathfrak{f}_\alpha}{2-\mathfrak{f}_\alpha}\right) \tag{8.55}$$

8.2.3 Population growth rate very large

When $\lambda \gg \max\{p, \tilde{p}\}$ then we have in for all values of $\omega - \alpha$ and $\tilde{\omega} - \tilde{\alpha}$

$$(1 - \mathfrak{f}_\alpha) \approx \sigma \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} \left(\frac{p}{\lambda}\right)^{-\alpha} (1 - \mathfrak{m}_{\tilde{\alpha}}) \tag{8.56}$$

8.3 Part 3. Putting the pieces together.

From 8.31

$$\left(1 - \frac{p\tilde{p}\pi}{\lambda}\right)\left(1 - \left(\frac{p\tilde{p}\pi}{\lambda}\right)^{1+\xi}\right)^{-1} = \min\left\{\frac{\tilde{u}p}{(1-\mathfrak{m}_{\tilde{\alpha}})} + \frac{u\tilde{p}}{(1-\mathfrak{f}_\alpha)}, \frac{\tilde{p}}{(1-\mathfrak{f}_\alpha)}, \frac{p}{(1-\mathfrak{m}_{\tilde{\alpha}})}\right\}$$

8.3.1 One reproductive age class

Case when $\omega = \alpha$ and $\tilde{\omega} = \tilde{\alpha} \Rightarrow \xi = 0$ and $(1 - \mathfrak{f}_\alpha) = \sigma \left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} \left(\frac{p}{\lambda}\right)^{-\alpha} (1 - \mathfrak{m}_{\tilde{\alpha}})$

$$1 = \min\left\{\frac{\tilde{u}p}{(1-\mathfrak{m}_{\tilde{\alpha}})} + \frac{\left(\frac{p}{\lambda}\right)^{\alpha} u\tilde{p}}{\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}(1-\mathfrak{m}_{\tilde{\alpha}})}, \frac{\left(\frac{p}{\lambda}\right)^{\alpha}\tilde{p}}{\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}(1-\mathfrak{m}_{\tilde{\alpha}})}, \frac{p}{(1-\mathfrak{m}_{\tilde{\alpha}})}\right\} \tag{8.57a}$$

$$(1-\mathfrak{m}_{\tilde{\alpha}}) = \min\left\{\tilde{u}p + \sigma^{-1}\left(\frac{\tilde{p}}{\lambda}\right)^{-\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{\alpha} u\tilde{p}, \sigma^{-1}\left(\frac{\tilde{p}}{\lambda}\right)^{-\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{\alpha}\tilde{p}, p\right\} \tag{8.57b}$$

$$(1-\mathfrak{f}_\alpha) = \min\left\{\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{-\alpha}\tilde{u}p + u\tilde{p}, \tilde{p}, \sigma p\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{-\alpha}\right\} \tag{8.57c}$$

$$(1-\mathfrak{f}_\alpha, 1-\mathfrak{m}_{\tilde{\alpha}}) = \begin{cases} \left(\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{-\alpha}\tilde{u}p + u\tilde{p}, \tilde{u}p + \sigma^{-1}\left(\frac{\tilde{p}}{\lambda}\right)^{-\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{\alpha}u\tilde{p}\right) & \text{no shortages} \\ \left(\tilde{p}, \sigma^{-1}\left(\frac{\tilde{p}}{\lambda}\right)^{-\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{\alpha}\tilde{p}\right) & \text{female limit} \\ \left(\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{-\alpha}p, p\right) & \text{male limit} \end{cases} \tag{8.58}$$

8.3.2 Number of reproductive age classes 3 or greater.

For $\mathfrak{f}_\alpha > \mathfrak{m}_{\tilde\alpha}$ when $\omega - \alpha$ is large we have $(1-\mathfrak{f}_\alpha) \approx A_{\omega-\alpha,\tilde\omega-\tilde\alpha}\left(\frac{1-\mathfrak{m}_{\tilde\alpha}}{2-\mathfrak{m}_{\tilde\alpha}}\right)$

$$\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde\omega-\tilde\alpha+1}\right)^{-1}$$

$$\approx \min\left\{\frac{\tilde{u}p}{(1-\mathfrak{m}_{\tilde\alpha})}+\frac{u\tilde{p}}{A_{\omega-\alpha,\tilde\omega-\tilde\alpha}\left(\frac{1-\mathfrak{m}_{\tilde\alpha}}{2-\mathfrak{m}_{\tilde\alpha}}\right)}, \frac{\tilde{p}}{A_{\omega-\alpha,\tilde\omega-\tilde\alpha}\left(\frac{1-\mathfrak{m}_{\tilde\alpha}}{2-\mathfrak{m}_{\tilde\alpha}}\right)}, \frac{p}{(1-\mathfrak{m}_{\tilde\alpha})}\right\} \tag{8.59}$$

Case (i) no shortages

$$\frac{p\tilde{p}}{A_{\omega-\alpha,\tilde\omega-\tilde\alpha}p-\tilde{p}} < \frac{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}{\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde\omega-\tilde\alpha+1}\right)} \tag{8.60a}$$

$$\frac{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}{\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde\omega-\tilde\alpha+1}\right)} \leq \left(\frac{2\,(1-u)\,\tilde{p}-A_{\omega-\alpha,\tilde\omega-\tilde\alpha}\tilde{u}p}{(1-u)\,\tilde{p}-A_{\omega-\alpha,\tilde\omega-\tilde\alpha}\tilde{u}p}\right)\frac{\tilde{p}}{A_{\omega-\alpha,\tilde\omega-\tilde\alpha}} \tag{8.60b}$$

or

$$\frac{up\tilde{p}}{A_{\omega-\alpha,\tilde\omega-\tilde\alpha}\,(1-\tilde{u})\,p-u\tilde{p}} < \frac{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}{\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde\omega-\tilde\alpha+1}\right)} \leq \frac{p\tilde{p}}{A_{\omega-\alpha,\tilde\omega-\tilde\alpha}p-\tilde{p}} \tag{8.61}$$

Case (ii) females limiting

$$\frac{p\tilde{p}}{A_{\omega-\alpha,\tilde\omega-\tilde\alpha}p-\tilde{p}} < \frac{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}{\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde\omega-\tilde\alpha+1}\right)} \tag{8.62}$$

and

$$\left(\frac{2\,(1-u)\,\tilde{p}-A_{\omega-\alpha,\tilde\omega-\tilde\alpha}\tilde{u}p}{(1-u)\,\tilde{p}-A_{\omega-\alpha,\tilde\omega-\tilde\alpha}\tilde{u}p}\right)\frac{\tilde{p}}{A_{\omega-\alpha,\tilde\omega-\tilde\alpha}} < \frac{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}{\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde\omega-\tilde\alpha+1}\right)} \tag{8.63}$$

Case (iii) males limiting

$$\frac{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}{\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde\omega-\tilde\alpha+1}\right)} \leq \frac{p\tilde{p}}{A_{\omega-\alpha,\tilde\omega-\tilde\alpha}p-\tilde{p}} \tag{8.64}$$

and

$$\frac{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}{\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)} \leq \frac{up\tilde{p}}{A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}\left(1-\tilde{u}\right)p-up\tilde{p}} \tag{8.65}$$

Then putting them together

$$\begin{pmatrix} 1-\mathfrak{f}_{\alpha} \\ 1-\mathfrak{m}_{\tilde{\alpha}} \end{pmatrix} = \begin{cases} \begin{pmatrix} \frac{\left(\tilde{u}pA_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}+u\tilde{p}\right)\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)+\tilde{u}p\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)} \\ \frac{\left(\tilde{u}pA_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}+u\tilde{p}\right)\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}-u\tilde{p}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)} \end{pmatrix} & \text{(i) no shortages} \\ \begin{pmatrix} \frac{\tilde{p}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)} \\ \frac{\tilde{p}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}-\tilde{p}\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)} \end{pmatrix} & \text{(ii) female limit} \\ \begin{pmatrix} \frac{A_{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}}p\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)+p\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)} \\ \frac{p\left(1-\left(\frac{p\tilde{p}\pi}{\lambda}\right)^{\tilde{\omega}-\tilde{\alpha}+1}\right)}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)} \end{pmatrix} & \text{(iii) male limit} \end{cases} \tag{8.66}$$

8.3.3 Population growth rate very large or maximum age of reproduction very large

When $\lambda \gg \max\{p,\tilde{p},\pi\}$, or $\tilde{\omega}$ and $\omega \to \infty$ then this implies that $\xi \to \infty$ and

$$(1-\mathfrak{f}_{\alpha}) \approx \sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{-\alpha}(1-\mathfrak{m}_{\tilde{\alpha}}) \tag{8.67}$$

$$\left(1-\frac{p\tilde{p}\pi}{\lambda}\right) \approx \min\left\{\frac{\tilde{u}p}{(1-\mathfrak{m}_{\tilde{\alpha}})}+\frac{\left(\frac{p}{\lambda}\right)^{\alpha}u\tilde{p}}{\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}(1-\mathfrak{m}_{\tilde{\alpha}})}, \frac{\left(\frac{p}{\lambda}\right)^{\alpha}\tilde{p}}{\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}(1-\mathfrak{m}_{\tilde{\alpha}})}, \frac{p}{(1-\mathfrak{m}_{\tilde{\alpha}})}\right\} \tag{8.68a}$$

$$(1-\mathfrak{m}_{\tilde{\alpha}}) \approx \min\left\{\frac{\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\tilde{u}p+\left(\frac{p}{\lambda}\right)^{\alpha}u\tilde{p}}{\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}, \frac{\left(\frac{p}{\lambda}\right)^{\alpha}\tilde{p}}{\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}, \frac{p}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}\right\} \tag{8.68b}$$

$$(1-\mathfrak{f}_{\alpha}) \approx \min\left\{\frac{\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\tilde{u}p+\left(\frac{p}{\lambda}\right)^{\alpha}u\tilde{p}}{\left(\frac{p}{\lambda}\right)^{\alpha}\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}, \frac{\tilde{p}}{\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}, \frac{\sigma p\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}}{\left(\frac{p}{\lambda}\right)^{\alpha}\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)}\right\} \tag{8.68c}$$

Putting them together

$$(1-\mathfrak{f}_\alpha, 1-\mathfrak{m}_{\tilde\alpha}) \approx \begin{cases} \left(\frac{\sigma\left(\frac{\tilde p}{\lambda}\right)^{\tilde\alpha}\tilde u p+\left(\frac{p}{\lambda}\right)^{\alpha}u\tilde p}{\left(\frac{p}{\lambda}\right)^{\alpha}\left(1-\frac{p\tilde p\pi}{\lambda}\right)}, \frac{\sigma\left(\frac{\tilde p}{\lambda}\right)^{\tilde\alpha}\tilde u p+\left(\frac{p}{\lambda}\right)^{\alpha}u\tilde p}{\sigma\left(\frac{\tilde p}{\lambda}\right)^{\tilde\alpha}\left(1-\frac{p\tilde p\pi}{\lambda}\right)}\right) & \text{no shortages} \\ \left(\frac{\tilde p}{\left(1-\frac{p\tilde p\pi}{\lambda}\right)}, \frac{\left(\frac{p}{\lambda}\right)^{\alpha}\tilde p}{\sigma\left(\frac{\tilde p}{\lambda}\right)^{\tilde\alpha}\left(1-\frac{p\tilde p\pi}{\lambda}\right)}\right) & \text{female limit} \\ \left(\frac{\sigma p\left(\frac{\tilde p}{\lambda}\right)^{\tilde\alpha}}{\left(\frac{p}{\lambda}\right)^{\alpha}\left(1-\frac{p\tilde p\pi}{\lambda}\right)}, \frac{p}{\left(1-\frac{p\tilde p\pi}{\lambda}\right)}\right) & \text{male limit} \end{cases} \tag{8.69}$$

8.4 Part 4. Population growth rate

From Equation 7.56, 7.44b and 7.43 the characteristic equation is

$$1 = \left(\sum_{i'=\alpha}^{\omega} \ell_{i'}\lambda^{-i'}\left(1-\mathfrak{f}_{i'}\right)\right)\sum_{i=\alpha}^{\omega}\sum_{j=\tilde\alpha}^{\tilde\omega}\sum_{h=0}^{\min\{\omega-i,\tilde\omega-j\}} f_h^{i,j}\mathcal{L}_h^{i,j}\mathcal{U}_{i-1,j-1}\ell_i\tilde\ell_j\lambda^{-(i+j+h)}\mathfrak{f}_{i-1}\mathfrak{m}_{j-1} \tag{8.70a}$$

$$1 = f\left(\sum_{i'=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^{i'}\left(1-\mathfrak{f}_{i'}\right)\right)\sum_{i=\alpha}^{\omega}\sum_{j=\tilde\alpha}^{\tilde\omega}\sum_{h=0}^{\min\{\omega-i,\tilde\omega-j\}} \lambda^{-1}z_h^{i,j} \tag{8.70b}$$

$$1 = \frac{f}{\lambda}\left(\sum_{i'=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^{i'}\left(1-\mathfrak{f}_{i'}\right)\right) \tag{8.70c}$$

$$1 = \frac{f}{\lambda}\left(1-\mathfrak{f}_\alpha\right)\frac{\left(\frac{p}{\lambda}\right)^{\alpha}}{2-\mathfrak{f}_\alpha}\left[\frac{\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)}{\left(1-\frac{p}{\lambda}\right)} + \frac{\left(1-\mathfrak{f}_\alpha\right)\left(1-\left[\left(\frac{p}{\lambda}\right)\left(\mathfrak{f}_\alpha-1\right)\right]^{\omega-\alpha+1}\right)}{\left(1+\frac{p}{\lambda}\left(1-\mathfrak{f}_\alpha\right)\right)}\right] \tag{8.70d}$$

8.4.1 One reproductive age class

Case when $\omega=\alpha$ and $\tilde\omega=\tilde\alpha \Rightarrow \xi=0$ and $(1-\mathfrak{f}_\alpha)=\sigma\left(\frac{\tilde p}{\lambda}\right)^{\tilde\alpha}\left(\frac{p}{\lambda}\right)^{-\alpha}(1-\mathfrak{m}_{\tilde\alpha})$

$$1-\mathfrak{f}_\alpha = \min\begin{cases} \sigma\left(\frac{\tilde p}{\lambda}\right)^{\tilde\alpha}\left(\frac{p}{\lambda}\right)^{-\alpha}\tilde u p + u\tilde p & \text{no shortages} \\ \tilde p & \text{female limit} \\ \sigma\left(\frac{\tilde p}{\lambda}\right)^{\tilde\alpha}\left(\frac{p}{\lambda}\right)^{-\alpha} p & \text{male limit} \end{cases} \tag{8.71}$$

The characteristic equation reduces to

$$1 = \frac{f}{\lambda}\left(\frac{p}{\lambda}\right)^{\alpha}(1 - \mathfrak{f}_{\alpha}) \tag{8.72}$$

$$1 = \begin{cases} \frac{f}{\lambda}\left(\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\tilde{u}p + \left(\frac{p}{\lambda}\right)^{\alpha}u\tilde{p}\right) & \text{no shortages} \\ \frac{f\tilde{p}}{\lambda}\left(\frac{p}{\lambda}\right)^{\alpha} & \text{female limit} \\ \frac{fp\sigma}{\lambda}\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} & \text{male limit} \end{cases} \tag{8.73}$$

For the case when there are no shortages and $\tilde{\alpha} \neq \alpha$ we let $\lambda = e^r$ and estimate by a Taylor series about $r = 0$

$$\begin{aligned} 0 &= 1 - \frac{f}{\lambda}\left(\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\tilde{u}p + \left(\frac{p}{\lambda}\right)^{\alpha}u\tilde{p}\right) && \text{(8.74a)} \\ &= \lambda^{\tilde{\alpha}+\alpha+1} - f\left(\sigma\lambda^{\alpha}\tilde{p}^{\tilde{\alpha}}\tilde{u}p + \lambda^{\tilde{\alpha}}p^{\alpha}u\tilde{p}\right) && \text{(8.74b)} \\ &= e^{(\tilde{\alpha}+\alpha+1)r} - f\left(\sigma e^{\alpha r}\tilde{p}^{\tilde{\alpha}}\tilde{u}p + e^{\tilde{\alpha}r}p^{\alpha}u\tilde{p}\right) && \text{(8.74c)} \end{aligned}$$

$$0 = \left(1 - f\left(\sigma\tilde{p}^{\tilde{\alpha}}\tilde{u}p + p^{\alpha}u\tilde{p}\right)\right) + \left(\tilde{\alpha} + \alpha + 1 - f\left(\sigma\alpha\tilde{p}^{\tilde{\alpha}}\tilde{u}p + \tilde{\alpha}p^{\alpha}u\tilde{p}\right)\right)r + O\left(r^2\right) \tag{8.75}$$

$$r \approx \frac{f\left(\sigma\tilde{p}^{\tilde{\alpha}}\tilde{u}p + p^{\alpha}u\tilde{p}\right) - 1}{\tilde{\alpha} + \alpha + 1 - f\left(\sigma\alpha\tilde{p}^{\tilde{\alpha}}\tilde{u}p + \tilde{\alpha}p^{\alpha}u\tilde{p}\right)} \tag{8.76}$$

If $\alpha = \tilde{\alpha} = 1$

$$\begin{aligned} \lambda &= \sqrt{f\left(\sigma\tilde{p}\tilde{u}p + pu\tilde{p}\right)} && \text{no shortages} \\ \lambda &= \sqrt{f\tilde{p}p} && \text{female limit} \\ \lambda &= \sqrt{\sigma f p\tilde{p}} && \text{male limit} \end{aligned} \tag{8.77}$$

8.4.2 Population growth rate very large or maximum age of reproduction very large

When $\lambda \gg \max\{p, \tilde{p}, \pi\}$, or $\tilde{\omega}$ and $\omega \to \infty$ then this implies $\xi \to \infty$

$$(1-\mathfrak{f}_\alpha) = \min \begin{cases} \left(\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} \tilde{u}p + \left(\frac{p}{\lambda}\right)^{\alpha} u\tilde{p}\right)\left(\frac{p}{\lambda}\right)^{-\alpha}\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1} & \text{no shortages} \\ \tilde{p}\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1} & \text{female limit} \\ \sigma p\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(\frac{p}{\lambda}\right)^{-\alpha}\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1} & \text{male limit} \end{cases} \tag{8.78}$$

$$1 = \frac{f}{\lambda}\left(\frac{p}{\lambda}\right)^{\alpha}(1-\mathfrak{f}_\alpha)$$

$$1 = \begin{cases} \frac{f}{\lambda}\left(\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}} \tilde{u}p + \left(\frac{p}{\lambda}\right)^{\alpha} u\tilde{p}\right)\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1} & \text{no shortages} \\ \frac{f\tilde{p}}{\lambda}\left(\frac{p}{\lambda}\right)^{\alpha}\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1} & \text{female limit} \\ \frac{fp}{\lambda}\sigma\left(\frac{\tilde{p}}{\lambda}\right)^{\tilde{\alpha}}\left(1-\frac{p\tilde{p}\pi}{\lambda}\right)^{-1} & \text{male limit} \end{cases} \tag{8.79}$$

To a first degree Taylor expansion (with caution)

$$\lambda \approx \begin{cases} \exp\left(\frac{f\left(\sigma\tilde{p}^{\tilde{\alpha}}\tilde{u}p + p^{\alpha}u\tilde{p}\right) - (1-p\tilde{p}\pi)}{1+(\tilde{\alpha}+\alpha)(1-p\tilde{p}\pi) - f(\sigma\alpha\tilde{p}^{\tilde{\alpha}}\tilde{u}p + \tilde{\alpha}p^{\alpha}u\tilde{p})}\right) & \text{no shortages} \\ \exp\left(\frac{f\tilde{p}p^{\alpha} - (1-p\tilde{p}\pi)}{1+\alpha(1-p\tilde{p}\pi)}\right) & \text{female limit} \\ \exp\left(\frac{\sigma fp\tilde{p}^{\tilde{\alpha}} - (1-p\tilde{p}\pi)}{1+\tilde{\alpha}(1-p\tilde{p}\pi)}\right) & \text{male limit} \end{cases} \tag{8.80}$$

Of course the value of lambda needs to be determined before we know whether we have a limiting case or not, so these estimates must be put back into the conditions for determining the case. This could presumably cause instabilities in the solution if we solve by iterating, since the conditions for determining the case are based on a fixed value of λ, whereas λ is itself dependent on which case is pertinent. In such cases the solution of the system may be dependent on initial conditions. From the characteristic equation however

$$1 = \frac{f}{p}\left(\sum_{i=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^{i+1}\left(1-\frac{1-(\mathfrak{f}_\alpha-1)^{i-\alpha+2}}{2-\mathfrak{f}_\alpha}\right)\right) \tag{8.81a}$$

$$= \frac{f}{p}(1-\mathfrak{f}_\alpha)\frac{\left(\frac{p}{\lambda}\right)^{\alpha+1}}{2-\mathfrak{f}_\alpha}\left[\frac{\left(1-\left(\frac{p}{\lambda}\right)^{\omega-\alpha+1}\right)}{\left(1-\frac{p}{\lambda}\right)}+\frac{(1-\mathfrak{f}_\alpha)\left(1-\left[\left(\frac{p}{\lambda}\right)(\mathfrak{f}_\alpha-1)\right]^{\omega-\alpha+1}\right)}{\left(1+\frac{p}{\lambda}(1-\mathfrak{f}_\alpha)\right)}\right] \tag{8.81b}$$

Thus λ increases monotonically with the fraction mated within the first reproductive age class $(1-\mathfrak{f}_\alpha)$, so when explicit solutions of λ are available the case that provides the correct value of fraction mated also provides the correct value of λ. For example from the semelparous case (one reproductive age class) we have

$$\lambda = \min\begin{cases} \approx \exp\left(\frac{f\left(\sigma\tilde{p}^{\tilde{\alpha}}\tilde{u}p+p^{\alpha}u\tilde{p}\right)-1}{\tilde{\alpha}+\alpha+1-f(\sigma\alpha\tilde{p}^{\tilde{\alpha}}\tilde{u}p+\tilde{\alpha}p^{\alpha}u\tilde{p})}\right) & \tilde{\alpha}\neq\alpha & \text{no shortages} \\ \left[f\left(\sigma\tilde{p}^{\alpha}\tilde{u}p+p^{\alpha}u\tilde{p}\right)\right]^{\frac{1}{\alpha+1}} & \tilde{\alpha}=\alpha & \\ \left(f\tilde{p}p^{\alpha}\right)^{\frac{1}{\alpha+1}} & & \text{female limit} \\ \left(\sigma f p\tilde{p}^{\tilde{\alpha}}\right)^{\frac{1}{\tilde{\alpha}+1}} & & \text{male limit} \end{cases} \tag{8.82}$$

This is not the method usually used to estimate λ. That method, proposed by Lotka [27], expands the characteristic equation in a Taylor series and uses the first two moments of the maternity function to estimate λ

$$\lambda \approx \frac{\kappa_1}{\kappa_2}\left(1-\sqrt{1-\frac{2\kappa_2\ln R_0}{\kappa_1^2}}\right)$$

where the cumulants $\kappa_1$and κ_2 are as defined in Equation 6.59. The problem here though is that the birth rates $\underline{\mathcal{B}}_i$ and $\underline{\tilde{\mathcal{B}}}_j$ are not actually constant (or even linear) with respect to λ. At this juncture we have not investigated the optimal way to estimate λ, or even if extending Lotka's method provides an improvement over the above method.

Chapter 9

Discussion and future work.

In this work I have hopefully provided a useful framework for the simulation of discrete-time two-sex age structured population models. I have shown the conditions necessary for geometric growth in these models in general, including direct proof that the homogeneity condition on marriage functions is a necessary condition for geometric growth and a stable age structure. Given this one condition all the other aspects of "normal" single-sex population structure apply, the population as a whole and all subgroups asymptotically approach a stable age structure for honest fertilities and both sexes necessarily grow at the same rate. I calculate the generation time for males and females and show that for discrete time models this generation time differs slightly (by 1 time step) from the generation time calculated from continuous time models. I also hope I have opened the door for more discussion on marriage functions and have provided some ideas of my own on how a function might be constructed from a more behaviorally based approach and still meet the conditions for marriage functions set forth by McFarland [31] and Fredrickson [11]. The explicit expression of the population structure in the general case is quite complicated and I have "distilled" the equations as much as possible in order to bring them to a point where at least numerical calculations can be performed and the general structure of solutions is apparent. Even in the case of age invariant parameters though, these expressions are still quite complicated. For numerical solutions simulation may be the quickest and simplest method.

Examining population dynamics with both sexes considered becomes more important as the life histories of the two sexes diverge, and/or the sex ratios become skewed away from dynamics adequately described by the female limiting case. It is the marriage function in conjunction with the fecundities of the particular reproductive pairs and described with regard to a particular classification (e.g. age) that gives the proper growth rates and dynamics for the population. In a way this is analogous to effective population size in population genetic models. In fact the effective population size for skewed sex ratios is proportional to the harmonic mean of the number of each sex, this is similar in form to the harmonic mean marriage function discussed in Chapter 7.

Ongoing work includes the collecting of data on age predispositions, initiation probabilities, and as many other direct estimates of marriage function parameters as possible without resorting to inverse methods (back calculating parameter estimates that give the best fit to population data). Although there is an huge number of factors that go into determining marriage rates it is hoped that some general agreement between the models prediction and the actual marriage rates will provide some validation or at least provide a guide to improving the model (or throwing it out completely).

Future work will include searching for optimal estimation methods for model variables and growth rates. In addition I will soon try projecting an actual (US?) population and comparing to historical data. Given success in these areas, inroads to stochastic versions of the model will provide some insight to confidence of projections, parameters and other information inaccessible from deterministic models such as probability of extinction or time to extinction. Applications to other types of population structuring or epidemic model (for example) is also a potentially fruitful area.

Appendix A

Manipulation of Sums Over Their Ranges

The following equivalencies exist in the manipulation of sums over their ranges,

$$C_h^{i,j}(t) = C_{h,i+h,j+h}(t) \ \text{, and } C_{h,i,j}(t) = C_h^{i-h,j-h}(t)$$

$$\begin{aligned}\sum_{i=\alpha}^{\omega-\eta}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}-\eta}\sum_{h=\eta}^{\min\{\omega-i,\tilde{\omega}-j\}} C_h^{i,j}(t) &= \sum_{i=\alpha}^{\omega-\eta}\sum_{h=\eta}^{\min\{\omega-i,\tilde{\omega}-\tilde{\alpha}\}}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}-h} C_h^{i,j}(t) \\ &= \sum_{h=\eta}^{\min\{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}\}}\sum_{i=\alpha}^{\omega-h}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}-h} C_h^{i,j}(t)\end{aligned}$$

$$\begin{aligned}\sum_{i=\alpha}^{\omega-\eta}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}-\eta}\sum_{h=\eta}^{\min\{\omega-i,\tilde{\omega}-j\}} C_{h,i+h,j+h}(t) &= \sum_{i=\alpha}^{\omega-\eta}\sum_{h=\eta}^{\min\{\omega-i,\tilde{\omega}-\tilde{\alpha}\}}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}-h} C_{h,i+h,j+h}(t) \\ &= \sum_{h=\eta}^{\min\{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}\}}\sum_{i=\alpha}^{\omega-h}\sum_{j=\tilde{\alpha}}^{\tilde{\omega}-h} C_{h,i+h,j+h}(t)\end{aligned}$$

$$\begin{aligned}\sum_{i=\alpha+\eta}^{\omega}\sum_{j=\tilde{\alpha}+\eta}^{\tilde{\omega}}\sum_{h=\eta}^{\min\{i-\alpha,j-\tilde{\alpha}\}} C_{h,i,j}(t) &= \sum_{i=\alpha+\eta}^{\omega}\sum_{h=\eta}^{\min\{i-\alpha,\tilde{\omega}-\tilde{\alpha}\}}\sum_{j=\tilde{\alpha}+h}^{\tilde{\omega}} C_{h,i,j}(t) \\ &= \sum_{h=\eta}^{\min\{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}\}}\sum_{i=\alpha+h}^{\omega}\sum_{j=\tilde{\alpha}+h}^{\tilde{\omega}} C_{h,i,j}(t)\end{aligned}$$

$$
\begin{aligned}
\sum_{i=\alpha+\eta}^{\omega}\sum_{j=\tilde{\alpha}+\eta}^{\tilde{\omega}}\sum_{h=\eta}^{\min\{i-\alpha,j-\tilde{\alpha}\}} C_h^{i-h,j-h}(t) &= \sum_{i=\alpha+\eta}^{\omega}\sum_{h=\eta}^{\min\{i-\alpha,\tilde{\omega}-\tilde{\alpha}\}}\sum_{j=\tilde{\alpha}+h}^{\tilde{\omega}} C_h^{i-h,j-h}(t) \\
&= \sum_{h=\eta}^{\min\{\omega-\alpha,\tilde{\omega}-\tilde{\alpha}\}}\sum_{i=\alpha+h}^{\omega}\sum_{j=\tilde{\alpha}+h}^{\tilde{\omega}} C_h^{i-h,j-h}(t)
\end{aligned}
$$

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