Mathematical models for the growth of diploid populations with overlapping generations

Louis Jensen
Iowa State University

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by

Louis Jensen

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Dean of Graduate College

Iowa State University
Ames, Iowa
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Mathematical models for the growth of diploid populations with overlapping generations

Louis Jensen

Under the supervision of Edward Pollak
From the Department of Statistics
Iowa State University

We have examined the currently used model which describes the growth of a population with overlapping generations. The basic assumption for this model is that the population consists of only one type of individual, say females. The females in the population survive to different ages with known probabilities and produce offspring at known rates according to age. The offspring are identical to the parents. If the population contains males, all of the infants are credited to the adult females. We show that the females and males grow at the same asymptotic rate. The parameter which determines the rate of growth is only a function of the survival probabilities and the birth rates of the females.

A model for population growth which incorporates the fact that females and males form couples before reproduction occurs is developed. The function used to describe the formation of couples is a quantitative measure of the maximum number of couples formed.

In one case we are able to completely solve the equations which describe the growth of the population. This case is when
couples are formed between females and males of the same age. We must assume that the ratio of females to males at birth is a constant. We show that the females and males in the population grow at the same asymptotic rate. The parameter which determines the rate of growth is a function of the survival probabilities and the birth rates of both the females and males. Every descriptive quantity which can be calculated for the currently used model can be calculated for the new model.

We have incorporated polygamy into the mating structure, provided the females and males of the same age form couples. If the number of wives that any male can have is sufficiently large, the equations which describe the production of offspring are identical to the equations for the growth of a population which credits both types of offspring to the females.

If couples are formed arbitrarily according to the ages of the females and males, or if the ratio of females to males at birth is not constant, we cannot solve the equations which describe the growth of the population. We are able to construct upper bounds to the solutions. The bounds are the solutions to the equations which describe the production of offspring in the currently used models. Thus, the rate of growth of a bisexual population which forms couples is overestimated.

The stochastic models for the growth of populations with overlapping generations are the age-dependent branching
processes. If a population consists of females, the equation which describes the generating function of the size of the population is derived. If couples are formed in a population consisting of females and males, we are not able to find the generating function for the size of the population explicitly. We are able to show that the probability of extinction for a population which forms couples is at least the probability of extinction of a population which credits the offspring to either adult.
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I. INTRODUCTION

We are going to consider several types of models which are used to describe the growth of populations. The type of model used should reflect a degree of realism with respect to the physical properties of the individuals in the population. For example, the generations in a population may be overlapping or nonoverlapping. Mathematically, the structure of the generations is relatively easy to incorporate into models for growth. However, there are characteristics of populations which are very difficult to incorporate into mathematical models. In biological populations for example, the individuals of a given species show a vast amount of genetic variation among themselves. This type of variation will not be incorporated into the models we will consider. Thus, we will make the convenient assumption that all of the individuals behave in an identical manner.

Models for population growth fall into two categories, the deterministic and the stochastic. The deterministic models for population growth are very easy to manipulate mathematically, since once the initial growth cycle is set up, the population evolves in a predetermined manner. The stochastic models allow a certain degree of randomness to be included into the growth process. We will consider both types of models.
The simplest type of deterministic model would be as follows. Suppose that a population initially consisted of one individual. This individual lives one unit of time, dies and produces exactly \( k \) progeny identical to itself. If this life cycle is then repeated, the size of the population in generation \( n \) is \( k^n \), \( n = 0, 1, \ldots \). Thus, if \( k \) is known the progress of the growth of the population is completely determined. A variation on this model incorporates a degree of randomness into the production of offspring. Suppose the initial individual produces a random number of offspring, say \( v \), at the time of its death. Let the random variable \( v \) have a distribution according to the probability generating function 
\[
    f(s) = \sum_{k=0}^{\infty} P[v = k]s^k, \\
    |s| < 1.
\]
Since each generation produces a random number of offspring, the size of the population is random. If the random variable \( X_n \), \( n = 0, 1, \ldots \) denotes the size of the population in generation \( n \), with \( X_0 = 1 \), then it can be shown that the probability generating function of \( X_n \) is
\[
    f_n(s) = f(f_{n-1}(s)), \quad n = 2, 3, \ldots \text{ where } f_0(s) = s \quad \text{and} \quad f_1(s) = f(s).
\]
It is then easy to show that if \( m \) is the mean number of offspring produced in any generation, then \( m \) completely determines the mean rate of growth and whether or not the population becomes extinct. This is proved in Harris (1963). This type of growth model is known as the Galton-Watson process.
Although these two introductory models do not incorporate the property of overlapping generations, which many populations have, they do illustrate a common deficiency. In sexually reproducing individuals, it is not one individual that is responsible for the production of offspring; it is two individuals, a female and a male. In the following chapters we are going to set up models for population growth which attempt to incorporate the property that, in a bisexual population, the females and males must interact before reproduction occurs. We should keep in mind that the models which are currently used to describe the growth of bisexual populations, including the human population, do not, on the whole, take this fact into account.

There are a few mathematical models for population growth which do incorporate the interaction of the females and males before reproduction occurs. Daley (1968) constructs bivariate Galton-Watson processes which incorporate this property. However, most of the models do not. The model which is usually used to describe the growth of the human population does not take into account the fact that both the females and the males together are responsible for the production of offspring, since it credits all of the offspring to the females in the population.

In the following chapter we will examine the model which is currently used to describe the growth of a population
in which generations are overlapping. It is assumed that the population consists of one type of individual, called females. These individuals survive to different ages with known probabilities and they produce female and male offspring at known rates according to age. Since it is assumed that only one type of individual is in the population many mathematical properties of the model can be determined.

We will construct a deterministic model for the growth of a bisexual population with overlapping generations. In this model we will incorporate the formation of couples between adult females and males in the population. The function we will use to describe the formation of couples is only a quantitative measure of the number of couples available. It should be noted that we are not able to actually describe mathematically the formation of a female-male bond, only the number of couples formed.

If the couples are formed in a very restrictive sense, we are able to solve completely the equations which describe the growth of the population. In this case we are able to compare every mathematical result with the corresponding result found with respect to the currently used model. We are also able to predict that a population which forms couples grows at slower rate than a population that does not form couples. However, when the couples are formed arbitrarily according to the function which describes couples,
we cannot solve the equations which describe the growth of the population. We are able to construct upper bounds to the solutions in terms of the functions which are related to the currently used models.

The stochastic models for the growth of populations with overlapping generations which consist of a single type of individual are the single type age-dependent branching processes. We are able to construct an age-dependent branching process for the growth of a bisexual population in which couples are formed according to the quantitative measure we introduce for the number of couples formed. However, due to the nature of the nonlinearity of the process, we are only able to construct lower bounds to the extinction probabilities in terms of the extinction probabilities corresponding to single-type age-dependent branching processes.

The mathematical technique we will use to describe the growth of a population, is to consider the problem from the point of view of renewal theory (see, for example Feller (1968)). That is, the equations which describe the growth of the population will be integral equations. The alternative technique available to us is matrix analysis. However, once we obtain the basic results we require with respect to the integral equations found in renewal theory, the use of matrix analysis seems pointless. By considering the growth of a population as a problem in renewal theory,
we will be able to write one integral equation which con­tains all of the information about the population. This is more appealing than considering a large array of numbers.

It should be noted that this approach to the discrete time model is not given elsewhere in such complete generality. But Lotka (1939) and Feller (1941) have used renewal equations in their models which were continuous in time. The results we will obtain are identical to the results from matrix anal­ysis. The definitions we will give for various quantities will differ from those given by other writers, but the final results are identical. This is especially true in the sections dealing with the concept of the reproductive value.

The notation we will use is somewhat natural. Whenever the letter $F$ is used in a function, we will be referring to females, likewise any function containing an $M$ refers to males. Otherwise, functions dealing with descriptive quantities about the females and males will be defined alphabetically. For example if the letter $P$ refers to something about the females, then $Q$ will refer to the same thing involving the males.
II. CLASSICAL GROWTH MODELS

A. The Currently Used Models

In this section we shall derive a model which describes the growth of a population. It is the simplest model in the sense that it is assumed that a population consists of only one type of individual. These individuals produce progeny which are identical to the parent. This model, since it is so simple, has a very long history and has been discovered independently by many persons; one of the earliest people to give an account of some of its properties was Euler (1760).

The functions used to describe the parameters in this model can be either continuous or discrete. The continuous version was presented as early as 1911 by Sharpe and Lotka (1911). Some of the other persons who have described this model include Lotka (1922), Haldane (1927), Fisher (1930), Rhodes (1940) and Moran (1962). Lotka (1939) and Feller (1941) present extensive bibliographies on the use of this model. These references refer to many situations in which a model of this type is applicable. A more up-to-date bibliography is presented by Keyfitz (1968). This bibliography references the use of this model by the demographers. The discrete versions of a model of this type were first presented by Bernardelli (1941) and Lewis (1942), and, independently, by Leslie (1945, 1948).
The functions we will define which characterize our model can be discrete or continuous. In either case, the basic assumptions we will make about the population are the same. We will suppose that our population consists of only one type of individuals, say females, and that only female offspring are produced. The probability that a female survives to a given age is the same for every female. These probabilities will depend only upon the age of the female and not on the time the event occurs. We will also suppose that the rate at which new females are born into the population depend only upon the age of the parent. These rates are assumed to be the same for every parent in a specified age.

The equations we will derive which describe the growth of our population are called renewal equations. These equations can be derived under the assumption of continuity of the underlying process. However, we will assume that the process is discrete. If continuity is assumed, the describing equations are similar to the equations we will derive. In fact, the mathematical techniques used to solve either the discrete or continuous equations are the same. This was shown by Feller (1941). The techniques and theorems developed by Feller (1941, 1968) with regard to the solution of equation of these type will be used extensively and they will be introduced when needed.
The model we will now describe is essentially the model given by Leslie (1945). Leslie approaches the problem from the point of view of matrix analysis and the use of the spectral decomposition. The approach we will use is to consider the model as a problem in renewal theory.

If the individuals in a population are all of the same type, say females, we can classify them according to age. We will say that a female is in age group \(x\) at time \(t\), where \(x\) and \(t\) are nonnegative integers, if the age is in the interval \([x, x+1)\) at time \(t\). The population is assumed to be homogeneous; that is, all of the females in a given age group behave in an identical manner. Let

\[
F(t, x) = \text{number of females in age group } x \text{ at time } t
\]

\[
P(x) = P(\text{any female survives from birth to age group } x)
\]

\[
b_1(x) = E(\text{number of female offspring a female parent in age group } x \text{ at time } t \text{ contributes to age group } 0 \text{ at time } t+1).
\]

The age dependent survival probabilities and birth rates are assumed to be known. The unknown quantity we want to obtain is \(F(t, x), t = 1,2,... \text{ and } x = 0,1,...\).

The ancestral females, that is the females alive at time \(t = 0\), may have different survival probabilities and different birth rates. If, however, these rates are identical to the rates for the descendants, we will say that the population is uniform in time. The number of ancestral females in each age group is assumed to be known.
Let \( n \) be the maximum age of survival for any individual; that is, \( P(x) = 0 \) if \( x > n \). Also, let \( s \) be the maximum age in which reproduction occurs; thus, \( b_1(x) = 0 \) if \( x > s \). The number of females in age group 0 at time \( t, t > 0 \), is equal to the female offspring of the ancestral individuals alive at time \( t - 1 \), plus the female offspring of the live descendants of the ancestral individuals at time \( t - 1 \). That is,

\[
F(t, 0) = \begin{cases} 
F_0(t-1) + \sum_{x=0}^{t-2} b_1(x) F(t-1, x), & t = 1, 2, \ldots, s+1 \\
\sum_{x=0}^{s} b_1(x) F(t-1, x), & t = s+2, s+3, \ldots 
\end{cases}
\]

(2.1)

where we will define \( \sum_{x=0}^{0} = 0 \). The expression \( F_0(t) \), \( t = 0, 1, \ldots, s \), denotes the female offspring of the ancestral individuals alive at time \( t \). Let us note that any female whose age is greater than \( s \) does not reproduce; thus Equation 2.1 follows. In these equations we have summed over the integers \( x \) between 0 and \( s \); clearly these summations are not minimal. For example, it might be reasonable to assume that \( b_1(0) = 0 \); that is, females in age group 0 do not reproduce. Thus, the summation should be over the set of integers \( x \in \mathbb{R} \) where \( R = \{x: b_1(x) > 0\} \) is the set of positive fertility. In the following pages, whenever we
sum over the consecutive integers between 0 and s it is to be understood that the summation is over the elements of the set R.

If we had supposed that the descriptive quantities in Equation 2.1 were continuous, then the analogous equation would be a Volterra integral equation of the second kind. This type of equation is also an example of the basic renewal equation as discussed in, for example, Feller (1966, 1968).

Equation 2.1 contains too many unknowns for us to obtain a solution at the moment. However, let us note that the females in age group x at time t are the females in age group 0 at time t - x that survive to reach age group x, if x \leq t. If x > t, the females in age group x at time t are the ancestral females in age group x - t at time 0 that survive to age group x, conditional on the event that they have survived to reach age group x - t. That is,

\[
F(t, x) = F(t-x, 0) P(x), \quad x \leq t
\]

\[
= F(0, x-t) P(x)/P(x-t), \quad x > t
\]

(2.2)

If we substitute Equations 2.2 into Equations 2.1 we have
\[
F(t, 0) = \begin{cases} 
F_0(t-1) + \sum_{x=0}^{t-2} b_1(x) P(x) F(t-x-1, 0), & \text{if } t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b_1(x) P(x) F(t-x-1, 0), & \text{if } t = s+2, s+3, \ldots,
\end{cases}
\]

where we have defined \( \sum_{x=0}^{-1} = 0 \). If the population is uniform in time then

\[
F_0(t) = \sum_{y=0}^{s-t} b_1(y+t) F(0, y) P(y+t)/P(y), \quad (2.4)
\]

\[
t = 0, 1, \ldots, s
\]

\[
= 0, \text{ otherwise.}
\]

Equation 2.3 is in a form that we can obtain a solution, since this equation is a linear function of the unknowns \( F(., 0) \).

The original formulation of this discrete model, as given by Lewis (1942), Leslie (1945, 1948) and presumably by Bernardelli (1941), was different than the formulation presented here. Let all of the notation introduced previously carry over, except that let \( p_x^t, x = 0, 1, \ldots, n-1 \), denote the probability that any female in age group \( x \) at time \( t \) survives to age group \( x+1 \) at time \( t+1 \). The relationship between \( P(x) \) and \( p_x^t \) is given by
\[ P(x) = \prod_{k=0}^{x-1} p_k, \quad x = 1, 2, \ldots, n, \quad \text{with} \quad P(0) = 1. \]

The results summarized by Equations 2.1 and 2.2 can also be written as

\[ F(t, 0) = \sum_{y=0}^{s} b_1(y) F(t-1, y) \]
\[ F(t, 1) = p_0 F(t-1, 0) \]
\[ F(t, 2) = p_1 F(t-1, 1) \]
\[ \vdots \]
\[ F(t, n) = p_{n-1} F(t-1, n-1), \]

for \( t = 1, 2, \ldots \). In matrix notation, considering only the ages in which reproduction takes place, these equations can be expressed as

\[ F(t) = AF(t-1), \quad t = 1, 2, \ldots \]

Where \( F(t) \) is the column vector

\[ F(t) = \{F(t, 0), F(t, 1), \ldots, F(t, s)\}^t \]

and \( A \) is a square matrix with elements

\[
A = \{ a_{xy} \} = \begin{cases} 
  b_1(y) & \text{if } x = 0 \\
  p_y & \text{if } x = y + 1 \\
  0 & \text{otherwise}, 
\end{cases}
\]
for $x, y = 0,1,\ldots,s$. Thus, we have that

$$F(t) = A^t F(0), t = 0,1,\ldots.$$  

Leslie (1945) constructed the spectral decomposition of the matrix $A$. However, a direct analysis of Equation 2.3 is possible and, at least to this writer, is more informative than the matrix decomposition approach.

B. Theoretical Results

Let us consider the form of Equation 2.3 in more detail. This equation can be written more generally as an integral equation having the form

$$u(t) = g(t) + \int_0^t u(t-x) h(x) \, d\mu[x]$$  

where $g(t)$ and $h(t)$ are known nonnegative functions.

We want to solve for the unknown function $u(t)$. The measure $\mu[\cdot]$ can be arbitrary, although we will be particularly interested in the case in which $\mu[\cdot]$ is the ordinary counting measure. For the results we desire, the structure of the measure is not important. It is the form of the equation that interests us. Equation 2.3a certainly has the same form as this integral equation. However, let us now look at Equation 2.3b. This equation can be written more generally as
\[ u(t) = \int_{0}^{\infty} u(t-x) h(x) \, d\mu[x], \quad \text{(II)} \]

for \( t \) sufficiently large.

If an equation having the same form as Equations I and II arose, many writers in the current literature state and solve Equation II. This equation is solved with the restriction that the solution reduces, for \( t \) small, to an arbitrarily prescribed function. Such a function, as we know, exists only under very special conditions. It is obvious that Equation II is not equivalent to Equation I, which is the much more general equation since it contains all of the information about the process we are trying to describe.

In Equation 2.3, we require, for \( t \) small, that the solution reduce to the offspring of the ancestral individuals occurring initially. The reason why many writers want to only consider the form of the general integral equation given by Equation II becomes evident if we examine Equation 2.3b in detail. This equation is an ordinary linear difference equation with constant coefficients, and equations of this type are easy to solve, at least in theory.

Feller (1941) became concerned about the existence and uniqueness of solutions having the form of Equation I, since the integral equation is incompletely stated if only Equation II is given. Feller showed that the correct equation to be considered is the more general integral equation given by
Equation I. It should be noted that Lotka (1939), recognized the existence of some of the difficulties which concerned Feller. In his 1939 paper he constructed the solution to his integral equation by considering the more general equation corresponding to Equation I.

The results that Feller (1941) obtained will be very useful to us. By assuming a very general hypothesis about the functions $g(t)$ and $h(t)$ occurring in Equation I and by using the Laplace transform, Feller proved two very useful theorems which deal with the existence, uniqueness, and the construction of the solution to integral equations having the form of Equation I. We will omit the proofs. The theorems we will state are respectively theorems 2 and 6 in Feller's paper. If $\mu[\cdot]$ is the counting measure, an alternative proof to Feller's theorem 6 can be found in Feller (1968). This alternate proof is based upon the theory of recurrent events. The theorems we will use are as follows.

**THEOREM:**

Let us suppose that $g(t)$ and $h(t)$ are $\mu$-measurable, non-negative, and bounded in every finite closed interval $0 \leq t \leq T$. Also, let us suppose that the integrals

$$\phi(r) = \int_0^\infty e^{-rt} h(t) \, d\mu[t] \quad \text{and} \quad \gamma(r) = \int_0^\infty e^{-rt} g(t) \, d\mu[t]$$
converge at least for $r > r^*$. Then there exists a unique solution $u(t)$ to Equation I which is bounded in every finite interval. With this function the integral

$$\omega(r) = \int_0^\infty e^{-rt} u(t) \, dt$$

converges at least for $r > r'$, where $r' = r^*$ if $\phi(r) \leq 1$ as $r \to r^* + 0$, and otherwise $r' > r^*$ is the solution to the characteristic equation $\phi(r) = 1$. For $r > r'$ it is true that

$$\omega(r) = \frac{\gamma(r)}{1-\phi(r)} .$$

**Theorem:**

The solution $u(t)$ to Equation I can be represented as an absolutely convergent series

$$u(t) = \sum_k A_k \exp(r_k t), \quad \text{for } t \geq 0,$$

where the $A_k$ are complex constants and the $r_k$ denote the distinct roots of the characteristic equation $\phi(r) = 1$, if and only if the Laplace transform $\omega(r)$ has an expansion of the form

$$\omega(r) = \frac{\gamma(r)}{1-\phi(r)} = \sum_k \frac{A_k}{r-r_k}$$

where $\sum |A_k|$ converges absolutely. The coefficients $A_k$ are determined by
\[ A_k = -\gamma(r_k)/\phi'(r_k) \]

where

\[ \phi'(r_k) = \left. \frac{d}{dr} \phi(r) \right|_{r = r_k} \]

In particular, it is necessary that \( \omega(r) \) be a single valued function. The number of roots of the characteristic equation may be finite or infinite.

If the characteristic equation has multiple roots there is an analogous result. That is, the Laplace transform \( \omega(r) \) is required to have an expansion of the form

\[ \omega(r) = k \left( \frac{A_k^{(1)}}{(r-r_k)} + \frac{A_k^{(2)}}{(r-r_k)^2} + \ldots + \frac{A_k^{(m_k)}}{(r-r_k)^{m_k}} \right), \]

where \( m_k \) is the multiplicity of the root \( r_k \). This leads formally to the solution \( u(t) \) having the expansion

\[ u(t) = \sum_k \exp(r_k t) \left( A_k^{(1)} + \frac{A_k^{(2)} t}{1!} + \ldots + \frac{A_k^{(m_k)} t^{m_k-1}}{(m_k-1)!} \right). \]

C. The Solution

We could set up Equation 2.3 in terms of a Lebesque-Stieltjes integral and use results from measure theory. However, we live in the age of the computer so that, computationally, all functions are discrete. Thus, we will only use the results from measure theory and not its notation.

These two theorems are clearly applicable, since the
known functions $F_0(\cdot)$, $b_1(\cdot)$ and $P(\cdot)$ are bounded, non-negative and measurable, with respect to the counting measure in our formulation. We will use these theorems to solve Equation 2.3. Let:

$$w(r) = \sum_{y=1}^{\infty} e^{-ry} F(y, 0)$$

$$\phi(r) = \sum_{y=0}^{\infty} e^{-r(y+1)} b_1(y) P(y)$$

$$\gamma(r) = \sum_{y=1}^{\infty} e^{-ry} F_0(y-1) .$$

If we take the Laplace transform of Equation 2.3 we have that

$$w(r) = \gamma(r) + \sum_{t=1}^{\infty} \sum_{x=0}^{t-2} e^{-rt} b_1(x) P(x) F(t-x-1, 0)$$

$$= \gamma(r) + \sum_{x=0}^{\infty} \sum_{t=x+2}^{\infty} e^{-rt} b_1(x) P(x) F(t-x-1, 0)$$

$$= \gamma(r) + \sum_{x=0}^{\infty} \sum_{y=1}^{\infty} e^{-r(x+y+1)} b_1(x) P(x) F(y, 0)$$

$$= \gamma(r) + \sum_{x=0}^{\infty} e^{-r(x+1)} b_1(x) P(x) \sum_{y=1}^{\infty} e^{-ry} F(y, 0)$$

$$= \gamma(r) + w(r) \phi(r) .$$

In the above manipulations, we have interchanged the order of summation, we have changed the index of summation by letting $y = t - x - 1$, and we have used the convolution
property of the Laplace transform.

We have that

\[ \omega(r) = \frac{\gamma(r)}{1 - \phi(r)}. \]

Thus, according to Feller's results we have that

\[ F(t, 0) = \sum F_k \exp(r_k t) \]

where the \( F_k \) are constants and \( r_k, k = 0,1,\ldots \), are the solutions to the characteristic equation \( \phi(r) = 1 \) and the constants are given by

\[ F_k = -\gamma(r_k)/\phi'(r_k), \quad k = 0,1,\ldots, \]

provided the solutions to \( \phi(r) = 1 \) are distinct.

Since we are dealing with a discrete process, we have, if we let \( r = \ln \omega \) that

\[ F(t, 0) = \sum F_k \mu_k^t \quad \text{(2.5)} \]

where \( \mu_k, k = 0,1,\ldots \) are the distinct solutions to the characteristic equation

\[ \phi(\mu) = \sum_{k=0}^{\infty} \mu^{-(x+1)} b_1(x) P(x) = 1 \quad \text{(2.6)} \]

and the constants are given by

\[ F_k = \sum_{x=1}^{s+1} \frac{\mu_k^{-x} F_0(x-1)}{\mu_k^{-(x+1)} b_1(x) P(x)} \quad \text{(2.7)} \]

for \( k = 0,1,\ldots \).
When \( t \to \infty \), we would like to know under what conditions the solution to Equation 2.3 is characterized by the first term in the series in Equation 2.5. That is, what are the solutions to the characteristic equation \( \phi(\mu) = 1 \)? For \( \mu \geq 0 \), \( \phi(\mu) \) is a monotonically decreasing function of \( \mu \). Thus, there exists only one positive \( \mu \), say \( \mu_0 \), such that \( \phi(\mu_0) = 1 \). All of the other solutions are either negative or complex. This result can also be obtained directly by using Descartes' rule of signs.

Thus, we have that there exists only one \( \mu_0 > 0 \) such that \( \phi(\mu_0) = 1 \), and obviously

\[
\mu_0 \leq 1 \text{ whenever } \phi(1) \leq 1.
\]

Let us note that

\[
\phi(1) = \sum_{x=0}^{S} b_1(x) P(x)
\]

is the expected number of total female offspring produced by any female during her length of life.

If the first term in the series of Equation 2.5 is to be dominant we would like to show that the other solutions of the characteristic equation are less, in absolute value, than \( \mu_0 \). Let \( \mu_j \) be any other solution of \( \phi(\mu) = 1 \). This solution is either negative or complex. We want to show that
\[ |\mu_j| < \mu_0, \text{ for any other solution } \mu_j. \]

Now, we have
\[ \mu_j = \rho e^{i\theta} = \rho (\cos \theta + i \sin \theta), \rho > 0, \]
and \( \phi(\rho e^{i\theta}) = 1. \) Thus, by equating real and imaginary parts of the characteristic equation, we have that
\[
1 = \sum_{x=0}^{s} \rho^{-(x+1)} \cos((x+1)\theta) b_1(x) P(x)
\]
and
\[
0 = \sum_{x=0}^{s} \rho^{-(x+1)} \sin((x+1)\theta) b_1(x) P(x).
\]
Since \( \cos((x+1)\theta) \leq 1 \) for any \( \theta \) and \( x \in \mathbb{R} \) we have
\[
1 \leq \sum_{x=0}^{s} \rho^{-(x+1)} b_1(x) P(x). \tag{2.9}
\]

We want to show that the inequality is strong. The proof will be by contradiction. However we must first make an assumption about \( R, \) the set of positive fertility. Leslie (1945) assumed that the females are fertile for at least two consecutive ages; that is, there is an \( x_0 \in R \) such that \( b_1(x_0) > 0 \) and \( b_1(x_0+1) > 0. \) We will make this assumption.

To show that the Inequality 2.9 is strong, let us suppose in Equation 2.8 that \( \cos((x_0+1)\theta) = 1 \) and \( \cos((x_0+2)\theta) = 1. \) Then \((x_0+1)\theta\) and \((x_0+2)\theta\) are both integer multiples of \( 2\pi; \) that is, \((x_0+1)\theta = k_12\pi\) and \((x_0+2)\theta = k_22\pi\) where \( k_1 \) and \( k_2 \) are integers. By subtraction, \( \theta = 2(k_2-k_1)\pi, \) which is
a multiple of $2\pi$. This is a contradiction, since we supposed that $\mu_j$ was negative or complex. Therefore $\rho < \mu_0$ or $|\mu_j| < \mu_0$.

We have shown that if there is an integer $x_0$ such that $b_1(x_0) > 0$ and $b_1(x_0 + 1) > 0$, then $\mu_0$ is the unique positive real solution of $\phi(\mu) = 1$ and all other solutions are negative or complex and have absolute value less than $\mu_0$. This is a sufficient condition. Sykes (1969) also gives a necessary condition. He proves the following

**THEOREM:**

There is only one positive real solution to the characteristic equation which is larger in absolute value than any other solution if and only if the greatest common divisor of all of the elements of $R$ is unity; that is, fertility is not a periodic function of age. The other solutions to the characteristic equation are either negative or complex.

The results of this theorem tell us some of the properties of the matrix $A$ introduced previously. This matrix has nonnegative elements and is called a nonnegative matrix. If fertility is not a periodic function of age, then this matrix is also irreducible (see, for example, Gantmacher (1959) or Karlin (1966) for the definitions). Nonnegative irreducible matrices have a very interesting characterization,
which is given by a theorem due to Perron and Frobenius (Gantmacher (1959)). This theorem says that any irreducible nonnegative matrix has a positive eigenvalue that is a simple root of the characteristic equation. This eigenvalue is larger in absolute value than any other eigenvalue of the matrix. The left and right eigenvectors corresponding to this eigenvalue can be chosen to have positive elements. This is an existence theorem corresponding to the spectral decomposition of the matrix $A$. Thus, we have that $A^t$, for $t$ sufficiently large, is given by the term in the spectral decomposition of the matrix $A$ corresponding to the maximal eigenvalue. The results of this theorem are applicable. Let us, however, return to our original formulation of the problem.

The solution to Equation 2.3, provided fertility is not a periodic function of age, is characterized by

$$F(t, 0) \sim F \mu_0^t, \quad t \to \infty$$  \hspace{1cm} (2.10)

where $F$ is a constant. By the symbol $\sim$ we mean that the left hand side of Equation 2.10 divided by the right hand side converges to unity as $t \to \infty$ through integer values. The constant $F$ is given by Equation 2.7, that is

$$F = \sum_{x=1}^{s+1} \mu_0^{-x} F_0(x-1) / \sum_{x=0}^{s} (x+1) \mu_0^{-(x+1)} b_1(x) P(x)$$  \hspace{1cm} (2.11)

and $\mu_0$ is the dominant positive real solution to
Thus, for $t$ sufficiently large we know the number of females in age group 0, provided we know the ancestors. Also, the number of females in age group 0 grows geometrically if $\mu_0 > 1$, remains constant if $\mu_0 = 1$, and the population becomes extinct if $\mu_0 < 1$, as $t \to \infty$. That is, the population grows, remains constant, or becomes extinct whenever the expected number of total offspring produced by any female during her life is greater than, equal to, or less than one.

The number of females in age group $x$ at time $t$ is obtained by using Equation 2.2. We have that

$$F(t, x) = F(t-x, 0) P(x), \ t \geq x$$

$$\sim F [\mu_0^{t-x} P(x), \ t \to \infty, \ (2.12)$$

for $x = 0, 1, \ldots, n$. The total number of females alive at time $t$ is

$$\sum_{y=0}^{n} F(t, y) \sim F [\mu_0^t \sum_{y=0}^{n} \mu_0^{-y} P(y), \ t \to \infty]. \ (2.13)$$

Let $f(t, x)$ denote the proportion of live females in age group $x$ at time $t$,

$$f(t, x) = F(t, x) / \sum_{y=0}^{n} F(t, y).$$

From Equations 2.12 and 2.13 we have that
\[ f(t, x) + f(x) = \mu_0^{-x} P(x) \sum_{y=0}^{n} \mu_0^{-y} P(y), \ t \to \infty \]  

for \( x = 0, 1, \ldots, n \), which says that for \( t \) sufficiently large, the distribution of females in age group \( x \) is a known function of age. Let us note that this is a stable age distribution since it does not depend upon the structure of the population of the ancestral females.

If the assumptions used in setting up this model for population growth are valid, then the growth rate and the other descriptive functions we have derived will describe the growth of the population. A model of this type is certainly valid for some populations which reproduce asexually. However, we must keep in mind that this model is currently used to describe the growth of many populations, including the human population. For a bisexual population, such as the human population, the role of the males and the reproduction cycle necessary for population growth, with respect to this model, is not at all clear.

Fisher (1930) derived many of the results we have given, although his model was continuous in all of the variables. He recognized that the main difficulty in this model is that it does not accurately take into account the role of reproduction for a bisexual population. With this difficulty in mind, Fisher says that in order to credit an offspring to both parents it is appropriate to credit each parent with
one half of each offspring produced. This is with respect to nonsex-linked characteristics. Possibly, Fisher had in mind that we could obtain a good approximation to the growth of a bisexual population by considering the growth of a population consisting only of females and a population consisting only of males. The progeny would be credited one half to each parent. However, it is not at all clear how Fisher envisioned the females and males to interact so that progeny could be produced.

Sharpe and Lotka (1911) considered the integral equation analogous to Equation 2.3. They found the asymptotic solution to their integral equation in the form $K \exp(r_0 t)$ analogous to Equation 2.10 where $r_0$ is the dominant solution to their characteristic equation and $K$ a constant. They also noted that there was a stable age distribution. The constant $K$ was found by Dublin and Lotka (1925) and Lotka (1939) using a complicated technique developed by Hertz (1908) and Herglotz (1908). The correct form of the constant was also found by Norton (1926) using successive approximations.

Many of the results presented for the discrete process have also been obtained by Leslie (1945, 1948) and by Goodman (1967, 1969) using the spectral decomposition of the matrix $A$ introduced previously. These results have also been derived by Pollak and Kempthorne (1970) using a combination of difference equations and matrices. However, the elegant theory
presented by Feller (1941) shows how simply solutions to a large class of integral equations can be constructed.

D. The Reproductive Value

The concept of the value of an individual in a population was introduced by Fisher (1930). Fisher constructed an analogy between the growth of a population and the growth of capital invested at compound interest. He regarded the birth of a child as the loaning to him of life. If this child later produced offspring, then this would be regarded as the payment of the debt. Fisher enlarges his analogy by considering not only the offspring newly born into the population, but the adults in any age group. He poses the following question: What will an individual in a given age group contribute to the ancestry of future generations? The answer to this question is given by the "reproductive value" of an individual. It should be noted that use of the word value as pertaining to Fisher's analogy is at least as old as De Moivre (1756). De Moivre uses the word value with respect to the investment of capital in the form of an annuity.

Let us recall the argument we used in deriving Equation 2.1. We said that at time $t$, the number of individuals in age group 0 are the offspring of the ancestral individuals alive at time $t - 1$, plus the offspring of the descendants of
the ancestral individuals at time $t - 1$. If we want to measure the contribution of an ancestor to the development of future generations, we must consider in detail the nonhomogeneous term in Equation 2.1. That is, the term which is a function of the ancestral individuals. This term is $F_0(t)$ which is defined explicitly in Equation 2.4. If we go back and follow this term throughout the construction of the solution to Equation 2.1, we will find that this term occurs only in the constant $F$ in Equation 2.10.

Let us consider this constant $F$ in more detail. This constant is explicitly defined by Equation 2.11. We found that

$$F = v \sum_{x=1}^{s+1} \mu_0^{-x} F_0(x-1)$$

where we will define

$$\frac{1}{v} = \sum_{x=0}^{s} (x+1) \mu_0^{-(x+1)} b_1(x) P(x)$$

and

$$= \sum_{x=0}^{s} x \mu_0^{-(x+1)} b_1(x) P(x) + 1$$

and where

$$F_0(x-1) = \sum_{y=0}^{s-x+1} b_1(x+y-1) P(0, y) P(y+x-1)/P(y)$$

for $x = 1, 2, \ldots, s+1$, denotes the number of female offspring contributed to the population by the ancestral individuals alive at time $x - 1$, provided the population is uniform in
time. It is interesting to speculate whether or not the constant $F$ can be represented as

$$F = \sum_{x=0}^{s} v(x) F(0, x);$$  \hspace{1cm} (2.15)

that is, as a linear combination of the number of ancestral females in the different age groups. If this can be done, then $v(x)$ would be a measure of the "reproductive value" of an ancestral female in age group $x$ with respect to the females in the stable age distribution. This is conditional on there being at least one ancestral female in age group $x$, $x \in \mathbb{R}$. We have

$$F = \sum_{x=1}^{s+1} \mu_0^{-x} F_0(x-1)$$

$$= \sum_{x=1}^{s+1} \mu_0^{-x} \sum_{y=0}^{s-x+1} b_1(y+x-1) F(0, y) P(y+x-1)/P(y)$$

by interchanging the order of summation. Thus,

$$v(z) = \text{coefficient of } F(0, z) \text{ in } F$$

$$= \sum_{x=1}^{s-z+1} \mu_0^{-x} b_1(z+x-1) P(z+x-1)/P(z)$$
where we have substituted $y = z + x - 1$. That is, the reproductive value of an ancestral female in age group $x$ is

$$v(x) = \frac{v \mu_0^x}{P(x)} \sum_{y=x}^{s} \mu_0^{-(y+1)} b_1(y) P(y), \quad x = 0, 1, \ldots, s$$

where we have defined $v(x) = 0$ if $x > s$, since any female of age greater than $s$ does not reproduce. Let us note that $v(0) = v$ or

$$\frac{1}{v(0)} = \sum_{x=0}^{s} (x+1) \frac{\mu_0^{-(x+1)} b_1(x) P(x)}{P(x)} \quad (2.17)$$

Thus, Equation 2.16 can be rewritten as

$$v(x) = \frac{v(0) \mu_0^x}{P(x)} \sum_{y=x}^{s} \mu_0^{-(y+1)} b_1(y) P(y), \quad x = 0, 1, \ldots, s$$

where we have defined $v(x) = 0$ if $s + 1, s + 2, \ldots, n$, (2.16)

The concept of value was first introduced by Fisher (1930) using a continuous model. Leslie (1948) also used the concept of value in his matrix algebra approach.
However, he only considered the ratio \( v(x)/v(0) \) and did not recognize the meaning of \( V(0) \) given in Equation 2.17.

Goodman (1967, 1969) was the first to derive correctly \( v(x) \), \( x = 0, 1, \ldots, s \), for the matrix algebra problem corresponding to Equations 2.2 and 2.3. In fact, the proportion of females in age group \( x \) in the stable age distribution, \( f(x) \) in Equation 2.14, and the value \( v(x) \) are related. Goodman (1967, 1969) shows that the vectors \( \{f(0), f(1), \ldots, f(x)\} \) and \( \{v(0), v(1), \ldots, v(s)\} \) are respectively the right and left eigenvectors corresponding to the eigenvalue \( \mu_0 \) of the matrix \( A \) introduced previously. These results are also shown to be correct by Pollak and Kempthorne (1971) using a different approach.

Fisher (1930) also introduced the concept of a total reproductive value for females alive at time \( t \). In terms of our notation this quantity is

\[
V(t) = \sum_{x=0}^{s} F(t, x) v(x), \quad t \geq 0. \tag{2.19}
\]

Let us note that \( V(0) = F \) from Equation 2.15. Now we have

\[
\Delta V(t) = V(t+1) - V(t)
= \sum_{x=0}^{s} F(t+1, x) v(x) - \sum_{x=0}^{s} F(t, x) v(s).
\]

The females in age group \( x > 0 \) at time \( t + 1 \) are the females alive in age group \( x - 1 \) at time \( t \) that survive
to age group \( x \). The females alive in age group 0 at time \( t + 1 \) are the offspring of the females alive at time \( t \).

Thus we have that

\[
\Delta V(t) = \sum_{x=1}^{s} F(t, x-1) v(x) \frac{P(x)}{P(x-1)} + \sum_{y=0}^{s-1} F(t, y) b_1(y) - \sum_{x=0}^{s} F(t, x) v(x)
\]

\[
= \sum_{x=0}^{s-1} F(t, x) v(x+1) \frac{P(x+1)}{P(x)} + \sum_{y=0}^{s} F(t, y) b_1(y) - \sum_{x=0}^{s} F(t, x) v(x).
\]

(2.20)

But, from Equation 2.18, we have

\[
v(x) = \frac{v(0) \mu^x}{P(x)} \sum_{y=x}^{s} \frac{\mu_0^{-y+1}}{b_1(y)} P(y)
\]

so that

\[
V(x+1) = \frac{v(0) \mu_0^x}{P(x+1)} \sum_{y=x+1}^{s} \frac{\mu_0^{-y+1}}{P(y)} b_1(y) P(y)
\]

\[
= \frac{v(0) \mu_0^x}{P(x+1)} \left\{ \sum_{y=x}^{s} \frac{\mu_0^{-y+1}}{b_1(y)} P(y) \right\}
- \mu_0^{-x+1} b_1(x) P(x)
\]

\[
= \frac{P(x)}{P(x+1)} \left\{ \frac{v(0) \mu_0^x}{P(x)} \sum_{y=x}^{s} \frac{\mu_0^{-y+1}}{b_1(y)} P(y) \right\}
\]
\[- v(0) b_1(x) \}

\[
= \frac{P(x)}{P(x+1)} \{ v(x) - v(0) b_1(x) \},
\]

\[x = 0,1,\ldots,s-1\]

or

\[
v(x+1) P(x+1)/P(x) = v(x) - v(0) b_1(x),
\]

\[v(x+1) P(x+1)/P(x) = \mu_0 v(x) - v(0) b_1(x), \quad (2.21)\]

\[x = 0,1,\ldots,s-1.\]

If we substitute this expression into Equation 2.20 we have

\[
\Delta V(t) = \mu_0 \sum_{x=0}^{s-1} F(t, x) v(x) - \sum_{x=0}^{s-1} F(t, x) b_1(x)
\]

\[+ v(0) \sum_{x=0}^{s} F(t, x) b_1(x) - \sum_{x=0}^{s} F(t, x) v(x)\]

\[= (\mu_0 - 1) \sum_{x=0}^{s} F(t, x) v(x) + F(t, s) \{ v(0) b_1(s) \]

\[- \mu_0 v(s) \} .
\]

However, if we evaluate Equation 2.18 at \(x = s\) we have

\[
\mu_0 v(s) = v(0) b_1(s), \text{ so that }
\]

\[
\Delta V(t) = (\mu_0 - 1) V(t), \quad t \geq 0 . \quad (2.22)
\]

This result was first given by Pollak and Kempthorne (1971) and it is the discrete version of the original given by
Fisher (1930, p. 30). That is, the rate of change in the total reproductive value increases if \( u_0 - 1 > 0 \), decreases if \( u_0 - 1 < 0 \), or if zero is \( u_0 - 1 = 0 \).

The number \( u_0 - 1 \) is the discrete analogue of what Fisher calls the Malthusian parameter of population growth. Fisher named this number after the English economist, T. R. Malthus who lived from 1766 to 1843. The name Malthusian parameter is somewhat appropriate since Malthus predicted that populations would grow geometrically unless checked by some external force. It should be noted that the ideas underlying the concept of the geometric growth of a population are not entirely due to Malthus. Two centuries before Malthus, Botero (1588) realized that populations would grow geometrically unless external forces were effecting the growth.

The concept of the existence of a Malthusian parameter is appealing in that all of the information regarding the eventual growth of a population is given by one number. However, we must remember that this number refers to a population in which the two functions which describe the births and the survival probabilities are constants with respect to the time variable.
E. A Two Sex Model

In the previous sections we have been concerned with a model in which we supposed that a population consisted of only one type of individual, and these individuals produced progeny which are identical to the parent. We can make a slight variation on this model and describe the growth of a population which consists of two different types of individuals. Let us suppose that a population consists of two types of individuals, say females and males, and that both types of progeny are produced. However, the progeny are produced in such a way that they are only credited to the adult females in the population. The adult males take no part in reproduction.

Let all of the notation introduced to describe the female population remain unchanged. However, let

\[ M(t, x) = \text{number of males in age group } x \text{ at time } t \]
\[ Q(x) = P(\text{any male survives from birth to age group } x) \]
\[ b_2(x) = E(\text{number of male offspring a female parent in age group } x \text{ at time } t \text{ contributes to age group } 0 \text{ at time } t + 1). \]

Since, according to this model, we have that both female and male offspring are attributed to only the adult females we can easily write down the renewal equations which describe the production of female and male offspring. The
equation which describes the production of female offspring is Equation 2.3. This equation is

\[
F(t, 0) = \begin{cases} 
F_0(t-1) + \sum_{x=0}^{t-2} b_1(x) P(x) F(t-x-1, 0), & \text{if } t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b_1(x) P(x) F(t-x-1, 0), & \text{if } t = s+2, s+3, \ldots,
\end{cases}
\]

(2.23)

where \( F_0(t), t = 0, 1, \ldots, s \), denotes the number of female offspring of the ancestral females alive at time \( t \). The number of male offspring in age group 0 at time \( t \) is equal to the male offspring of the ancestral females alive at time \( t-1 \) plus the male offspring of the descendants of the ancestral females alive at time \( t-1 \). That is,

\[
M(t, 0) = \begin{cases} 
M_1(t-1) + \sum_{x=0}^{t-2} b_2(x) P(x) F(t-x-1, 0), & \text{if } t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b_2(x) P(x) F(t-x-1, 0), & \text{if } t = s+2, s+3, \ldots.
\end{cases}
\]

(2.24)

In this renewal equation \( M_1(t), t = 0, 1, \ldots, s \), represents the male offspring of the ancestral females alive at time \( t \).
If the population is uniform in time this function is

\[ M_1(t) = \sum_{y=0}^{t} b_2(y+t) F(0, y) \frac{P(y+t)}{P(y)}, \]

\[ t = 0, 1, \ldots, 3, \]

\[ = 0, \text{ otherwise}, \]

which is similar to Equation 2.4. Let us note that the right hand side of Equations 2.23 and 2.24 are not functions of the males in the population.

We have already found the solution to Equation 2.23. The solution is characterized by Equation 2.10, that is,

\[ F(t, 0) \sim F \mu_0^t, \quad t \rightarrow \infty \]

(2.25)

where \( F \) is a constant and \( \mu_0 \) is the dominant positive real solution to the characteristic equation \( \phi(\mu) = 1 \), defined by Equation 2.6. The constant \( F \) is stated in Equation 2.11.

We can use Equation 2.25 to solve Equation 2.24, since the right hand side of Equation 2.24 is only a function of \( F(t, 0) \). If we substitute Equation 2.25 into Equation 2.24 we find that

\[ M(t, 0) \sim F \mu_0^t \sum_{x=0}^{S} \mu_0^{-(x+1)} b_2(x) P(x), \quad t \rightarrow \infty \]

since \( M_1(t) = 0 \) for \( t \) sufficiently large. That is,

\[ M(t, 0) \sim M \mu_0^t, \quad t \rightarrow \infty \]

(2.26)

where \( M \) is a constant and \( \mu_0 \) is the solution which is
larger in absolute value than any other solution to the characteristic equation \( \phi(\mu) = 1 \), given by Equation 2.11. The constant \( M \) is

\[
M = F \sum_{x=0}^{s} \mu_0^{-(x+1)} b_2(x) P(x).
\]

Equations 2.25 and 2.26 show that the numbers of infant females and males in the population at time \( t \) grow at the same rate, for \( t \) sufficiently large. This rate of growth is determined by the implicit growth rate \( \mu_0 \), which is only a function of the females in the population.

Equation 2.26 describes the number of males in age group 0 at time \( t \). We must find a way to describe the number of males in the other age groups at time \( t \). We can compute this number if we can find the sex ratio of females to males at birth. Let

\[
S(t, x) = F(t, x)/M(t, x)
\]

denote the sex ratio at time \( t \) for females and males in age group \( x \). The sex ratio at birth is

\[
S(t, 0) = F(t, 0)/M(t, 0)
\]

\[
+ \frac{1}{S} \sum_{x=0}^{s} \mu_0^{-(x+1)} b_2(x) P(x), \quad t \to \infty \tag{2.27}
\]

\[
= 1/S, \text{ say}
\]
where we have used the results from Equations 2.25 and 2.26. Let us note that if $b_1(\cdot) = b_2(\cdot)$ then $S(t, 0) \to 1$ as $t \to \infty$, since the denominator in Equation 2.27 would be the characteristic equation $\phi(\mu_0) = 1$.

We can now find the number of males in the different age groups at time $t$. The males in age group $x$ at time $t$ are the males in age group $0$ at time $t - x$ that survive to age group $x$. That is,

$$M(t, x) = M(t-x, 0) Q(x), \quad t > x.$$ 

Thus, we have

$$M(t, x) = F(t-x, 0) Q(x)/S(t-x, 0), \quad t > x$$

$$\sim S F \mu_0^{t-x} Q(x), \quad t \to \infty$$

(2.28)

for $x = 0, 1, \ldots, n$. If we let $m(t, x)$ denote the proportion of live males in age group $x$ at time $t$, we have

$$m(t, x) = M(t, x)/\sum_{y=0}^{n} M(t, y).$$

So, analogous to Equation 2.14 we have that

$$m(t, x) + m(x) = \mu_0^{-x} Q(x)/\sum_{y=0}^{n} \mu_0^{-y} Q(y), \quad t \to \infty$$

(2.29)

for $x = 0, 1, \ldots, n$. That is, the proportion of males in age group $x$ converges to a stable age distribution which does not depend upon the structure of the ancestral individuals.
Let us now consider the sex ratio of females to males in age group \( x \) at time \( t \). We have,

\[
S(t, x) = \frac{F(t, x)}{M(t, x)}
\]

\[
= \frac{[F(t-x, 0) P(x)]/[M(t-x, 0) Q(x)]}{, \ t > x}
\]

\[
= S(t-x, 0) P(x)/Q(x)
\]

\[
\to \frac{[P(x)]/[SQ(x)], \ t \to \infty}{, (2.30)}
\]

for \( x = 0, 1, \ldots, n \) where the constant \( S \) is defined in Equation 2.27. This shows, that according to this model for population growth, the ratio of females to males in the same age group stabilizes. The overall sex ratio at time \( t \) is given by

\[
S(t) = \frac{\sum_{x=0}^{n} F(t, x)}{\sum_{x=0}^{n} M(t, x)}
\]

\[
= \frac{\sum_{x=0}^{n} F(t-x, 0) P(x)}{\sum_{x=0}^{n} M(t-x, 0) Q(x)}, \ t > x
\]

\[
\to \frac{\sum_{x=0}^{n} \mu^{-x}_0 P(x)}{[S \sum_{x=0}^{n} \mu^{-x}_0 Q(x)], \ t \to \infty}{, (2.31)}
\]

Thus, we have that the overall sex ratio stabilizes.

Let us now consider the possibility of the existence of a reproductive value for an ancestral male. We have, from Equation 2.26 that
\[ M(t, 0) \sim M \mu_0^t, t \to \infty \]

where \( M \) is a constant defined to be

\[
M = F \sum_{x=0}^{s} \mu_0^{-(x+1)} b_2(x) P(x).
\]

In this equation, \( F \) is also a constant given by Equation 2.11, and by Equation 2.15.

The reproductive value for an ancestral female in age group \( x \) was defined to be the coefficient of \( F(0, x) \) in the constant \( F \) given by Equation 2.15. Let us call the value \( v_f(x) \) determined from Equation 2.15 \( v_f(x) \). We showed that \( v_f(x) > 0 \) for \( x = 0, 1, \ldots, s \). Let us now consider the possibility of a reproductive value for the ancestral males. Let \( v_m(x) \) denote this quantity, where \( v_m(x) \) is defined to be the coefficient of \( M(0, x) \) in the constant \( M \). However, from Equation 2.15 we have

\[
M = \sum_{x=0}^{s} v_f(x) F(0, x) \sum_{y=0}^{s} \mu_0^{-(y+1)} b_2(y) P(y).
\]

Therefore,

\[ v_m(x) = \text{coefficient of } M(0, x) \text{ in } M \]

\[ = 0, x = 0, 1, \ldots, n, \]

since the formulation of this model does not depend upon the existence of ancestral males.
F. Comments on the Use of the Model

This model is currently used to describe the growth of the human population. Its use to predict the growth of a bisexual population was introduced into the literature by Karmel (1947). It has also been extensively studied by Goodman (1967, 1969). This model is called, by these writers, the female marriage dominance model for population growth. Possibly the reason that many people believe that it accurately describes the true nature of the growth of a bisexual population is that the mother of a child is always known, while the father is not necessarily known. This model is female dominant, in the sense that all of the offspring are attributed to only the females in the population. The use of the word marriage in the name of this model is very misleading since there is not even any structure to incorporate the formation of couples. The role of the males, with respect to the growth of a population, is not depicted accurately. The males do not take part in reproduction, they are born, they age, and they die. They do not have any "value". The ability of this model to accurately describe the growth of a bisexual population is doubtful.

It is clear, that in the models we have been describing, we could easily reverse the roles of the females and the males. That is, we could easily suppose that adult males
produce male offspring, and if females occur in the population, the infant females are produced only by the adult males. The renewal equations which describe the production of offspring according to this model are

\[
M(t, 0) = \begin{cases} 
M_0(t-1) + \sum_{x=0}^{t-2} b_2(x) M(t-x-1, 0) Q(x) & t = 1, 2, \ldots, s+1 \\
\sum_{x=0}^{s} b_2(x) M(t-x-1, 0) Q(x) & t = s+2, s+3, \ldots 
\end{cases}
\tag{2.32}
\]

and

\[
F(t, 0) = \begin{cases} 
F_1(t-1) + \sum_{x=0}^{t-2} b_1(x) M(t-x-1, 0) Q(x) & t = 1, 2, \ldots, s+1 \\
\sum_{x=0}^{s} b_1(x) M(t-x-1, 0) Q(x) & t = s+2, s+3, \ldots 
\end{cases}
\tag{2.33}
\]

In these two equations \( b_1(x) \) and \( b_2(x) \) now respectively denote the average number of female and male offspring an adult male in age group \( x \) at time \( t \) contributes to age group \( 0 \) at time \( t + 1 \). The functions \( F_1(t) \) and \( M_0(t) \), \( t = 0, 1, \ldots, s \), respectively represent the number of female and male offspring produced by the ancestral males alive at time \( t \). These functions are
\[ F_1(t) = \sum_{y=0}^{s-t} b_1(y+t) M(0, y) \frac{Q(y+t)}{Q(y)}, \]
\[ t = 0, 1, \ldots, s \]  
\[ = 0, \text{ otherwise}, \]  
and
\[ M_0(t) = \sum_{y=0}^{s-t} b_2(y+t) M(0, y) \frac{Q(y+t)}{Q(y)}, \]
\[ t = 0, 1, \ldots, s \]  
\[ = 0, \text{ otherwise}. \]

We could easily solve Equations 2.32 and 2.33, since they are linear renewal equations. The results of the solutions are totally analogous to each of the equations given previously. The only equation that will be different is the characteristic equation corresponding to Equation 2.32. This equation is
\[ \phi(v) \equiv \sum_{x=0}^{s} v^{-(x+1)} b_2(x) Q(x) = 1. \]  
\[ (2.36) \]

The solutions to this equation completely describe the growth of our population. This model is entitled, naturally, the male marriage dominance model for population growth.

The utility of a model for population growth in which both types of offspring are attributed to one parent is only a mathematical convenience. These types of models do not take into account the obvious requirement that in a bisexual population, the production of offspring is a function of both
the adult females and males.

The use of these types of models has been questioned by several writers, among whom is Hajnal (1948). Hajnal points out the obvious fact that a model which attributes both types of offspring to one parent is not at all realistic. Karmel (1948) concurs with Hajnal's comments, but he presents the case that this type of model is a good approximation to the true model. This sort of erroneous reasoning occurs even today. Goodman (1968) discusses the stochastic versions of the female and male marriage dominance models. He makes the comment that for a bisexually reproducing population, the true model for population growth lies somewhere between the two extremes of female and male marriage dominance. A statement of this type seems to imply a complete noncomprehension of basic biology.
III. A NEW GROWTH MODEL

A. A Basic Bisexual Model

We will consider an elementary model to describe the growth of a population consisting of both females and males in which couples must be formed before reproduction can occur; that is, the females and males must interact before reproduction. The complete analysis of the model depends upon two assumptions. These assumptions are:

(1) only females and males in the same age group form couples
(2) at birth, the ratio of females to males is a known constant.

Assumption 1 is not realistic, but Assumption 2 is valid, as we will show. If these assumptions are not made, an upper bound to the solution of the describing equations can be found.

The individuals in a population can be classified according to age, type and time. We will say that an individual belongs to age group \( x \) at time \( t \), where \( x \) and \( t \) are nonnegative integers, whenever the age of the individual is contained in the interval \( [x, x+1) \) at time \( t \). We will also make the assumption that the females and the males are homogeneous with respect to age; that is, all of the females in a specified age group behave in an identical manner, and the same is true about the males in a given age group. Let
\[ F(t, x) = \text{number of females in age group } x \text{ at time } t \]
\[ M(t, x) = \text{number of males in age group } x \text{ at time } t \]
\[ C(t, x) = \text{number of couples formed at time } t \text{ with the females and males both in age group } x \]
\[ P(x) = P(\text{any female survives from birth to age group } x) \]
\[ Q(x) = P(\text{any male survives from birth to age group } x) \]
\[ b_1(x) = E(\text{number of female offspring a couple in age group } x \text{ at time } t \text{ contributes to age group } 0 \text{ at time } t+1) \]
\[ b_2(x) = E(\text{number of male offspring a couple in age group } x \text{ at time } t \text{ contributes to age group } 0 \text{ at time } t+1). \]

The number of couples at time \( t \) with the females and males both in age group \( x \) is a function of \( F(t, x) \) and \( M(t, x) \). For the moment, we will not define the function \( C(t, x) \) more explicitly. Following the notation introduced in the previous chapter let \( R \) denote the set of positive fertility. We will assume that this set is the same for the production of both females and males; that is, \( R = \{x: b_1(x) > 0\} \) and \( R = \{x: b_2(x) > 0\} \). All of the functions except \( F(t, x) \) and \( M(t, x) \) defined above are assumed to be known. The unknowns we want to solve for are \( F(t, x) \) and \( M(t, x) \), for \( t = 1, 2, \ldots \) and \( x = 0, 1, \ldots \).

The ancestral males and females are \( F(0, x) \) and \( M(0, x) \) for \( x = 0, 1, \ldots \). These individuals are also assumed to be known. These initial individuals may have different survival
probabilities and different birth rates as compared to the individuals alive at time $t, \ t > 0$. We will call our population uniform in time, if the survival probabilities and the birth rates for the ancestral individuals are the same as the rates for the descendants. Actually, we are most interested in the case in which the survival probabilities and the birth rates are the same for all of the individuals in the population, including the ancestral individuals.

Let $n$ be the maximum age to which any female or male can survive; that is, $P(x) = 0$ and $Q(x) = 0$ for any $x > n$. Also, let $s$ be the last age group in which reproduction can occur; that is, $b_1(x) = 0$ and $b_2(x) = 0$ for $x > s$.

Clearly, the quantities of interest are the number of females and males in age group 0 at time $t$. Once we have found expressions for these two quantities then, as we did previously, we can obtain the females and males in the other age groups by aging the infants. At time $t, \ t > 0$, the number of females in age group 0 is equal to the female offspring produced by the couples formed from the ancestral individuals alive at time $t - 1$, plus the number of female offspring produced by the couples formed from the descendants of the ancestral individuals. A similar statement about the males in age group 0 at time $t$ is also true. Thus we have our basic renewal equations,
\[
F(t, 0) = \begin{cases}
F^*(t-1) + \sum_{x=0}^{t-2} b_1(x) C(t-1, x), & t = 1, 2, \ldots, s+1 \\
\sum_{x=0}^{s} b_1(x) C(t-1, x), & t = s+2, s+3, \ldots
\end{cases} \tag{3.1}
\]

and
\[
M(t, 0) = \begin{cases}
M^*(t-1) + \sum_{x=0}^{t-2} b_2(x) C(t-1, x), & t = 1, 2, \ldots, s+1 \\
\sum_{x=0}^{s} b_2(x) C(t-1, x), & t = s+2, s+3, \ldots
\end{cases} \tag{3.2}
\]

where we define \( \Sigma^* = 0 \) and where \( F^*(t) \) and \( M^*(t) \) for \( t = 0, 1, \ldots, s \), denote the female and male offspring from the couples formed by the ancestral individuals alive at time \( t \). Let us note that no couples produce offspring if their age is greater than \( s \), the maximum age of positive fertility. Whence Equations 3.1 and 3.2 follow since the ancestral individuals no longer contribute offspring if their age is greater than \( s \).

In these two equations we have summed over the consecutive integers \( x \) between \( 0 \) and \( s \). These sums could be over the set of integers \( x \in \mathbb{R} \), where \( \mathbb{R} \) is the set of positive fertility. In the following pages, whenever equations similar to Equations 3.1 and 3.2 occur, we will sum over all of the integers \( x \) between \( 0 \) and \( s \) and mean that the summation
The important question we must answer at this time is:

What is a reasonable choice for the function

\[ C(t, x) = \text{the number of couples formed at time } t \text{ with the females and males both in age group } x? \]

We would like this function to at least have the following properties:

1. the function \( C(t, x) \) is zero if there are no females or if there are no males in age group \( x \) at time \( t \)

2. the function \( C(t, x) \) should denote the operation of the pairing of the females and the males in age group \( x \) at time \( t \).

Many functions such as the product \( F(t, x) M(t, x) \) satisfy Property 1, but certainly not Property 2. However, let us note that the maximum number of couples that can be formed in a given age group is equal to the minimum of the numbers of females or males in the age group. Thus, a reasonable function which describes the number of couples formed with the females and males in age group \( x \) at time \( t \) is

\[ C(t, x) = \min \{F(t, x), M(t, x)\}, \quad (3.3) \]

for \( x = 0, 1, \ldots, s \) and \( t = 0, 1, \ldots \)

The choice of this function to describe the number of couples is an upper bound to the number of couples formed,
since in many populations there are females and males who do not reproduce. However, we will suppose that Equation 3.3 is an equality. This choice of the function $C(t, x)$ certainly satisfies Properties 1 and 2. However, there are other implications in the choice of this function.

It is implicit in the choice of this function $C(t, x)$ that couples need not be permanent, since the females and males can change partners as they age. However, if permanent couples are formed then $\min\{F(t, x), M(t, x)\}$ is an upper bound to the true situation. Also, this function does not specify what actually happens to widows and widowers if they do not want to remate, since according to this model remating is possible as the females and males age.

The greatest virtue in this choice of the function $C(t, x)$ is that the emphasis for reproduction is placed upon the less numerous sex. If couples are formed, this emphasis is very valid since it is indeed true that the less numerous sex is the controlling factor in the growth of a population.

Let us now substitute Equation 3.3 into Equations 3.1 and 3.2. We have

$$F(t, 0) = \begin{cases} 
F^*(t-1) + \sum_{x=0}^{t-2} b_1(x) \min\{F(t-1, x), M(t-1, x)\}, \\
& t = 1, 2, \ldots, s+1, \\
& t = s+2, s+3, \ldots
\end{cases} \quad (3.4)$$
and

\[
M(t, 0) = \begin{cases} 
  \sum_{x=0}^{t-2} b_2(x) \min\{F(t-1, x), M(t-1, x)\}, \\
  \sum_{x=0}^{s} b_2(x) \min\{F(t-1, x), M(t-1, x)\}, \\
  t = 1, 2, \ldots, s+1, \\
  t = s+2, s+3, \ldots 
\end{cases} 
\]  (3.5)

The females and males in age group \(x\) at time \(t\) are the females and males in age group \(0\) at time \(t-x\) that survive to age \(x\), provided \(x \leq t\). If \(x > t\), the individuals in age group \(x\) at time \(t\) are the individuals in age group \(x-t\) at time \(0\) that survive to age \(x\) given that they have survived to age \(x-t\). That is

\[
F(t, x) = F(t-x, 0) P(x), \quad x \leq t 
\]

\[
= F(0, x-t) P(x)/P(x-t), \quad x > t 
\]  (3.6)

and

\[
M(t, x) = M(t-x, 0) Q(x), \quad x \leq t 
\]

\[
= M(0, x-t) Q(x)/Q(x-t), \quad x > t. 
\]  (3.7)

If we use these two identities in Equations 3.4 and 3.5, we have that
\[ F(t, 0) = \begin{cases} 
F^*(t-1) + \sum_{x=0}^{t-2} b_1(x) \min\{F(t-x-1, 0) P(x), \\
M(t-x-1, 0) Q(x)\}, \\
t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b_1(x) \min\{F(t-x-1, 0) P(x), \\
M(t-x-1, 0) Q(x)\}, \\
t = s+2, s+3, \ldots, 
\end{cases} \quad (3.8) \]

and
\[ M(t, 0) = \begin{cases} 
M^*(t-1) + \sum_{x=0}^{t-2} b_2(x) \min\{F(t-x-1, 0) P(x), \\
M(t-x-1, 0) Q(x)\}, \\
t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b_2(x) \min\{F(t-x-1, 0) P(x), \\
M(t-x-1, 0) Q(x)\}, \\
t = s+2, s+3, \ldots. 
\end{cases} \quad (3.9) \]

In these equations we have defined \( \Sigma = 0 \). If the population is uniform in time, \( F^*(t) \) and \( M^*(t) \), as in Equation 2.4, are given by
\[ F^*(t) = \sum_{y=0}^{s-t} b_1(y+t) \min\{F(0, y) P(y+t)/P(y), \\
M(0, y) Q(y+t)/Q(y)\}, \\
t = 0, 1, \ldots, s, \\
= 0, \text{ otherwise} \]
and
\[ M^*(t) = \sum_{y=0}^{s-t} b_2(y+t) \min\{F(0, y) \frac{P(y+t)}{P(y)}, M(0, y) \frac{Q(y+t)}{Q(y)} \}, \]
\[ t = 0, 1, \ldots, s \]
\[ = 0, \text{ otherwise}. \]

A complete analysis of Equations 3.8 and 3.9 appears to be impossible since the function \( \min\{\cdot, \cdot\} \) can be very oscillatory. These two renewal equations are nonlinear in the unknowns. However, an upper bound to the solutions of Equations 3.8 and 3.9 can be obtained. We will discuss the upper bound in the next chapter.

C. The Solution

As we noted previously, our renewal Equations 3.8 and 3.9 are nonlinear in the unknowns \( F(t, 0) \) and \( M(t, 0) \). If, however, we make a simple assumption then these two equations become linear in the unknowns. The assumption is:

Let us suppose that the number of females in age group 0 at time \( t \) is proportional to the number of males in age group 0 at time \( t \), \( t > 0 \). That is,
\[ \frac{F(t, 0)}{M(t, 0)} = \frac{p}{q} \text{ for all } t > 0, \]
where \( p \) and \( q \) are known positive numbers such that \( p + q = 1 \). This says that at birth, the ratio of females to males is a known constant. At least for the human population,
this appears to be a valid assumption. A justification is given in the Appendix.

If we make this assumption then we have that

\[
\begin{align*}
\min\{F(t-x-1, 0) P(x), M(t-x-1, 0) Q(x)\} \\
&= F(t-x-1, 0) \min\{P(x), (q/p) Q(x)\} \\
&= \left(\frac{1}{p}\right) F(t-x-1, 0) \min\{pP(x), qQ(x)\},
\end{align*}
\]

and

\[
\min\{F(t-x-1, 0) P(x), M(t-x-1, 0) Q(x)\} \\
&= \left(\frac{1}{q}\right) M(t-x-1, 0) \min\{pP(x), qQ(x)\}.
\]

Thus, by the use of a simple reasonable assumption we have introduced the very desirable mathematical property of linearity into our renewal equations. The renewal Equations 3.8 and 3.9 have simplified to

\[
pF(t, 0) = \begin{cases} 
\frac{t-2}{p} F^*(t-1) + \sum_{x=0}^{t-2} b_1(x) F(t-x-1, 0) \\
& \cdot \min\{pP(x), qQ(x)\}, \\
& t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b_1(x) F(t-x-1, 0) \\
& \cdot \min\{pP(x), qQ(x)\} \\
& t = s+2, s+3, \ldots, 
\end{cases}
\]

and
which are of the same form as the basic renewal equation studied in the last chapter. The theorems we stated in that chapter are thus applicable. However, before applying these theorems, let us consider Equations 3.12 and 3.13 in more detail. These two equations give us a relationship between \( b^1(x) \) and \( b^2(x) \). This relationship is given by the following theorem:

**Theorem:**

Let us suppose that the population is uniform in time and that \( b^1(x) \) and \( b^2(x) \) denote respectively the average number of female and male offspring produced by a couple in age group \( x \). Then \( F(t, 0)/M(t, 0) = p/q \) for all \( t \geq 0 \) if and only if \( b^1(x)/b^2(x) = p/q \) for all \( x \in \mathbb{R} \), where \( p, q > 0 \) and \( p + q = 1 \). This is true provided \( F(0, x) \) and \( M(0, x) \) are positive for \( x \in \mathbb{R} \).

**Proof:**

If \( b^1(x)/b^2(x) = p/q \) for all \( x \in \mathbb{R} \) then by looking at Equations 3.8, through 3.11 it is obvious that
\[ \frac{F(t, 0)}{M(t, 0)} = \frac{p}{q} \text{ for all } t > 0. \]

Let us now suppose that \( \frac{F(t, 0)}{M(t, 0)} = \frac{p}{q} \text{ for all } t > 0. \) From Equation 3.12 we have

\[
F(t, 0) = \begin{cases} 
F^*(t-1) + \frac{1}{p} \sum_{x=0}^{t-2} b_1(x) F(t-x-1, 0) & \cdot \min\{pP(x), qQ(x)\}, \\
& t = 1,2,\ldots,s+1, \\
\frac{1}{p} \sum_{x=0}^{s} b_1(x) F(t-x-1, 0) & \cdot \min\{pP(x), qQ(x)\}, \\
& t = s+2,s+3,\ldots 
\end{cases}
\]

and by substituting \( M(t, 0) = \frac{q}{p} F(t, 0) \) into Equation 3.13 and simplifying we also have

\[
F(t, 0) = \begin{cases} 
(p/q) \cdot F^*(t-1) + \frac{1}{q} \sum_{x=0}^{t-2} b_2(x) F(t-x-1, 0) & \cdot \min\{pP(x), qQ(x)\}, \\
& t = 1,2,\ldots,s+1, \\
\frac{1}{q} \sum_{x=0}^{s} b_2(x) F(t-x-1, 0) & \cdot \min\{pP(x), qQ(x)\}, \\
& t = s+1,s+2,\ldots 
\end{cases}
\]

If we subtract the first of these equations from the second and use Equations 3.10 and 3.11 we have that
\[
0 = \sum_{y=0}^{s-t+1} \left[ \frac{p}{q} b_2(y+t-1) - b_1(y+t-1) \right] \\
\cdot \min\{F(0, y) P(y+t-1)/P(y), M(0, y) Q(y+t-1)/Q(y)\}
\]
\[
+ \sum_{x=0}^{t-2} \left[ \frac{1}{q} b_2(x) - \frac{1}{p} b_1(x) \right] F(t-x-1, 0) \\
\cdot \min\{pP(x), qQ(x)\},
\]
\[
t = 1, 2, \ldots, s+1,
\]

and
\[
0 = \sum_{x=0}^{s} \left[ \frac{1}{q} b_2(x) - \frac{1}{p} b_1(x) \right] F(t-x-1, 0) \\
\cdot \min\{pP(x), qQ(x)\},
\]
\[
t = s+2, s+3, \ldots
\]

However,
\[
\min\{F(0, y) P(y+t-1)/P(y), M(0, y) Q(y+t-1)/Q(y)\} > 0,
\]
for \( y = 0, 1, \ldots, s-t+1, y \in \mathbb{R} \), and \( t = 1, 2, \ldots, s+1 \), since in the hypothesis of the theorem we assumed that \( F(0, y) > 0 \) and \( M(0, y) > 0 \) for \( y \in \mathbb{R} \). Also, we have
\[
F(t-x-1, 0)\{\min pP(x), qQ(x)\} > 0
\]
for \( x = 0, 1, \ldots, t-2 \), and \( t = 1, 2, \ldots, s+1 \). Thus the only way in which the right hand side of Equation 3.14 can be equal to zero is that
\[
(p/q) b_2(y+t-1) - b_1(y+t-1) = 0
\]
for \( y = 0,1,\ldots,s-t+1 \), and \( t = 1,2,\ldots,s+1 \), and that
\[
\frac{1}{q} b_2(x) - \frac{1}{p} b_1(x) = 0
\]
for \( x = 0,1,\ldots,t-2 \), and \( t = 1,2,\ldots,s+1 \). Likewise from Equation 3.15 we have that
\[
\frac{1}{q} b_2(x) - \frac{1}{p} b_1(x) = 0
\]
for \( x = 0,1,\ldots,s \) and \( t = s+2,s+3,\ldots \). These equations say that
\[
b_1(x)/b_2(x) = p/q \quad \text{for all } x \in \mathbb{R},
\]
which is the result we wanted to prove.

From the proof of this theorem we also have a

**COROLLARY:**

If the population is not uniform in time then
\[
b_1(x)/b_2(x) = p/q \quad \text{for } x \in \mathbb{R} \quad \text{if and only if } F(t, 0)/M(t, 0) = p/q \quad \text{for } t = s+2,s+3,\ldots.
\]

We have shown that if we make Assumption 2 or its equivalent as given by the previous theorem, then the equations which describe the growth of our population are linear in the unknowns. Also, at least for \( t \) sufficiently large, we need only solve for \( F(t, 0) \) and we can obtain \( M(t, 0) \) as a multiple of \( F(t, 0) \); that is, \( M(t, 0) = (q/p) F(t, 0) \).

Let \( b_1(x) = pb(x) \) and \( b_2(x) = qb(x) \) where \( p,q > 0 \) and \( p + q = 1 \), and where
\[ b(x) = E(\text{number of offspring a couple in age group } x \text{ at time } t \text{ contributes to age group 0 at time } t+1). \]

A proportion \( p \) of the offspring are females and a proportion \( q \) of the offspring are males. Equations 3.12 and 3.13 now become, after some simplification,

\[
F(t, 0) = \begin{cases} 
F^*(t-1) + \sum_{x=0}^{t-2} b(x) F(t-x-1, 0) \min\{pP(x), qQ(x)\}, & t = 1, 2, \ldots, s+1 \\
\sum_{x=0}^{s} b(x) F(t-x-1, 0) \min\{pP(x), qQ(x)\}, & t = s+2, s+3, \ldots 
\end{cases} \quad (3.16)
\]

and

\[
M(t, 0) = \begin{cases} 
M^*(t-1) + \sum_{x=0}^{t-2} b(x) M(t-x-1, 0) \min\{pP(x), qQ(x)\}, & t = 1, 2, \ldots, s+1 \\
\sum_{x=0}^{s} b(x) M(t-x-1, 0) \min\{pP(x), qQ(x)\}, & t = s+2, s+3, \ldots 
\end{cases} \quad (3.17)
\]

where \( M(t, 0)/q = F(t, 0)/p, \quad t = 1, 2, \ldots \). An implicit result in the previous theorem is that if the population is uniform in time then

\[ F^*(t)/p = M^*(t)/q, \quad t = 0, 1, \ldots, s \]
\[ F^*(t) = M^*(t) = 0, \text{ otherwise} \]

Thus, we need only apply the theorems of Feller to solve for \( F(t, 0) \) in Equation 3.16 and can then immediately find
Let \( R = \{x: b(x) > 0\} \) be such that fertility is not a periodic function of age; that is, \( R \) satisfies Sykes' theorem in the previous chapter. Thus, for \( t \) sufficiently large the unique solution to Equation 3.12 and 3.13 is characterized by

\[
F(t, 0) \sim F^* \lambda_0^t, \quad t \to \infty,
\]

\[
M(t, 0) \sim M^* \lambda_0^t, \quad t \to \infty,
\]

where \( F^* \) and \( M^* \) are constants, and \( \lambda_0 \) is the unique positive real solution which is larger in absolute value than any other solution to the characteristic equation

\[
\phi(\lambda) = \sum_{x=0}^{s} \lambda^{-x} b(x) \min\{pP(x), qQ(x)\} = 1. \tag{3.19}
\]

Let us note that this characteristic equation is common to both Equations 3.16 and 3.17.

The constants are

\[
F^* = v^* \sum_{y=1}^{s+1} \lambda_0^{-y} F^*(y-1) \tag{3.20}
\]

and

\[
M^* = v^* \sum_{y=1}^{s+1} \lambda_0^{-y} M^*(y-1)
\]

where we define

\[
1/v^* = \sum_{y=0}^{s} (y+1) \lambda_0^{-(y+1)} b(y) \min\{pP(y), qQ(y)\}.
\]
Also, as we found in the previous chapter, we have that

\[ \lambda_0 \leq 1 \text{ whenever } \phi(1) \geq 1. \]

We should note that the characteristic equation, corresponding to the renewal equation describing the production of infant females given in the previous chapter, when evaluated at unity was equal to the mean number of offspring any female produced during her life time. This is no longer true for the characteristic equation given by Equation 3.19.

Let us note that if the population is uniform in time then

\[ \frac{F^*}{p} = \frac{M^*}{q}, \]

otherwise we can say nothing about the relationship between the constants \( F^* \) and \( M^* \). Thus, for \( t \) sufficiently large, we have characterized the number of females and males in age group 0 at time \( t \).

The number of females and males in age group \( x \) at time \( t \) can be found by using Equations 3.6 and 3.7 in the same manner as we found the number of females in age group \( x \) in the previous chapter. We have

\[ F(t, x) = F(t-x, 0) P(x) \sim F^* \lambda_0^{t-x} P(x), t \to \infty, \]

and

\[ M(t, x) = M(t-x, 0) Q(x) \sim M^* \lambda_0^{t-x} Q(x), t \to \infty. \]

for \( x = 0, 1, \ldots, n \). That is, for \( t \) sufficiently large we
know the number of females and males in the different age
groups at time \( t \). Also, as \( t \) becomes large our population
of females and males grows geometrically if \( \lambda_0 > 1 \), remains
constant if \( \lambda_0 = 1 \), and the population becomes extinct if
\( \lambda_0 < 1 \).

Let \( f(t, x) \) and \( m(t, x) \) denote respectively the
proportion of females and males in age group \( x \) at time
\( t \); that is,

\[
f(t, x) = \frac{F(t, x)}{\sum_{y=0}^{n} F(t, y)}
\]

and

\[
m(t, x) = \frac{M(t, x)}{\sum_{y=0}^{n} M(t, y)},
\]

for \( x = 0, 1, \ldots, n \) and \( t \geq 0 \). Then we obtain results
similar to Equations 2.14 and 2.29 in the previous chapter,
and have that

\[
f(t, x) \to f(x) = \frac{\lambda_0^{-x} P(x)}{\sum_{y=0}^{n} \lambda_0^{-y} P(y)}, \quad t \to \infty \tag{3.21}
\]

and

\[
m(t, x) \to m(x) = \frac{\lambda_0^{-x} Q(x)}{\sum_{y=0}^{n} \lambda_0^{-y} Q(y)}, \quad t \to \infty
\]

for \( x = 0, 1, \ldots, n \). Thus for \( t \) sufficiently large, the
proportions of females and males in the different age groups
are only a function of age. Note that these equations do not
depend upon the structure of the population of ancestors and
are valid even if the population is not uniform in time.
Equation 3.21 has the same form as Equation 2.14 in the
previous chapter, but the two equations are not necessarily equal, since \( \lambda_0 \neq \mu_0 \) in general.

In the previous chapter we considered a "two sex" model for the growth of a population. With respect to this model we found a stabilization of the sex ratios. Let us now consider these ratios for our new model. An important hypothesis was assumed for our new model, namely that for any time \( t \), the sex ratio of females to males at birth is a constant. That is,

\[
S(t, 0) = \frac{F(t, 0)}{M(t, 0)} = \frac{p}{q} \text{ for all } t \geq 0.
\]

This ratio should be compared with Equation 2.27. With respect to Equation 2.27, we found that in the currently used model for population growth, the sex ratio at birth stabilized only asymptotically.

We can also find the sex ratio of females to males in age group \( x \) at time \( t \). We have

\[
S(t, x) = \frac{F(t, x)}{M(t, x)}
\]

\[
= \frac{[F(t-x, 0) P(x)]/[M(t-x, 0) Q(x)]}{[pP(x)]/[qQ(x)]}, \text{ for any } t \geq x
\]

\[
= S(t-x, 0) P(x)/Q(x)
\]

\[
= \frac{[pP(x)]/[qQ(x)]}, \text{ for any } t \geq x, \quad (3.22)
\]

for \( x = 0,1,\ldots,n \) and \( t = 0,1,2,\ldots \). In Equation 2.30 we found that the sex ratio for females and males in age group
x at time $t$ stabilized only when $t \to \infty$. Equation 3.22 shows that for our new model for population growth the sex ratio at time $t$ for females and males in age group $x$ is a known constant as soon as $t \geq x$. That is, the sex ratio stabilizes much faster in our new model.

The overall sex ratio at time $t$ is given by

$$S(t) = \frac{\sum_{x=0}^{n} F(t, x)}{\sum_{x=0}^{n} M(t, x)}$$

$$= \frac{\sum_{x=0}^{n} F(t-x, 0) P(x)}{\sum_{x=0}^{n} M(t-x, 0) Q(x)}, \quad t \geq x$$

$$\to \frac{[F^* \sum_{x=0}^{t-x} \lambda_0^{-x} P(x)]}{[M^* \sum_{x=0}^{t-x} \lambda_0^{-x} Q(x)]}, \quad t \to \infty.$$

However, if the population is uniform in time, we showed that $F^*/p = M^*/q$. Thus we have that

$$S(t) \to \frac{\sum_{x=0}^{n} \lambda_0^{-x} P(x)}{\sum_{x=0}^{n} \lambda_0^{-x} Q(x)}, \quad t \to \infty. \quad (3.23)$$

That is, the overall sex ratio stabilizes as $t \to \infty$. Equation 2.31 gives the asymptotic over all sex ratio for the currently used model for population growth. The form is similar to Equation 3.23.

The above sex ratios should be compared with the corresponding sex ratios given in the previous chapter. We have commented on the rates of approach to the stable sex ratios. The functional forms of the sex ratios for the two models are very similar, as is to be expected. However, the
ratios are not equal since, in general the implicit growth parameters $\mu_0$ and $\lambda_0$ are not equal.

Let us now consider the proportion of couples in age group $x$ at time $t$; let $c(t, x)$ denote this proportion.

We have

$$c(t, x) = \frac{\min\{F(t, x), M(t, x)\}}{\sum_{y=0}^{n} \min\{F(t, y), M(t, y)\}}$$

for $x = 0, 1, ..., n$. However, we have that

$$\min\{F(t, x), M(t, x)\} = \min\{F(t-x, 0) P(x), M(t-x, 0) Q(x)\}$$

$$= \min\{F_0^{t-x} P(x), M_0^{t-x} Q(x)\}, \ t \to \infty$$

but if the population is uniform in time then $F_0^{t}/p = M_0^{t}/q$, so that

$$\min\{F(t, x), M(t, x)\}$$

$$= (1/p) F_0^{t-x} \min\{pP(x), qQ(x)\}, \ t \to \infty.$$  

If we substitute this into Equation 3.24 we have that

$$c(t, x) = \frac{\lambda_0^{-x} \min\{pP(x), qQ(x)\}}{\sum_{y=0}^{n} \lambda_0^{-y} \min\{pP(y), qQ(y)\}}$$

as $t \to \infty$, for $x = 0, 1, ..., n$. That is, for $t$ sufficiently large, $c(x)$ denotes the proportion of couples in age group $x$. This proportion is a stable age distribution of couples since
c(x) does not depend upon the structure of the ancestral population provided the population is uniform in time. If the population is not uniform in time this result does not hold.

D. The Reproductive Value

Let us now consider the possibility of the existence of a reproductive value for the ancestral females and males. We have shown that the solutions to Equations 3.12 and 3.13 are characterized by

\[ F(t, 0) \sim F* \lambda_0^t, \quad t \to \infty, \]

and

\[ M(t, 0) \sim M* \lambda_0^t, \quad t \to \infty, \]

where \( \lambda_0 \) is the dominant positive solution to the characteristic equation \( \phi(\lambda) = 1 \), and \( F* \) and \( M* \) are constants given by

\[ F* = v* \sum_{y=1}^{s+1} \lambda_0^{-y} F*(y-1), \]

and

\[ M* = v* \sum_{y=1}^{s+1} \lambda_0^{-y} M*(y-1), \]

where we have defined

\[ 1/v* = \sum_{x=0}^{s} (x+1) \lambda_0^{-(x+1)} b(x) \min\{pP(x), qQ(x)\}. \quad (3.26) \]

Let us note that \( 1/v* \) is similar in structure to \( 1/v(0) \),
given in Equation 2.17, but these two expressions have different interpretations, since \( \frac{1}{v^*} \) is not the mean age of a couple at the time of birth of their offspring.

It is interesting to ask whether or not we can define a reproductive value for an ancestral female or male in age group \( x \), say \( v_f(x) \) and \( v_m(x) \) respectively. In Equation 2.15 the reproductive value of a female in age group \( x \), \( v(x) \), was defined to be the coefficient of the number of ancestral females in age group \( x \); that is, the coefficient of \( F(0, x) \) in the expansion of the constant \( F \). We also supposed that the population was uniform in time.

We cannot make the same definition for \( v_f(x) \) and \( v_m(x) \) since in this model reproduction involves both sexes. In order to see this, let us note that if the population is uniform in time then from Equation 3.10 we have

\[
F^*(x-1) = p \sum_{y=0}^{s-x+1} b(y+x-1) \min\{F(0, y) P(y+x-1)/P(y) M(0, y) Q(y+x-1)/Q(y)
\]

for \( x = 1, 2, \ldots, s+1 \), and

\[
M^*(x-1)/q = F^*(x-1)/p, \ x = 1, 2, \ldots, s+1.
\]

Thus, it makes no sense to talk about the coefficients of \( F(0, x) \) and of \( M(0, x) \) in the constants \( F^* \) and \( M^* \).

However, we can make a similar definition for the reproductive value of a couple if we assume that the ancestral
population has equal numbers of females and males in each of the possible age groups. Let

\[ F(0, x) = C(x) \quad \text{and} \quad M(0, x) = C(x), \]

for \( x = 0, 1, \ldots, s \), where the symbol \( C(x) \) means that there are an equal number of females and males in age group \( x \) at time 0. That is, \( C(x) \) denotes the number of ancestral couples in age group \( x \). Thus, it seems reasonable to define the reproductive value of an ancestral couple in age group \( x \) with respect to the growth of the female population to be the coefficient of \( C(x) \) in the constant \( F^* \). We will call this coefficient \( v_f(x) \). Likewise, we will call the coefficient of \( C(x) \) in the constant \( M^* \), say \( v_m(x) \), the reproductive value of an ancestral couple in age group \( x \) with respect to the growth of the male population.

The constant \( F^* \) is

\[ F^* = v^* \sum_{x=1}^{s+1} \lambda_0^{-x} F^*(x-1) \]

\[ = pv^* \sum_{x=1}^{s+1} \sum_{y=0}^{s-x+1} \lambda_0^{-x} b(y+x-1) C(y) \min\{P(y+x-1)/P(y), Q(y+x-1)/Q(y)\} \]

\[ = pv^* \sum_{y=0}^{s} \sum_{x=1}^{s-y+1} \lambda_0^{-x} b(y+x-1) \min\{P(y+x-1)/P(y), Q(y+x-1)/Q(y)\}, \]

where we have interchanged the order of summation.
Thus, we have that

\[ v_f(z) = \text{coefficient of } C(z) \text{ in } v^* \sum_{x=1}^{s+1} \lambda_0^{-x} F^*(x-1) \]

\[ = p v^* \sum_{x=1}^{s-z+1} \lambda_0^{-x} b(z+x-1) \min \left\{ \frac{P(z+x-1)}{P(z)}, \frac{Q(z+x-1)}{Q(z)} \right\} \]

\[ = p v^* \lambda_0^z \sum_{y=z}^{s} \lambda_0^{-(y+1)} b(y) \min \left\{ \frac{P(y)}{P(z)}, \frac{Q(y)}{Q(z)} \right\}, \]  \hspace{1cm} (3.25)

for \( z = 0,1,\ldots,s \), where we have substituted \( y = z + x - 1 \).

Likewise, since \( M^*/q = F^*/p \), we have that

\[ v_m(z) = q v^* \lambda_0^z \sum_{y=z}^{s} \lambda_0^{-(y+1)} b(y) \min \left\{ \frac{P(y)}{P(z)}, \frac{Q(y)}{Q(z)} \right\}, \]  \hspace{1cm} (3.26)

for \( z = 0,1,\ldots,s \).

We have now shown that the reproductive values for an ancestral couple in age group \( x \) with respect to the growth of the females and males are, respectively

\[ v_f(x) = p v^* \lambda_0^x \sum_{y=x}^{s} \lambda_0^{-(y+1)} b(y) \min \left\{ \frac{P(y)}{P(x)}, \frac{Q(y)}{Q(x)} \right\}, \]

\[ x = 0,1,\ldots,s \]

\[ = 0, \text{ otherwise} \]

and

\[ v_m(x) = q v^* \lambda_0^x \sum_{y=x}^{s} \lambda_0^{-(y+1)} b(y) \min \left\{ \frac{P(y)}{P(x)}, \frac{Q(y)}{Q(x)} \right\}, \]

\[ x = 0,1,\ldots,s \]

\[ = 0, \text{ otherwise}. \]
We have defined \( v^x = 0 \) and \( v^m = 0 \) if \( x > s \), since any individual of age greater than \( s \) does not reproduce.

In these equations we have defined

\[
1/v^* = \sum_{x=0}^{s} (x+1) \lambda_0^{-(x+1)} b(x) \min\{pP(x), qQ(x)\}.
\]

These reproductive values follow from a definition similar to the definition of the reproductive value we gave previously.

In the previous chapter, we also considered the concept of a total reproductive value. If we follow this analogy we could consider two total reproductive values given by

\[
V_f(t) = \sum_{x=0}^{s} P(t, x) v_f(x), \quad t \geq 0,
\]

and

\[
V_m(t) = \sum_{x=0}^{s} M(t, x) v_m(x), \quad t \geq 0.
\]

We could also look at \( \Delta V_f(t) \) and \( \Delta V_m(t) \). However a decomposition similar to Equation 2.22 does not exist, since in this model an individual has two parents, not one parent as previously assumed.

E. Extensions of the Basic Model

The basic model we have considered in the last few sections has several limitations, the greatest being that couples are only formed between females and males in the same age group. We will relax this assumption in a later chapter. Another limitation we have introduced into the
model is that we have supposed that the maximum number of possible couples between females and males in the same age group are formed. We can relax this assumption, in a limited sense, and still retain all of the results presented in this chapter.

The function which expresses the fact that the maximum number of couples between females and males in the same age group are formed is given by Equation 3.3. That is,

\[ C(t, x) = \min\{F(t, x), M(t, x)\} \]  \hspace{1cm} (3.27)

for \( x = 0,1,\ldots,s \) and \( t = 0,1,\ldots \). For a bisexual reproducing population this function is certainly an upper bound to the true state of nature. In the human population, for example, there are females and males who for various reasons do not reproduce. There can also be widows and widowers in the population who do not desire to remate. Equation 3.27 does not take these possibilities into account.

Let \( F'(t, x) \) and \( M'(t, x) \) respectively denote the number of females and males in age group \( x \) at time \( t \) who do not take part in reproduction. These two functions also include the possibility of the existence of widows and widowers. We have that the number of females and males who are available to form couples are respectively \( F(t,x) - F'(t, x) \) and \( M(t, x) - M'(t, x) \). Thus, the maximum number of couples that can be formed between females and males
in the same age group is given by

\[ C(t, x) = \min\{F(t, x) - F'(t, x), M(t, x) - M'(t, x)\} \]

(3.28)

for \( x = 0,1,\ldots,s \) and \( t = 0,1,\ldots \).

If we substituted this function into renewal Equations 3.1 and 3.2 we could mimic the development presented in the early part of this chapter. If we were to do this, we would find that our renewal equations remained nonlinear. That is, unless we were to make some additional assumptions about the functions \( F'(t, x) \) and \( M'(t, x) \). If we assume that the numbers of females and males in age group \( x \) at time \( t \) who do not take part in reproduction are respectively proportional to the number of females and males in age group \( x \) at time \( t \) then the describing renewal equations are linear. Thus, let \( F'(t, x) = fF(t, x) \) and \( M'(t, x) = mM(t, x) \) where \( f \) and \( m \) are known real numbers between 0 and 1. Equation 3.28 then becomes

\[ C(t, x) = \min\{(1-f)F(t, x), (1-m)M(t, x)\}. \]  

(3.29)

If we use this function to describe the number of couples formed, if we again suppose that at birth the ratio of females to males is a constant, and if we mimic the steps followed in the initial parts of this chapter, then the renewal equations corresponding to Equations 3.16 and 3.17 become
\[ F(t, 0) = F^*(t-1) + \sum_{x=0}^{t-2} b(x) F(t-x-1, 0) \min\{p(1-f) P(x), q(1-m) Q(x)\} \]
\[ t = 1, 2, \ldots, s+1, \]  
\[ F(t, 0) = \sum_{x=0}^{s} b(x) F(t-x-1, 0) \min\{p(1-f) P(x), q(1-m) Q(x)\} \]
\[ t = s+2, s+3, \ldots \]  

and
\[ M(t, 0) = M^*(t-1) + \sum_{x=0}^{t-2} b(x) M(t-x-1, 0) \min\{p(1-f) P(x), q(1-m) Q(x)\} \]
\[ t = 1, 2, \ldots, s+1, \]  
\[ M(t, 0) = \sum_{x=0}^{s} b(x) M(t-x-1, 0) \min\{p(1-f) P(x), q(1-m) Q(x)\} \]
\[ t = s+2, s+3, \ldots \]  

where \( F^*(t) \) and \( M^*(t) \) are now given by
\[ F^*(t) = p \sum_{y=0}^{s-t} b(y+t) \min\{ (1-f) F(0, y) P(y+t)/P(y), (1-m) M(0, y) Q(y+t)/Q(y) \}, \]
\[ t = 0, 1, \ldots, s \]  
\[ = 0, \text{ otherwise}, \]

and
\[ M^*(t) = q \sum_{y=0}^{s-t} b(y+t) \min\{ (1-f) F(0, y) P(y+t)/P(y), (1-m) M(0, y) Q(y+t)/Q(y) \}, \]
\[ t = 0, 1, \ldots, s, \]  
\[ = 0, \text{ otherwise}. \]
The solutions to these renewal equations are easily found. The only significant difference between the solutions to these two equations and the solutions to Equations 3.16 and 3.17 is found in the characteristic equation. The characteristic equation common to Equations 3.30 and 3.31 is

\[ \phi^*(\lambda) = \sum_{x=0}^{\infty} \lambda^{-(x+1)} b(x) \min\{p(1-f) P(x), q(1-m) Q(x)\} = 1. \] (3.34)

All of the results we found for the model presented initially in this chapter carry over to this version of the model. The only difference occurs in the solutions to the characteristic equations. Let \( \lambda_1 \) be the solution to Equation 3.34 which is larger in absolute value than any other solution. Let us compare the two characteristic equations given by Equations 3.19 and 3.34. Since the numbers \( f \) and \( m \) are proportions we have, at least for \( \lambda \) real and positive, that

\[ \phi^*(\lambda) \leq \phi(\lambda) \]

and the inequality is strong if both \( f \) and \( m \) are strictly positive. Since these two characteristic equations are monotone functions, we have that \( \lambda_1 \leq \lambda_0 \) where \( \lambda_0 \) is the dominant solution to characteristic Equation 3.19.

Let us note that \( \lambda_1 < \lambda_0 \) whenever \( f \) and \( m \) are positive. Thus, the rate of growth for this population is at most the rate of growth of a population in which the maximum number
of couples is formed. This is to be expected.

Another variation on this model is also possible. We can easily introduce the possibility of having a polygamous population. If we suppose that any male in age group \( x \) at time \( t \) can have at most \( w \) wives from the females in age group \( x \) at time \( t \), then the function which describes the maximum number of couples formed is

\[
C(t, x) = \min\{F(t, x), wM(t, x)\},
\]

\( x = 0, 1, \ldots, s \), and \( t = 0, 1, \ldots \). If we again assume that at birth the ratio of females to males is a known constant then the renewal equations which describe the growth of the population are given by Equations 3.30 and 3.31 in which \( 1-f \) is replaced by 1 and \( 1-m \) is replaced by \( w \).

These equations are

\[
F(t, 0) = \begin{cases} 
F^*(t-1) + \sum_{x=0}^{t-2} b(x) F(t-x-1, 0) \min\{pP(x), wQ(x)\}, & t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b(x) F(t-x-1, 0) \min\{pP(x), wQ(x)\}, & t = s+2, s+3, \ldots,
\end{cases}
\]
and

\[ M(t, 0) = \begin{cases} 
M^*(t-1) + \sum_{x=0}^{t-2} b(x) M(t-x-1, 0) \min\{pP(x), wqQ(x)\}, & t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b(x) M(t-x-1, 0) \min\{pP(x), wqQ(x)\}, & t = s+2, s+3, \ldots,
\end{cases} \tag{3.36} \]

where \( F^*(t) \) and \( M^*(t) \) are given by

\[ F^*(t) = p \sum_{y=0}^{s-t} b(y+t) \min\{F(0, y) P(y+t)/P(y), wM(0, y) Q(y+t)/Q(y)\}, \]
\[ = 0, \text{ otherwise}, \tag{3.37} \]

and

\[ M^*(t) = q \sum_{y=0}^{s-t} b(y+t) \min\{F(0, y) P(y+t)/P(y), wM(0, y) Q(y+t)/Q(y)\}, \]
\[ t = 0, 1, \ldots, s, \tag{3.38} \]
\[ = 0, \text{ otherwise}. \]

Let us consider the function \( \min\{pP(x), wqQ(x)\} \), for \( x = 0, 1, \ldots, s \), in more detail. If we make the assumption that the proportions \( p \) and \( q \) are of the same order and that the number \( w \) is sufficiently large then we have
\[ \min\{pP(x), wQ(x)\} = pP(x) \quad (3.39) \]

for \( x = 0, 1, \ldots, s \). Also, let us assume that the ancestral population has an equal number of females and males in each age group; that is

\[ F(0, x) = C(x) \quad \text{and} \quad M(0, x) = C(x) \]

for \( x = 0, 1, \ldots, s \).

Thus, for \( w \) sufficiently large, we have

\[
F^*(t) = \sum_{y=0}^{s-t} b(y+t) C(y) \min\{P(y+t)/P(y), wQ(y+t)/Q(y)\}
\]

\[
= \sum_{y=0}^{s-t} b(y+t) F(0, y) P(y+t)/P(y)
\]

\[ = F_0(t), \ \text{say, for} \ t = 0, 1, \ldots, s, \quad (3.40) \]

and

\[ F^*(t) = F_0(t) = 0, \ \text{otherwise}. \]

Let us note that if in Equation 2.4 we let \( b_1(x) = pb(x) \) then the function \( F_0(t) \) defined by Equation 3.40 is identical to the function \( F_0(t) \) in Equation 2.4. We also have

\[
M^*(t) = \sum_{y=0}^{s-t} b(y+t) C(y) \min\{P(y+t)/P(y), wQ(y+t)/Q(y)\}
\]

\[
= \sum_{y=0}^{s-t} b(y+t) F(0, y) P(y+t)/P(y)
\]
and

\[ M^*(t) = M_1(t) = 0, \text{ otherwise.} \]

If in Equation 2.24 we let \( b_2(x) = q_b(x) \) then the function \( M_1(t) \) defined above is identical to the function \( M_1(t) \) defined with respect to Equation 2.24.

Let us now substitute Equations 3.39 and 3.40 into Equation 3.35. This equation becomes

\[
F(t, 0) = \begin{cases} 
F_0(t-1) + p \sum_{x=0}^{t-2} b(x) F(x) F(t-x-1, 0), & t = 1, 2, \ldots, s+1, \\
p \sum_{x=0}^{s} b(x) P(x) F(t-x-1, 0), & t = s+2, s+3, \ldots.
\end{cases}
\]

This equation is identical to Equation 2.3, if in Equation 2.3 we let \( b_1(x) = pb(x) \), for \( x = 0, 1, \ldots, s \). Thus, Equation 3.42 describes the production of female offspring in a population such that the offspring are credited to only the adult females.

If we now substitute Equations 3.39 and 3.41 into Equation 3.36 we find that
\[ M(t, 0) = \begin{cases} 
M_1(t-1) + p \sum_{x=0}^{t-2} b(x) P(x) M(t-x-1, 0), & t = 1, 2, \ldots, s+1, \\
q \sum_{x=0}^{s} b(x) P(x) M(t-x-1, 0), & t = s+2, s+3, \ldots.
\end{cases} \]

However, we have assumed that \( M(t, 0)/q = F(t, 0)/p \). If we use this assumption then this equation becomes

\[ M(t, 0) = \begin{cases} 
M_1(t-1) + q \sum_{x=0}^{t-2} b(x) P(x) F(t-x-1, 0), & t = 1, 2, \ldots, s+1, \\
q \sum_{x=0}^{s} b(x) P(x) F(t-x-1, 0), & t = s+2, s+3, \ldots.
\end{cases} \]

Let us note that this equation is identical to Equation 2.24 if we let \( b_2(x) = q b(x) \) for \( x = 0, 1, \ldots, s \) in this equation. That is, Equation 3.43 describes the production of male offspring in a population in which the offspring are credited to only the adult females in the population.

We have introduced the possibility of having a polygamous population. This population is structured in such a manner that only couples are formed between females and males in the same age groups, and any male can have at most \( w \) wives. If \( w \) is sufficiently large, the renewal Equations 3.35 and 3.36 which describe the production of female and
male offspring from the couples formed by the adult females and males assume an interesting form. These two equations become Equations 3.42 and 3.43. However, Equations 3.42 and 3.43 describe the production of female and male offspring in a bisexual population which credits the offspring to only the adult females in the population. So, if in a polygamous population the number of wives any male can have is sufficiently large, and if couples are formed according to the structure we have imposed, then the classical models for the growth of a bisexual population appear to be valid.
IV. A COMPARISON WITH THE CLASSICAL MODELS

We have developed a model for the growth of a bisexual population in which couples must be formed before reproduction occurs. The couples were formed between females and males in the same age group. We showed that if we made the assumption that the ratio of females to males at birth was a known constant then we could solve the renewal equations which described the growth of our population.

At this point it would be desirable to compare the rate of growth of a population in which coupling occurs with the rate of growth of a unisexual population as predicted by the classical models. We will make a comparison between the two models without making any assumption about the ratio of females to males at birth.

We considered two types of classical models for population growth. The first model was based on the assumption that a population consisted only of females, and that only female offspring were produced. In the second type of model we considered it was supposed that a population could consist of both females and males. However, we made the assumption that both the female and the male offspring were attributed only to the mature females and that the mature males played no part in reproduction.

Let all of the notation introduced in the initial pages of the previous chapter remain. The renewal equations which
describe the growth of our bisexual population are Equations 3.8 and 3.9. These equations are

\[
F(t, 0) = \begin{cases} 
F^*(t-1) + \sum_{x=0}^{t-2} b_1(x) \min\{F(t-x-1, 0) P(x), M(t-x-1, 0) Q(x)\}, \\
M(t-x-1, 0) Q(x) \\
t = 1, 2, \ldots, s+1, \\
s+2, s+3, \ldots.
\end{cases}
\]

(4.1)

and

\[
M(t, 0) = \begin{cases} 
M^*(t-1) + \sum_{x=0}^{t-2} b_2(x) \min\{F(t-x-1, 0) P(x), M(t-x-1, 0) Q(x)\}, \\
M(t-x-1, 0) Q(x) \\
t = 1, 2, \ldots, s+1, \\
s+2, s+3, \ldots.
\end{cases}
\]

(4.2)

The functions \( F^*(t) \) and \( M^*(t) \) which describe the female and male offspring of the ancestral individuals are, if the population is uniform in time, given by Equations 3.10 and 3.11. These equations are
\[ F^*(t) = \sum_{y=0}^{s-t} b_1(y+t) \min\{F(0, y) P(y+t)/P(y), M(0, y) Q(y+t)/Q(y)\} \]
\[ = 0, \text{ otherwise} \]

and

\[ M^*(t) = \sum_{y=0}^{s-t} b_2(y+t) \min\{F(0, y) P(y+t)/P(y), M(0, y) Q(y+t)/Q(y)\} \]
\[ = 0, \text{ otherwise}. \]

A. The Construction of Upper Bounds

In order to compare the rate of growth of this bisexual population with the rate of growth of the classical unisexual population we will use the fact that \( \min\{a, b\} \leq a \) and \( \leq b \) with equality whenever \( a = b \). Let us use this inequality in Equations 4.3 and 4.4. We have

\[ F^*(t) \leq \sum_{y=0}^{s-t} b_1(y+t) F(0, y) P(y+t)/P(y) \]
\[ = F_0(t), \text{ say, for } t = 0, 1, \ldots, s \] (4.5a)

and
\[ F^*(t) \leq \sum_{y=0}^{s-t} b_1(y+t) M(0, y) Q(y+t)/Q(y) \]

\[ = F_1(t), \text{say, for } t = 0, 1, \ldots, s \] (4.5b)

with

\[ F^*(t) = F_0(t) = F_1(t) = 0, \text{otherwise.} \]

Let us note that the quantity \( F_0(t) \) defined by Equation 4.5a is identical to the \( F_0(t) \) defined by Equation 2.4. Also, we find that

\[ M^*(t) \leq \sum_{y=0}^{s-t} b_2(y+t) F(0, y) P(y+t)/P(y) \]

\[ = M_1(t), \text{say, for } t = 0, 1, \ldots, s \] (4.6a)

and

\[ M^*(t) \leq \sum_{y=0}^{s-t} b_2(y+t) M(0, y) Q(y+t)/Q(y) \]

\[ = M_0(t), \text{say, for } t = 0, 1, \ldots, s \] (4.6b)

with

\[ M^*(t) = M_1(t) = M_0(t) = 0, \text{otherwise.} \]

Let us recall the definition of the function \( F_0(t) \). This function was first defined in Equation 2.1, and if the population was uniform in time, \( F_0(t) \) was written out explicitly in Equation 2.4. The function \( F_0(t) \) was defined to represent the number of female offspring of the ancestral
individuals alive at time $t$. Let us also remember that it was defined with respect to a population of females which produced only female offspring. With respect to $F_0(t)$ defined by Equation 4.5a, we have that $b_1(x)$ denotes the average number of female offspring a female parent in age group $x$ at time $t$ contributes to age group 0 at time $t+1$.

We will now consider the function $M_1(t)$ defined by Equation 4.6a. In the second type of classical model for population growth that we considered, the population consisted of both females and males. However, the female and male offspring were attributed only to the mature females. The function $M_1(t)$ defined by Equation 4.6a is related to a model of this type. That is, $M_1(t)$ denotes the number of male offspring of the mature ancestral females alive at time $t$, provided that both the female and the male offspring are attributed to only the mature females. Let us note that $M_1(t)$ is identical to the function $M_{12}(t)$ defined in Equation 2.24. Thus, with respect to $M_1(t)$, we have that $b_2(x)$ refers to the average number of male offspring a female parent in age group $x$ at time $t$ contributes to age group 0 at time $t+1$.

The classical bisexual model for population growth we presented previously attributed both types of offspring to the mature females in the population. We also noted that
we could easily develop a bisexual model for population growth in which both types of offspring are attributed only to the mature males in the population. Equations 2.32 and 2.33 describe the growth of this type of a population. The functions $M_0(t)$ and $F_1(t)$ defined respectively by Equations 4.6b and 4.5b are related to this type of a model for the growth of a bisexual population.

The function $M_0(t)$ defined by Equation 4.6b denotes the number of male offspring of the mature ancestral males alive at time $t$, provided the population consists of only males and that the male offspring are attributed to the adult males. Thus, in this equation, $b_2(x)$ represents the average number of male offspring an adult male in age group $x$ at time $t$ contributes to age group 0 at time $t+1$. Let us also note that $M_0(t)$ defined by Equation 4.6b is identical to $M_0(t)$ defined in Equation 2.35. The function $F_1(t)$ defined by Equation 4.5b is similar in structure to $M_0(t)$. Let us note that if in Equation 4.5b we let $b_1(x)$ denote the average number of female offspring a mature male in age group $x$ at time $t$ contributes to age group 0 at time $t+1$, then $F_1(t)$ represents the number of female offspring of the ancestral males alive at time $t$. The function $F_1(t)$ defined by Equation 4.5b is identical to $F_1(t)$ introduced in Equation 2.34.

In the following pages let us keep in mind the definitions
of the functions $b_1(x)$ and $b_2(x)$. These functions as defined in the previous chapter denoted, respectively, the average number of female and male offspring a couple in age group $x$ at time $t$ contributed to age group 0 at time $t + 1$. We should remember that the function $b_1(\cdot)$ always refers to the production of female offspring and $b_2(\cdot)$ always refers to the production of male offspring. However, in the following pages the type of parent credited with the offspring will change.

If we again use the inequality that $\min\{a, b\} \leq a$ and $\leq b$ in Equations 4.1 and 4.2 and use the functions defined by Equations 4.5 and 4.6, eight inequalities are possible. Of these eight inequalities, only four are of interest. These four inequalities are

$$
F(t, 0) \leq \begin{cases} 
F_0(t-1) + \sum_{x=0}^{t-2} b_1(x) F(t-x-1, 0) P(x), & t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b_1(x) F(t-x-1, 0) P(x), & t = s+2, s+3, \ldots,
\end{cases}
$$

(4.7)

and
Let us compare these four inequalities with Equations 2.3, 2.24, 2.32 and 2.33. The right hand side of Inequality 4.7 is identical to the right hand side of Equation 2.3, and therefore describes the growth of a population of females such that the offspring are all females. That is, in Inequality 4.7 \( b_1(x) \) denotes the average number of female offspring that an adult female in age group \( x \) at time \( t \) contributes to age group \( 0 \) at time \( t + 1 \). Let us replace
any \( F(t, x) \) appearing in the right hand side of Inequality 4.7 by \( F_1(t, x) \). We have that

\[
F(t, 0) \leq F_1(t, 0) \quad \text{for all } t > 0
\]

where \( F_1(t, 0) \) solves a renewal equation having the same form as Equation 2.3, i.e., \( F_1(t, 0) \) is the solution of

\[
F_1(t, 0) = \begin{cases} 
F_0(t-1) + \sum_{x=0}^{t-2} b_1(x) F_1(t-x-1, 0) P(x), & t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b_1(x) F_1(t-x-1, 0) P(x), & t = s+2, s+3, \ldots.
\end{cases} \tag{4.11}
\]

Let us now look at the right hand side of Inequality 4.8. Let us interpret \( b_1(x) \) in this inequality as representing the average number of female offspring an adult male in age group \( x \) at time \( t \) contributes to age group \( 0 \) at time \( t + 1 \). If we make this interpretation, then the right hand side of this inequality is identical to the right hand side of Equation 2.33. That is, the right hand side of this inequality describes the growth of the females in a population which consists of both females and males. However, the population is structured such that both the female and male offspring are attributed only to the males.

If we replace any \( M(t, x) \) appearing in the right hand side of Inequality 4.8 by \( M_1(t, x) \), then we also have that
\[ F(t, 0) \leq F_2(t, 0), \text{ say, for all } t > 0, \]

where the function \( F_2(t, 0) \) is the solution to

\[
F_2(t, 0) = \begin{cases} 
F_1(t-1) + \sum_{x=0}^{t-2} b_1(x) M_1(t-x-1, 0) Q(x), & \text{if } t = 1, 2, \ldots, s+1, \\
\sum_{x=0}^{s} b_1(x) M_1(t-x-1, 0) Q(x), & \text{if } t = s+2, s+3, \ldots .
\end{cases}
\]

(4.12)

Let us note that the right hand side of this equation is a function of \( M_1(t, 0) \) only. Thus, \( F_2(t, 0) \) denotes the number of females in age group 0 at time \( t \), provided the female offspring are due only to the males. That is, Equation 4.12 has the same basic form as Equation 2.33.

Since Equation 4.11 has the same form as the renewal equation we have studied, we immediately have the solution, and it is characterized by

\[ F_1(t, 0) \sim F_1 \mu_0^t, \quad t + \infty, \]

(4.13)

where \( F_1 \) is a constant and \( \mu_0 \) is the unique positive real solution that is larger in absolute value than any other solution to the characteristic equation

\[ \phi_1(\mu) \equiv \sum_{x=0}^{s} \mu^{-(x+1)} b_1(x) P(x) = 1. \]

(4.14)

The constant \( F_1 \) is given by
\[
F_1 = \sum_{x=1}^{s+1} \mu_0^{-x} F_0(x-1) / \sum_{x=0}^{s} (x+1) \mu_0^{-(x+1)} b_1(x) p(x), \quad (4.15)
\]

where the function \( F_0(x-1) \) is defined by Equation 4.5.

Let us note that Equation 4.12 is not of the same form as the basic renewal equation. We cannot solve this equation for the unknown \( F_2(t, 0) \), because this equation is also a function of \( M_1(t, 0) \), which, for the moment, is also unknown. We will return to this equation and solve it later.

We have that Equations 4.11, 4.13, 4.14, and 4.15 respectively are identical to Equations 2.3, 2.10, 2.6, and 2.11, except that there is not a subscript on the function \( F(t, 0) \) appearing in the latter four equations. Thus, we have that the two characteristic equations \( \phi(\mu) = 1 \) and \( \phi_1(\mu) = 1 \) defined respectively by Equations 2.6 and 4.14 are identical, i.e., \( \phi(\mu) = \phi_1(\mu) \) for all \( \mu \). The constants \( F \) and \( F_1 \) given respectively by Equations 2.11 and 4.15 are also identical. We will leave the subscript on \( \phi_1(\mu) \) and \( F_1 \) since it will become useful later. Let us note that Equations 4.11, 4.13, 4.14, and 4.15 give us one upper bound to the number of females in age group 0 at time \( t \). However, these equations describe the growth of a population consisting of only females which produce only female offspring. This is true provided we interpret the function \( b_1(x) \) as the average number of female offspring that an adult female
in age group \( x \) at time \( t \) contributes to age group \( 0 \) at time \( t + 1 \).

We will now look at Inequalities 4.9 and 4.10. First, let us consider Inequality 4.10. The right hand side of this inequality describes the growth of a population of males such that the male offspring are attributed only to the adult males. That is, if we interpret \( b_2(x) \) as being the average number of male offspring an adult male in age group \( x \) at time \( t \) contributes to age group \( 0 \) at time \( t + 1 \). Thus, the right hand side of Inequality 4.10 is identical to the right hand side of Equation 2.32. If we replace any \( M(t, 0) \) appearing in the right hand side of this inequality by \( M_1(t, 0) \) then we have that

\[
M(t, 0) \leq M_1(t, 0), \text{ for all } t > 0.
\]

The function \( M_1(t, 0) \) represents the number of males in age group \( 0 \) at time \( t \). However, these males are the offspring of other males in the population; that is \( M_1(t, 0) \) is a solution to an equation having the same form as Equation 2.32. This equation is

\[
M_1(t, 0) = \begin{cases} 
M_0(t-1) + \sum_{x=0}^{t-2} b_2(x) M_1(t-x-1, 0) Q(x), & t = 1,2,\ldots,s+1, \\
\sum_{x=0}^{s} b_2(x) M_1(t-x-1, 0) Q(x), & t = s+2,s+3,\ldots .
\end{cases}
\]
The function $M_0(t)$, which denotes the number of male offspring of the ancestral males of our population alive at time $t$, is given by Equation 4.6b, and it is identical to Equation 2.35.

Let us now look at the right hand side of Inequality 4.9. One of the classical models used to describe the growth of a population was a bisexual model. In this model it was supposed that the population consists of both females and males. However, when reproduction occurs, both the female and male offspring are attributed only to the mature females. The right hand side of Inequality 4.9 is related to this type of model for population growth. That is, it describes the number of infant males in the population at time $t$, provided that the males are attributed only to the adult females. This is true if we interpret $b_2(x)$ as representing the average number of male offspring a mature female in age group $x$ at time $t$ contributes to age group 0 at time $t + 1$. Thus, the right hand side of Inequality 4.9 is identical to the right hand side of Equation 2.24.

Let us replace any $F(t, x)$ occurring in the right hand side of this inequality by $F_1(t, x)$. Also, let $M_2(t, 0)$ denote the number of males in age group 0 at time $t$. We have the restriction that these males are the offspring of only the adult females occurring in the population. We have that

$$M(t, 0) \leq M_2(t, 0), \text{ for all } t > 0,$$
where $M_2(t, 0)$ is the solution to

$$
M_2(t, 0) = \begin{cases}
t - 2 & \text{if } t = 1, 2, \ldots, s + 1, \\
\sum_{x=0}^{s} b_2(x) F_1(t-x-1, 0) P(x) & \text{if } t = s + 2, s + 3, \ldots.
\end{cases}
$$

(4.17)

Let us note that this equation has the same structure as Equation 2.24, except for the subscripts. The function $M_1(t)$, given by Equation 4.6a, represents the number of male offspring from the ancestral females alive at time $t$.

We can immediately solve Equation 4.16, since it is a renewal equation, but the solution to Equation 4.17 is not immediately available. The solution to Equation 4.16 is characterized by

$$
M_1(t, 0) \sim M_1 v_0^t, \quad t \to \infty.
$$

(4.18)

In this equation $M_1$ is a constant and $v_0$ is the unique positive real solution which is larger in absolute value than any other solution to the characteristic equation

$$
\phi_2(v) \equiv \sum_{x=0}^{s} v^{-(x+1)} b_2(x) Q(x) = 1.
$$

(4.19)

The constant $M_1$ is given by

$$
M_1 = \sum_{x=1}^{s+1} v_0^{-x} M_0(x-1)/ \sum_{x=0}^{s} (x+1) v_1^{-(x+1)} b_2(x) Q(x).
$$

(4.20)
Let us note that the characteristic equation \( \phi_2(v) = 1 \) is the same equation given by Equation 2.36.

We have now characterized the solutions to Equations 4.11 and 4.16. The solutions are given respectively by Equations 4.13 and 4.18. With these two solutions, it is now possible to characterize the solutions to Equations 4.12 and 4.17.

If we substitute Equation 4.18 into Equation 4.12, we have that

\[
F_2(t, 0) \sim M_1 \nu_0^t \sum_{x=0}^S \nu_0^{-(x+1)} b_1(x) Q(x), \quad t \to \infty. \tag{4.21}
\]

This solution is valid since \( F_1(t) = 0 \) for \( t \) sufficiently large. Likewise, by substituting Equation 4.13 into Equation 4.17, we find that

\[
M_2(t, 0) \sim F_1 \nu_0^t \sum_{x=0}^S \nu_0^{-(x+1)} b_2(x) P(x), \quad t \to \infty, \tag{4.22}
\]

since \( M_1(t) = 0 \) for \( t \) sufficiently large.

The upper bound to the solution to Equations 4.1 and 4.2 is now available. The number of females in age group 0 at time \( t \) is bounded above by the solutions to Equations 4.11 and 4.12. That is,

\[
F(t, 0) \leq F_1(t, 0) \sim F_1 \nu_0^t, \quad t \to \infty, \tag{4.23}
\]

and

\[
F(t, 0) \leq F_2(t, 0) \sim M_1 \nu_0^t \sum_{x=0}^S \nu_0^{-(x+1)} b_1(x) Q(x), \quad t \to \infty. \tag{4.24}
\]
The number of males in age group 0 at time $t$ is bounded above by the solutions to Equations 4.16 and 4.17. That is,

$$M(t, 0) \leq M_1(t, 0) \sim M_1 \nu_0^t, \quad t \to \infty,$$  

(4.25)

and

$$M(t, 0) \leq M_2(t, 0) \sim F_1 \mu_0^t \sum_{x=0}^{S} \mu_0^{-(x+1)} b_2(x) P(x), \quad t \to \infty.$$  

(4.26)

In these four equations $F_1$ and $M_1$ are constants given respectively by Equations 4.15 and 4.20, and $\mu_0$ and $\nu_0$ are the dominant solutions to their respective characteristic equations given by Equations 4.14 and 4.19.

Let us note that in general we cannot compare the right hand sides of Equations 4.23 and 4.24 with an inequality. This is true since we have not made any assumptions about an inequality between $P(x)$ and $Q(x)$ nor between $b_1(x)$ and $b_2(x)$ for $x = 0, 1, \ldots, s$. For exactly the same reason, we cannot compare the right hand sides of Equations 4.25 and 4.26 with an inequality.

**B. The Interpretation of the Upper Bounds**

In the previous pages we have constructed upper bounds to the solutions to Equations 4.1 and 4.2. These two equations describe the manner in which female and male offspring are produced, provided that the adult females and males
in the same age group form couples. In these two equations we made no assumption about the ratio of females to males at birth.

We are able to compare this means of attributing offspring to a couple with two versions of the classical models for the growth of a bisexual population. The first version of the classical model for the growth of a bisexual population we used was to suppose that a population consisted of both females and males. Offspring of both types were produced; however all of the offspring were credited to only the mature females in the population. The mature males took no part in reproduction. The equations which describe the production of female and male progeny for a model of this type are given respectively by Equations 4.11 and 4.17.

In the second version of the classical model, we interchanged the role of the two sexes. That is, we again supposed that the population consisted of both females and males. However, when reproduction occurred, we made the assumption that both of the female and male offspring were attributed only to the adult males. The mature females played no role in reproduction. Equations 4.16 and 4.12 respectively describe the growth of the male and female population.

We have, according to the two classical models, that there are two ways of obtaining female offspring. The first
way is that the mature females produce the female offspring. The second way is that the mature males produce the female offspring. Equations 4.23 and 4.24 show that if couples are formed between females and males in the same age group, then the number of female offspring, produced at time \( t \), is at most the number of female offspring produced at time \( t \) as predicted by either of the classical models for the production of female progeny. This is true provided \( t \) is very large.

Likewise, according to the classical models there are two ways to obtain male offspring. In the first way we could suppose that mature males are credited with producing the male offspring. The second would be to make the assumption that the male offspring are attributed only to the mature females. Now, according to the analysis we have given, Equations 4.25 and 4.26 show that if couples are formed between females and males in the same age group, then the number of male offspring produced at time \( t \) is less than or equal to the number produced at time \( t \) as predicted by either of the classical models, for \( t \) sufficiently large.

We have constructed two upper bounds to the solutions to Equations 4.1 and 4.2. These two renewal equations describe the production of offspring if couples are formed between the adult females and males in the same age group. However, in these two equations, we have only considered the
case in which the maximum number of couples is formed. For a bisexually reproducing population, there are individuals who do not take part in reproduction. Thus, the maximum number of couples formed is an upper bound to the actual number formed. Thus, the upper bounds we have constructed are bounds for upper bounds to the true state of nature.

C. A Comparison of Characteristic Equations

We will now consider some consequences of the results from the previous pages when we make the assumption that the ratio of females to males at birth is a known constant. Thus, let us suppose that \( b_1(x) = pb(x) \) and \( b_2(x) = qb(x) \) where \( p, q > 0 \) and \( p + q = 1 \) which is equivalent to supposing that at birth the ratio of females to males is a constant. The connotation of \( b(x) \) is that it represents the average total number of offspring a parent in age group \( x \) at time \( t \) contributes to age group \( 0 \) at time \( t + 1 \). The word parent refers to adult female, to adult male, or to a couple, depending upon the model. A proportion \( p \) of the offspring are female and a proportion \( q \) are male.

If we make this change in notation, then the equations we want to consider are the characteristic equations given by Equations 4.14 and 4.19. These two equations become
\[
\phi_1(\mu) \equiv p \sum_{x=0}^{s} \mu^{-(x+1)} b(x) P(x) = 1 \tag{4.27}
\]

and
\[
\phi_2(\nu) \equiv q \sum_{x=0}^{s} \nu^{-(x+1)} b(x) Q(x) = 1 \tag{4.28}
\]

We want to compare these two equations with the characteristic equation which determines the rate of growth of the population in which couples are formed, that is, with Equation 3.19. This equation is
\[
\phi(\lambda) \equiv \sum_{x=0}^{s} \lambda^{-(x+1)} b(x) \min\{pP(x), qQ(x)\} = 1. \tag{4.29}
\]

If we use the inequality \(\min\{a, b\} \leq a\) and \(\leq b\), then at least for \(\lambda\) real and positive, we have that
\[
\phi(\lambda) \leq p \sum_{x=0}^{s} \lambda^{-(x+1)} b(x) P(x)
\]

\[= \phi_1(\lambda)\]

and
\[
\phi(\lambda) \leq q \sum_{x=0}^{s} \lambda^{-(x+1)} b(x) Q(x)
\]

\[= \phi_2(\lambda).\]

The functions \(\phi_1(\cdot)\) and \(\phi_2(\cdot)\) are respectively defined by Equations 4.27 and 4.28. We know, at least for \(\lambda\) real and positive that the three characteristic equations \(\phi(\lambda)\), \(\phi_1(\lambda)\), and \(\phi_2(\lambda)\) are monotone decreasing functions of \(\lambda\). Also, these three characteristic equations are such that
\[ \phi(\lambda) \leq \phi_1(\lambda) \text{ and } \phi(\lambda) \leq \phi_2(\lambda) \, . \]

This implies that

\[ \lambda_0 \leq \mu_0 \text{ and } \lambda_0 \leq \nu_0 \]

where \( \lambda_0 \), \( \mu_0 \) and \( \nu_0 \) are the unique positive real solutions which are larger in absolute value than any other solutions to their respective characteristic equations

\[ \phi(\lambda) = 1, \; \phi_1(\mu) = 1, \text{ and } \phi_2(\nu) = 1. \]

This shows that the rate of growth, as predicted by either of the classical models for population growth, is an upper bound to the rate of growth predicted if couples are formed between females and males in the same age group. That is, the growth rate for a bisexual population in which couples are formed is at most the rate predicted by either of the classical modes for the growth of a bisexual population.

It should be noted that we do not know which of the numbers \( \mu_0 \) or \( \nu_0 \) is smaller. This is true since in Equations 4.27 and 4.28 we have not made any assumptions about a comparison between the survival probabilities for the females and males.
V. THE GENERAL STRUCTURE OF
THE COUPLES

In the previous chapters we have been quite restrictive
in specifying the mating structure of our population. We
have considered only the case in which couples are formed
between females and males in the same age group. In this
chapter we will drop this restriction and impose an arbitrary
structure on the formation of the couples.

As before, we will suppose that the population consists
of both females and males that are classified according to
age and time. We will also assume that for any time, all
of the females in a given age group behave identically.
The same assumption is true for the males in the population;
so that for any time the males in a specified age group behave
in an identical manner. The adult females and males will
form couples and female and male offspring will be produced.

We will use the following notation. Let

\[ F(t, x) = \text{number of females in age group } x \text{ at time } t \]
\[ M(t, x) = \text{number of males in age group } x \text{ at time } t \]
\[ P(x) = \text{P(any female survives from birth to age group } x) \]
\[ Q(x) = \text{P(any male survives from birth to age group } x) \].

In this more general model, the couples are formed between
females and males in different age groups. Thus, the number
of couples formed at time \( t \) will be a function of both ages.
Also, the functions describing the birth of the offspring will be a function of both ages. We will however, suppose that these functions are only age dependent and not time dependent. Thus, we also let

\[ C(t; x, y) = \text{number of couples formed, with the adult female in age group } x \text{ and the adult male in age group } y, \text{ at time } t. \]

\[ B_1(x, y) = E(\text{number of female offspring a couple, at time } t, \text{ contributes to age group 0 at time } t + 1 \text{ if the adult female is in age group } x \text{ and the adult male is in age group } y.). \]

\[ B_2(x, y) = E(\text{number of male offspring a couple, at time } t, \text{ contributes to age group 0 at time } t + 1 \text{ if the adult female is in age group } x \text{ and the adult male is in age group } y.). \]

If we are going to form couples between females and males in different age groups, we must partition the number of live females in a given age group into subclasses according to the age of the male half of the couple. Likewise, we must partition the number of males in a given age according to the age of the female used in forming the couple. We will suppose that these partitions are only dependent upon the ages of the females and males involved and not on time. Thus, let

\[ I(x, y) = P(\text{a female in age group } x \text{ couples with a male in age group } y) \]

\[ J(x, y) = P(\text{a male in age group } y \text{ couples with a female in age group } x) \]
The unknowns we want to solve for are the number of females and males in the various age groups at time \( t \).

We assume that we know the survival probabilities, the birth rates for both female and male offspring, and the partition probabilities for both the adult females and males. Presently, we shall explicitly state the form of the function which describes the formation of the couples.

Let \( n \) be the maximum age to which any individual can survive. We will suppose that this age is the same for both females and males; that is, \( P(x) = 0 \) and \( Q(x) = 0 \) for any age \( x > n \). Let \( s \) be the maximum age in which reproduction occurs; that is \( B_1(x, y) = 0 \) and \( B_2(x, y) = 0 \) for any age \( x > s \) and any age \( y > s \). The restrictions we have on the partition probabilities are that

\[
0 \leq I(x, y) \leq 1, \quad 0 \leq J(x, y) \leq 1, \quad \text{for all } x \text{ and } y,
\]

\[
\sum_{y=0}^{s} I(x, y) = 1, \quad \text{for all } x = 0, 1, \ldots, s
\]

and

\[
\sum_{x=0}^{s} J(x, y) = 1, \quad \text{for all } y = 0, 1, \ldots, s.
\]

However, in general we have that

\[
\sum_{x=0}^{s} I(x, y) \neq 1, \quad \text{for } y = 0, 1, \ldots, s
\]
and
\[ \sum_{y=0}^{s} J(x, y) \neq 1, \text{ for } x = 0, 1, \ldots, s. \]

The function we are most concerned about is the function which describes the formation of the couples. Previously we noted that if couples were formed between females and males in the same age group, then the maximum number of couples possible was equal to the minimum of the number of females and males in that age group. We will construct couples in the same manner in this more general content.

We have partitioned our population of females and males according to the preference they have for the age of a mate. Thus, we have that \( I(x, y) F(t, x) \) represents the expected number of females in age group \( x \) at time \( t \) that are available to form a couple with a male in age group \( y \). We also have that \( J(x, y) M(t, y) \) is the expected number of males in age group \( y \) at time \( t \) that can form a couple with a female in age group \( x \). Thus, the maximum number of couples that can be formed between the two age groups is the minimum of these two expected values. We will take

\[ C(t; x, y) = \min\{I(x, y) F(t, x), J(x, y) M(t, y)\}. \quad (5.1) \]

It should be noted that Equation 3.3 is a special case of Equation 5.1. That is, if we define the partition probabilities to be
1 if \( x = y \) 

\[
I(x, y) = \begin{cases} 
1 & \text{if } x = y \\ 
0 & \text{if } x \neq y
\end{cases}
\]

and 

\[
J(x, y) = \begin{cases} 
1 & \text{if } x = y \\ 
0 & \text{if } x \neq y
\end{cases}
\]

then Equation 5.1 is identical to Equation 3.3.

We are now in a position to write down the two renewal equations which describe the production of female and male offspring in age group 0 at time \( t \). Some females in age group 0 at time \( t \) are the female offspring of the couples formed from the ancestral individuals alive at time \( t - 1 \).

In addition, there are female offspring of couples alive at time \( t - 1 \) formed from the descendants of the original ancestral individuals. A similar statement about the production of males in age group 0 at time \( t \) is also true.

As we noted in previous sections, the females and males in age group \( x \) at time \( t \) are the infant females and males in age group 0 at time \( t - x \) that survive to age \( x \), provided \( x \leq t \). If \( x > t \), the females and males in age group \( x \) at time \( t \) are the original ancestral individuals in age group \( x - t \) at time 0 that survive to age group \( x \) given that they were alive at age \( x - t \). That is

\[
P(t, x) = P(t-x, 0) \frac{P(x)}{P(x-t)}, \quad x \leq t
\]

\[
= P(0, x-t) \frac{P(x)}{P(x-t)}, \quad x > t
\]
and

\[ M(t, x) = M(t-x, 0) Q(x), \quad x \leq t \]
\[ = M(0, x-t) Q(x)/Q(x-t), \quad x > t. \]

If we use these two identities in Equation 5.1 we have an expression for the couples formed by the adults in terms of the infants. That is,

\[ C(t; x, y) = \min\{I(x, y) F(t-x, 0) P(x), \]
\[ J(x, y) M(t-y, 0) Q(y)\} \quad (5.2) \]

for \( x \leq t \) and \( y \leq t \). If \( x > t \) and \( y > t \) we have an equation for the couples formed by the ancestral females and males. This equation is

\[ C(t; x, y) = \min\{I(x, y) F(0, x-t) P(x)/P(x-t), \]
\[ J(x, y) M(0, y-t) P(y)/P(y-t)\}, \quad (5.3) \]

for \( x > t \) and \( y > t \). It is possible to form couples between ancestral individuals and descendants of the ancestors. However, for the sake of simplicity, we will not consider this possibility.

Thus, since the infants produced at time \( t \) are the offspring of the couples alive at time \( t-1 \), the renewal equations which describe the production of females and males are,
\[
F(t, 0) = \begin{cases} 
F^*(t-1) + \sum_{x=0}^{t-2} \sum_{y=0}^{t-2} B_1(x, y) \\
\cdot \min\{I(x, y) F(t-x-1, 0) P(x), \\
J(x, y) M(t-y-1, 0) Q(y)\}, \\
t = 1, 2, \ldots, s+1, 
\end{cases}
\]  
(5.4)

\[
M(t, 0) = \begin{cases} 
M^*_0(t-1) + \sum_{x=0}^{t-2} \sum_{y=0}^{t-2} B_2(x, y) \\
\cdot \min\{I(x, y) F(t-x-1, 0) P(x), \\
J(x, y) M(t-y-1, 0) Q(y)\}, \\
t = s+2, s+3, \ldots, 
\end{cases}
\]  
(5.5)

In these two equations we define $\Sigma = 0$ and $F^*_0(t)$ and $M^*_0(t)$ to be, respectively, the number of female and male offspring produced by the couples formed from the ancestral
females and males alive at time \( t \). These functions are given by

\[
F_0^*(t) = \sum_{x=0}^{s-t} \sum_{y=0}^{s-t} B_1(x+t, y+t) \cdot \min\{I(x+t, y+t) F(0, x) P(x+t)/P(x), J(x+t, y+t) M(0, y) Q(y+t)/Q(y)\},
\]

\[
t = 0, 1, \ldots, s,
\]

\[
= 0, \text{ otherwise},
\]

and

\[
M_0^*(t) = \sum_{x=0}^{s-t} \sum_{y=0}^{s-t} B_2(x+t, y+t) \cdot \min\{I(x+t, y+t) F(0, x) P(x+t)/P(x), J(x+t, y+t) M(0, y) Q(y+t)/Q(y)\},
\]

\[
t = 0, 1, \ldots, s,
\]

\[
= 0, \text{ otherwise}.
\]

When we were considering the special case in which couples were formed between females and males in the same age groups, we proved an interesting theorem. This theorem said that the hypothesis that the ratio of females to males at birth is a constant is equivalent to the hypothesis that the number of females and male offspring produced by the couples in the various age groups is also proportional. This theorem is also true for the more general mating system we are now considering. That is, if we mimic the proof of this theorem, it is possible
to prove that if we suppose that $F(t, 0)/p = M(t, 0)/q$ for all $t \geq 0$ where $p, q > 0$ and $p + q = 1$ then this is equivalent to assuming that $B_1(x, y)/p = B_2(x, y)/q$ for every age $x$ and $y$ in which reproduction occurs.

If couples are formed between females and males in the same age groups, this theorem lead us to the conclusion that the renewal equations which describe the production of female and male offspring are linear in the unknowns. With respect to the more general case we are now considering, this result no longer holds. That is, Equations 5.4 and 5.5 are still nonlinear in the unknowns $F(\cdot, 0)$ and $M(\cdot, 0)$. Thus, since we cannot solve Equations 5.4 and 5.5 explicitly, we will construct some meaningful upper bounds to the solutions.

However, since it is reasonable to assume, at least for the human population, that at birth the ratio of females to males is a constant, we will let $B_1(x, y) = pB(x, y)$ and $B_2(x, y) = qB(x, y)$, where $p, q > 0$ and $p + q = 1$. Thus $B(x, y)$ represents the average number of offspring a couple, with the adult female in age group $x$ and the adult male in age group $y$ at time $t$, contributes to age group $0$ at time $t + 1$. A proportion $p$ of the total number of offspring produced are females and a proportion $q$ are males.

The renewal equations which describe the production of infants, i.e., Equations 5.4 and 5.5, become
The two functions $F^*_0(t)$ and $M^*_0(t)$, which respectively describe the production of female and male infants from the ancestral individuals alive at time $t$, become
\[ F_s^*(t) = p \sum_{x=0}^{s-t} \sum_{y=0}^{s-t} B(x+t, y+t) \]
\[ \cdot \min\{I(x+t, y+t) F(0, x) P(x+t) P(x), \]
\[ J(x+t, y+t) M(0, y) Q(y+t/Q(y))\}, \]
\[ t = 0,1,\ldots,s, \quad (5.10) \]

\[ = 0, \text{ otherwise,} \]

and

\[ M_s^*(t) = q \sum_{x=0}^{s-t} \sum_{y=0}^{s-t} B(x+t, y+t) \]
\[ \cdot \min\{I(x+t, y+t) F(0, x) P(x+t)/P(x), \]
\[ J(x+t, y+t) M(0, y) Q(y+t)/Q(y)\}, \]
\[ t = 0,1,\ldots,s, \quad (5.11) \]

\[ = 0, \text{ otherwise.} \]

We want to construct upper bounds to the solutions to Equations 5.8 and 5.9. In order to do this, we will use the fact that \(\min\{a,b\} \leq a\) and \(\leq b\) in our renewal equations. Let us first use this inequality in Equation 5.10. We have

\[ F_s^*(t) \leq p \sum_{x=0}^{s-t} F(0, x) P(x+t)/P(x) \sum_{y=0}^{s-t} B(x+t, y+t) I(x+t, y+t) \]
\[ = F_0(t), \text{ say, for } t = 0,1,\ldots,s, \quad (5.12) \]

and

\[ F_s^*(t) \leq q \sum_{y=0}^{s-t} M(0, y) Q(y+t)/Q(y) \sum_{x=0}^{s-t} B(x+t, y+t) J(x+t, y+t) \]
\[ = F_1(t), \text{ say, for } t = 0,1,\ldots,s, \quad (5.13) \]
with
\[ F_0^*(t) = F_0(t) = F_1(t) = 0, \text{ otherwise.} \]

Let us consider parts of Equations 5.12 and 5.13 in more detail. First, let us look at the function
\[ \sum_{y=0}^{s-t} B(x+t, y+t) I(x+t, y+t) = b_f(x+t), \text{ say,} \quad (5.14) \]
for \( x = 0, 1, \ldots, s \) and \( t = 0, 1, \ldots \). Let us note that the equations we are manipulating describe the production of offspring from the ancestral individuals in the population. Now, \( B(x, y) \) denotes the average number of offspring a couple, with the female in age group \( x \) and the male in age group \( y \) at time \( t \), contributes to age group 0 at time \( t + 1 \). Also, \( I(x, y) \) is the probability that a female in age group \( x \) couples with a male in age group \( y \). Thus, if \( t = 0 \) in Equation 5.14, we have that \( b_f(x) \) is the expected number of offspring any female in age group \( x \) produces as a result of the matings with the available males in the various age groups. Let us now consider \( b_f(x + t) \) for \( t > 0 \). In Equation 5.14, let \( z = y + t, \) then we have
\[ b_f(x + t) = \sum_{z=t}^{s} B(x+t, z) I(x+t, z), \]
or
\[ b_f(x + t) = \sum_{z=0}^{s} B(x+t, z) I(x+t, z) - \sum_{z=0}^{t-1} B(x+t, z) I(x+t, z), \]
for \( t = 1, 2, \ldots, s \). So, we have that \( b_f(x+t) \) is the expected number of offspring produced by an ancestral female in age group \( x + t \) such that the males that take part in the mating are also ancestral individuals, provided \( t = 1, 2, \ldots, s \). What we have stated is true for \( x = 0, 1, \ldots, s \) and \( t = 0, 1, \ldots \). The index \( t \) can range over all of the nonnegative integers since the function \( B(x, y) \) is zero for \( x > s \) and \( y > s \). It then follows that \( b_f(x+t) \) defined in Equation 5.14 is zero for \( x + t > s \). Thus, we have that the function \( b_f(\cdot) \), defined by Equation 5.14, refers to the production of offspring by the females in the population. Let us remember that a proportion \( p \) of the total offspring are females and a proportion \( q \) are males.

If we substitute Equation 5.14 into Equation 5.12, we have that

\[
F^*(t) < F_0(t), \quad t = 0, 1, \ldots
\]

where

\[
F_0(t) = p \sum_{x=0}^{s-t} b_f(x+t) F(0, x) P(x+t)/P(x), \quad (5.15)
\]

\[
t = 0, 1, \ldots, s,
\]

\[
= 0, \text{ otherwise}.
\]

Thus, this equation represents the number of female offspring produced by the ancestral females alive at time \( t \), provided the offspring are credited to the females. This equation
has the same structure as Equation 2.4.

We will now consider part of Equation 5.13 in more detail. Let us look at:

\[ \sum_{x=0}^{s-t} B(x+t, y+t) J(x+t, y+t) = b_m(y+t), \text{ say,} \quad (5.16) \]

for \( y = 0,1, \ldots, s \), and \( t = 0,1, \ldots \). If \( t = 0 \) in this equation, \( b_m(y) \) is the expected number of offspring a male in age group \( y \) contributes to the population as a result of the matings with the females in the different age groups.

Let \( z = x + t \) in Equation 5.16. We find that

\[ b_m(y+t) = \sum_{z=0}^{s} B(z, y+t) J(z, y+t) - \sum_{z=0}^{t-1} B(z, y+t) J(z, y+t) \]

for \( t = 1,2, \ldots, s \). Thus, we have that \( b_m(y+t) \) represents the expected number of offspring produced by an ancestral male in age group \( y + t \) such that the females that are available for mating are ancestral females, provided \( t = 1,2, \ldots, s \). So, the function \( b_m(\cdot) \) refers to the production of offspring, provided the offspring are credited to the males in the population. If we substitute Equation 5.16 into Equation 5.13 we find that

\[ F_0^*(t) \leq F_1(t), \quad t = 0,1, \ldots \]
where

$$F_1(t) = p \sum_{y=0}^{s-t} b_m(y+t) M(0, y) \frac{Q(y+t)}{Q(y)},$$

$$t = 0, 1, \ldots, s$$

(5.17)

$$= 0, \text{ otherwise.}$$

Thus, since a proportion $p$ of the total number of offspring produced are females, we have that $F_1(t)$ represents the number of female offspring produced by the ancestral males alive at time $t$. We should note that this equation has the same form as Equation 2.34.

If we use the two functions defined by Equations 5.14 and 5.16 in Equation 5.11, we obtain two inequalities. These two inequalities are

$$M^*(t) \leq q \sum_{x=0}^{s-t} F(0, x) \frac{P(x+t)}{P(x)} \sum_{y=0}^{s-t} B(x+t, y+t) I(x+t, y+t)$$

$$= q \sum_{x=0}^{s-t} b_f(x+t) (x+t) \frac{F(0, x)}{P(x)}$$

$$= M_1(t), \text{ say, for } t = 0, 1, \ldots, s$$

(5.18)

and

$$M^*_0(t) \leq q \sum_{y=0}^{s-t} M(0, y) \frac{Q(y+t)}{Q(y)} \sum_{x=0}^{s-t} B(x+t, y+t) J(x+t, y+t)$$

$$= q \sum_{y=0}^{s-t} b_m(y+t) M(0, y) \frac{Q(y+t)}{Q(y)}$$

$$= M_0(t), \text{ say, for } t = 0, 1, \ldots, s,$$

(5.19)
with

\[ M_0^*(t) = M_1^*(t) = M_0(t) = 0, \text{ otherwise} \]

A proportion \( q \) of the offspring produced by the parents are males. Thus, \( M_1(t) \) denotes the number of male offspring produced by the ancestral females alive at time \( t \). This equation has a form similar to the function \( M_1(t) \) defined in Equation 2.24. Also, if the offspring are attributed to the adult males in the population, then Equation 5.19 represents the number of male offspring produced by the ancestral males alive at time \( t \). This function has the same form as Equation 2.35.

We are now in a position to form inequalities for Equations 5.8 and 5.9. If we use the functions defined by Equations 5.14 through 5.19 and if we again use the inequality that \( \min\{a,b\} \leq a \) and \( \leq b \) we find that

\[
F(t, 0) \leq \begin{cases} 
F_0(t-1) + p \sum_{x=0}^{t-2} b_f(x) F(t-x-1, 0) P(x), \\
t = 1, 2, \ldots, s+1,
\end{cases}
\]

and

\[
F(t, 0) \leq \begin{cases} 
\sum_{x=0}^{s} p b_f(x) F(t-x-1, 0) P(x), \\
t = s+2, s+3, \ldots,
\end{cases}
\]
and
\[
F(t, 0) \leq \begin{cases} 
F_1(t-1) + p \sum_{x=0}^{t-2} b_m(x) M(t-x-1, 0) Q(x), \\
&\text{if } t = 1, 2, \ldots, s+1,
\end{cases}
\]

and
\[
M(t, 0) \leq \begin{cases} 
M_1(t-1) + q \sum_{x=0}^{t-2} b_f(x) F(t-x-1, 0) P(x), \\
&\text{if } t = 1, 2, \ldots, s+1,
\end{cases}
\]

Let us note that Equations 5.20 through 5.23 have the same basic form as Equations 4.7 through 4.10. Thus, all of the results we obtained with regards to Equation 4.7, 4.8, 4.9, and 4.10 apply respectively to Equation 5.20, 5.21, 5.22, and 5.23. That is, the right hand side of Equations
5.20 and 5.22 describe the production of infants for a bisexual population. However, the population is constructed in such a manner that both types of offspring are credited only to the adult females in the population. Thus, if couples are formed among the adult females and males in the various age groups, then the renewal equations which describe the production of infants are bounded above by the renewal equations which describe the production of female and male offspring in a so called bisexual population in which all of the offspring are attributed to the adult females.

The right hand sides of Equations 5.21 and 5.23 also describe the production of female and male offspring for a bisexual population. However, all of the offspring are attributed to the adult males in the population. We have that if couples are formed among the adult females and males in different age groups then the numbers of infant females and males produced are at most the numbers of females and males produced as predicted by a model in which all the infants are credited to the adult males in the population.

We could equate the right hand sides of Equations 5.20 through 5.23 to the appropriate quantities and solve the four renewal equations. However, the equations and solutions we would obtain are analogous to all of the results we found in the later sections of the previous chapter. Thus, all of the results with respect to the upper bounds we found in
the previous chapter now apply to the more general model we have considered in this chapter.
VI. STOCHASTIC MODELS FOR POPULATION GROWTH

A. Classical Age-Dependent Branching Processes

The stochastic versions of the type of growth models we have been discussing are known as the single type age-dependent branching processes. The basic idea underlying these processes is that initially there is one individual alive. This individual lives a random length of life. At the end of its life, it is replaced by a random number of progeny that are identical to the parent. The life cycle is then repeated, with all lines of ancestry developing independently of each other. The process then continues as long as individuals are present in the population.

Since the age-dependent branching processes describe the growth of a population which consists of only one type of individual, the model cannot be used to describe the growth of a bisexually reproducing population. However, as a mathematical model for the growth of an asexually reproducing organism or any object that reproduces by fission, the results from the age-dependent branching processes may be valid.

Many of the mathematical properties of this type of model for population growth were given by Bellman and Harris (1952). They were interested in the growth of a population that reproduced by fission; that is, when every individual
split into two identical individuals at the end of its life. Harris (1963) gives an elegant account of the mathematical properties of the general age-dependent branching process. An attempt was made by Goodman (1968) to use this type of model to describe the growth of a bisexually reproducing population.

The notation we will use is the notation given by Harris (1963). It should be noted that some of the symbols we have used previously in a specific connotation will be reused. However, the interpretation of the symbols is not necessarily the same.

Let the nonnegative integer valued random variable \( X(t) \) represent the size of the population at time \( t \). The time variable \( t \) can be either discrete or continuous. We will assume that any individual in the population lives a random length of life, denoted by \( \ell \). Actually, there are a collection of random variables which describe the length of life, one for each individual. We will assume that all of these random variables are independent and identically distributed. Let \( G(t) \) be the known common probability distribution function for these random variables; that is

\[
P[\ell \leq t] = G(t), \ t \geq 0 .
\] (6.1)

Let the random variable \( v \) represent the number of offspring any individual contributes to the population at the end of
its life. The random variable \( v \) does not depend upon time, and it is distributed independently of \( l \). We will let \( f(s) \) be the known probability generating function for the offspring; that is,

\[
f(s) = \sum_{k=0}^{\infty} P[v=k]s^k, \quad |s| \leq 1, \quad (6.2)
\]

where \( P[v=k] > 0 \) for each \( k \), and \( f(1) = 1 \). To avoid trivialities, we will exclude the cases in which \( P[v=0] = 1 \) and \( P[v=1] = 1 \).

We want to find the probability generating function of the random variable, \( X(t) \), which denotes the size of the population at time \( t \) as a function of Equations 6.1 and 6.2. Let

\[
F(s, t) = \sum_{k=0}^{\infty} P[X(t)=k]s^k, \quad t \geq 0, \quad |s| \leq 1 \quad (6.3)
\]

represent the generating function of \( X(t) \).

Let us recall that at time 0 the population consists of only one ancestral individual. Thus, at time \( t \) two events are possible. We have that either the initial ancestral individual is still alive, or this individual has died and produced progeny. If, at time \( t \), the initial individual is still alive this is equivalent to having \( l > t \). That is,
\[ P[X(t) = 1] = P[\lambda > t] \]
\[ = 1 - P[\lambda \leq t] \]
\[ = 1 - G(t), \quad t < \lambda, \quad (6.4) \]

so the generating function at time \( t, \quad t < \lambda, \) is \( s. \)

We will now consider the situation after the initial individual has died and produced progeny. That is, we want to find a general expression for \( P[X(t) = k], \quad k = 0, 1, \ldots, \) and \( t \geq \lambda. \) Let us suppose that the initial progeny were produced at time \( u, \quad 0 \leq u \leq t, \) and that exactly \( n, \quad n = 0, 1, \ldots, \) offspring were produced. The probability of this event is

\[ P[v = n] \, dG(u), \quad n = 0, 1, \ldots. \]

During the remaining \( t - u \) units of time, each of the \( n \) offspring age, die, and leave offspring, such that at time \( t \) the population consists of exactly \( k \) individuals. If we use the theorem of total probability, we find that at time \( t, \quad t > \lambda, \)

\[ P[X(t) = k] = \int_0^t \sum_{n=0}^\infty P[v = n] \sum_{j=1}^n P[X(t-u) = k_j] \, dG(u), \quad (6.5) \]

for \( k = 0, 1, \ldots, \) where the summation in the center of the integrand is over the set of nonnegative integers \( k_1, k_2, \ldots, k_n \) such that \( k_1 + k_2 + \ldots + k_n = k. \) Let us multiply this equation by \( s^k \) and sum over the integers \( k = 0, 1, \ldots; \) we
will then obtain the generating function. If we do this summation, and if we use the monotone convergence theorems so that we can interchange summation and integration, the right hand side of Equation 6.5 becomes

\[
\int_0^t \sum_{n=0}^\infty \sum_{k=0}^\infty s^k \sum_{k_1+k_2+\ldots+k_n=k} \prod_{j=1}^n P[X(t-u)=k_j] \, dG(u) .
\]

Now, the inner sum,

\[
\sum_{k=0}^\infty s^k \sum_{k_1+k_2+\ldots+k_n=k} \prod_{j=1}^n P[X(t-u)=k_j] ,
\]

is the generating function of the n-fold convolution of the distribution expressed by Equation 6.3 with itself and equals \([F(s, t-u)]^n, n = 0,1,\ldots\). Thus, the generating function corresponding to Equation 6.5 becomes

\[
\int_0^t \sum_{n=0}^\infty P[v=n] (F(s, t-u))^n \, dG(u) .
\]

The inner sum in this equation is the generating function for the offspring defined in Equation 6.2 with s replaced by F(s, t-u). That is, the generating function at time t, t > \ell, is given by

\[
\int_0^t f[F(s, t-u)] \, dG(u), \quad t > \ell .
\] (6.6)

If we now combine Equations 6.4 and 6.6 we obtain
the probability generating function for the size of the population for any $t$. That is, we find that

$$F(s, t) = s(1-G(t)) + \int_0^t f[F(s, t-u)] dG(u), \quad t \geq 0, \quad |s| < 1. \quad (6.7)$$

This is a functional integral equation for the unknown generating function $F(s, t)$, and the solution is unknown in general. If however, the generating function for the offspring, $f(s)$, has finite moments then it can be shown that the unknown generating function $F(s, t)$ also has finite moments, Harris (1963). It is easy to show that the moments satisfy linear integral equations having the same form as the renewal equation. We could set up and solve the integral equations for the moments of the generating function $F(s, t)$. However, we are more interested in a bisexual age-dependent branching process. So, with this note, we will conclude the study of the singletype age-dependent branching process.

Harris (1963), in addition to finding the moments of the generating function $F(s, t)$, also discusses many properties of this function. In particular, he gives results dealing with the probability of extinction. We will use some of these results later, which we will introduce when necessary. It should be noted that it is easy to set up a multitype age-dependent branching process. That is, an age-dependent branching process which consists of several different types of individuals. Each of these individuals can produce all of the types of offspring. It must however, be assumed that
all lines develop independently. The multivariate integral equation for the generating function of the size of the population at time \( t \) is similar to Equation 6.7. This integral equation is derived by Mode (1968).

There are stochastic models which are not branching processes for populations with overlapping generations. These models are due to Moran (1962).

B. A Bisexual Age-Dependent Branching Process

We want to describe the growth of a population which consists of two types of individuals, say females and males. However, we want to restrict the population in such a manner that the two types of individuals must interact before reproduction occurs. The idea we have in mind is that initially there is one female and one male in the population. Each of these individuals lives a random length of life. The two individuals form a couple which also lives a random length of life. At the end of the life of the couple, a random number of offspring are produced. These consist of random numbers of females and males. The offspring age, form couples, and reproduce so that the life cycle is repeated.

Let the nonnegative integer valued random variable \( X(t) \) denote the size of the population of females at time \( t \). We must remember that at time 0 there is exactly one female in the population. Any female that is born into the population lives a random length of life. Let the random variable \( \ell_f \) represent the length of life of any female. Also, if \( G_f(t) \)
is the known probability distribution function for the random variable $l_f$, we have

$$P[l_f \leq t] = G_f(t), \ t \geq 0 . \tag{6.8}$$

We want the population to also consist of males, so let $Y(t)$ be a nonnegative integer valued random variable which represents the number of males in the population at time $t$. Initially there is only one male alive. All of the males born into the population live a random length of life. For any male, let the random variable $l_m$ describe the length of life. We will suppose that the random variable has a known probability distribution function $G_m(t)$; that is

$$P[l_m \leq t] = G_m(t), \ t \geq 0 . \tag{6.9}$$

We will assume that the two random variables $l_f$ and $l_m$, which describe the length of life of the females and males, are independently distributed.

We will form the maximum number of couples between the females and males alive at time $t$. Let the nonnegative integer valued random variable $Z(t)$ denote the couples formed at time $t$. Thus,

$$Z(t) = \min\{X(t), Y(t)\}, \ t \geq 0 .$$

Now, a couple is viable as long as both the female and the male are alive. Thus if we let the random variable $\eta$ represent the life of a couple, we have that

$$\eta = \min\{l_f, l_m\}$$

Thus, it is implicit that for any generation, the couples are
formed the instant that the first death occurs in the population. If we let \( G(t) \) be the probability distribution for the random variable \( l \), we have

\[
G(t) = P[l \leq t] = P[\min\{l_f, l_m\} \leq t] = 1 - P[\min\{l_f, l_m\} > t] = 1 - P[l_f > t, l_m > t] = 1 - P[l_f > t] P[l_m > t],
\]

since the random variables \( l_f \) and \( l_m \) are independent. Thus

\[
G(t) = 1 - [1 - P[l_f \leq t]] [1 - P[l_m \leq t]] = 1 - [1 - G_f(t)] [1 - G_m(t)], ~ t \geq 0, \tag{6.10}
\]

and \( G(t) \) is a probability distribution function since both \( G_f(t) \) and \( G_m(t) \) are.

At the instant the first individuals in a given generation die, the couples are formed and offspring are produced. Let the random variables \( v_f \) and \( v_m \) respectively represent the number of female and male offspring any couple produces. The random variables \( v_f \) and \( v_m \) are supposed to be independent of the time variable and the two random variables \( l_f \) and \( l_m \). Let the probability generating function of the random variables \( v_f \) and \( v_m \) be

\[
h(s_1, s_2) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} p[v_f = i, v_m = j] s_1^i s_2^j, \quad |s_1| < 1, \quad |s_2| < 1. \tag{6.11}
\]
Let us suppose that the random variable $v$ represents the total number of offspring produced, i.e., $v = v_f + v_m$, and that $v$ has probability generating function
\begin{equation}
    f(s) = \sum_{k=0}^{\infty} P(v=k)s^k, \quad |s| < 1. \tag{6.12}
\end{equation}

We show in the Appendix that, at least for the human population, a fixed proportion of the total number of births for a given year are females, and a fixed proportion are males. It is possible to incorporate this fact into the probability generating functions given by Equations 6.11 and 6.12. So, with respect to the total number of offspring born, let us suppose that $p$ is the probability that any offspring is a female and $q$ is the probability of a male, where $p, q > 0$ and $p + q = 1$. This gives us a relationship between Equations 6.11 and 6.12. We have,
\begin{equation}
    h(s_1, s_2) = f(ps_1 + qs_2), \quad |s_1| < 1, \quad |s_2| < 1. \tag{6.13}
\end{equation}

The coefficient of $s_1^i s_2^j$ in Equation 6.11 is $P(v_f = i, v_m = j)$. If we use the definition of the probability generating function $f(\cdot)$ given by Equation 6.12 in Equation 6.13, we are able to find the coefficient of $s_1^i s_2^j$ in the right hand side of Equation 6.13. After some manipulation, we find that this coefficient is
That is, from Equation 6.13 we have that

\[ P[v = i + j] \binom{i+j}{j} p^i q^j \]

for \( i,j = 0,1,\ldots \). These equations illustrate the binomial structure of the distribution of female and male offspring.

We want to find the probability generating functions for the three random variables \( X(t), Y(t), \) and \( Z(t) \). In Equation 6.3 we gave a general probability generating function for the random variable \( X(t) \). It has the form

\[ F(s, t) = \sum_{k=0}^{\infty} P[X(t) = k]s^k, \quad |s| < 1. \quad (6.14) \]

In this equation the random variable and the generating function is a function of \( t \). There are other types of probability generating functions, and at this point, it will be convenient for us to introduce and use one of them. Let us consider a generating function having the form

\[ F^*(s, t) = \sum_{k=0}^{\infty} P[X(t) \leq k]s^k, \quad |s| \leq 1 \quad (6.15) \]

There is a relationship between Equations 6.14 and 6.15. The relationship is given as a problem by Feller (1968). We will state this as the following
THEOREM:

For $|s| < 1$ we have that

$$F^*(s, t) = \frac{F(s, t)}{1-s}. \quad (6.16)$$

PROOF:

The proof of this theorem is easy. If $|s| < 1$ the coefficient of $s^k$ in $F(s, t)/(1-s)$ is

$$P[X(t) = k] + P[X(t) = k - 1] + \ldots + P[X(t) = 0],$$

for $k = 0, 1, \ldots$. But this equals $P[X(t) \leq k]$, which is the coefficient of $s^k$ in $F^*(s, t)$.

Let the probability generating functions for the three random variables $X(t)$, $Y(t)$, and $Z(t)$ be given respectively by

$$F(s, t) = \sum_{k=0}^{\infty} P[X(t) = k]s^k, \quad |s| \leq 1, \quad (6.17)$$

$$M(s, t) = \sum_{k=0}^{\infty} P[Y(t) = k]s^k, \quad |s| \leq 1, \quad (6.18)$$

$$C(s, t) = \sum_{k=0}^{\infty} P[Z(t) = k]s^k, \quad |s| \leq 1. \quad (6.19)$$

We can also define three other generating functions having the same structure as Equation 6.15. These three functions will be denoted respectively by $F^*(t, s)$, $M^*(t, s)$, and $C^*(t, s)$. 
We will now consider the random variable $Z(t)$ which denotes the number of couples formed at time $t$; that is,

$$Z(t) = \min\{X(t), Y(t)\}, \ t \geq 0.$$ 

Now, we have that

$$P[Z(t) < k] = P[\min\{X(t), Y(t)\} < k]$$

$$= 1 - P[\min\{X(t), Y(t)\} \geq k]$$

$$= 1 - P[X(t) > k, Y(t) > k]$$

$$\geq 1 - P[X(t) > k]$$

$$= P[X(t) \leq k], \ k = 0, 1, \ldots.$$ 

That is,

$$P[X(t) \leq k] \leq P[Z(t) \leq k], \ t \geq 0, \ (6.20)$$

for $k = 0, 1, \ldots$. If we multiply both sides of this equation by $s^k$, sum over the integers $k = 0, 1, \ldots$, and use the definitions of the probability generating functions $F^*(s, t)$ and $C^*(s, t)$ we have that

$$F^*(s, t) \leq C^*(s, t), \ t \geq 0, \ |s| \leq 1. \ (6.21)$$

However, if we use Equation 6.16 this implies that

$$\frac{F(s, t)}{1-s} \leq \frac{C(s, t)}{1-s}, \ t \geq 0, \ |s| < 1. \ (6.22)$$
Thus, for $|s| < 1$ we have that

$$F(s, t) \leq C(s, t), \quad t \geq 0. \tag{6.23}$$

The probability generating function $F(s, t)$ on the left hand side of Inequality 6.23 is the generating function for the size of the female population at time $t$. However, in the population we are considering, both female and male offspring are produced according to the probability generating function $f(ps_1 + qs_2)$ given by Equation 6.13. The generating function for the females produced is then $f(ps + q)$. Thus, if all of the offspring are credited to the females in the population, and the life length of the females is governed by the distribution $G(t)$ given by Equation 6.10, then the integral equation for $F(s, t)$ is similar to Equation 6.7. In fact, this equation becomes the inequality

$$F(s, t) \geq s(1-G(t)) + \int_0^t f[pF(s, t-u) + q] \, dG(u), \quad t \geq 0 \tag{6.24}$$

which follows from reasoning similar to that given by Daley (1968, p. 320). The solution to this inequality, for $|s| < 1$, is then a lower bound to the generating function $C(s, t)$ describing the couples in the population at time $t$.

We can also find another lower bound to the function $C(s, t)$. If we mimic the steps used in obtaining Equation 6.20 we find that
$P[Y(t) \leq k] \leq P[Z(t) \leq k], \ t \geq 0,$  \hspace{1cm} (6.25)

for $k = 0, 1, \ldots$. It then follows that the probability generating functions $M(s, t)$ and $C(s, t)$ are, for $|s| < 1$ such that

$$M(s, t) \leq C(s, t), \ t \geq 0.$$ \hspace{1cm} (6.26)

If, in the initial pages of this chapter, we had supposed that the particles in the population were males, and that male offspring were produced according to the generating function $f(s)$ given by Equation 6.2, then the function $M(s, t)$ would satisfy Equation 6.7 with $M(s, t)$ replacing $F(s, t)$. However, in connection with Inequality 6.26, we are considering a population in which both female and male offspring are produced. These offspring are produced according to the generating function $f(ps_1 + qs_2)$ given by Equation 6.13. Let us suppose that all of the offspring are attributed to the males in the population, and that the random variable $\xi$ with distribution function $G(t)$ governs the length of life of any male. If both female and male offspring are produced, then the male offspring are produced according to the probability generating function $f(p + qs)$. Thus, analogous to Inequality 6.24, the generating function for the size of the male population at time $t$, provided the males produce all of the offspring, satisfies the following inequality.
\[ M(s, t) \geq s(1 - G(t)) + \int_0^t f[p + qM(s, t-u)] \, dG(u), \quad t \geq 0. \]  

(6.27)

The solution to this inequality is a lower bound to the generating function \( C(s, t) \), for \( |s| < 1 \) and \( t \geq 0 \).

We have that each of the solutions to Inequalities 6.24 and 6.27 is a lower bound to the function \( C(s, t) \) for \( t \geq 0 \) and \( |s| < 1 \). In general, we cannot solve these two integral inequalities. We will derive some other properties of these lower bounds.

Let us now try to construct upper bounds. To do this, let us examine the random variable \( Z(t) \) in more detail. We have

\[ Z(t) = \min\{X(t), Y(t)\}, \quad t \geq 0. \]

Let \( k \) be any nonnegative integer, and let us consider the set \( \{Z(t) \leq k\} \). This symbol is to be interpreted as meaning the set of \( Z(t)'s \) such that \( Z(t) \leq k \). We have that

\[ \{Z(t) \leq k\} = \{\min\{X(t), Y(t)\} \leq k\} \]

\[ = \{X(t) \leq k\} \cup \{Y(t) \leq k\}, \quad t \geq 0, \]

for \( k = 0,1,\ldots \). Thus we have that

\[ P[Z(t) \leq k] = P[X(t) \leq k] + P[Y(t) \leq k] \]

\[ - P[X(t) \leq k, Y(t) \leq k], \quad t \geq 0. \]  

(6.28)
for \( k = 0,1,\ldots \). If we could find an appropriate upper bound for \( P[X(t) \leq k, \, Y(t) \leq k] \), we would be satisfied. The Tchebychev type of inequalities are sometimes useful in this context. But, for the inequality we desire, these methods fail. Since a probability is subadditive, it is true that

\[
P[Z(t) \leq k] \leq P[X(t) \leq k] + P[Y(t) \leq k].
\]

The right hand side of this inequality can be greater than unity. Thus, any generating functions obtained by using this inequality would not give us any useful results.

Let us now return to the two lower bounds we have constructed. If \( |s| < 1 \) we have that

\[
F(s, t) \leq C(s, t), \quad t \geq 0 \tag{6.28}
\]

and

\[
M(s, t) \leq C(s, t), \quad t \geq 0 \tag{6.29}
\]

where \( F(s, t) \) and \( M(s, t) \) are solutions to Inequalities 6.24 and 6.27. As we noted previously, we cannot in general solve Inequalities 6.24 and 6.27. However, these two inequalities and the above inequalities are valid if we set \( s = 0 \).

If we set \( s = 0 \) in the probability generating function for an age-dependent branching process we can obtain the probability that the population becomes extinct. For example, if \( s = 0 \) in Equation 6.3 we have that
The probability that \( X(t) = 0 \) for \( t \geq 0 \) is related to the probability generating function for the production of offspring. Harris (1963) proves the following

**THEOREM:**

Let us assume that the offspring in an age-dependent branching process are produced according to the probability generating function \( f(s) \). Then the probability of extinction, i.e., of the event \( [X(t) = 0 \text{ for sufficiently large } t] \), is the smallest nonnegative root \( r \) of the equation \( f(s) = s \). If the extinction probability \( r \) is 0, then \( F(0, t) = 0 \) for all \( t \). If \( r > 0 \), then \( F(0, t) < r \) for each \( t \geq 0 \), \( F(0, t) \) is a nondecreasing function of \( t \), and \( \lim_{t \to \infty} F(0, t) = r \).

This theorem is a combination of Theorems 5.2 and 9.3 in Chapter 6 of Harris (1963).

If we let \( s = 0 \) in Equations 6.28 and 6.29 we have

\[
\lim_{t \to \infty} P[X(t) = 0] \leq \lim_{t \to \infty} P[Z(t) = 0]
\]

and

\[
\lim_{t \to \infty} P[Y(t) = 0] \leq \lim_{t \to \infty} P[Z(t) = 0].
\]
It then follows that

\[
\min \{ \lim_{t \to \infty} P[X(t) = 0], \lim_{t \to \infty} P[Y(t) = 0] \} \leq \lim_{t \to \infty} P[Z(t) = 0].
\]

However, we have noted that the generating function \( F(s, t) \),
is the generating function for the number of females alive
at time \( t \). But the population is such that offspring of
both types are produced. The probability generating function
which describes the production of the females is \( f(ps + q) \).
Let \( r_f \) be the smallest nonnegative root of \( f(ps + q) = s \).
Likewise, we saw that \( M(s, t) \) is the generating function
which describes the number of males alive at time \( t \), these
males being in a population which attributes both types of
offspring to the males. The probability generating function
for the production of males is \( f(p + qs) \). Let \( r_m \) be the
smallest nonnegative root of \( f(p + qs) = s \).

According to Harris' theorem, in addition to the
probabilities \( r_f \) and \( r_m \) being the smallest nonnegative
roots of their respective generating functions, we have
that

\[
\lim_{t \to \infty} F(0, t) = \lim_{t \to \infty} P[X(t) = 0] = r_f
\]

and

\[
\lim_{t \to \infty} M(0, t) = \lim_{t \to \infty} P[Y(t) = 0] = r_m.
\]
Thus, Inequality 6.30 becomes

$$\min\{r_f, r_m\} \leq \lim_{t \to \infty} P[Z(t) = 0] \leq 1.$$  \hspace{1cm} (6.31)

This inequality says that the probability of extinction for a population of females and males who form couples before reproduction occurs is greater than or equal to the probability of extinction of a population which produces both female and male offspring in such a manner that the offspring are attributed to the females. Also, the probability of extinction for the couples is greater than or equal to the probability of extinction of a bisexual population which attributes both types of offspring to the males.

The results we have obtained with respect to the probabilities of extinction, allow us to infer that a bisexual population which forms couples grows at a rate which is slower than the rate given for a bisexual population which attributes both type of offspring to only one type of adult. We should note that we have not proved this result. The only proof we have is with respect to the inequality on the survival probabilities given by Inequality 6.31.

Let us consider a specific example. Let us suppose that when offspring are produced, exactly two are formed: That is, the generating function for the total number of offspring, given by Equation 6.12, is
If any offspring is a female with probability \( p \) and a male with probability \( q \), then the generating function for both types of offspring, i.e., Equation 6.13, is given by

\[
f(p s_1 + q s_2) = p^2 s_1^2 + 2pq s_1 s_2 + q^2 s_2^2,
\]

\[|s_1| \leq 1, \quad |s_2| \leq 1.\]

If both types of offspring are credited to the females, then \( f(ps + q) \) is the generating function for the female offspring. The smallest nonnegative root of \( f(ps + q) = s \) is \( \min\{1, q^2/p^2\} \). Likewise, if both types of offspring are attributed to the males, then \( f(p + qs) \) is the generating function for the production of male offspring. Also, the smallest nonnegative root of \( f(p + qs) = s \) is \( \min\{1, p^2/q^2\} \). Thus, for a population which forms couples and produces offspring according to a binary branching process, we have the following inequality for the probability of extinction,

\[
\min\{1, q^2/p^2, p^2/q^2\} \leq \lim_{t \to \infty} P[Z(t) = 0].
\]

In the Appendix we consider some data on the number of females and males born in the U.S. over several years. From this data, the probability that any offspring born is
a female is estimated to be 0.486, i.e., $p = 0.486$. The probability of obtaining a male is then $q = 0.514$. Thus, if there is binary reproduction, we have the following probability for extinction

$$\min\{1, \frac{q^2}{p^2}, \frac{p^2}{q^2}\} = \frac{p^2}{q^2} = 0.893$$

$$< \lim_{t \to \infty} P[Z(t) = 0].$$

The lower bound probability of extinction 0.893 is quite large. The probability that the line survives is no larger than 0.107.

Daley (1968) constructed the Galton-Watson process which corresponds to the age-dependent branching process we have been considering. He found necessary and sufficient conditions with respect to the mean number of female and male offspring produced so that the probability that the line becomes extinct is one.
VII. SUMMARY AND CONCLUSIONS

We have been considering models for the growth of populations with overlapping generations. In both the deterministic and the stochastic models the survival probabilities and the functions which described the production of offspring depended only upon the age of the individuals in the population. It would be more realistic to let the survival probabilities and the birth rates be also functions of time. It may be realistic to assume in some species the average number of live births produced per female is not a function of time. However, the use of modern medicine has changed the probabilities of survival for humans and domestic animals drastically within the last century. It is also true, for the human population, that the birth rates are changing. With respect to the properties of the models we have also assumed that all of the individuals in the population in a given age are identical. This is not realistic since there exists a great amount of genetic variability between individuals in a given species. That is, it should be noted that the models should be improved so that they become more realistic with regard to the underlying assumptions used to describe the growth of a population.

The models that are currently used to describe the growth of a bisexual population with overlapping generations lack, as we have noted, one major property. That is, they
do not incorporate the obvious fact that the production of offspring is a function of both of the adult females and the adult males in the population. In a limited sense we have tried to correct this deficiency. We have not been completely successful in incorporating the formation of couples into the growth models. However, if couple formation can be described according to the quantitative measure of the maximum number of couples available which we have used, then we have been able to compare the rate of growth of a population forming couples with the rate as predicted by the currently used model.

The model that is currently used to describe the growth of a bisexual population with overlapping generations credits the offspring produced to only the adult females in the population. When this model is valid, we have shown that both the females and the males grow asymptotically in numbers at the same rate, as is demonstrated by Equations 2.25 and 2.26. The parameter $\mu_0$ in these two equations is the solution which is larger in absolute value than any other solution to the characteristic equation given by Equation 2.6. This characteristic equation is obtained solely from the renewal equation which describes the production of female offspring, that is, from Equation 2.3. Thus, this characteristic equation is only a function of the survival probabilities and the birth rates for the females. The male offspring
are credited to the adult females in the population. The males play no role in reproduction; they are born, they age, and they die.

It is shown that there does exist an asymptotic stabilization of the distribution of females and males in the population according to age. For this result to be true, it is necessary that the survival probabilities and birth rates are only age dependent.

The currently used model introduces the concept of the reproductive value of an individual in a specified age group. It is shown that the value is a measure of the contribution of an ancestral individual in a given age to the growth of future generations. The reproductive value for an ancestral female is given by Equation 2.18 and the value is positive as long as a female is fertile. The reproductive value of an ancestral male is found to be zero. This is not surprising, since the males play no role in reproduction.

Along the same lines as the model currently used to describe the growth of a bisexual population, we introduce a model in which couples must be formed before reproduction occurs. The function we use to describe the formation of couples, is only a quantitative measure of the maximum number of couples that can be formed. If the maximum number of couples is formed, and if the couples are only formed between females and males of the same age, we can solve the
renewal equations which describe the production of offspring if we assume that the ratio of females to males at birth is a known constant. In this special case, we are able to calculate every descriptive function that was also available from the currently used model.

We have shown that the females and the males asymptotically grow in numbers at the same rate. This is demonstrated in Equation 3.18. However, the parameter $\lambda_0$, which completely determines the rate of growth of both the females and the males in the population is the solution which is larger in absolute value than any other solution to the characteristic equation given by Equation 3.19. This characteristic equation is common to the two renewal equations which describe the production of female and male offspring. That is, this characteristic equation is a function of the survival probabilities of both the females and the males, and it is also a function of the birth rates for the females and the males.

We have also shown that the distribution of females and males in the population according to age eventually stabilizes. The distribution by age is similar to that predicted by the currently used model. Since however, the age distributions for each of the models are functions of their respective growth rates $\mu_0$ and $\lambda_0$, these distributions are not identical.
The concept of the reproductive value is also valid for this model. However we must now refer to the reproductive value of an ancestral couple with respect to the growth of the females and the males in the population. The definition of the reproductive value we made in connection with the currently used model is valid for the new model, provided we assume that there are an equal number of ancestral females and males in each age group. The reproductive value of an ancestral couple with respect to the growth of the females and males is positive as long as the couple is fertile.

We have been able to incorporate a certain degree of polygamy into the mating structure, provided couples are formed between females and males in the same age group. If the number of wives that any male can have is sufficiently large, then the renewal equations which describe the production of female and male offspring are identical to the renewal equations for the growth of a population in which all of the offspring are attributed to the females. This result is strictly a consequence of the choice of the function which describes the formation of the number of couples.

The assumption that the ratio of females to males at birth was a constant, enabled us to solve the renewal equations which described the production of offspring. However, if we do not make this assumption, we are able to compare the rate of growth of a population which forms couples between
females and males in the same age group with the rate of
growth as predicted by the currently used models which attrib­
ute the offspring to only one type of parent. This is a
mathematical consequence of the function which describes the
formation of the maximum number of couples. The renewal equa­tions which describe the number of female and male offspring
produced when couples are formed are bounded above by the
solutions to renewal equations which describe the production
of offspring in populations which credit either the adult fe­
male or adult males with all of the offspring. Thus, a
population which forms couples grows at most as fast as a
population which credits the offspring to only one parent.

If we assume that at birth the ratio of females to males
is a constant, then the rate of growth of a population
which forms couples as described by the solution to the char­
acteristic equation which is larger in absolute value than
any other solution, can be compared to the rate of growth as
predicted by the use of the currently used models. The
dominant solution to the characteristic equations, which
determine the growth of a population which attributes the off­
spring to either of the parents in the population, is greater
than or equal to the implicit growth rate when couples are
formed. This result is conditional on the maximum number
of couples being formed. Thus, if the maximum number is not
formed, the rate of growth of a population as predicted by the
currently used models is probably greatly overestimated.

We have also shown in the general situation in which couples are formed arbitrarily according to the ages of the females and males, that the solution to the renewal equations which describe the production of offspring are bounded above. They are bounded above by the solutions to the renewal equations which describe the production of offspring as formulated by the currently used models for population growth. Thus, the rates of growth of a bisexual population which forms couples is overestimated.

The stochastic models, which describe the growth of a population with overlapping generations, are the age-dependent branching processes. If a population consists of only one type of individual, then the functional integral equation which describes the generating function for the size of the population at time \( t \) has the form of Equation 6.7. If, however, the maximum number of couples are formed in each generation we have not been able to find the generating function for the size of the female and male population at time \( t \). We can only construct lower bounds in terms of the age-dependent branching processes which attribute all of the offspring to either the adult females or males in the population. In particular, the probability of extinction for a population that forms couples is greater than or equal to the probability of extinction of a population which attributes all of the offspring to either type of adult.
We have constructed models for the growth of bisexual populations with overlapping generations in which couples are formed. In all cases, we have been able to compare these models with the currently used models for the growth of a bisexual population. The comparisons we have made are mathematical consequences of the function we have used to describe the formation of couples.
VIII. LITERATURE CITED

Arbuthnott, J. 1710. An argument for divine providence, taken from the constant regularity observed in the births of both sexes. Philosophical Transactions of the Royal Society 27: 186-190.


IX. ACKNOWLEDGMENTS

The author wishes to express his thanks to the many teachers who have guided and enlightened him during his years as a student. These people have helped with their encouragement and patience as the author learned to understand mathematics, statistics, and genetics. In particular, the author is indebted to Dr. Edward Pollak for directing the research which led to this dissertation and for his help in learning to understand population genetics. A special word of thanks is due to Professor Oscar Kempthorne for his guidance and encouragement as the author learned statistics.

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X. APPENDIX

An assumption we made was that the ratio of females to males at birth was a constant. To test the validity of this assumption, the following data was obtained from the Statistical Abstracts of the United States (1970). In this data the numbers we give refer to the total number of registered live births in the U.S., and these numbers are in units of 1000. The probabilities \( p \) and \( q \) refer respectively to the estimated probability of obtaining a female and a male for the given year.

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To test the hypothesis that at birth the ratio of females to males is a constant, a \( \chi^2 \) goodness of fit test was performed. The calculated value of \( \chi^2 \) was 0.13. If the hypothesis is true, the probability of obtaining this value or a larger value is greater than 0.995. We have no reason to reject the hypothesis. So, according to this data, it is reasonable to assume that the ratio of females to males at birth is a constant.

Data similar to the above is given by Arbuthnott (1710) for the city of London between the years 1629-1710. Due to
the historical interest in this data, we list it on the following pages.

In this data, the numbers given refer to the number of christened female and male infants in the city of London. The probabilities \( p \) and \( q \) are the estimated probabilities of

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obtaining a female and a male in a specified year.

We tested the hypothesis that the ratio of females to males at birth was a constant. The calculated value, according to Arbuthnott's data, of $\chi^2$ was 174.69. The probability of this value occurring, if the hypothesis is true, is less than 0.005. Thus, according to this data, we reject the hypothesis that at birth the ratio of females to males is constant.

Arbuthnott's paper is interesting in the history of the construction of tests for a statistical hypothesis. According to Hacking (1965), Arbuthnott was the first person to publish the reasoning behind his statistical inference.

Arbuthnott considers two different statistical inferences he wants to make from his data. The first is that he wants to test the null hypothesis that there are equal numbers of both sexes born; that is, that the probability that any infant born is a male is 1/2. The alternative hypothesis he considers is that there are more males born than females. Presumably, he arrived at this alternative by looking at his data. Arbuthnott constructs a test for his hypothesis by assuming that the distribution of births is analogous to the outcomes possible from tossing a fair coin. He notes, that according to his data, there were more males than females born for 82 consecutive years. Thus, the chance of this event occurring is $(1/2)^{82}$, which is very small. Arbuthnott then rejects his
null hypothesis in favor of his alternative hypothesis since this number is so small. We should note, that if in his data, there were $N$ years in which more females than males were born and $82-N$ years for more males than females, then if his null hypothesis is true, the chance of this event occurring is also $(1/2)^{82}$ for any $N$. So, if we follow Arbuthnott's reasoning then we would reject his null hypothesis in favor of any alternative hypothesis.

Arbuthnott rejects his hypothesis in favor of the alternative that there are always more males than females born. He then says: "From whence it follows, that it is Art, not Chance, that governs." The title of his paper follows from this statement.

The second hypothesis that Arbuthnott considers is that at birth the ratio of females to males is a constant. The alternative he considers is that the ratio is not constant. He accepts the hypothesis. However, the reason why he accepts the hypothesis is that he says that every male is entitled to have a mate, so the hypothesis must be true. We have already noted, that according to his data, this hypothesis is false.