Dynamics of Population Growth

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In the Department of Mathematics

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PROJECT TITLE: Dynamics of Population Growth

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# Table of Contents

Introduction ...................................... 6

Age-Specific Life History Parameters
Leslie Matrix
Definition of Variables
Iteration of Matrix

The Basic Model .................................. 10

Process and Observations

The Genetic Model ............................... 14

Expanded Leslie Matrix

The Genetic Experiment ......................... 15

Process and Observations
Frequency of b Allele

Conclusion ....................................... 20

Graphs ........................................... 22

Life History Graphs
Genetic Genotype Graphs
Genetic Graphs
Ratio of Frequency of b Allele

Addendum ....................................... 46

Appendix A .................................... 47

Appendix B .................................... 49

Appendix C .................................... 50

Appendix D .................................... 51

Appendix E .................................... 55

Bibliography .................................. 60
Introduction:

This project represents an effort to combine the sciences of mathematics and biology. Population dynamics does exactly this. The study of populations is inevitably a quantitative one, and so involves mathematics; the growth that a hypothetical population experiences as generations pass can be simulated and described mathematically. Populations in nature are dynamic entities. Their numbers fluctuate over time either in response to obvious environmental stimuli, such as the change in seasons, or for reasons not yet identified. These factors which influence population growth and size, and the mechanisms involved, are of biological interest.

The purpose of this project was to explore the dynamics of population growth based upon genetic information and age-specific life history parameters--survivorship and fecundity--using a mathematical model. P.H Leslie's "On The Use of Matrices in Certain Population Mathematics", Readings in Ecology and Ecological Genetics by David Mertz et al, and Charles King and Wyatt Anderson's "Age-Specific Selection. II. The Interaction Between r and K During Population Growth" were the main resources used for the development of the mathematical model.

The Leslie Matrix describes age-specific life history
information in a compact format. Usually, fecundity, the number of female offspring per female of a given age class, is given the variable name \( m(x) \) or \( a_i \), where \( x \) and \( i \) are age classes. The other age-specific life history variable, survivorship, is the probability that a female will survive from birth to age \( x \), and is given the variable name \( l(x) \); the Leslie Matrix uses this variable in a proportion--\( l(x)/l(x-1) \), denoted by \( b_i \), where \( x \) and \( i \) are the age classes. This results in the proportion of individuals alive at age \( x \) that will survive to the next age class. The Leslie Matrix compactly describes the age-specific life history information since the fecundity values comprise the first row of the matrix and the survivorship values constitute the sub-diagonal of the matrix. The general appearance of the Leslie Matrix is shown below for \( n \) age classes.

\[
\begin{array}{ccccccc}
  a_1 & a_2 & a_3 & \ldots & a_i & \ldots & a_{n-1} & a_n \\
  b_1 & 0 & 0 & \ldots & 0 & \ldots & 0 & 0 \\
  0 & b_2 & 0 & \ldots & 0 & \ldots & 0 & 0 \\
  0 & 0 & b_3 & \ldots & 0 & \ldots & 0 & 0 \\
  \vdots & \vdots & \vdots & \ddots & \vdots & \ddots & \vdots & \vdots \\
  \vdots & \vdots & \vdots & \ddots & b_i & \ddots & \ddots & \vdots \\
  0 & 0 & 0 & \ldots & 0 & \ldots & b_{n-1} & 0 \\
\end{array}
\]

The most valuable variable determined from the Leslie Matrix is the dominant eigenvalue, the eigenvalue of greatest absolute value, since it is used to calculate the intrinsic rate of increase, the stable age distribution, and the age specific reproductive values. The dominant
eigenvalue of the matrix represents the finite rate of increase, usually denoted by $\lambda$ (lambda). Lambda represents the rate of increase per individual once the stable age distribution is attained (Mertz et al 13). The intrinsic rate of increase is the natural logarithm of the dominant eigenvalue and is an indicator of the population's capacity for sustained change in numbers based on its life history information (Mertz et al 13). Thus, "the higher a population's $r$ (intrinsic rate of increase), the higher is this capacity" (Mertz et al 13). The stable age distribution is the eigenvector that corresponds to the dominant eigenvalue. As the name implies, this is the distribution of the population once it reaches stability. That is the distribution in which the proportion of individuals in each age group will not change relative to the total population. The reproductive values, which represent the number of female offspring expected from a female that has survived to age $x$, are based on lambda in this fashion:

$$v(x) = \left[\lambda^x / l(x)\right] \times \sum_{y=x}^{\infty}[\lambda^y \times m(y) \times l(y)].$$

In this equation, $x$ represents the age class for which the reproductive value is being calculated; the $y$ variable is the "dummy" variable.

Directly from the standard life history parameters, another parameter describing a characteristic of the population can be determined. This value is the net
reproductive rate, which represents the average number of females produced in the next generation by each female in the present generation. The mathematical equation for the net reproductive rate is:

\[ R = \sum_{x} m(x) l(x) \].

The net reproductive rate is an indicator of how the population is changing. If \( R < 1 \), the population size is decreasing; if \( R > 1 \), the population size is increasing; and if \( R = 1 \), the population size is remaining constant.

The carrying capacity is the population size at which the population growth rate is zero. Carrying capacity is also defined as the number of individuals which can be sustained indefinitely in the given environmental conditions. Thus, this value, denoted by \( K \), is used to control population growth—that is, inhibit exponential growth—by multiplying the Leslie matrix by the scalar multiple \((K - \text{total})/K\).\(^1\) If a population size exceeds its carrying capacity, the population will decrease since the scalar multiple will be negative. Similarly, if the population size is less than its carrying capacity, the population will increase in size. There exist situations in which the population can so greatly exceed its carrying capacity that the population can become extinct in the next generation.

\(^1\)Complications arose with this use of carrying capacity. Please see addendum for further details.
It is necessary to iterate the Leslie Matrix to explore the dynamics of the population. This is accomplished by multiplying the matrix by the initial distribution of the population, denoted by $v_0$, yielding a new population vector. If the matrix is called $M$, one iteration of the population will be $v_1 = M \ast v_0$. The second iteration is $v_2 = M \ast v_1$, or equivalently, $v_2 = M \ast (M \ast v_0) = M^2 \ast v_0$. The pattern that evolves is $v_n = M^n \ast v_0$. The inclusion of the carrying capacity results in a scalar multiple of the equation, yielding, $v_n = \left[ \frac{\prod_{i=0}^{n-1} [(K_{\text{total}})_{i}]/K} \right] \ast M^n \ast v_0$.

The Basic Model:

Twelve fictitious data sets are generated and the population dynamics of each are analyzed. These twelve data sets are created from four fecundity and three survivorship patterns in all possible combinations. The four fecundity patterns represent age-specific fecundity that is constant, monotonically increasing, monotonically decreasing, and peaking at an intermediate age. Total fecundity for an individual surviving to maximum age is the same for all cases; this value is ten. The survivorship patterns represent classic survivorship patterns: rapid early decline with slow late decline, steady decline, and slow early decline with rapid late decline. These survivorship patterns are not the proportional values that are the
elements of the sub-diagonal of the Leslie Matrix; the proportional values are calculated from the given values. The matrix has five age classes, which is an arbitrary value. The four fecundity and three survivorship data sets are shown below.

Data Sets: Fecundity

<table>
<thead>
<tr>
<th>Age Classes</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
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<tr>
<td></td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>3</td>
<td>4</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

Survivorship

<table>
<thead>
<tr>
<th>Age Classes</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>0.25</td>
<td>0.17</td>
<td>0.08</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.75</td>
<td>0.5</td>
<td>0.25</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.92</td>
<td>0.83</td>
<td>0.75</td>
<td>0</td>
</tr>
</tbody>
</table>

Additional information is necessary before the population can undergo iterations. The number of generations (iterations), the initial population size and distribution, and the carrying capacity are arbitrarily assigned. The number of generations equals 20; the initial population size equals 100 and is distributed based on the stable age distribution; and K, the carrying capacity, equals 10,000. The total population size was calculated every generation and plotted on a generations versus population size graph for every combination of life history characteristics (Life History Graphs). The simulation model is coded in Mathematica.

The main conclusion to come from this model deals with
population growth. The simulation results suggest that the fecundity pattern is more important than the survivorship pattern in determining the population dynamics during the growth phase. Different survivorship patterns will vary population size, but changes in fecundity will influence both the total population size and how the population reaches its equilibrium population size. For example, different survivorship patterns result in different equilibria values for the population size, see graphs of H1, H2, and H3. The fecundity patterns, however, significantly affect the dynamics of the population growth, see graphs of H2, H5, H8, and H11.

Other observations can be made from the graphs resulting from the simulations. In particular, the population patterns for graphs H7, H8, and H9 are situations where the population excessively exceeds its carrying capacity and, thus, must become extinct. Notice also that graphs H10, H11, and H12 are not all of the same pattern. This, mathematically, can be attributed to the life history patterns; when the fecundity value is high, the survivorship value drops suddenly and when the fecundity value is low, the survivorship is slowly declining.

The other variables calculated from the Leslie Matrix also give information about the population dynamics. The values for lambda, the stable age distribution, intrinsic rate of increase, net reproductive rate, and reproductive
values can be found in Tables 1a, 1b, and 1c. These data reflect the main result observed from the graphs--the fecundity pattern more significantly affect the dynamics than the survivorship pattern.

Table 1a: Eigenvalue and Eigenvector

<table>
<thead>
<tr>
<th>Data</th>
<th>( \lambda )</th>
<th>stable age distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>H1</td>
<td>2.797</td>
<td>( {0.941, 0.336, 0.030, 0.007, 0.001} )</td>
</tr>
<tr>
<td>H2</td>
<td>2.911</td>
<td>( {0.942, 0.324, 0.083, 0.019, 0.003} )</td>
</tr>
<tr>
<td>H3</td>
<td>2.966</td>
<td>( {0.943, 0.318, 0.099, 0.030, 0.009} )</td>
</tr>
<tr>
<td>H4</td>
<td>1.339</td>
<td>( {0.795, 0.594, 0.111, 0.056, 0.020} )</td>
</tr>
<tr>
<td>H5</td>
<td>1.642</td>
<td>( {0.827, 0.504, 0.230, 0.093, 0.028} )</td>
</tr>
<tr>
<td>H6</td>
<td>1.811</td>
<td>( {0.843, 0.465, 0.236, 0.118, 0.059} )</td>
</tr>
<tr>
<td>H7</td>
<td>4.667</td>
<td>( {0.978, 0.209, 0.011, 0.002, 0.000} )</td>
</tr>
<tr>
<td>H8</td>
<td>4.709</td>
<td>( {0.978, 0.208, 0.033, 0.005, 0.000} )</td>
</tr>
<tr>
<td>H9</td>
<td>4.725</td>
<td>( {0.978, 0.207, 0.040, 0.008, 0.001} )</td>
</tr>
<tr>
<td>H10</td>
<td>1.914</td>
<td>( {0.618, 0.323, 0.042, 0.015, 0.004} )</td>
</tr>
<tr>
<td>H11</td>
<td>2.169</td>
<td>( {0.898, 0.414, 0.143, 0.044, 0.010} )</td>
</tr>
<tr>
<td>H12</td>
<td>2.261</td>
<td>( {0.901, 0.398, 0.162, 0.065, 0.026} )</td>
</tr>
</tbody>
</table>

Table 1b: Intrinsic Rate of Increase \( (r) \) and Net Reproductive Rate \( (R) \)

<table>
<thead>
<tr>
<th>Data</th>
<th>( r )</th>
<th>( R )</th>
</tr>
</thead>
<tbody>
<tr>
<td>H1</td>
<td>1.029</td>
<td>3.00</td>
</tr>
<tr>
<td>H2</td>
<td>1.069</td>
<td>5.00</td>
</tr>
<tr>
<td>H3</td>
<td>1.087</td>
<td>7.00</td>
</tr>
<tr>
<td>H4</td>
<td>0.292</td>
<td>2.33</td>
</tr>
<tr>
<td>H5</td>
<td>0.496</td>
<td>5.00</td>
</tr>
<tr>
<td>H6</td>
<td>0.594</td>
<td>8.33</td>
</tr>
<tr>
<td>H7</td>
<td>1.541</td>
<td>3.67</td>
</tr>
<tr>
<td>H8</td>
<td>1.550</td>
<td>5.00</td>
</tr>
<tr>
<td>H9</td>
<td>1.553</td>
<td>5.67</td>
</tr>
<tr>
<td>H10</td>
<td>0.649</td>
<td>4.51</td>
</tr>
<tr>
<td>H11</td>
<td>0.774</td>
<td>7.50</td>
</tr>
<tr>
<td>H12</td>
<td>0.816</td>
<td>9.17</td>
</tr>
</tbody>
</table>
Table 1c: Reproductive Values

<table>
<thead>
<tr>
<th>Data</th>
<th>$V_0$</th>
<th>$V_1$</th>
<th>$V_2$</th>
<th>$V_3$</th>
<th>$V_4$</th>
</tr>
</thead>
<tbody>
<tr>
<td>H1</td>
<td>2.797</td>
<td>2.230</td>
<td>2.568</td>
<td>2.336</td>
<td>2.000</td>
</tr>
<tr>
<td>H2</td>
<td>2.911</td>
<td>2.653</td>
<td>2.527</td>
<td>2.343</td>
<td>2.000</td>
</tr>
<tr>
<td>H3</td>
<td>2.966</td>
<td>2.066</td>
<td>2.794</td>
<td>2.609</td>
<td>2.000</td>
</tr>
<tr>
<td>H4</td>
<td>1.339</td>
<td>1.792</td>
<td>4.230</td>
<td>4.406</td>
<td>4.000</td>
</tr>
<tr>
<td>H5</td>
<td>1.642</td>
<td>2.696</td>
<td>3.713</td>
<td>4.210</td>
<td>4.000</td>
</tr>
<tr>
<td>H6</td>
<td>1.011</td>
<td>3.200</td>
<td>4.409</td>
<td>4.996</td>
<td>4.000</td>
</tr>
<tr>
<td>H7</td>
<td>4.667</td>
<td>3.115</td>
<td>2.146</td>
<td>1.000</td>
<td>0.000</td>
</tr>
<tr>
<td>H8</td>
<td>4.709</td>
<td>3.341</td>
<td>2.142</td>
<td>1.000</td>
<td>0.000</td>
</tr>
<tr>
<td>H9</td>
<td>4.725</td>
<td>3.427</td>
<td>2.191</td>
<td>1.000</td>
<td>0.000</td>
</tr>
<tr>
<td>H10</td>
<td>1.914</td>
<td>3.662</td>
<td>5.066</td>
<td>3.000</td>
<td>0.000</td>
</tr>
<tr>
<td>H11</td>
<td>2.169</td>
<td>4.702</td>
<td>4.922</td>
<td>3.000</td>
<td>0.000</td>
</tr>
<tr>
<td>H12</td>
<td>2.262</td>
<td>5.114</td>
<td>5.197</td>
<td>3.000</td>
<td>0.000</td>
</tr>
</tbody>
</table>

The Genetic Model:

The genetic model is similar to the basic model since the Leslie Matrix remains the basis. It is assumed that there are two alleles for a single gene locus, and only one gene is of interest. Thus, there are three possible genotypes: two homozygous classes and one heterozygous class. It is also assumed that there are three age groups. With this information, the 9x9 matrix given below, is generated that contains age-specific life history information for each genotype. The $a_{ij}$, $ab_{ij}$, and $bb_{ij}$ indicate the number of offspring of the given genotype produced by females in the $i$th age class by females of the $j$th genotype, where $j = 1$ indicates $aa$, $j = 2$ indicates $ab$, and $j = 3$ indicates $bb$. The $b_{ij}$ values indicate the proportional survivorship for an individual in the $i$th age class with the $j$th genotype.
<table>
<thead>
<tr>
<th>$aa_{11}$</th>
<th>$aa_{12}$</th>
<th>$aa_{13}$</th>
<th>$aa_{21}$</th>
<th>$aa_{22}$</th>
<th>$aa_{23}$</th>
<th>$aa_{31}$</th>
<th>$aa_{32}$</th>
<th>$aa_{33}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$ab_{11}$</td>
<td>$ab_{12}$</td>
<td>$ab_{13}$</td>
<td>$ab_{21}$</td>
<td>$ab_{22}$</td>
<td>$ab_{23}$</td>
<td>$ab_{31}$</td>
<td>$ab_{32}$</td>
<td>$ab_{33}$</td>
</tr>
<tr>
<td>$bb_{11}$</td>
<td>$bb_{12}$</td>
<td>$bb_{13}$</td>
<td>$bb_{21}$</td>
<td>$bb_{22}$</td>
<td>$bb_{23}$</td>
<td>$bb_{31}$</td>
<td>$bb_{32}$</td>
<td>$bb_{33}$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>$b_{11}$</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>$b_{12}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>$b_{13}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

| 0 | 0 | 0 | $b_{21}$ | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | $b_{22}$ | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | $b_{23}$ | 0 | 0 | 0 |

It should be noted that the assumptions can be expanded to include additional genes and age groups. This model can simulate the dynamics of genotypic distribution as dictated by genotypic and age-specific life history characteristics. For instance, selection for a particular genotype or a reproductive advantage for an individual with a particular age and genotype combination can be modelled with this matrix. However, this was not how the model was exercised for this project. For this project, this model simulated the genetic impact of immigrants on an otherwise genetically homogeneous population.

The Genetic Experiment:

Observing the impact of immigrants on a homogeneous population indicates the susceptibility of this population to foreign alleles. The model developed to study the impact of immigrants begins with the basic Leslie Matrix. The initial population is homogeneous for the aa genotype, while the immigrants are of bb genotype. The basic matrix is necessary to determine a distribution of the aa genotype in
an initial population vector (based upon the eigenvector) and to ascertain which age class has the greatest reproductive potential (has the highest reproductive value). Before discussing the details of this process, the data sets will be presented.

As with the basic model, twelve fictitious data sets were generated from four fecundity and three survivorship data sets. In a manner similar to the basic model, the fecundity patterns represent age-specific fecundity that is peaking, monotonically increasing, monotonically decreasing, and remaining constant. The total fecundity for an individual surviving to maximum age is three for all cases. The survivorship patterns, likewise, represent the three classic types: slow early decline with rapid late decline, consistent decline, and rapid early decline with slow late decline. The data sets are given below.

**Data Sets:**

**Fecundity:**

<table>
<thead>
<tr>
<th>Age Classes:</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>1</td>
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<td></td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

**Survivorship:**

<table>
<thead>
<tr>
<th>Age Classes:</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.75</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.25</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

From the above information, a basic Leslie matrix is created, which facilitates the examination of the
susceptibility of a population to the incorporation of genes from immigrant individuals. The dominant eigenvalue, lambda, and the corresponding eigenvector, as well as the reproductive values, are calculated from the basic Leslie matrix. With this information, the size of the initial population (one hundred) is distributed among the aa homozygous class based upon the stable age distribution; the number of individuals in the heterozygous class is initially zero; and the number of individuals in the bb homozygous class is one, where the value of one was placed in the age group with the highest reproductive value. Thus, the elements of the initial population vector summed to 101. This vector has the following appearance:

\[ \text{pv} = \{aa_1, ab_1, bb_1, aa_2, ab_2, bb_2, aa_3, ab_3, bb_3\} \]

The subscripts indicate the age group for an individual with the given genotype.

Before iterations of the model are made, the number of generations and the carrying capacity must be assigned. The number of generations equals 20 and the carrying capacity equals 10,000. One of the main differences between the basic and the genetic models is that the matrix in the genetic model must be recalculated after each generation to account for the changes in the distribution of genotypes. The changes in genotypes will change the elements in the first three rows of genetic matrix, since these rows are based upon the genetic probability that an offspring of the
particular genotype is possible.

Analysis was made on the total population within each genotype (Genetic Genotype Graphs) and changes in total population size (Genetic Graphs). The genotype graphs of aa and ab follow the pattern of the total population graphs. The bb graphs demonstrate how the bb genotype enters the population. The results of all of these graphs are expected to be similar to the results for the basic model with the same general life history characteristics--it is expected that the fecundity pattern will have a greater affect on the dynamics than the survivorship pattern. It appears that this is an accurate expectation; the fecundity pattern in the genetic graphs does appear to more strongly affect the dynamics of growth than does the survivorship pattern. However, for all of these graphs, the similarities are more striking than the differences. The only significantly different growth pattern is found in graphs for G3, G7 and G11. In the total population graph for G10, it appears that this might be a different pattern from the others with the same fecundity (G2 and G6). However, it is more likely that this combination of life history characteristics simply requires more generations to achieve its stable population size. A similar result is also observed in the genetic genotype graphs.

The ratio of the final frequency of the b allele to its initial frequency is an indicator of how susceptible the
population is to immigrant alleles. The frequency of the \( b \) allele, denoted by \( q_b \), was calculated by adding the proportion of \( bb \) homozygotes and one half the proportion of heterozygotes. The ratio, \( z = q_b / q_b \), is the frequency in the \( n \)th generation divided by the frequency in the initial population, \( q_b \). Since the immigrants are specifically chosen to be reproductively successful, it is known that this genotype will successfully infiltrate the population, as is indicated by the genetic genotype graphs. However, the tolerance of the initial population to perturbation, which is indicated by the degree to which \( z \) is greater than one, is not known. Table 2 has the equilibrium values of \( z \) and the changes in frequency are indicated in the Allele Frequency Ratio Graphs.

Table 2: Allele Frequency Ratio

<table>
<thead>
<tr>
<th>Survivorship</th>
<th>Fecundity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>peaking</td>
</tr>
<tr>
<td>slow early decline</td>
<td>G1</td>
</tr>
<tr>
<td>steady decline</td>
<td>G5</td>
</tr>
<tr>
<td>rapid early decline</td>
<td>G9</td>
</tr>
</tbody>
</table>

The greatest \( z \) value is found in G1. The G1 life history characteristics are peaking fecundity and slow early decline in survivorship. Thus, a population with these characteristics will be most susceptible to the
incorporation of immigrant alleles—it is most responsive to genetic manipulation. In other words, with slow early decline in survivorship, a peaking fecundity allows for the most favorable results for introducing foreign alleles into a population. On the other hand, with constant decline or rapid early decline in survivorship, the most favorable fecundity pattern is monotonically decreasing—greatest fecundity effort at an early age.

It should also be noted that this analysis does not have the same sort of results as the analysis of population size. The survivorship and fecundity patterns do not seem to directly influence which life history combination is least susceptible to foreign alleles. Previously, the fecundity pattern greatly influenced the dynamics, but the allele frequency ratio does not remain similar for the same fecundity patterns nor for the same survivorship patterns. Thus, the patterns must be compared individually.

Conclusion:

The Leslie Matrix is a valuable tool for exploring the dynamics of populations. Using typical age-specific life history patterns, predictable population dynamics are observed. The Leslie Matrix is also moldable to incorporate the genetic information. Traditionally, genetic studies have excluded the concept of age, and age-specific studies have excluded the concept of genotypes. Thus, this
particular approach combining genetic information with age-
specific life history patterns, has not been extensively
explored.
G2 total population

G6 total population

G10 total population
Addendum

The carrying capacity scalar was taken from Anderson and King. However, it was inadvertently used differently than they used it. For my analysis, K modifies both the fecundity and the survivorship since it is multiplied by the entire matrix. Anderson and King choose K to modify only the fecundity—-the first row of the matrix. There exists an inherent problem with both of these approaches.

If the total population is greater than the carrying capacity, then the scalar is negative. If the scalar is multiplied by the entire matrix or only the first row of the matrix, there will be negative individuals. This is impossible; there can neither be negative individuals born nor negative total population sizes.

The intent of including carrying capacity in the model was to allow the environment to have some control on how a population will grow. If the total population size is greater than the carrying capacity, the population should get smaller and approach K. If the total population is less than K, the population should increase and approach K. With the model as it is, carrying capacity works as it should for populations with sizes less than K, but not for sizes greater than K.
Appendix A

**Fecundity**: The expected number of daughters born to a female at age x or i, denoted m(x) or a_i.

**Finite Rate of Increase**: The eventual rate of increase for the population. Mathematically, the dominant eigenvalue (λ) of the Leslie Matrix.

**Intrinsic Rate of Increase**: Natural logarithm of the finite rate of increase.

**K-selection**: Selection based upon the carrying capacity of the environment. Mathematically, 
\[ \frac{(K - \text{total population})}{K} \]
would be the constant that is multiplied by the Leslie Matrix.

**Leslie Matrix**: An n x n matrix which exemplifies age class divisions and has m(x) values along the first row, proportional l(x) values along the subdiagonal, and zero values elsewhere.

**Net Reproductive Rate**: The expected lifetime production of daughters for a newborn female. Mathematically,
\[ R = \sum_{x} m(x) l(x). \]

**Proportional \( l(x) \) values:** Mathematically, the proportion of females that survive from birth to age \( i \) divided by the proportion of females that survive from birth to age \( (i-1) \), denoted by \( b_i, l(i)/l(i-1) \).

**Reproductive Values:** The expected number of daughters that can be born to a females from age \( x \) until death. Mathematically,

\[ v(x) = \lambda^x / l(x) \times \sum_{y=x}^{\infty} [\lambda^{-y} \times m(y) l(y)]. \]

**Stable Age Distribution:** The distribution of the population by age groups to which the population approaches as generations pass. Mathematically, the eigenvector that corresponds to the dominant eigenvalue of the Leslie Matrix.

**Survivorship:** The proportion of females that live from birth to age \( x \), denoted \( l(x) \).
Appendix B

Data Sets for Life Histories Program

<table>
<thead>
<tr>
<th>Set</th>
<th>Fecundity</th>
<th>Survivorship</th>
</tr>
</thead>
<tbody>
<tr>
<td>H1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2 2 2 2 2</td>
<td>0.25 0.17 0.08 0</td>
</tr>
<tr>
<td>H2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2 2 2 2 2</td>
<td>0.75 0.5 0.25 0</td>
</tr>
<tr>
<td>H3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2 2 2 2 2</td>
<td>0.92 0.83 0.75 0</td>
</tr>
<tr>
<td>H4</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>1 2 3 4</td>
<td>0.25 0.17 0.08 0</td>
</tr>
<tr>
<td>H5</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>1 2 3 4</td>
<td>0.75 0.5 0.25 0</td>
</tr>
<tr>
<td>H6</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>1 2 3 4</td>
<td>0.92 0.83 0.75 0</td>
</tr>
<tr>
<td>H7</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>3 2 1 0</td>
<td>0.25 0.17 0.08 0</td>
</tr>
<tr>
<td>H8</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>3 2 1 0</td>
<td>0.75 0.5 0.25 0</td>
</tr>
<tr>
<td>H9</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>3 2 1 0</td>
<td>0.92 0.83 0.75 0</td>
</tr>
<tr>
<td>H10</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>3 4 3 0</td>
<td>0.25 0.17 0.08 0</td>
</tr>
<tr>
<td>H11</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>3 4 3 0</td>
<td>0.75 0.5 0.25 0</td>
</tr>
<tr>
<td>H12</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>3 4 3 0</td>
<td>0.92 0.83 0.75 0</td>
</tr>
</tbody>
</table>
Appendix C

Data Sets for Genetic Program

<table>
<thead>
<tr>
<th></th>
<th>Fecundity</th>
<th>Survivorship</th>
</tr>
</thead>
<tbody>
<tr>
<td>G1</td>
<td>0 2 1</td>
<td>1 1 0</td>
</tr>
<tr>
<td>G2</td>
<td>0 1 2</td>
<td>1 1 0</td>
</tr>
<tr>
<td>G3</td>
<td>2 1 0</td>
<td>1 1 0</td>
</tr>
<tr>
<td>G4</td>
<td>1 1 1</td>
<td>1 1 0</td>
</tr>
<tr>
<td>G5</td>
<td>0 2 1</td>
<td>1 0.75 0</td>
</tr>
<tr>
<td>G6</td>
<td>0 1 2</td>
<td>1 0.75 0</td>
</tr>
<tr>
<td>G7</td>
<td>2 1 0</td>
<td>1 0.75 0</td>
</tr>
<tr>
<td>G8</td>
<td>1 1 1</td>
<td>1 0.75 0</td>
</tr>
<tr>
<td>G9</td>
<td>0 2 1</td>
<td>1 0.25 0</td>
</tr>
<tr>
<td>G10</td>
<td>0 1 2</td>
<td>1 0.25 0</td>
</tr>
<tr>
<td>G11</td>
<td>2 1 0</td>
<td>1 0.25 0</td>
</tr>
<tr>
<td>G12</td>
<td>1 1 1</td>
<td>1 0.25 0</td>
</tr>
</tbody>
</table>
Appendix D

Life History Parameters Program

(* Clear Files *)

DeleteFile["matrix.m"]
DeleteFile["values.m"]
DeleteFile["reprovals.m"]
DeleteFile["pop.m"]

(* Calculate Leslie Matrix values *)

a1 = m0
a2 = m1
a3 = m2
a4 = m3
a5 = m4

b1 = l1
b2 = 12 / l1
b3 = l3 / l2
b4 = l4 / l3

(* Put values in matrix form and output the matrix *)

m = {{a1, a2, a3, a4, a5},
    {b1, 0, 0, 0, 0},
    {0, b2, 0, 0, 0},
    {0, 0, b3, 0, 0},
    {0, 0, 0, b4, 0}}

Put[Leslie Matrix, "matrix.m"]
PutAppend[Format[MatrixForm[m], OutputForm], "matrix.m"]

(* Calculate the eigenvalues and eigenvectors and
determine the dominant eigenvalue and corresponding
eigenvector *)

eigen = Eigenvalues[m]
age = Eigenvectors[m]

Which[Abs[eigen[[1]]] >= Abs[eigen[[2]]] &
       Abs[eigen[[1]]] >= Abs[eigen[[3]]] &
       Abs[eigen[[1]]] >= Abs[eigen[[4]]] &
       Abs[eigen[[1]]] >= Abs[eigen[[5]]], la = eigen[[1]],
       Abs[eigen[[2]]] >= Abs[eigen[[1]]] &
       Abs[eigen[[2]]] >= Abs[eigen[[3]]]]
Abs[eigen[[2]]] >= Abs[eigen[[4]]] &&
Abs[eigen[[2]]] >= Abs[eigen[[5]], la = eigen[[2]],
Abs[eigen[[3]]] >= Abs[eigen[[1]], &&
Abs[eigen[[3]]] >= Abs[eigen[[2]], &&
Abs[eigen[[3]]] >= Abs[eigen[[4]], &&
Abs[eigen[[3]]] >= Abs[eigen[[5]], la = eigen[[3]],
Abs[eigen[[4]]] >= Abs[eigen[[1]], &&
Abs[eigen[[4]]] >= Abs[eigen[[2]], &&
Abs[eigen[[4]]] >= Abs[eigen[[3]], &&
Abs[eigen[[4]]] >= Abs[eigen[[5]], la = eigen[[4]],
Abs[eigen[[5]]] >= Abs[eigen[[1]], &&
Abs[eigen[[5]]] >= Abs[eigen[[2]], &&
Abs[eigen[[5]]] >= Abs[eigen[[3]], &&
Abs[eigen[[5]]] >= Abs[eigen[[4]], &&
Abs[eigen[[5]]] >= Abs[eigen[[5]], newage = age[[1]],,
Abs[eigen[[1]]] >= Abs[eigen[[1]], &&
Abs[eigen[[2]]] >= Abs[eigen[[3]], &
Abs[eigen[[2]]] >= Abs[eigen[[4]], &
Abs[eigen[[2]]] >= Abs[eigen[[5]], newage = age[[2]],
Abs[eigen[[3]]] >= Abs[eigen[[1]], &
Abs[eigen[[3]]] >= Abs[eigen[[2]], &
Abs[eigen[[3]]] >= Abs[eigen[[4]], &
Abs[eigen[[3]]] >= Abs[eigen[[5]], newage = age[[3]],
Abs[eigen[[4]]] >= Abs[eigen[[1]], &
Abs[eigen[[4]]] >= Abs[eigen[[2]], &
Abs[eigen[[4]]] >= Abs[eigen[[3]], &
Abs[eigen[[4]]] >= Abs[eigen[[5]], newage = age[[4]],
Abs[eigen[[5]]] >= Abs[eigen[[1]], &
Abs[eigen[[5]]] >= Abs[eigen[[2]], &
Abs[eigen[[5]]] >= Abs[eigen[[3]], &
Abs[eigen[[5]]] >= Abs[eigen[[4]], &
Abs[eigen[[5]]] >= Abs[eigen[[5]], newage = age[[5]],

(* If stable age distribution contains all negative entries, change to all positive entries *)

If[newage[[1]] < 0 && newage[[2]] < 0 && newage[[3]] < 0 &&
newage[[4]] < 0 && newage[[5]] < 0, newage = -1 newage]

(* Normalize dominant eigenvector for population iterations *)

normal = newage . {1, 1, 1, 1, 1}
k = 1/normal
rv = k newage (* normal vector*)

(* Calculate and output intrinsic rate of increase and net reproductive rate *)
\[ r = \log(1 + a) \quad (* \text{intrinsic rate of increase} *) \]
\[ R = 11m1 + 12m2 + 13m3 + 14m4 \quad (* \text{net reproductive rate} *) \]

Put[eigenvalues, eigen, "values.m"]
PutAppend[dominant eigenvalue, la, "values.m"]
PutAppend[eigenvectors, age, "values.m"]
PutAppend[dominant eigenvector, newage, "values.m"]
PutAppend[intrinsic, r, "values.m"]
PutAppend[net reproductive, R, "values.m"]

(* Calculate and output reproductive values *)

\[
\begin{align*}
    v0 &= (1 / 10) * (l0m0 + (l1m1 / la) + (l2m2 / la^2) + \\
         & \quad (l3m3 / la^3) + (l4m4 / la^4)) \\
    v1 &= (la / l1) * (l1m1 / la) + (l2m2 / la^2) + \\
         & \quad (l3m3 / la^3) + (l4m4 / la^4)) \\
    v2 &= (la^2 / l2) * (l2m2 / la^2) + (l3m3 / la^3) + \\
         & \quad (l4m4 / la^4)) \\
    v3 &= (la^3 / l3) * (l3m3 / la^3) + (l4m4 / la^4)) \\
    v4 &= (la^4 / l4) * (l4m4 / la^4)
\end{align*}
\]

Put[REPRODUCTIVE VALUES, "reprovals.m"]
PutAppend[group one, v0, "reprovals.m"]
PutAppend[group two, v1, "reprovals.m"]
PutAppend[group three, v2, "reprovals.m"]
PutAppend[fourth group, v3, "reprovals.m"]
PutAppend[fifth group, v4, "reprovals.m"]

(* Iterations of generations; K, PN, GN inputed *)

initial = PN n
pop[1] = ((K - PN)/K) . initial

Put[GENERATIONS, "pop.m"]
PutAppend[Initial population, initial, "pop.m"]
PutAppend[First generation, pop[1], "pop.m"]

Do[
    P = pop[j] . {1, 1, 1, 1, 1};
    pop[j+1] = ((K - P) / K) . pop[j];
    If[pop[j+1] . {1, 1, 1, 1, 1} < 0,
        pop[j+1] = {0, 0, 0, 0, 0}];
    PutAppend[P, "pop.m"];
    PutAppend[(j+1) generation, pop[j+1], "pop.m"];
    {j, 1, GN - 1}]

(* Plot total population size *)

Do[total[i] = pop[j] . {1, 1, 1, 1, 1}, {i, 1, GN}]
t = Table[total[i], {i, 1, GN}]
<<X11.m (* set up graphics window *)

w = ListPlot[t, PlotJoined -> True, AxesLabel -> 
{generations, size}, PlotLabel -> "H1 Total Population"]
PSPrint[w] (* change H-value with changing data sets *)
Appendix E

3x3 Genetic Matrix Program

(* Clear files *)

DeleteFile["new.m"]
DeleteFile["result.m"]

(* Create standard Leslie matrix from situations where
fecundity and survivorship are identical for different
genotypes *)

b1 = 11
b2 = 11
b3 = 11
b4 = 12/11
b5 = 12/11
b6 = 12/11

s = {
{m111, m211, m311},
{b1, 0, 0},
{0, b4, 0}}

(* Calculate dominant eigenvalue and eigenvector of
standard Leslie matrix *)

vals = Eigenvectors[s]
vecs = Eigenvectors[s]
Put[{eigenvalues, vals, eigenvectors, vecs, "new.m"]

Which[vals[[1]]] >= vals[[2]]] &&
   vals[[1]] >= vals[[3]], la = vals[[1]],
   Which[vals[[2]]] >= vals[[1]]] &&
   vals[[2]] >= vals[[3]], la = vals[[2]],
   Which[vals[[3]]] >= vals[[1]]] &&
   vals[[3]] >= vals[[2]], la = vals[[3]]

Which[vals[[1]]] >= vals[[2]]] &&
   vals[[1]] >= vals[[3]], newage = vecs[[1]],
   Which[vals[[2]]] >= vals[[1]]] &&
   vals[[2]] >= vals[[3]], newage = vecs[[2]],
   Which[vals[[3]]] >= vals[[1]]] &&
   vals[[3]] >= vals[[2]], newage = vecs[[3]]}
(If stable age distribution contains all negative entries, change to all positive entries *)

If[newage[[1]] < 0 && newage[[2]] < 0 && newage[[3]] < 0,
newage = -1 newage]

(* Normalize dominant eigenvector for age and genotype population vector *)

sum = newage . {1, 1, 1}
k = 1/sum
nv = k newage (* normal vector *)

PutAppend[lambda, la, distribution, newage, "new.m"]

(* Reproductive values: calculate and determine which is greatest *)

v0 = (1/10) * (10*m111 + (11*m211/la) + (12*m311/la^2))
v1 = (1a/11) * ((11*m211/la) + (12*m311/la^2))
v2 = (la^2/12) * (12*m311/la^2)

Which[N[v0] > N[v1] && N[v0] > N[v2], v = {1, 0, 0},
N[v1] > N[v0] && N[v1] > N[v2], v = {0, 1, 0},
N[v2] > N[v0] && N[v2] > N[v1], v = {0, 0, 1}]

PutAppend[age one, v0, age two, v1, age three, v2, "new.m"]

(* Initial genetic population vector (pv); PN is initial population size *)

aa1 = PN nv[[1]]
aa2 = PN nv[[2]]
aa3 = PN nv[[3]]

ab1 = 0
ab2 = 0
ab3 = 0

bb1 = v[[1]]
bb2 = v[[2]]
bb3 = v[[3]]

pv = {aa1, ab1, bb1, aa2, ab2, bb2, aa3, ab3, bb3}

Put[Initial population vector, pv, "result.m"]

Do[
   (* proportions in genotypes *)
   total[i] = pv . {1, 1, 1, 1, 1, 1, 1, 1};]
propaa = (pv . [1, 0, 0, 1, 0, 0, 1, 0, 0, 0]) / total[i];
propab = (pv . [0, 1, 0, 0, 1, 0, 0, 1, 0, 0]) / total[i];
propbb = (pv . [0, 0, 1, 0, 0, 1, 0, 0, 1, 0]) / total[i];

props = {propaa, propab, propbb};

(* frequency of b allele and ratio of allele *)

q[i] = propbb + .5*propab;
rat[i] = q[i]/q[1];

(* proportions in genotypes and age groups *)

prop1 = pv[[1]] / total[i];
prop2 = pv[[2]] / total[i];
prop3 = pv[[3]] / total[i];
prop4 = pv[[4]] / total[i];
prop5 = pv[[5]] / total[i];
prop6 = pv[[6]] / total[i];
prop7 = pv[[7]] / total[i];
prop8 = pv[[8]] / total[i];
prop9 = pv[[9]] / total[i];

props2 = {prop1, prop2, prop3, prop4, prop5, prop6, prop7, prop8, prop9};

(* Create first three rows of matrix *)

(* Capital letters are genotypes of offspring *)

(* mated with aa *)

AA1 = props . [1, .5, 0];
AB1 = props . [0, .5, 1];
BB1 = props . [0, 0, 0];

(* mated with ab *)

AA2 = props . [.5, .25, 0];
AB2 = props . [.5, .5, .5];
BB2 = props . [0, .25, .5];

(* mated with bb *)

AA3 = props . [0, 0, 0];
AB3 = props . [1, .5, 0];
BB3 = props . [0, .5, 1];

(* multiply all elements by respective fecundity to generate appropriate numbers of daughters per individual per genotype and age group and create matrix *)
m = {{m111*AA1, m121*AA2, m131*AA3, m211*AA1, m221*AA2, m231*AA3, m311*AA1, m321*AA2, m331*AA3},
{m112*AB1, m122*AB2, m132*AB3, m212*AB1, m222*AB2, m232*AB3, m312*AB1, m322*AB2, m332*AB3},
{m113*BB1, m123*BB2, m133*BB3, m213*BB1, m223*BB2, m233*BB3, m313*BB1, m323*BB2, m333*BB3},
\[b1, 0, 0, 0, 0, 0, 0, 0, 0\],
\[0, b2, 0, 0, 0, 0, 0, 0, 0\],
\[0, 0, b3, 0, 0, 0, 0, 0, 0\],
\[0, 0, 0, b4, 0, 0, 0, 0, 0\],
\[0, 0, 0, 0, b5, 0, 0, 0, 0\],
\[0, 0, 0, 0, 0, b6, 0, 0, 0\]};

(* Iterate population one generation with carrying
capacity K for total population *)

cap[i] = N[(K - total[i])/K];
new = (cap[i] m) . pv;

If[new . {1, 1, 1, 1, 1, 1, 1, 1, 1} < 0,
new = {0, 0, 0, 0, 0, 0, 0, 0, 0}];

(* total population within genotypes *)

g1[i] = new[[1]] + new[[4]] + new[[7]];
g2[i] = new[[2]] + new[[5]] + new[[8]];
g3[i] = new[[3]] + new[[6]] + new[[9]];

(* re-assign population vector *)

pv = new;

PutAppend[genotype proportions, props, age and genotype proportions, props2, population size, total[i], allele frequency, q[i], i generation population vector, new, "result.m"],
{i, 1, GN}]

(* Set up to plot population within genotypes, allele
frequency ratio, and total population size *)

t1 = Table[g1[i], {i, 1, GN}]
t2 = Table[g2[i], {i, 1, GN}]
t3 = Table[g3[i], {i, 1, GN}]
t4 = Table[rat[i], {i, 1, GN}]}
t = Table[total[i], {i, 1, GN}]

<<X11.m (* initialize graphics *)

w1 = ListPlot[t1, PlotJoined -> True,
AxesLabel -> {generations, size},
PlotLabel -> "G1 genotype aa"]

w2 = ListPlot[t2, PlotJoined -> True,
AxesLabel -> {generations, size},
PlotLabel -> "G1 genotype ab"]

w3 = ListPlot[t3, PlotJoined -> True,
AxesLabel -> {generations, size},
PlotLabel -> "G1 genotype bb"]

w4 = ListPlot[t4, PlotJoined -> True,
AxesLabel -> {generations, ratio},
PlotLabel -> "G1 b allele frequency ratio"]

w = ListPlot[t, PlotJoined -> True,
AxesLabel -> {generations, size},
PlotLabel -> "G1 total population"]

(* change G-value with change in data set *)

PSPrint[w1]
PSPrint[w2]
PSPrint[w3]
PSPrint[w4]
PSPrint[w]
Bibliography


