Solutions to exercise sheet 1

Sex, Ageing and Foraging Theory

1 Leslie Matrix

a. The Leslie matrix is given by

$$\mathbf{L} = \begin{pmatrix} 0.456 & 1.68 & 3.40 & 3.40 & 3.40 & 3.40 \\ 0.52 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.60 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.71 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.71 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.71 & 0 \end{pmatrix}, \quad (1)$$

where the first row (effective fecundities) is obtained by multiplying age-specific fecundities m_a by the survival probability of newborns, p_0.

b. By iterating the $\mathbf{L}$ matrix in R,

```
tmax=10 # Maximum number of years for which to iterate
n=c(1000,0,0,0,0,0) # Initial population vector
ps=c(1000,rep(0,tmax-1)) # vector with initial pop. size and zeroes
# for the others (to be filled during iteration).

for(i in 2:tmax) # For tmax-1 years,
{
    n = L %*% n # Iterate the matrix
    ps[i] = sum(n) # Compute the size of the population
}
```

we obtain the plot presented in Figure 1. The population of wild boars experiences exponential growth.

c. Using R,

```
eig=eigen(L)
# Growth rate (lambda) is the leading eigenvalue of L
lambda = eig$values[1]
# Stable age distribution (u) is the leading eigenvector scaled
# such that its elements sum to 1.
u = eig$vectors[,1]/sum( eig$vectors[,1] )
```

This yields

$$\begin{aligned} \lambda &= 1.648 \\ \mathbf{u} &= (0.662, 0.209, 0.076, 0.033, 0.014, 0.006) \end{aligned} \quad (2)$$

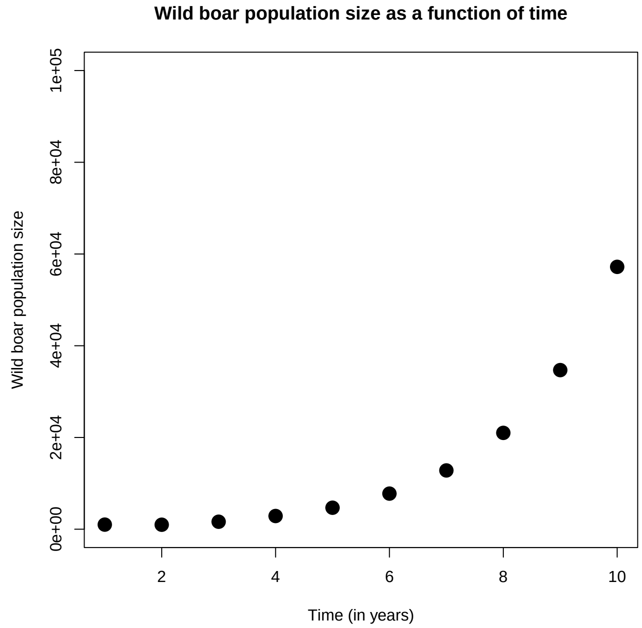

Figure 1: Population size as a function of time

d. To compute R_0, we need to build a vector of survival probabilities to age a (l_a), multiply it by age-specific fecundities (m_a) and sum the elements of the resulting vector,

```
# Age specific fecundities
m=c(0.57, 2.1, 4.25, 4.25, 4.25, 4.25)
p0=0.8 # Survival probability of newborns
# Age-specific survival probabilities
psurv=c(0.52,0.60,0.71,0.71,0.71)

l=c(p0, rep(0,5)) #  Survival to age 'a' vector
for(i in 1:5)
{
    l[i+1] = l[i]*psurv[i]
}
R0 = sum( l * m ) # Compute R0
```

This yields $R_0 = 4.058$. This tells us that each individual leaves on average 4.058 successful offspring, indicating that the population will grow indefinitely.

2 Individual-based simulations

We observe a good match between Leslie matrix predictions and simulation results (Figure 2).

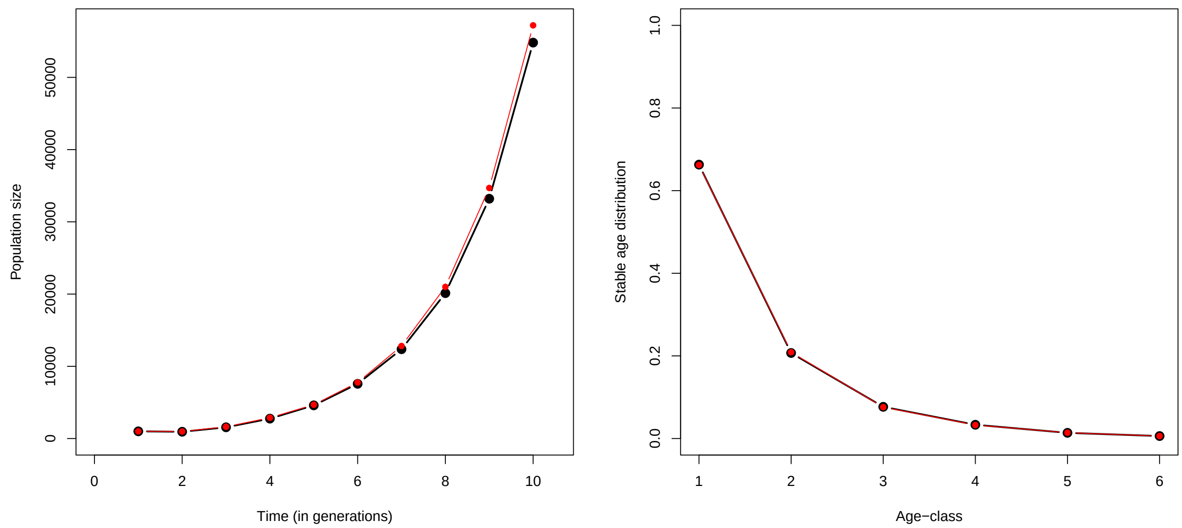

Figure 2: Population size as a function of time (right-hand panel) and stable age distribution (left-hand panel). Red dots and lines depict predictions from the Leslie matrix, black dots and line depict simulation results.

3 Density regulation

a. To modify the simulation program, we need to add a parameter to the function DYN() and modify how P0 is calculated in the time loop. For the parameter we have on line 14

```
DYN=function(n0, n_a, Fec, P, p0, gamma, nt, nmax).
```

Further down the code (line 36), we modify the code as follows

```
P0 = p0/(1+gamma*length(A)) # Length(A) corresponds to population size.
```

The population first grows and then stabilises at an equilibrium size due to density-regulation. The larger the population, the harder it becomes for newborns to survive to maturity, which limits population growth (Figure 3).

b. The Leslie matrix $\mathbf{L}_{\text{reg}}(N_t)$ associated with this new model depends on population size at time t. We obtain it by modifying the first row of the previous matrix (eq. 1), yielding

$$\mathbf{L}_{\text{reg}}(N_t) = \begin{pmatrix} \frac{0.456}{1+\gamma N_t} & \frac{1.68}{1+\gamma N_t} & \frac{3.40}{1+\gamma N_t} & \frac{3.40}{1+\gamma N_t} & \frac{3.40}{1+\gamma N_t} & \frac{3.40}{1+\gamma N_t} \\ 0.52 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.60 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.71 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.71 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.71 & 0 \end{pmatrix}, \tag{3}$$

where

$$N_t = \sum_{i=1}^{6} n_{i,t} \tag{4}$$

denotes population size at time t. To iterate this matrix numerically, we have to update it with the new population size at each generation. Using R,

```
# Leslie matrix
Lreg = matrix(0, nrow = 6, ncol = 6) # This will be our Leslie matrix.
p0=0.8 # density-independent establishment probability
gam=0.0005 # density-dependence
tmax=100

fec= c( 0.57, 2.10, 4.25, 4.25, 4.25, 4.25) # Fecundities
surv=c(0.52, 0.60, 0.71, 0.71, 0.71) # Survival probabilities
nv=c(1000,0,0,0,0,0) # Initial population

P0=p0/(1+gam*sum(nv))  # Density-dependent survival probability
for(i in 1:ncol(L)) # For each column,
{
    Lreg[1,i] = fec[i]*P0 # Add the effective fecundity to the first row
    if(i < ncol(Lreg))
    {
        Lreg[i+1,i] = surv[i] # And survival to the corresponding row
    }
}

results=matrix(0,ncol=6,nrow=tmax) # Matrix of results
results[1,]=nv # First row of results is the initial population
for(i in 2:tmax) # For tmax-1 generations,
{
    nv = Lreg %*% nv # Iterate the matrix
    results[i,]=nv # Store the results
    P0=p0/(1+gam*sum(nv))  # Calculate the new survival probability
    Lreg[1,] = fec*P0 # Modify the matrix
}
```

The population size is predicted to increase and reach a plateau, much like what we observed in our simulation.

c. To calculate R_0, we use the same approach as in exercise 1 (question d), but we need to include the fact that the survival probability of newborns changes with time.

```
la[1] = 1 # Vector of cumulated survival probabilities
# given maturity has been reached
for(i in 2:6)
{
    la[i]=la[i-1]*surv[i-1]
}

R0=rep(0,tmax) # Vector that will contain R0 values
vp0 = p0/(1 + gam*rowSums(results)) # p0(Nt) for each time point.
for(i in 1:tmax)
{
    # Calculate R0 for each time point
    R0[i] = vp0[i]*sum( fec*la  )
}
```

We obtain the plot shown in Figure 4. R_0 decreases through time and reaches $R_0 = 1$, indicating that individuals produce on average one successful offspring in their life so that the population remains stable (i.e. equilibrium is reached).

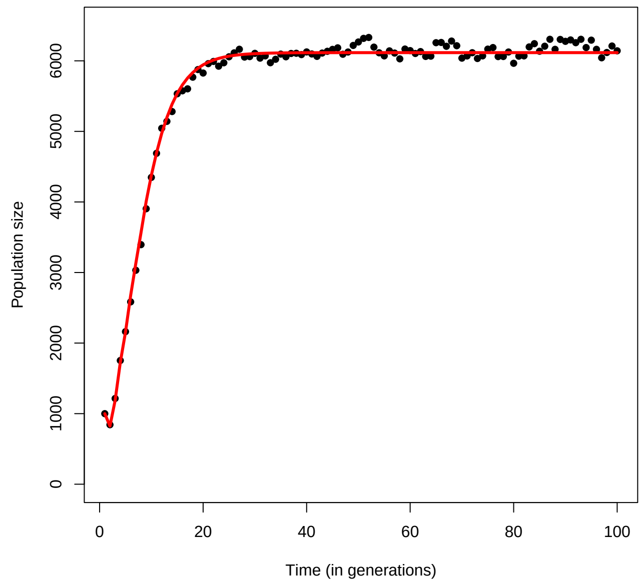

Figure 3: Population size as a function of time in a simulation (black dots), and as predicted by the Leslie matrix (red line).

4 Selection

a. Selection is stabilising around the trait value $x = 2$, as fecundity is maximised for this value. The parameter ω controls the width of the peak around $x = 2$, that is how steeply fecundity drops when x moves away from the optimum. Thus, it controls the strength of selection on trait x.

b. Since the mutant is rare, we may neglect its effect on density-dependent survival. Thus, its lifetime reproductive success is given by

$$R_0(y, x) = \frac{m_1(y)}{m_1(x)}. \tag{5}$$

Setting $y = x$ thus yields

$$R_0(x, x) = \frac{m_1(x)}{m_1(x)} = 1. \tag{6}$$

c. The selection gradient acting on x is given by

$$s(x) = \left.\frac{\partial R_0(y, x)}{\partial y}\right|_{y=x} = 2\omega(2 - x), \tag{7}$$

and the singular strategy x^* is therefore

$$s(x^*) = 0 \Leftrightarrow x^* = 2. \tag{8}$$

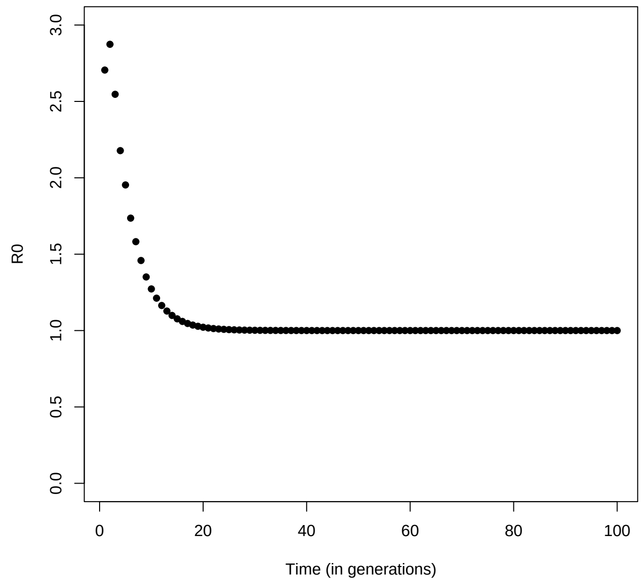

Figure 4: Population size as a function of time

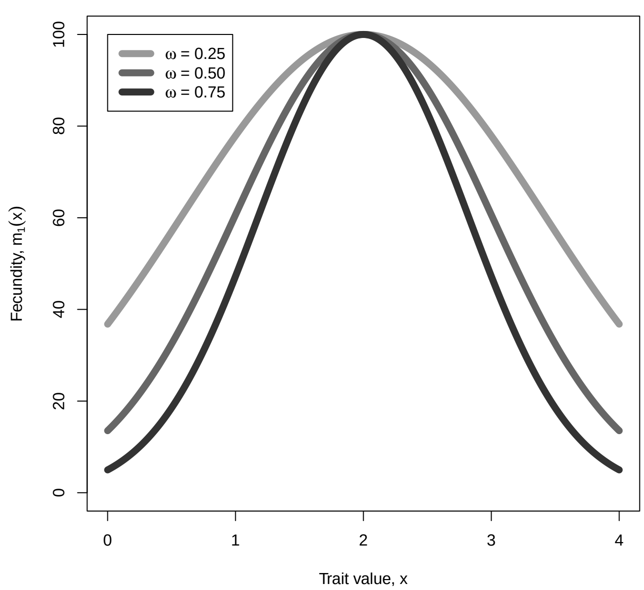

Figure 5: Fecundity $m_1(x)$ as a function of x for $\omega = 0.25, 0.50, 0.75$ (shades of grey).