EEB 200B: Lloyd-Smith PS 2

Gaurav Kandlikar

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Question 1A: Complete the final two columns of the life table.

Age, i	Fecundity, b_i	Number observed n_i	Yearly survival, s_i	Cumulative survival, l_i
0	0.6	50	0.3	1
1	1.5	15	0	0.3
2	0	0	-	0

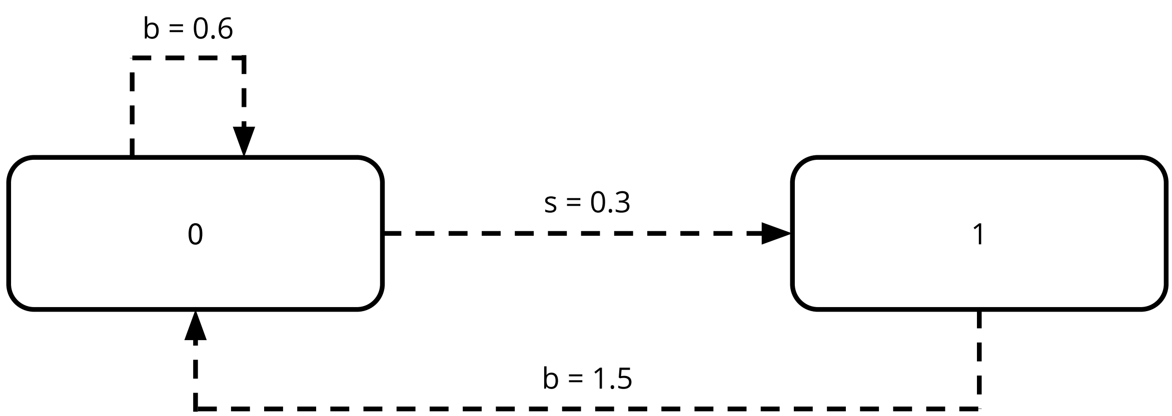
Question 1B: Compute R_0 for this population. Do you expect it to grow or shrink over time?

The basic reproductive rate R_0 can be calculated as

$$\sum_{n=1}^{i} l_i b_i = (1 * 0.6) + (0.3 * 1.5) = 1.05$$

This means that each new offspring is expected to leave behind, on average, 1.05 offsprings of its own- so the population is expected to grow.

Question 1C: Draw the life cycle graph for this population. How many age classes are needed?



Question 1D: Write down the Leslie matrix that describes the dynamics of the system.

$$\mathbf{L} = \begin{bmatrix} 0.6 & 1.5 \\ 0.3 & 0 \end{bmatrix}$$

Question 1E: Calculate the eigenvalues for this matrix by hand. Find the stable age distribution.

I will calculate the eigenvalues by using the matrix determinant approach:

$$\left[\begin{vmatrix} 0.6 & 1.5 \\ 0.3 & 0 \end{vmatrix} - \lambda \mathbf{I} \right] = 0$$

$$\left[\begin{vmatrix} 0.6 & 1.5 \\ 0.3 & 0 \end{vmatrix} - \lambda \begin{vmatrix} 1 & 0 \\ 0 & 1 \end{vmatrix} \right] = 0$$

$$\left[\begin{vmatrix} 0.6 & 1.5 \\ 0.3 & 0 \end{vmatrix} - \begin{vmatrix} \lambda & 0 \\ 0 & \lambda \end{vmatrix} \right] = 0$$

$$\left[\begin{vmatrix} (0.6-\lambda) & (1.5-0) \\ (0.3-0) & (0-\lambda) \end{vmatrix} \right] = 0$$

$$(0.6-\lambda) * (0-\lambda) - (0.3 * 1.5) = 0$$
$$\lambda^2 - 0.6\lambda - 0.45 = 0$$

Solving this quadratic equation for λ:

```
quad <- function(a,b,c) {
  to_return <- numeric(2)
  to_return[1] <- (-b+sqrt((b^2)-4*a*c))/(2*a)
  to_return[2] <- (-b-sqrt((b^2)-4*a*c))/(2*a)

  return(to_return)
}

lambdas <- quad(a = 1, b = -0.6, c = -0.45); lambdas
```

```
## [1]  1.035 -0.435
```

Here, $\lambda_1 = 1.035$ and $\lambda_2 =$ -0.435. The dominant eigenvalue 1.035 is the long term population growth rate; the eigenvector associated with this eigenvalue will describe the stable age distribution.

To calculate the eigenvectors associated with λ_1, we can use the equation $\mathbf{L}\bar{w}_1 = \lambda_1 \bar{w}_1$:

$$\begin{vmatrix} 0.6 & 1.5 \\ 0.3 & 0 \end{vmatrix} \begin{vmatrix} w_{11} \\ w_{12} \end{vmatrix} = \lambda \begin{vmatrix} w_{11} \\ w_{12} \end{vmatrix}$$

$$0.6(w_{11}) + 1.5(w_{12}) = 1.03w_{11}$$
$$0.3(w_{11}) + 0(w_{12}) = 1.03w_{12}$$
$$0.29(w_{11}) = w_{12}$$

```
c12 <- .29/(1+.29)
c11 <- 1-c12
c(c11, c12)
```

```
## [1] 0.775 0.225
```

Question 1F: Calculate the eigenvalues and eigenvectors for this matrix with `R`.

```
ll <- matrix(c(0.6, 1.5, 0.3, 0), byrow = T, ncol = 2); ll
```

```
##      [,1] [,2]
## [1,]  0.6  1.5
## [2,]  0.3  0.0
```

```
ll_eigen <- eigen(ll)

# Take a look at the eigenvalues
ll_eigen$values
```

```
## [1]  1.035 -0.435
```

```
dom_eigval <- ll_eigen$values[1]
# Normalize the first eigenvector to get stable age distrib
sad <- as.matrix(ll_eigen$vectors[,1]/(sum(ll_eigen$vectors[,1]))); sad
```

```
##       [,1]
## [1,] 0.775
## [2,] 0.225
```

Question 1G: Confirm the result in part F by showing that the dominant eigenvector and eigenvalue satisfy the eigenvalue equation $L\bar{v}_1 = \lambda_i \bar{v}_1$

```
round(ll %*% sad, 5) == round(dom_eigval * sad, 5)
```

```
##      [,1]
## [1,] TRUE
## [2,] TRUE
```

Question 1H: A survey of variegated wombats across UCLA campus in 2015 observed population sizes of 2000 and 1000. What are the expected population sizes by age for 2016?

```
p2015 <- matrix(c(2000, 1000), ncol = 1)

p2016 <- ll %*% p2015; p2016
```

```
##      [,1]
## [1,] 2700
## [2,]  600
```

Question 1I: If nothing else changes, by what proportion will population grow or shrink from the year 2067 to 2068? And from 2068 to 2069?

The population should proportionally grow as λ- here, $\lambda = 1.035$

Question 1J: The answer to part I is based on model prediction for long term growth of a population. Give three reasons why this prediction might not come true.

Long term dynamics may be influenced by a number of parameters...

1. The long term prediction assumes that both survival and fecundity estimates remain constant- we know that this is an unrealistic assumption, especially when the environment changing in a directional way, as it is now. Warmer temperatures, for instance, might drive down s_0 or other variables for a number of reasons. If a parameter to which the table is particularly sensitive changes even slightly, the long-term trajectory of the population might change drastically.

2. This model does not account for any low-probability events- for example, a freak landslide during a torrential El Nino strom might destroy the wombats' territory and lead to a population crash. The population could then enter some sort of extinction vortex. Similarly, a disease may spread through the population to drive it out.

3. Let's consider the sad reality that UCLA campus security is unlikely to allow population of marsupials roaming around in the Mildred Mathais gardens to boom!

Question 1K: Use `R` to simulate the dynamics of the population for 50 time steps. Plot the absolute number in each age class and the proportion in each age class. Confirm predictions for long term population growth rate and stable age distrubution.

```r
# First I will write a function to go through the generations
project <- function(ll, init, t){
  to_return <- matrix(0, nrow = 2, ncol = t+1)
  to_return[, 1] <- init

  for(time in 2:(t+1)) {
    to_return[, time] <- as.vector(ll %*%(to_return[,time-1]))
  }
  return(to_return)
}

generations <- 50

population_trajectory <- project(ll, init = c(2000, 1000), generations)

prop <- function(x) {return(c(x[1]/sum(x), x[2]/sum(x)))}
population_trajectory_props <- apply(population_trajectory, 2, prop)

par(mfrow = c(1,2))
matplot(t(population_trajectory), ylab = "N", xlab = "Time",
        main = "Population growth over time", lty = 1, lwd = 3, type = "l")
text(x = c(33, 40), y = c(10000, 1500), c("Age = 0", "Age = 1"))
matplot(t(population_trajectory_props), ylab = "N", xlab = "Time", xlim = c(-5, 50),
        main = "Population growth over time", lty = 1, lwd = 3, type = "l")
text(x = c(30, 30), y = c(0.7, 0.3), c("Age = 0", "Age = 1"))
abline(h = sad[1], col = "black", lty = 2, lwd = 2)
abline(h = sad[2], col = "red", lty = 2, lwd = 2)
```

Question 1L: Will an absolute in crease of 0.01 in b_0 or s_0 have a greater impact on the long term growth rate of wombats? What about a relative increase of 1% in those two parameters?

To get at this question, we need to calculate the Sensitivity and Elasticity matrices for this Leslie matrix. We can calculate the sensitivity matrix **S** as:

$$\mathbf{S} = \frac{\bar{v}_1 \bar{w}_1^T}{\bar{v}_1 \cdot \bar{w}_1}$$

Then, the elasticity matrix **E** can be calculated as

$$\mathbf{E} = \mathbf{S}\frac{L_{i,j}}{\lambda}$$

We still have not calculated the *left eigenvectors* for our Leslie Matrix. Let's do that first so that we have v_is:

```
left_eigens <- eigen(t(ll))
v1 <- left_eigens$vectors[,1]; v1
```

```
## [1] 0.568 0.823
```

```
# let's also make a vector W11- currently the first eigenvector is stored as 'sad'
w1 <- sad
```

With both of these components in hand, we can use the formulae above to calculate **S** and **E**:

```r
# Sensitivity matrix:
ss <- (v1 %*% t(w1))/as.numeric(v1%*%w1)
print("The Sensitivty matrix:"); ss
```

```
## [1] "The Sensitivty matrix:"

##       [,1]  [,2]
## [1,] 0.704 0.204
## [2,] 1.021 0.296
```

```r
ee <- ss*(ll/dom_eigval)
print("The Elasticity matrix:"); ee
```

```
## [1] "The Elasticity matrix:"

##       [,1]  [,2]
## [1,] 0.408 0.296
## [2,] 0.296 0.000
```

The Sensitivity matrix $\mathbf{S}$ above predicts that an absolute increase of 0.01 in S_0 will have a greater impact on λ than the same increase in b_0.

Conversely, the Elasticity matrix $\mathbf{E}$ predicts that a 1% increase in b_0 will impact λ more than the same proportional increase in s_0.

We can verify this prediction by manually perturbing the values of s_0 and b_0. First, let's verify for an absolue change of 0.01:

```r
# increase b0 by 0.01
ll_s1 <- matrix(c(0.6+0.01, 1.5, 0.3, 0), byrow = T, ncol = 2)
lambda_s1 <- eigen(ll_s1)$values[1]

# increase s0 by 0.01
ll_s2 <- matrix(c(0.6, 1.5, 0.3+0.01, 0), byrow = T, ncol = 2)
lambda_s2 <- eigen(ll_s2)$values[1]
```

Recall that above, we predicted that perturbing s_0 by 0.01 will have a greater impact on λ than increasing b_0 by the same amount. Let's verify the prediction:

```r
# Check that difference is higher when we change s0 by 0.1
# than when we change b0 by 0.1
lambda_s2 - dom_eigval > lambda_s1 - dom_eigval
```

```
## [1] TRUE
```

Now, let's verify for a proportional increase of 1%:

```r
# increase b0 by 1%
ll_e1 <- matrix(c(1.01*0.6, 1.5, 0.3, 0), byrow = T, ncol = 2)
lambda_e1 <- eigen(ll_e1)$values[1]

# increase s0 by 0.01
ll_e2 <- matrix(c(0.6, 1.5, 1.01*0.3, 0), byrow = T, ncol = 2)
lambda_e2 <- eigen(ll_e2)$values[1]
```

Recall that above, we predicted that perturbing b_0 by 1% will have a greater impact on λ than increasing s_0 by the same proportion. Let's verify the prediction:

```
# Check that difference is higher when we change b0 by 1%
# than when we change s0 by 1%
lambda_e1 - dom_eigval > lambda_e2 - dom_eigval
```

```
## [1] TRUE
```

Hurray!

Question 1M: What is weird about the Elasticity matrix? Play around with different values in the Leslie matrix and develop an intuitive explanation.

Let's recall the Elasticity matrix **E**:

```
print("The elasticity matrix:"); ee
```

```
## [1] "The elasticity matrix:"
```

```
##       [,1]  [,2]
## [1,] 0.408 0.296
## [2,] 0.296 0.000
```

One surprising feature of this matrix is that the elasticities are equal for b_1 and s_0. The best intuitive explanation I can come up for this phenomenon is that both of these parameters eventually determine the reproductive output of a new-born individual one year from birth. So, the same proportional increase in either of these parameters will impact the reproductive value, and therefore λ in the same way.

It will be fun to iterate over a range of s_0s and check whether this holds:

```
s0s <- seq(from = 0.5, to = 2.5, by = 0.1)
ratios_s0b1 <- numeric(length(s0s))
for(ii in 1:length(s0s)) {
  current_ll <- matrix(c(0.6, s0s[ii], 1.5, 0), byrow = T, ncol = 2)
  lambda <- eigen(current_ll)$values[1]
  w1 <- eigen(current_ll)$vectors[,1]
  v1 <- eigen(t(current_ll))$vectors[,1]
  ss <- (v1 %*% t(w1))/as.numeric(v1%*%w1)
  ee <- ss*(current_ll/lambda)
  ratios_s0b1[ii] <- ee[1,2]/ee[2,1]
}
ratios_s0b1
```

```
##  [1] 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
```

Sure enough, the ratio of the elasticies of s_0 and b_1 remains 1 for many values of s_0. To confirm, we can also iterate over a range of b_0s:

```r
b0s <- seq(from = 0.1, to = 1.5, by = 0.1)
ratios_s0b1 <- numeric(length(b0s))
for(ii in 1:length(b0s)) {
  current_ll <- matrix(c(b0s[ii], 0.3, 1.5, 0), byrow = T, ncol = 2)
  lambda <- eigen(current_ll)$values[1]
  w1 <- eigen(current_ll)$vectors[,1]
  v1 <- eigen(t(current_ll))$vectors[,1]
  ss <- (v1 %*% t(w1))/as.numeric(v1%*%w1)
  ee <- ss*(current_ll/lambda)
  ratios_s0b1[ii] <- ee[1,2]/ee[2,1]
}
ratios_s0b1
```

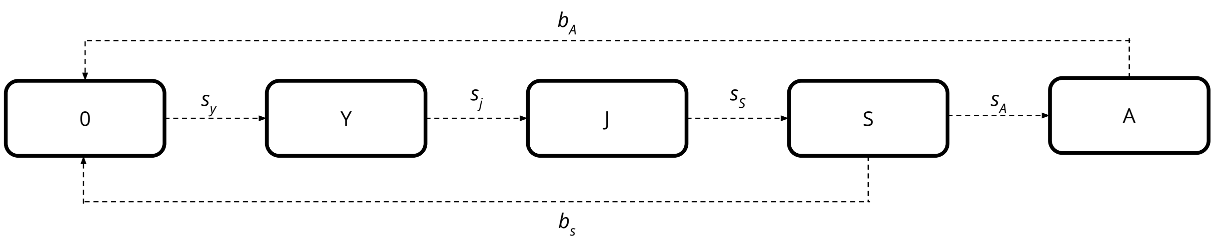
```
##  [1] 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
```

Woohoo!

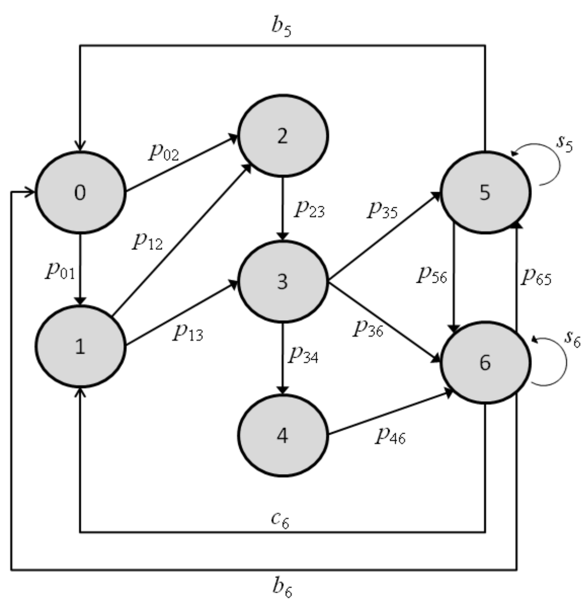
Question 2: Consider some more complex stage-structured populations.

Question 2A: Draw the life cycle graph corresponding to the Leslie matrix:

$$\mathbf{L} = \begin{bmatrix} 0 & 0 & b_s & b_A \\ S_Y & 0 & 0 & 0 \\ 0 & S_J & 0 & 0 \\ 0 & 0 & S_S & S_A \end{bmatrix}$$



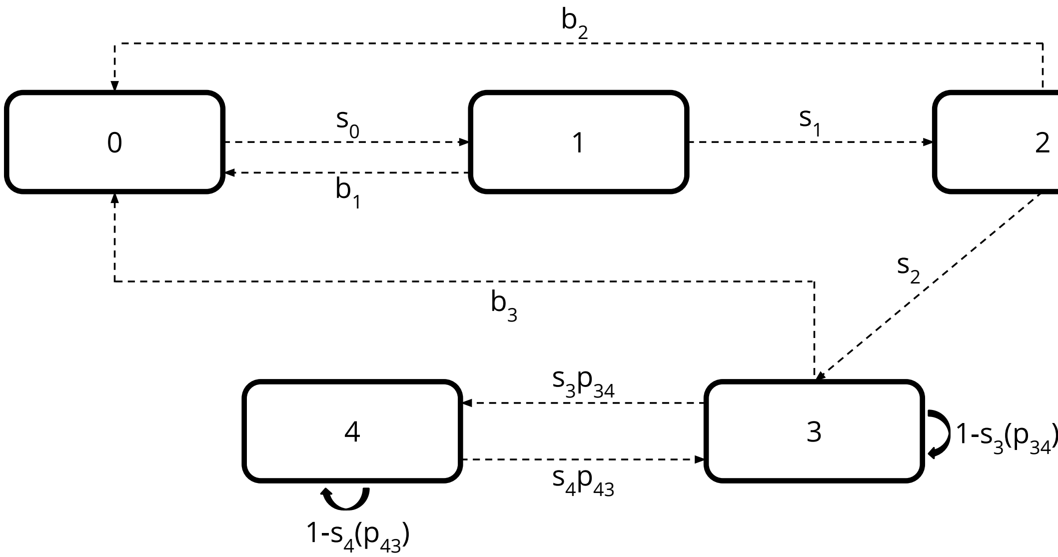
Question 2B: Write the Leslie matrix corresponding to this life cycle graph:



$$\mathbf{L} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & b_5 & b_6 \\ p_{01} & 0 & 0 & 0 & 0 & 0 & c_6 \\ p_{02} & p_{12} & 0 & 0 & 0 & 0 & 0 \\ 0 & p_{13} & p_{23} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & p_{34} & 0 & 0 & 0 \\ 0 & 0 & 0 & p_{35} & 0 & s_5 & p_{65} \\ 0 & 0 & 0 & p_{36} & p_{46} & p_{56} & s_6 \end{bmatrix}$$

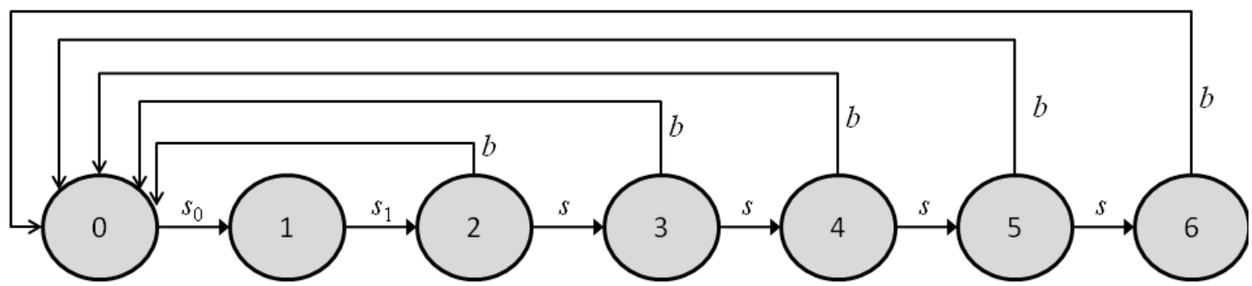
Question 2C: Draw the life cycle graph corresponding to this Leslies matrix. What is a biological explanation for the stage classes labeled 3 and 4?

$$\mathbf{L} = \begin{bmatrix} 0 & b_1 & b_2 & b_3 & 0 \\ s_0 & 0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 & 0 \\ 0 & 0 & s_2 & s_3(1-p_{34}) & s_4 p_{43} \\ 0 & 0 & 0 & s_3 p_{34} & s_4(1-p_{43}) \end{bmatrix}$$



Stage 3 might be an adult stage with peak fecundity that the organisms stay in for some time, before they leave that stage into a period of zero fecundity (Stage 4). Organisms in stage 4 may return to Stage 3. This might happen if individuals in Stage 3 give birth and are unable to give birth for some period of time immediately thereafter, but are able to give birth again after some time.

Question 2D: Write an age structured Leslie matrix corrresponding to this life cycle. And write a stage-structured matrix with as few groups as possible. Is the stage structured matrix an exact match for this life cycle?



$$\mathbf{L} = \begin{bmatrix} 0 & 0 & b & b & b & b & b \\ S_0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S & 0 \end{bmatrix}$$

The stage structured work can be done with a 3X3 Leslie matrix:

$$\mathbf{L} = \begin{bmatrix} 0 & 0 & b & b \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S & S \end{bmatrix}$$

The full matrix tells us that this members of this species live for no longer than 6 years- this information is lost when we make a Lefkovitch(!) matrix.