INSA 4-BIM
TP3 : Leslie models

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Abstract

This tutorial will focus on a particular subset of matrix models in population dynamics, known as Leslie models. We will mainly study two models and use the commands provided in the `popbio` R package.

This tutorial will be used to grade your coding ability in R. Please answer the question in an R script and e-mail this script to the teacher's address. I should be able to run this script smoothly.

You can download an R script to fill up at `https://tinyurl.com/srbpt7n`
This document without solutions can be downloaded at `https://tinyurl.com/qsroj5l`
This document including solutions may be found at `https://tinyurl.com/urakoof`

1 Dynamics of a Squirrel population

The life table of a cohort of the eastern gray squirrel (*Sciurus carolinensis*) enables to provide the parameter set for a population dynamics model shown in table 1

Age class (years)	1	2	3	4	5	6	7
P_i	0.46	0.77	0.65	0.67	0.64	0.88	0
f_i	0.32	0.57	0.57	0.57	0.57	0.57	0.57

Table 1: Parameter set for the eastern gray squirrel population dynamics

Exercise 1

In R, store the parameter set in table 1 in a variable named `parameters` the following way

```
parameters <- matrix(data = c(0.46, 0.77, 0.65, 0.67, 0.64, 0.88,
    0, 0.32, 0.57, 0.57, 0.57, 0.57, 0.57, 0.57), ncol = 2, byrow = FALSE,
    dimnames = list(NULL, c("survival", "fertility")))
```

In R, Write three functions with the following names and description:

- `fertility.m(parset)`: takes a parameter set table such as `parameters` with two columns (first is survival, second is fertility) and an unknown row number and returns the *fertility* part of the Leslie matrix. The size of the returned matrix should match the number of rows in the `parset` argument.

- `survival.m(parset)`: takes a parameter set table such as `parameters` with two columns (first is survival, second is fertility) and an unknown row number and returns the *survival* part of the Leslie matrix. The size of the returned matrix should match the number of rows in the `parset` argument. Pay attention to the last survival probability: a non-zero rate should be allowed and provide a survival probability indicating that individuals might survive in the last age class.

- `leslie.m(parset)`: takes a parameter set table such as `parameters` with two columns (first is survival, second is fertility) and an unknown row number and returns the full Leslie matrix. The size of the returned matrix should match the number of rows in the `parset` argument.

For instance, the following commands should provide the following results

```
fertility.m(parset = parameters[1:3, ])

##      [,1] [,2] [,3]
## [1,] 0.32 0.57 0.57
## [2,] 0.00 0.00 0.00
## [3,] 0.00 0.00 0.00

survival.m(parset = parameters[1:3, ])

##      [,1] [,2] [,3]
## [1,] 0.00 0.00 0.00
## [2,] 0.46 0.00 0.00
## [3,] 0.00 0.77 0.65

leslie.m(parset = parameters[1:3, ])

##      [,1] [,2] [,3]
## [1,] 0.32 0.57 0.57
## [2,] 0.46 0.00 0.00
## [3,] 0.00 0.77 0.65
```

Exercise 2

We now store the Leslie matrix for the squirrel model into a variable named `l.squirrels` with the following command

```
l.squirrels <- leslie.m(parset = parameters)
```

Load (possibly also install before loading) the `diagram` R package. Use the `plotmat` function in this package to plot a diagram of the model.

Exercise 3

Write a generic R function named `timetable` that computes and returns the age structure for a given time range. `timetable` must use the following arguments

- `x0` the initial number of individuals in each class of the model

- `l.mat` the Leslie matrix of the model

- `tmax` the number of time steps to be computed.

The returned matrix should contain `tmax`+ 1 lines (lines are timesteps) and as many columns as there are age classes in the model. For instance, the following command should return the following results:

```
timetable(x0 = c(10, 0, 0), l.mat = leslie.m(parameters[1:3,
    ]), tmax = 5)

##             [,1]     [,2]     [,3]
## [1,] 10.000000 0.000000 0.000000
## [2,]  3.200000 4.600000 0.000000
## [3,]  3.646000 1.472000 3.542000
## [4,]  4.024700 1.677160 3.435740
## [5,]  4.202257 1.851362 3.524644
## [6,]  4.409046 1.933038 3.716567
```
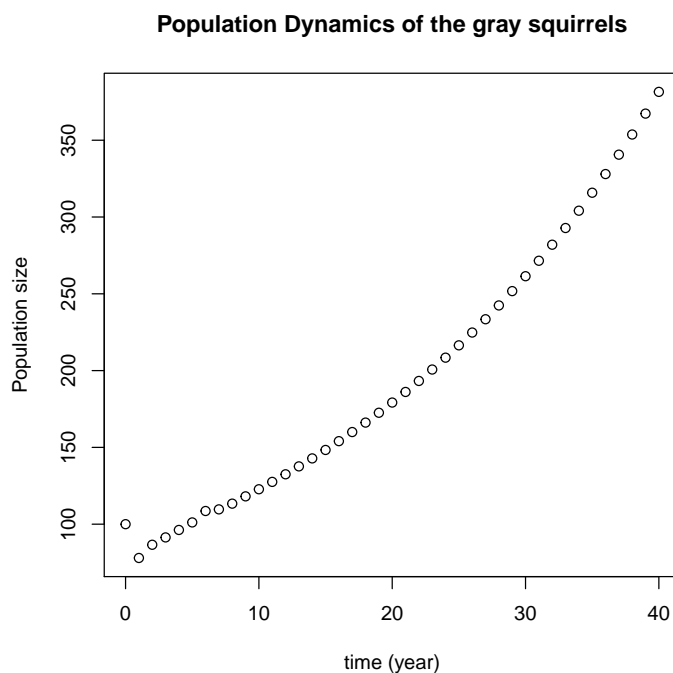
Exercise 4

We provide the following R function that computes the total population size at each time step from a time table returned by the `timetable` function.

```r
popsize <- function(tt) {
    return(apply(tt, MARGIN = 1, FUN = sum))
}
```

Use your `timetable` function to compute the time table of grey squirrels for `tmax`=40 timesteps and an initial population of 100 young squirrels of age class 1, store the result in a variable named `tt.squirrels` then compute and plot the total population size with time. You should produce the following figure:

Population Dynamics of the gray squirrels

Exercise 5

We provide the following commands to compute the growth rate from the population time table in `tt.squirrels`.

```r
growthrate <- function(ps) {
    tmax <- length(ps)
    return(ps[-1]/ps[-tmax])   # The growth rate is the ratio of consecutive pop sizes
}
ps.squirrels <- popsize(tt.squirrels)
gr.squirrels <- growthrate(ps.squirrels)
```

Plot the growth rate for the 25 first time steps and check that it converges to the leading eigenvalue of the Leslie matrix. You should produce the following figure:

Growth rates of the gray squirrel population
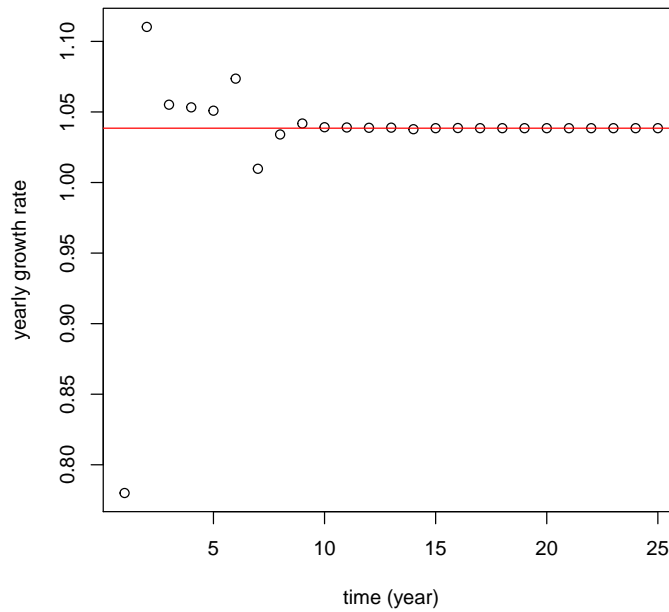
How long does it take for the growth rate to converge to the leading eigenvalue up to the 8th decimal?

Exercise 6

Write an R function called `plot.timetable(tt)` that takes as input a timetable `tt` as returned by your `timetable` function and plots the size of each age class as a function of time on the same figure. The following command should produce the following figure, note that sets of different colors are easily obtained with the `rainbow()` command:

```
plot.timetable(tt = timetable(x0 = c(10, 0, 0), l.mat = leslie.m(parameters[0:3,
    ]), tmax = 25))
```
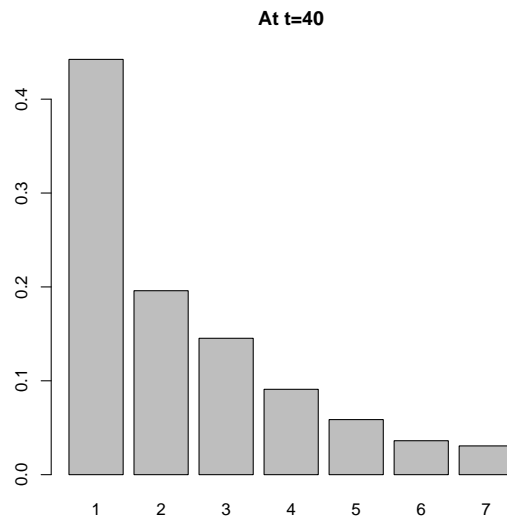
Population dynamics of each class
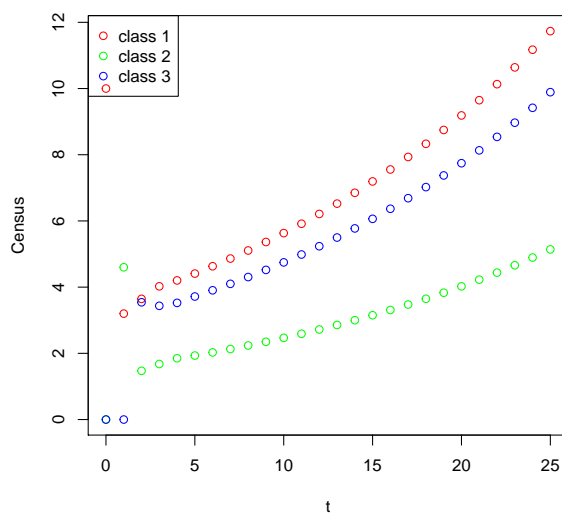
Exercise 7

The following command plots the age-structure of the population at $t = 40$. Generate a figure where this plot is shown next to the theoretical stable age-structure predicted by the Leslie matrix.

```
agedistribution50 <- tt.squirrels[41, ]/sum(tt.squirrels[41,
    ])
barplot(agedistribution50, names.arg = 1:7, main = "At t=40")
```


At t=40

Exercise 8

The `popbio` R package is a library of R functions dedicated to the analysis of matrix-based population models. Mainly, the `pop.projection` function enables to quickly replicate the analyses we have done so far.

Load the `popbio` R package (you might need to install it) and replicate the analyses on population dynamics, growth rate and age structure using the `pop.projection` function.

Exercise 9

What is the result of the following command

```
eigen.analysis(A = l.squirrels)
```

Especially, explain what are the reproductive values, sensitivity, elasticity and the damping ratio. Compute the reproductive values and the damping ratio without the help of the `popbio` library.

Exercise 10

The net reproductive rate R_0 is defined as the expected number of offspring of a single individual during its life. Compute the net reproductive rate in this model, does it match the result of the following command?

```
net.reproductive.rate(A = l.squirrels)
```

Explain why and propose a fixed command.

Exercise 11

The generation time is defined as the time needed for the population to increase by the net reproductive rate. Compute the generation time of the population. Does your computation match the result of the following command? Explain.

```
generation.time(A = l.squirrels)
```

Exercise 12

In order to stop the rapid development of the squirrel population, it is decided to catch squirrels between 1 and 2 years old. The survival probability from the first year to the second year reduced from 0.46 to 0.36.

What kind of analysis could this decision be based on? Can you make a prediction about the effect on the population growth rate without computing the eigenvalues of the new Leslie matrix? Check your predictions.

2   Dynamics of a salmon population

The life cycle of a salmon is shown on figure 1. Adult salmons feed in the ocean but travel to freshwater streams to breed and die after reproduction. Young salmons leave their birthplace between the first and the second year to reach the ocean and grow for one to several years before they become adult and ready for their final trip to the freshwater stream where they were born. Any barrier on their migration trip (dam on the river, overfishing...) may endanger the populations. Population studies are thus needed to predict the impact of any decision affecting the environment of the species.
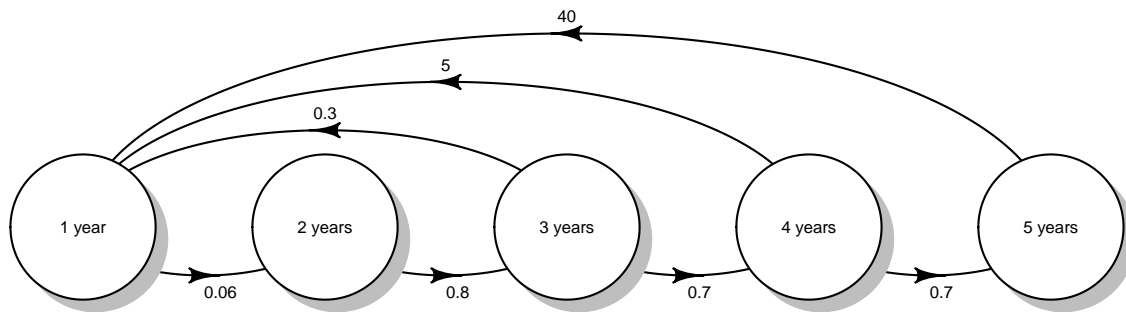

Figure 1: Life cycle of a salmon

Exercise 13

Inspired by the code in exercise 1] write the R commands to put the parameter set for the salmon in a variable named `parsalmon` and use your `leslie.m` function to put the corresponding Leslie matrix in a variable named `l.salmon`.

Exercise 14

With the help of the appropriate function in the `popbio` package, find the stable age structure, reproductive values and asymptotic growth rate of the population.

Exercise 15

In the following cases, predict the effect of the decision on the species' long term survival. Check your prediction by computing the asymptotic growth rate with a modified Leslie matrix.

1. An electricity company wants to build a dam on the river. This dam would not affect the upward migration of the adults but could severely impair the survival rate of the downward migrating one-year old salmons. How-much could the survival of the young salmons be reduced without threatening the species' long term survival?

2. The electricity company managed to corrupt local politicians and to build a dam that reduce the survival of the young salmons by $\frac{1}{3}$: the survival probabililty of the young salmons is now 0.04 and the salmon populations are starting to decline. A local nature protection association propose to create a fishing-free area, enabling to increase the number of newborns. What minimal relative increase of the number of newborn would you recommand?

3. In spite of all the efforts of the nature protection association, the average number of offsprings was only increased by 20%. The fertility parameters of the third, fourth and fifth years salmons are now 0.36, 6, 48. Confronted with protests of the inhabitants, the electricity company decides to conduct a green washing campaign. They propose to protect the salmon's breeding area and modify the dam. They claim that these changes will increase the survival probability of the young salmons. What minimum relative increase should be achieved to ensure the populations' persistance?

Exercise 16

The electricity company successfully managed to increase the survival probability of young salmons by 25%. The survival probability of the young salmons is now 0.05. The salmon population starts to increase again and reaches the steady age structure. Unfortunately, a chemical company sitting next to the river is destroyed by a fire and all the yound salmons are killed. This kind of drama had previously happened in other places and the local fishermen said it took several decades for the populationn to recover the steady age structure. Explain why this has taken so long.

We propose a way to model this feeling with the following procedure: explain how this works.

```
parsalmon4 <- matrix(data = c(0.05, 0.8, 0.7, 0.7, 0, 0, 0, 0.36,
    6, 48), ncol = 2, byrow = FALSE, dimnames = list(NULL, c("survival",
    "fertility")))
l.salmon4 <- leslie.m(parset = parsalmon4)
easa4 <- eigen.analysis(l.salmon4)

steadystage <- easa4[["stable.stage"]]/sum(easa4[["stable.stage"]])

init <- 500 * steadystage
init[1] <- 0

pp <- pop.projection(A = l.salmon4, n = init, iterations = 100)


steadystage <- easa4[["stable.stage"]]/sum(easa4[["stable.stage"]])
adjustment <- function(N) {
    freq <- N/sum(N)
    pval <- replicate(100, chisq.test(rmultinom(1, 500, prob = freq),
        p = steadystage)$p.value)
    x <- sum(pval > 0.5)
    return(binom.test(x, n = 100, alternative = "less")$p.value)
}
par(mfrow = c(1, 2))
plot(pp[["pop.changes"]], xlab = "Time elapsed since the catastrophy",
    ylab = "Population growth rate")
abline(h = easa4[["lambda1"]], col = "red")

plot(apply(pp[["stage.vectors"]], MARGIN = 2, FUN = adjustment),
    xlab = "Time elapsed since the catastrophy", ylab = "Feeling that recovery has happened")
```