Leslie Matrix I

Formal Demography
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Outline

1. Matrix Dynamics

2. Matrix Powers

3. Life-Cycle Graphs

   (a) Irrucibility/Primitivity
   (b) Post-Reproductive Life

4. Eigenvalues and Eigenvectors

A Simple Example

Assume 2 Age-Classes

The population is now described by the following model:

$$n_1(t+1) = f_1 n_1(t) + f_2 n_2(t) \quad (1)$$

$$n_{2(t+1)} = p_1 n_1 \quad (2)$$

n_1 is the number in stage 1. n_2 is the number in stage 2, f_1 is the fertility of stage 1 individuals, f_2 is the fertility of stage 2 individuals, and p_1 is the survivals of 1's to age class 2

The question we wish to answer: Is there a unique exponential growth rate for such a population analogous to the unstructured case?

Figuring Out Age Structure

Imagine you start with a total population size ($N(0) = n_1(0) + n_2(0)$) of 10. What will the population look like in one time step?

If there are 10 ones and zero twos

$$n_1(1) = 10f_1 \tag{3}$$
$$n_2(1) = 10p_1 \tag{4}$$

If there are zero ones and 10 twos

$$n_1(1) = 10f_2 \tag{5}$$
$$n_2(1) = 0 \tag{6}$$

Hmmmm. . .

A structured population will grow exponentially only when the ratios between the different classes of the population remain constant

In the age-structured case, we call this the stable age distribution

In the state-structured case, we call it the stable stage distribution

Matrices Provide a Compact Notation

Manipulation of Matrices

1. A matrix is a rectangular array of numbers

$$\mathbf{A} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

2. A vector is simply a list of numbers

$$\mathbf{n(t)} = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}$$

3. A scalar is a single number: $\lambda = 1.05$

Index Conventions

We refer to individual matrix elements by indexing them by their row and column positions

A matrix is typically named by a capital (bold) letter (e.g., $\mathbf{A}$)

An element of matrix $\mathbf{A}$ is given by a lowercase a subscripted with its indices

These indices are subscripted following the the lowercase letter, first by row, then by column

For example, a_{21} is the element of $\mathbf{A}$ which is in the second row and first column

The Leslie Matrix

This matrix is a special matrix used in demography and population biology

It is referred to as a Leslie Matrix after its inventor Sir Paul Leslie (Leslie 1945, 1948)

A Leslie Matrix contains:

- age-specific fertilities along the first row
- age-specific survival probabilities along the subdiagonal
- Zeros everywhere else

Here is a 5×5 Leslie matrix:

$$\mathbf{A} = \begin{bmatrix} 0 & F_2 & F_3 & F_4 & F_5 \\ P_1 & 0 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 & 0 \\ 0 & 0 & P_3 & 0 & 0 \\ 0 & 0 & 0 & P_4 & 0 \end{bmatrix} \tag{7}$$

The Leslie matrix is a special case of a **projection matrix** for an age-classified population

With age-structure, the only transitions that can happen are from one age to the next and from adult ages back to the first age class

Can you imagine a projection matrix structured by something other than age?

The Life Cycle Diagram

It is useful to think of the matrix entries in a life-cycle manner:

The entry a_{ij} is the transition probability of going from (st)age j to (st)age i

$$a_{ij} = a_{i \leftarrow j} \tag{8}$$

Note (Especially for Sociologists): The column-to-row convention of the Leslie Matirx is transposed from the convention commonly found in sociological applications (e.g., social mobility matrices)

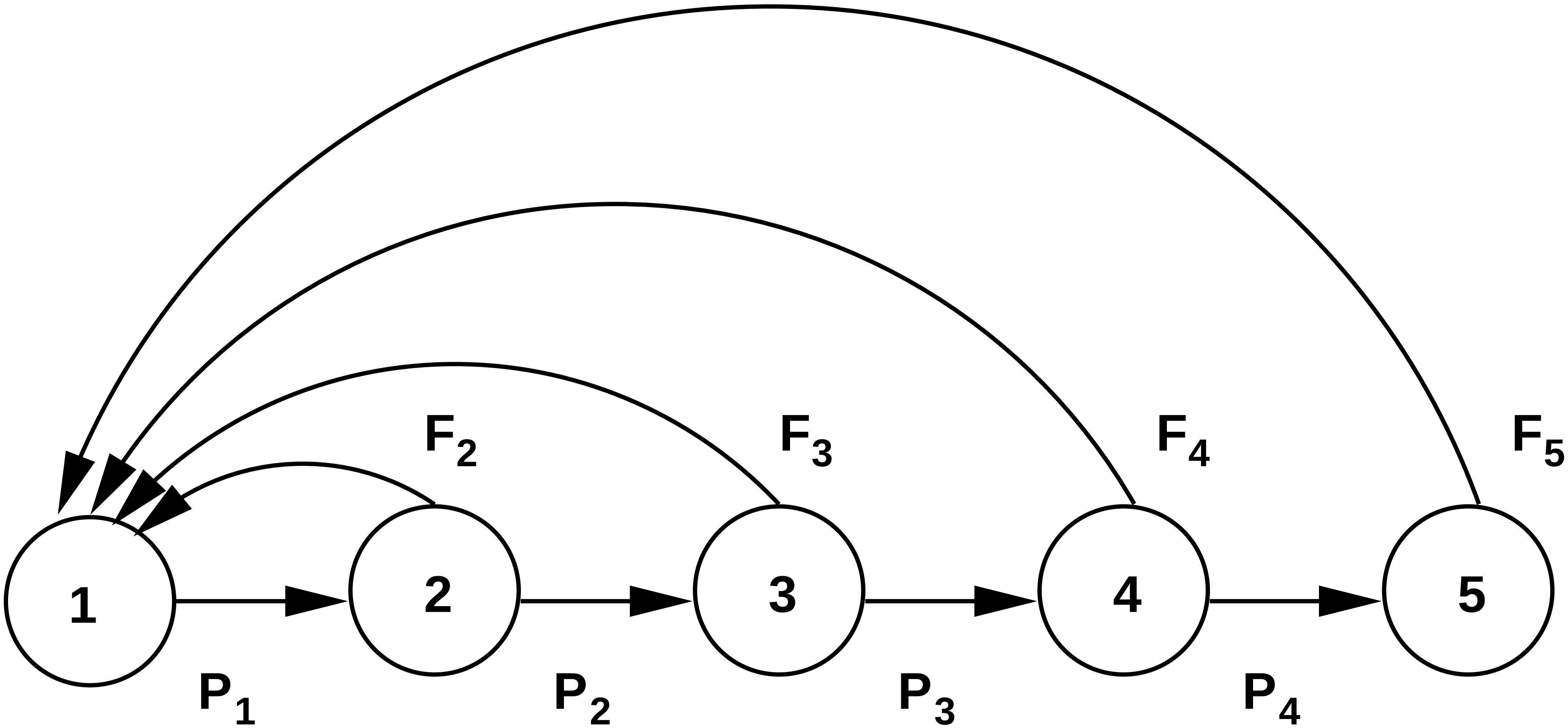
Life Cycle Diagram

We formalize this life-cycle approach by noting the linkages between the projection matrix and the life-cycle graph

A life-cycle graph is a digraph (or directed graph) composed two things:

- Nodes, which represent the states (ages, stages, subgroups, localities, etc.)
- Edges, which represent transitions between states

Here is a simple age-structured life cycle with five ages and reproduction in age classes 2-5


F2
F3
F4
F5
1
2
3
4
5
P1
P2
P3
P4

Desirable Properties of Matrices

Every demographic matrix is non-negative (all its entries are greater than or equal to zero)

In general, we are only interested in non-negative matrices

We have seen that it is important for the elements of a structured population model to come to some sort of stable distribution

Not all population models do this

To evaluate the conditions for convergence, we use the life cycle graph

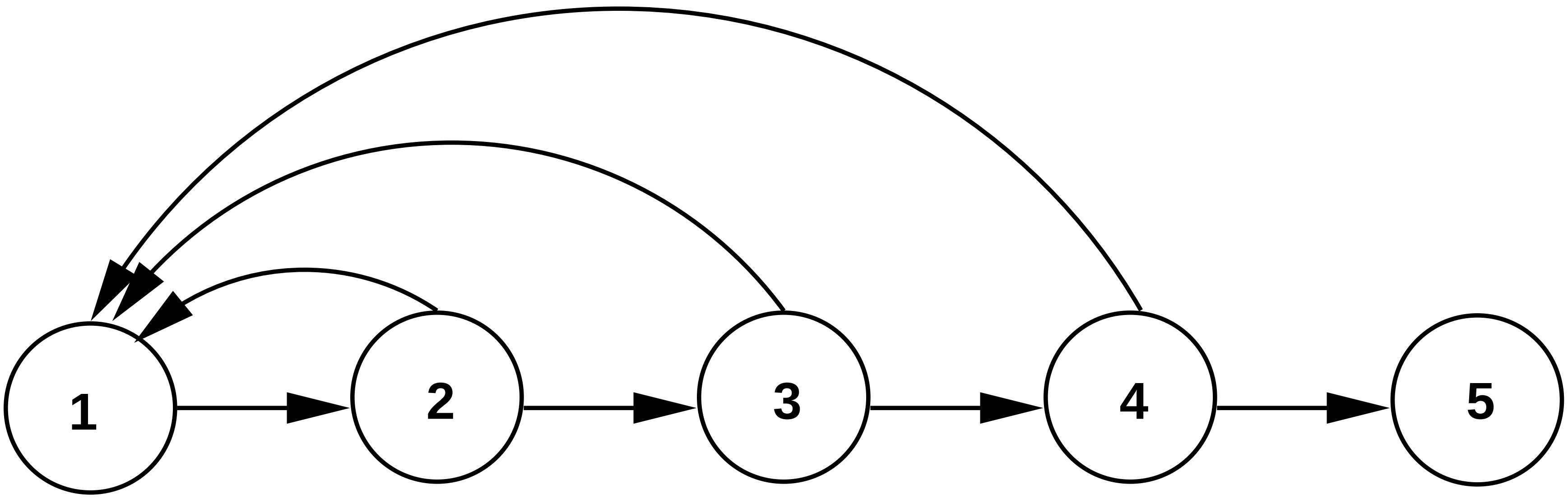
Irreducible Matrices: A matrix is irreducible if and only if there is a path between every node and every other node in the life cycle graph

Irreducibility is necessary but not sufficient for stability

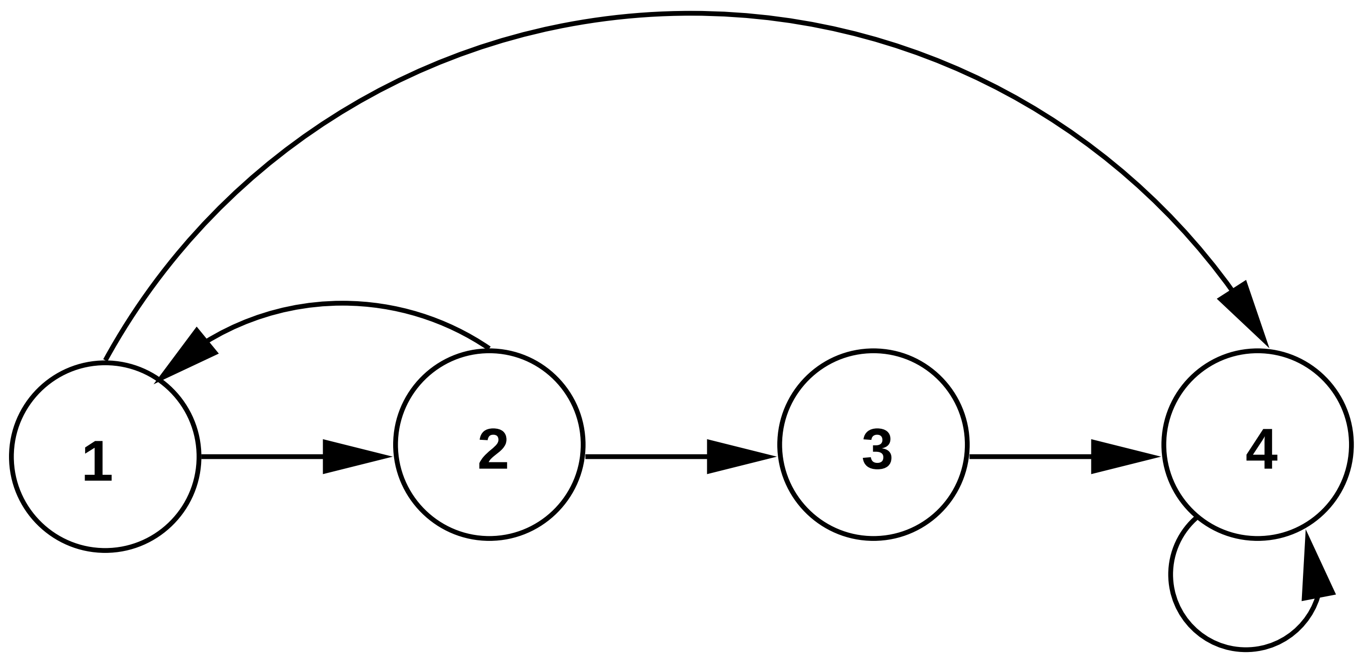
Primitivity: An irreducible non-negative matrix is primitive if all its elements become positive when raised to sufficiently high powers

A matrix is primitive if the greatest common divisor of all loops in the corresponding life-cycle graph is 1

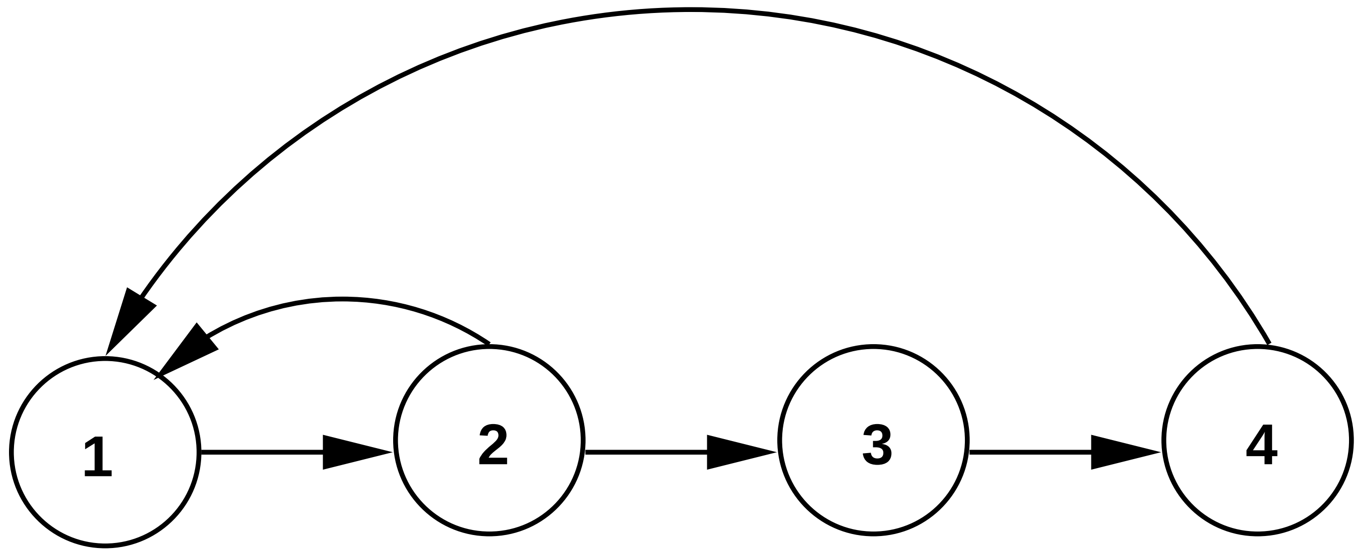
A Reducible Life Cycle



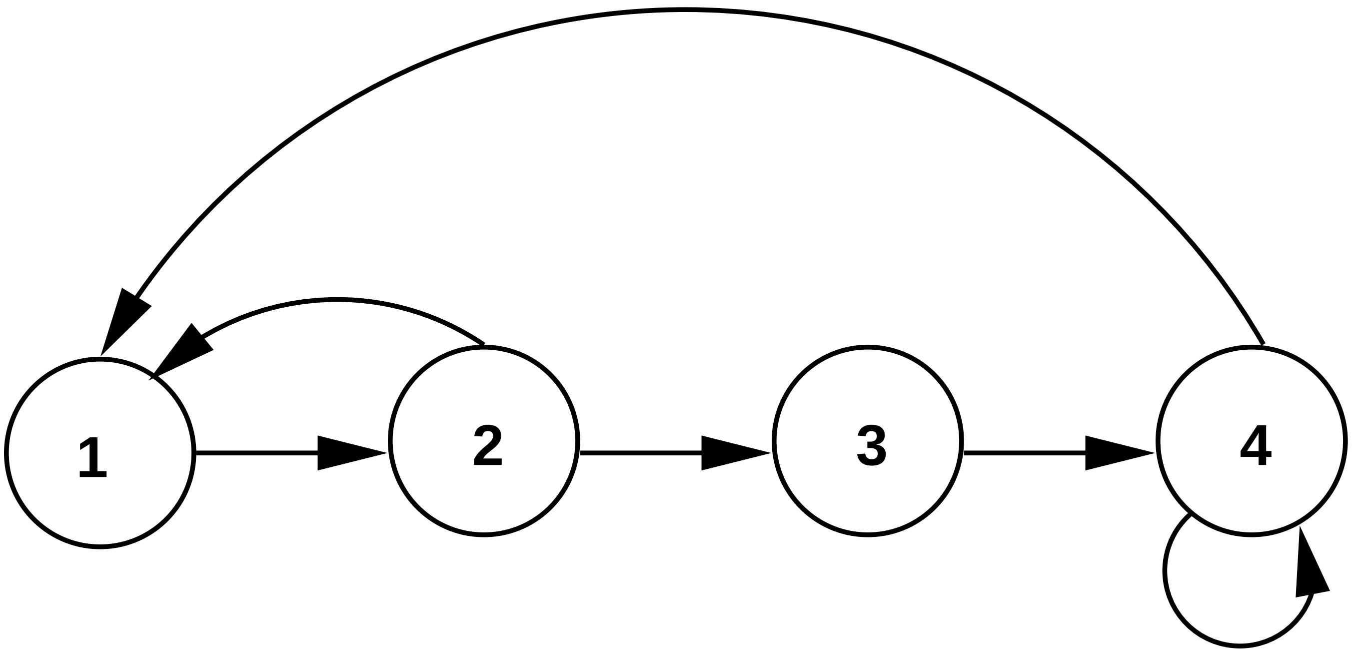
Another (Wierd) Reducible Life Cycle



An Imprimitive Life Cycle



Life Cycles with Self-Loops Are Primitive



Compact Notation

Having redefined the population model in matrix form, we can write it in a more compact notation of matrix algebra:

$$\mathbf{n(t+1) = An(t)} \tag{9}$$

(Matrices contain much, much more than just a pretty face of notation)

Let's now assume that there is a solution to the exponential growth model in a structured population

Write the population model as:

$$\mathbf{A}\mathbf{n} = \lambda\mathbf{n} \tag{10}$$

Now solve for λ . . .

The rules of linear algebra make this a little trickier than just dividing both sides by $\mathbf{n}$

$$\mathbf{An} - \lambda\mathbf{n} = 0 \tag{11}$$

$$\mathbf{An} - \lambda\mathbf{In} = 0 \tag{12}$$

$$(\mathbf{A} - \lambda\mathbf{I})\mathbf{n} = 0 \tag{13}$$

$\mathbf{I}$ is an identity matrix of the same rank as $\mathbf{A}$ (ones along the diagonal, zeros elsewhere)

It's a fact of linear algebra, that the solution to equation 10 exists only if the determinant of the matrix $(\mathbf{An} - \lambda \mathbf{I})$ is zero

For the 2×2 case of equation 10, the determinant is simple

For any 2×2 matrix the determinant is given by:

$$\det \begin{bmatrix} a & b \\ c & d \end{bmatrix} = ad - bc$$

Determinants of matrices of larger rank are, necessarily, more complex the calculation

$$(\mathbf{A} - \lambda \mathbf{I}) = \begin{bmatrix} f_1 & f_2 \\ p_1 & 0 \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix} = \begin{bmatrix} f_1 - \lambda & f_2 \\ p_1 & -\lambda \end{bmatrix}$$

$$\det(\mathbf{A} - \lambda \mathbf{I}) = -(f_1 - \lambda)\lambda - f_2 p_1$$

$$\lambda^2 - f_1 \lambda - f_2 p_1 = 0$$

Use the quadratic equation to solve for λ:

$$\frac{-f_1 \pm \sqrt{f_1^2 - 4 f_2 p_1}}{2 f_1}$$

Numerical Example

Perhaps it makes more sense to use numbers . . .

Define:

$$\mathbf{A} = \begin{bmatrix} 1.5 & 2 \\ 0.5 & 0 \end{bmatrix} \tag{14}$$

$$\det(\mathbf{A} - \lambda \mathbf{I}) = \begin{bmatrix} 1.5 - \lambda & 2 \\ 0.5 & -\lambda \end{bmatrix}$$

$$\lambda^2 - 1.5\lambda - 1 = 0$$

$$(\lambda - 2)(\lambda + 0.5) = 0$$

Eigenvectors

Remember when we started this, we found that for a population to grow exponentially, it must maintain constant ratios between its age classes?

There is a special vector that goes hand-in-hand with the eigenvalue called, strangely enough, an $eigenvector$

Let's keep up with our example. Remember that the eigenvalues of this model are $\lambda = 2$ and $\lambda = -0.5$

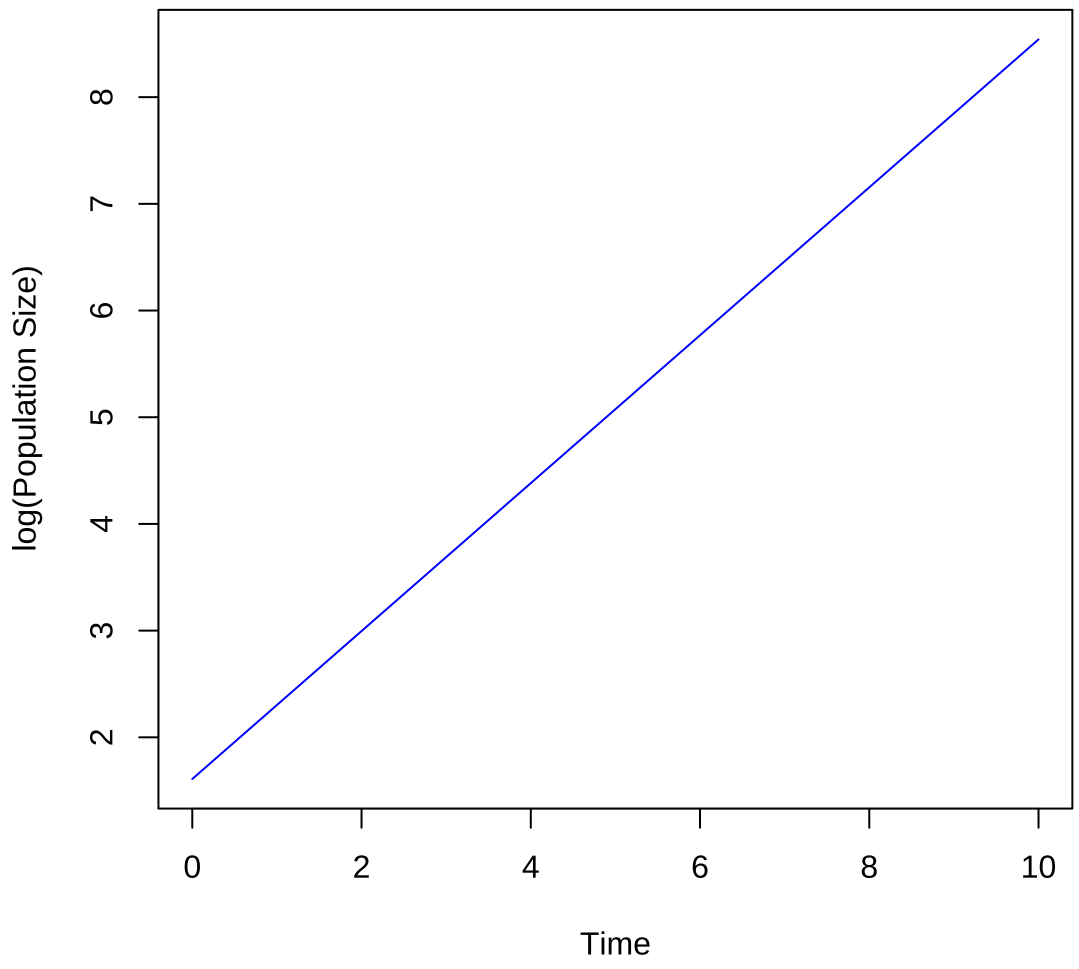
That means that we can write our model as:

$$\mathbf{A} = \left[\begin{array}{cc} 1.5 & 2 \\ 0.5 & 0 \end{array} \right] \left[\begin{array}{c} n_1 \\ n_2 \end{array} \right] = \left[\begin{array}{c} 2n_1 \\ 2n_2 \end{array} \right] \tag{15}$$

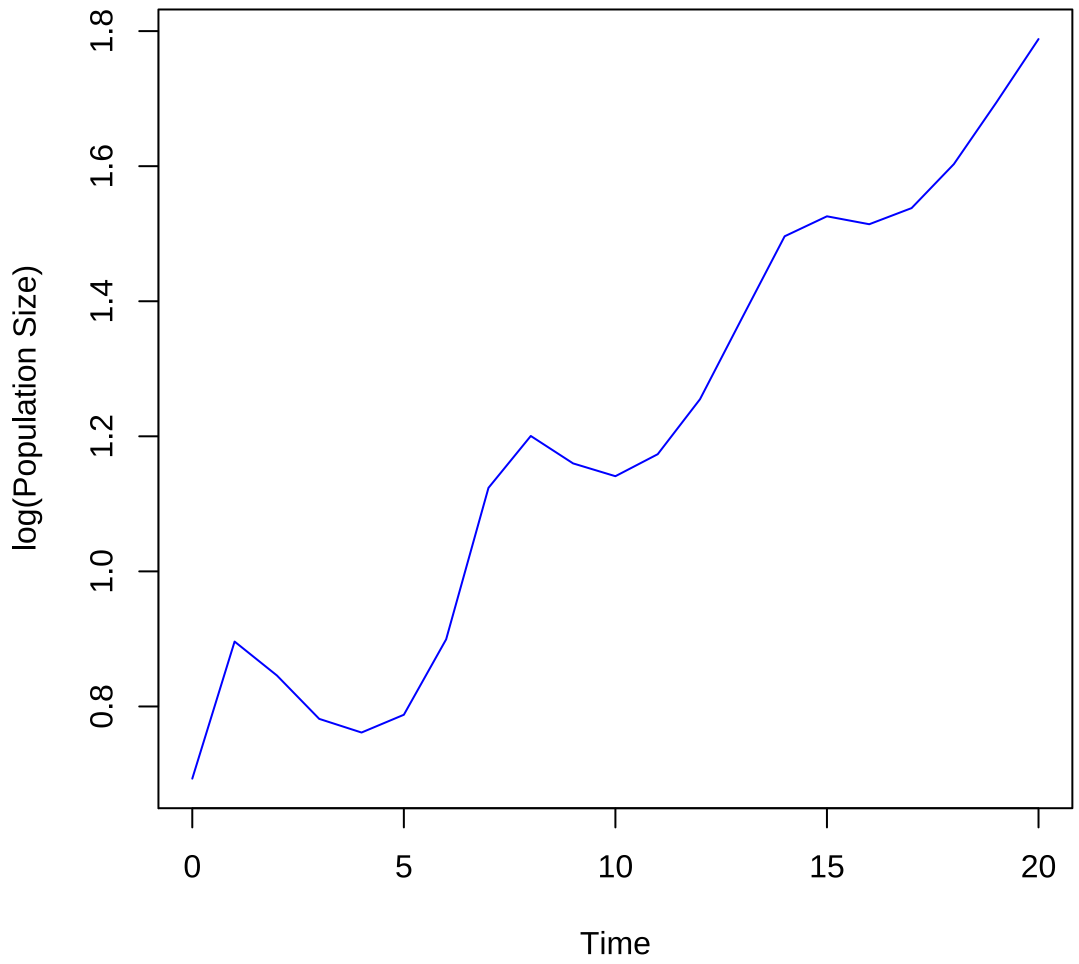
Solve this system to two equations and find that $n_1 = 4n_2$ is a solution

If there are four times the number of stage ones as there are stage twos, the population will grow exponentially

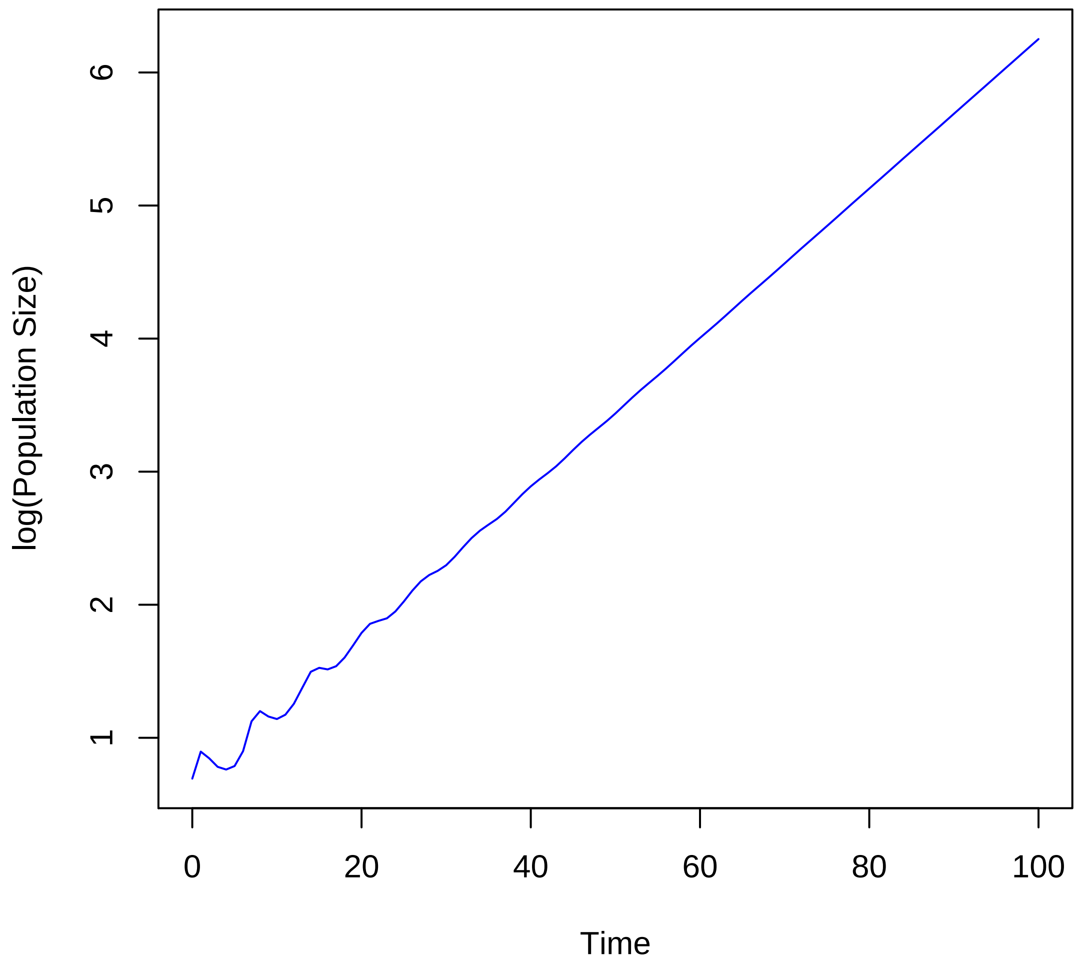
```
> no <- matrix(c(4,1),nrow=2)
> N <- NULL
> N <- cbind(N,no)
> pop <- no
> for (i in 1:10)
+ pop <- A%*%pop
+ N <- cbind(N,pop)
> plot(0:10,log(apply(N,2,sum)),type="l", col="blue", xlab="Time",
> ylab="Population Size")
> N[1,]/N[2,]
 [1] 4 4 4 4 4 4 4 4 4 4 4
```


8
7
6
5
4
3
2
log(Population Size)
0
2
4
6
8
10
Time

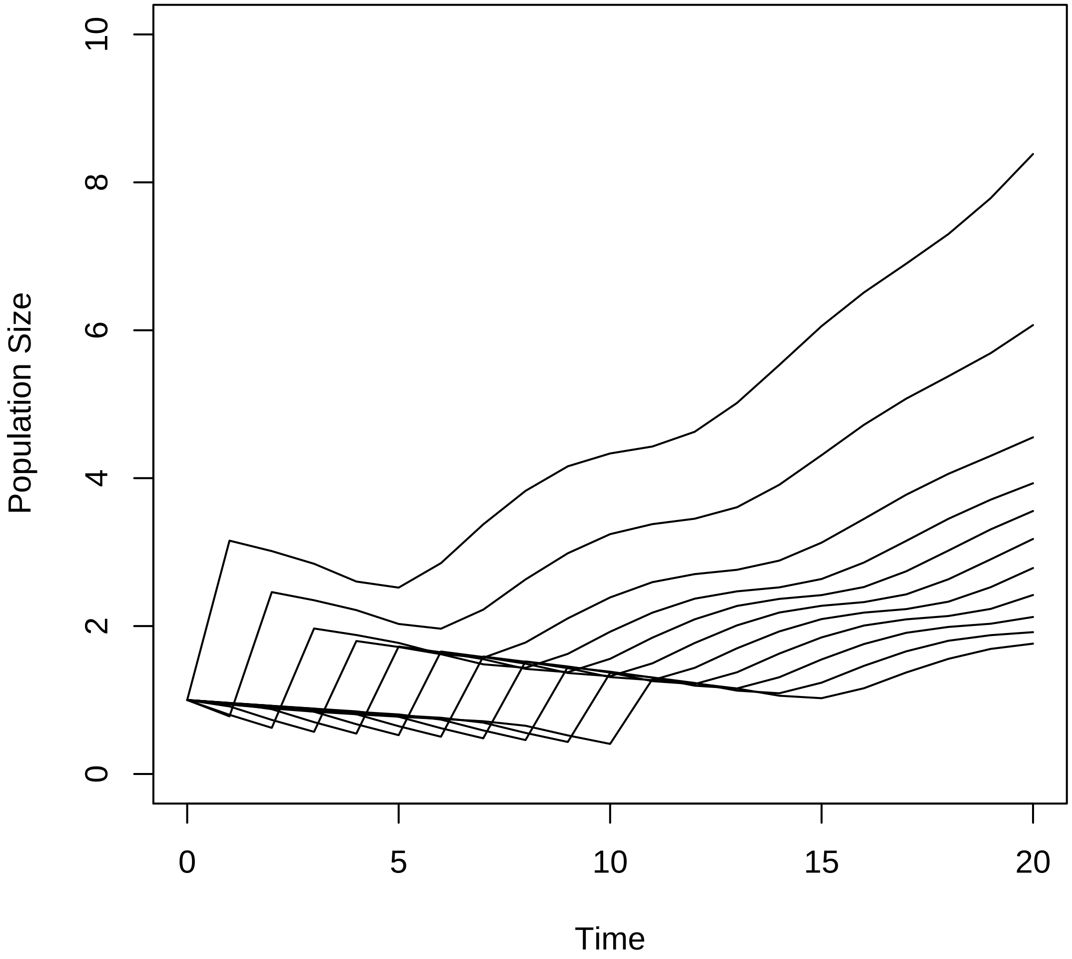
Projection (The Simplest Form of Analysis)



Here is a projection of a population that didn't start at its stable age distribution



Note that if we let it run long enough, the oscillations dampen and we see the straight line on semilog axes, indicating geometric increase


Population Size
0
2
4
6
8
10
0
5
10
15
20
Time

Some Plotting Notes...

Just for Grins, Here's how I did the plots:

First, I made a 7×7 Leslie matrix using the following commands (which you will see again repeatedly)

```
> px <- c(.92,.95,.95,.95,.95,.95) # some arbitrary survival probs.
> mx <- c(0,0,.05,.1,.25,.5,1)     # some arbitrary fertilities
> lx <- c(1,px)                    # a quick way to get lx from px
> lx <- cumprod(lx)
> lx
[1] 1.0000000 0.9200000 0.8740000 0.8303000 0.7887850 0.7493457 0.7118785
> sum(lx*mx)                       # the net reproduction number
[1] 1.410478

> k <- length(px)+1                # i.e., 7
> A <- matrix(0, nrow=k, ncol=k)   # make a 7x7 matrix of zeros
> A[row(A) == col(A)+1] <- px      # put px on the subdiag
> A[1,] <- mx                      # put mx on first row
```

I then typed the following into a text editor and saved it in my working directory

```
oscillate.plot <- function(tmax, A=A){
```

```
  no <- matrix(c(0,0,0,0,0,1,1),nrow=7)
  pop <- no
  N <- NULL
  N <- cbind(N,pop)
  for (i in 1:tmax){
    pop <- A%*%pop
    N <- cbind(N,pop)
  }
N
}
```

I then do the rest at the R command line

```
> source("oscillate.plot.r")
> N <- oscillate.plot(tmax=20)
> plot(0:20,log(apply(N,2,sum)),type="l",col="blue",xlab="Time",
+ ylab="log(Population Size)")
> N1 <- oscillate.plot(tmax=100)
> plot(0:100,log(apply(N1,2,sum)),type="l",col="blue",xlab="Time",
+ ylab="log(Population Size)")
```

Fun facts about Eigenvalues

1. A theorem from linear algebra (The Perron-Frobenius Theorem) guarantees that one eigenvalue will be positive and absolutely greater than all others. This is called the dominant eigenvalue of the projection matrix

2. The dominant eigenvalue of the projection matrix is the asymptotic growth rate of the population described by that matrix

3. The dominant eigenvalue of the projection matrix is the fitness measure of choice for age-structured populations

4. $\log(\lambda) = r$. That is, the logarithm of the dominant eigenvalue gives the annual rate of increase of the population

5. By calculating the eigenvalues of a projection matrix, you get lots of other important information

Left Eigenvectors of the Projection Matrix

In matrix algebra, multiplication is not commutative

$\mathbf{AB} \neq \mathbf{BA}$

Thus, the left eigenvector of a matrix is distinct from the right eigenvector

$$\mathbf{v}^* \mathbf{A} = \lambda \mathbf{v}^* \tag{16}$$

where the asterisk denotes the complex-conjugate transpose

If $\mathbf{\Lambda}$ is a matrix with the eigenvalues of the projection matrix along the diagonal and zeros elsewhere, we have

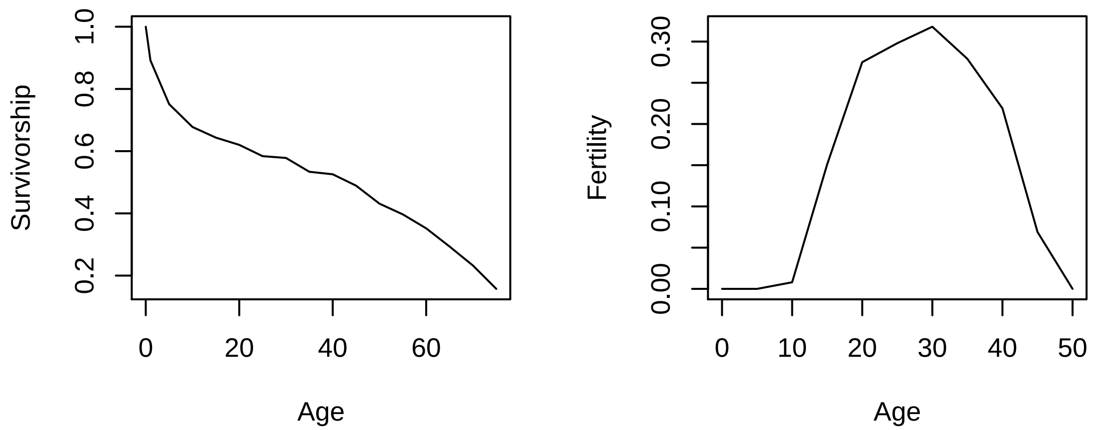
$$\begin{aligned} \mathbf{AU} &= \mathbf{U\Lambda} && (17) \\ \mathbf{\Lambda} &= \mathbf{U^{-1}AU} && (18) \\ \mathbf{U^{-1}A} &= \mathbf{\Lambda U}^{-1} && (19) \end{aligned}$$

Equation 19 is the matrix formula for an eigensystem (Equation 16), suggesting that the rows of $\mathbf{U^{-1}}$ must be the left eigenvectors of $\mathbf{A}$.

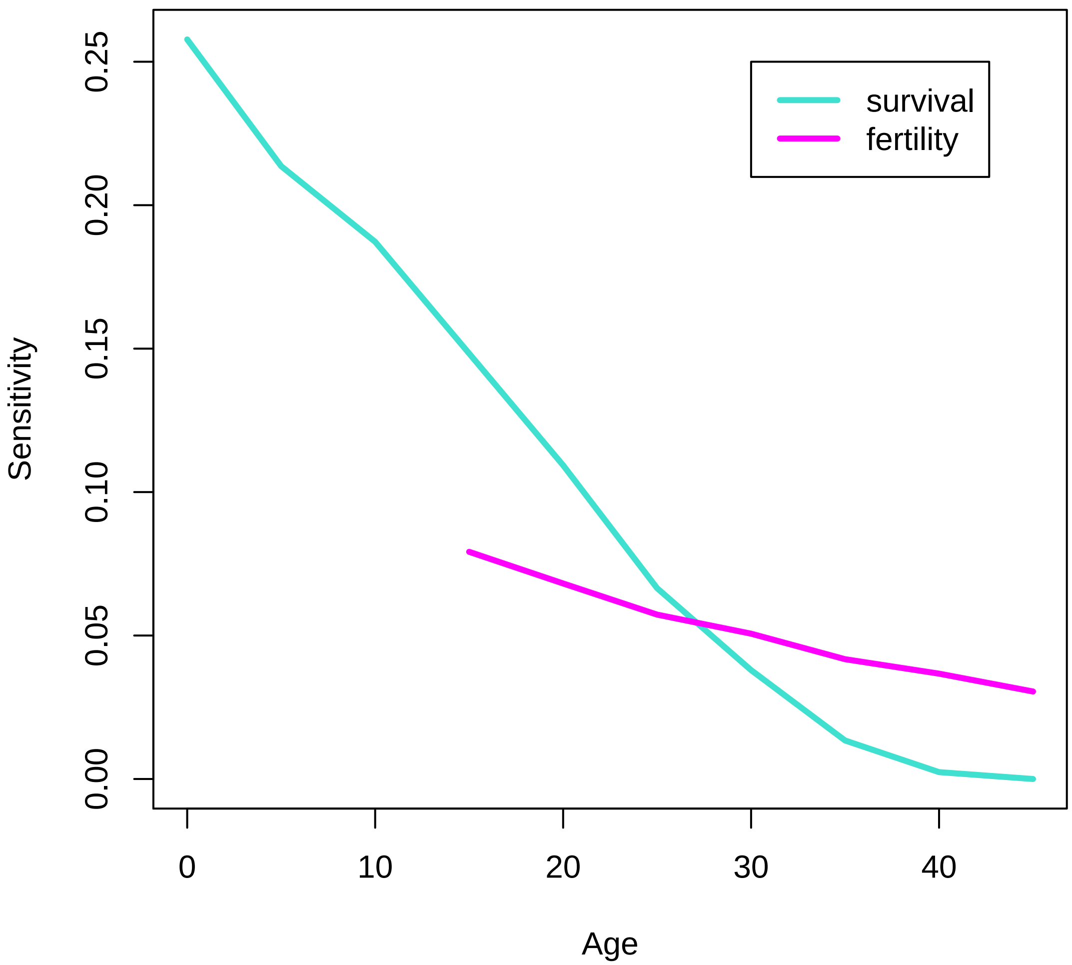
In R, we calculate the matrix of reproductive value vectors, $\mathbf{V}$, by using the the function `solve`, which inverts the matrix of right eigenvectors. While we need the complex parts for the calculations, the first left eigenvector will be made up only of real numbers. We therefore use the function `Re()` to extract only these real parts (the imaginary parts have a coefficient of 0).

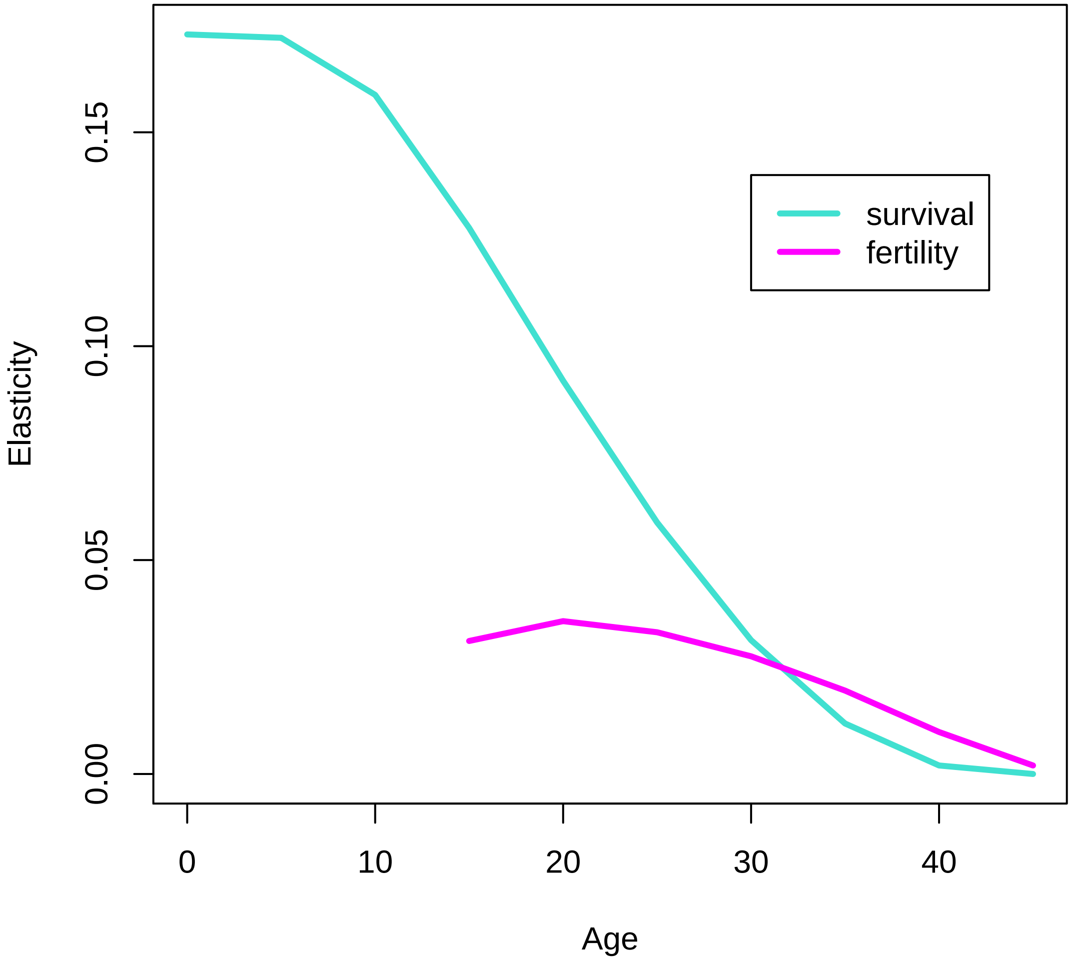
```
U <- ev$vectors
V <- solve(Conj(U))
v <- abs(Re(V[1,]))
plot(age,v/v[1],pch=16,col="red",type="b", xlab="Age",
     ylab="Reproductive Value")
```

Leslie Matrix Example: The Ache



$$
\mathbf{A} = \begin{bmatrix}
0.00 & 0.01 & 0.16 & 0.45 & 0.60 & 0.66 & 0.62 & 0.54 & 0.31 & 0.03 \\
0.75 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.90 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.95 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.96 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.94 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.99 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.92 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.98 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.93 & 0.00
\end{bmatrix}
$$


survival
fertility
Sensitivity
0.00
0.05
0.10
0.15
0.20
0.25
0
10
20
30
40
Age


0.00
0.05
0.10
0.15
Elasticity
0
10
20
30
40
Age
survival
fertility