

Solutions to exercise sheet 1

Sex, Ageing and Foraging Theory

1 Population dynamics

- a. To incorporate age-specific survival probabilities and fecundities, we modify the simulation program as follows.

First, we modify the function **IND_ACT()** so that it now receives the survival probability of the individual (**psuv**) and the probability of survival of newborn offspring from age 0 to age 1 (**p0**) as separate arguments, and uses them at the right moments. Specifically, we add parameter **p0** on line 3,

```
IND_ACT = function(age, fec, psuv, p0){
```

and change the survival probability of survival of newborns in the core of the function on line 6,

```
no_new_n1 = rbinom(1, size = no_offspring, prob = p0)
```

Second, we modify the arguments specified to function **DYN()** on line 26, so that it now takes three arguments in addition to initial population size **n0** and time of the simulation **FinalYear**:

- A vector **Fec** that gives fecundities at age 1 to 6,
- A second vector **Psuv** that gives survival probabilities at age 1 to 6,
- A real number **p0** between 0 and 1 that gives the survival probability of newborns from age 0 to age 1.

Thus, line 26 now reads:

```
DYN = function(n0, FinalYear, Fec, Psuv, p0){
```

Finally, we modify the loop over individuals so that the function **IND_ACT()** now receives the age-specific fecundity and survival probability corresponding to the individual, and the survival probability of newborns as specified on line 3 (see above). Namely, with the age of the i^{th} individual given by **Population[i]**, the fecundity of that individual is given by **Fec[Population[i]]** and its survival probability is given by **Psuv[Population[i]]**, so that line 36 now reads

```
NextPopulation = c(NextPopulation, IND_ACT(age = Population[i], fec = Fec[  
Population[i] ], psuv = Psuv[ Population[i] ], p0=p0))
```

- b. The stochastic dynamics of the wild boar population over ten years are plotted in red in Figure 1, which shows that the population rapidly increases in size. This implies that each wild boar more than replaces itself over its lifetime (i.e. brings more than one offspring to maturity over its lifetime on average), so that $R_0 > 1$.

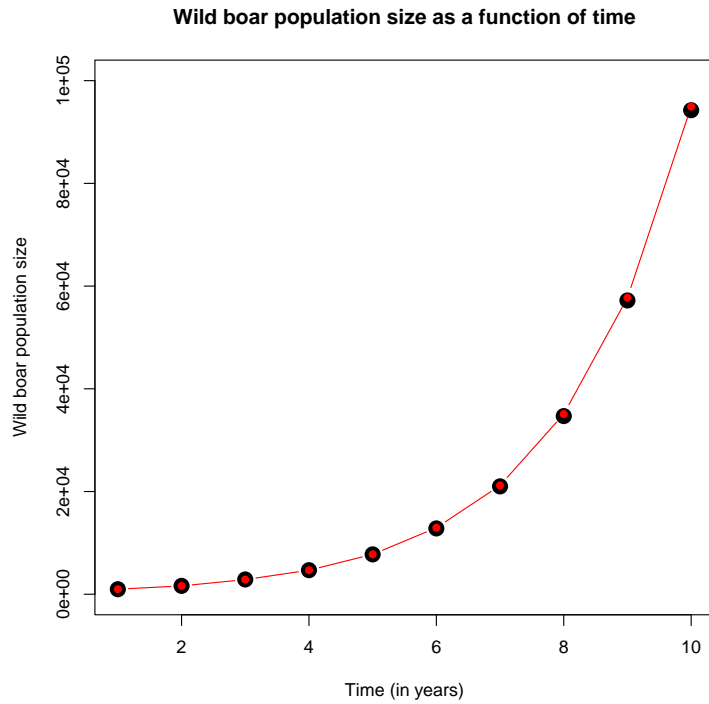


Figure 1: Population dynamics of the wild boar population as a function of time. The prediction from the Leslie matrix is shown in black, and the simulation results are shown in red.

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

```
L = matrix(0, nrow = 6, ncol = 6) # This will be our Leslie matrix, for now it is
  filled with zeroes.
p0=0.8 # Establishment probability
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

for(i in 1:ncol(L)) # For each column,
{
  L[1,i] = fec[i]*p0 # Add the effective fecundity to the first row
  if(i < ncol(L))
  {
    L[i+1,i] = surv[i] # And survival to the corresponding row
  }
}
```

```

tmax=10 ### Number of timesteps for which we wish to predict population dynamics
n=c(1000,0,0,0,0,0) # Initial population vector
ps=rep(0,tmax) # Vector in which we will record population size
for(i in 1:tmax) # For 10 years,
{
  n = L %*% n # Iterate the matrix
  ps[i] = sum(n) # Compute the size of the population
}

```

we obtain a vector that contains predicted average population size over time. Figure 1 shows how the prediction compares to the dynamics of the simulated population. We observe a good match between the two, suggesting that the Leslie matrix can accurately predict the dynamics of the wild boar population in this case.

2 Density regulation

- a. To modify the simulation program, we copy and paste the function **DYN()** below and name this new function **DYN_REG()** to differentiate it from the previous one. We modify the new function as follows. First, we modify the parameters given to **DYN_REG()** to reflect the new assumption of our model, i.e. we replace parameter **p0** with two new parameters **c** and **gam**, so that line 93 in the solution Rscript reads

```
DYN_REG = function(n0, FinalYear, Fec, Psuv, c, gam){
```

Second, we recalculate the survival probability of newborns each year, because it depends on population size. To do so, we add a line in the loop over years that computes the value **p0** on line 101,

```
p0=c/(1+gam*length(Population))
```

Finally, we modify the newborn survival probability given to function **IND_ACT()** in line 105,

```
NextPopulation = c(NextPopulation, IND_ACT(age = Population[i], fec = Fec[
Population[i] ], psuv = Psuv[ Population[i] ], p0=p0))
```

By running this simulation program for the parameters given in the exercise sheet, we observe that 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. The simulated population is shown in red in Figure 2.

- 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

$$\mathbf{L}_{\text{reg}}(N_t) = \begin{pmatrix} \frac{0.456}{1 + \gamma N_t} & \frac{1.68}{1 + \gamma N_t} & \frac{3.40}{1 + \gamma N_t} & \frac{3.40}{1 + \gamma N_t} & \frac{3.40}{1 + \gamma N_t} & \frac{3.40}{1 + \gamma N_t} \\ 0.52 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.60 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.71 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.71 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.71 & 0 \end{pmatrix}, \quad (2)$$

where

$$N_t = \sum_{i=1}^6 n_{i,t} \quad (3)$$

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.
c=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, 0) # Survival probabilities
nv=c(1000,0,0,0,0,0) # Initial population

p0=c/(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=c/(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 (black line in Fig. 2).

3 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

$$R_0(y, x) = \frac{m_1(y)}{m_1(x)}. \quad (4)$$

Setting $y = x$ thus yields

$$R_0(x, x) = \frac{m_1(x)}{m_1(x)} = 1. \quad (5)$$

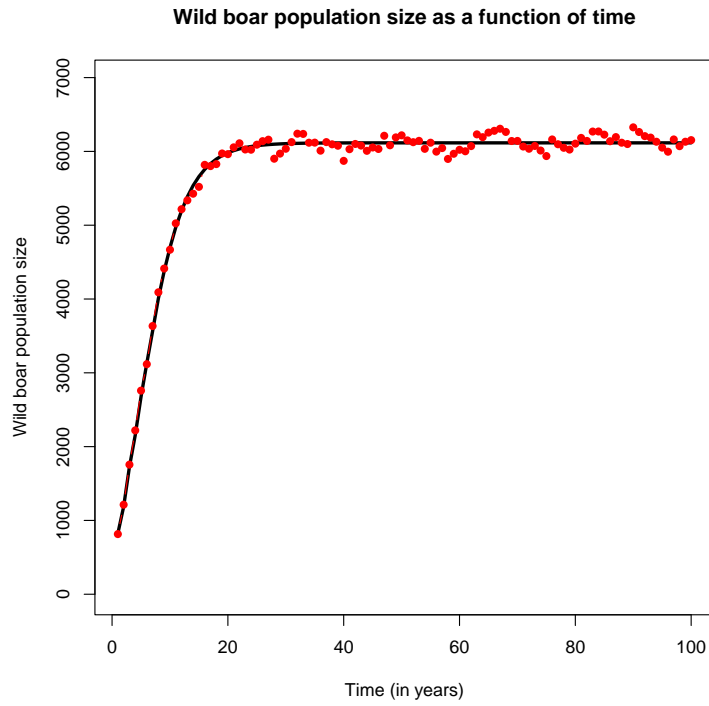


Figure 2: Population size as a function of time in a simulation (in red), and as predicted by the Leslie matrix (black line).

c. The selection gradient acting on x is given by

$$s(x) = \left. \frac{\partial R_0(y, x)}{\partial y} \right|_{y=x} = 2\omega(2 - x), \quad (6)$$

and the singular strategy x^* is therefore

$$s(x^*) = 0 \Leftrightarrow x^* = 2. \quad (7)$$

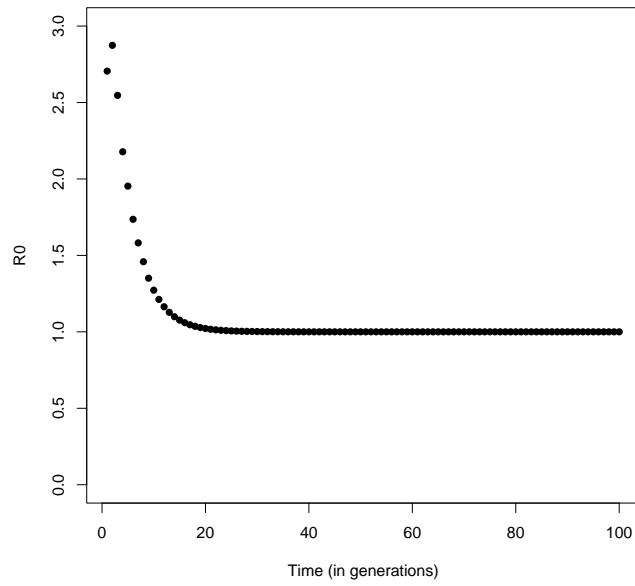


Figure 3: Population size as a function of time

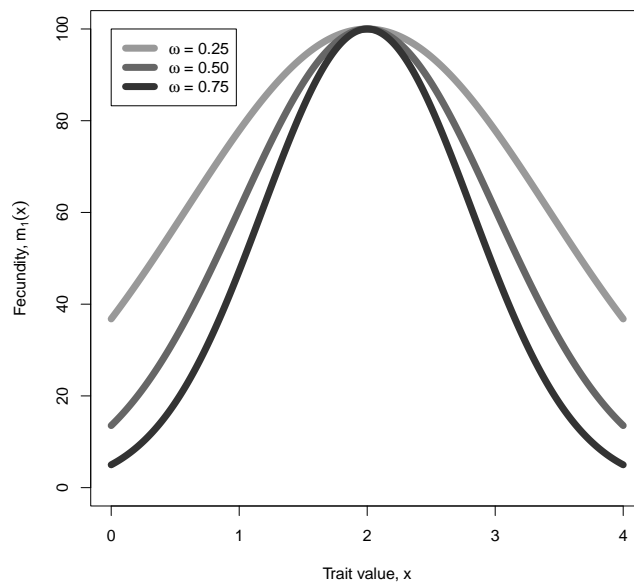


Figure 4: Fecundity $m_1(x)$ as a function of x for $\omega = 0.25, 0.50, 0.75$ (shades of grey).