1 R code

1. Given a vector of animal activity levels (`activity`) and a vector of air temperatures in degrees C (`temp`), write R code to calculate the mean of animal activity when air temperatures are above freezing.

```
mean(activity[temp>0])
```

2. Consider a frog population consisting of tadpoles, juveniles, and adults. (We will only count females.) Each year every adult female has 25 female offspring that survive to the tadpole stage. 10% of the tadpoles survive to become juveniles. 25% of the juveniles survive to become adults. 50% of the adults survive until the next year.

   Write down R code to construct a matrix and calculate the state of the (female) population after 5 years if it starts from 5 (female) tadpoles (zero juveniles, zero adults).

```
M <- matrix(c(0,0,25,
              0.1,0,0,
              0,0.25,0.5),byrow=TRUE,nrow=3)
X <- c(5,0,0)
for (i in 1:5) {
  X <- M %*% X
}
```

   or:

```
X <- c(5,0,0)
library(expm)
(M %^% 5 ) %*% X

##          [,1]
## [1,] 0.78125
## [2,] 0.15625
## [3,] 0.09375
```

3. Consider the discrete-time Ricker model,

$$x(t+1) = x(t)e^{r(1-x(t)/k)}$$

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where $r = 0.3$ and $k = 1$ are constants and $x(0) = 0.1$. Write no more than five lines of R code (semicolons are not allowed) to calculate and print out $x(10)$.

Use for loop

```
r <- 0.3
k <- 1
x <- 0.1
for(i in 1:10) x <- x * exp(r*(1-(x/k)))
print(x)

## [1] 0.7273
```

4. Suppose you would like to numerically solve the following continuous-time model,

$$\frac{dx}{dt} = rx(1 - e^{-bx}) \tag{1}$$

Write an R function that computes $\frac{dx}{dt}$, which can be passed to the `ode` function in the `deSolve` package. Also define an example of state and parameter vectors that you will need to use this function with `ode`.

```
state <- c(x = 1)
pars <- c(r = 0.4, b = 0.5)
gfun <- function(time, state, pars) {
    with(c(as.list(state), as.list(pars)), {
        dx <- r*x*(1-exp(-b*x))
        return(list(x = dx))
    })
}
```

Going a little further (this wouldn't be on the exam),

```
library(deSolve)
times <- seq(0, 10, length = 100)
soln <- ode(state, times, gfun, pars)
plot(soln)
```

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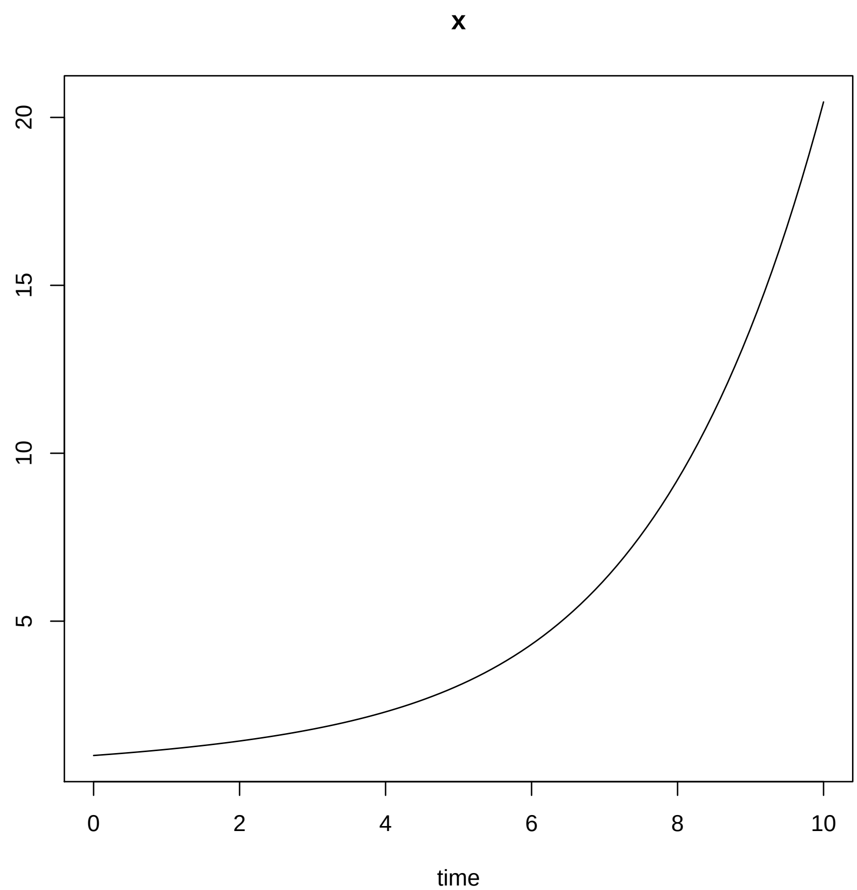

2 Delta method

A tree falls in a forest and makes a sound, 'because' many woodland animals are around to hear it. The average distance, d of animals from the tree is $E(d) = 10$m (in metres) with a variance of $Var(d) = 10\text{m}^2$. If the intensity, I, of the sound in each animal's ear follows the inverse-square law $I = \frac{1}{d^2}$, find an approximation to the mean and variance of the intensities of the sound in the animals' ears throughout the forest. Recall that the delta method equations are: $E(f(X)) \approx f(E(X)) + \frac{1}{2}f''(E(X))Var(X)$ and $Var(f(X)) \approx f'(E(X))^2 Var(X)$.

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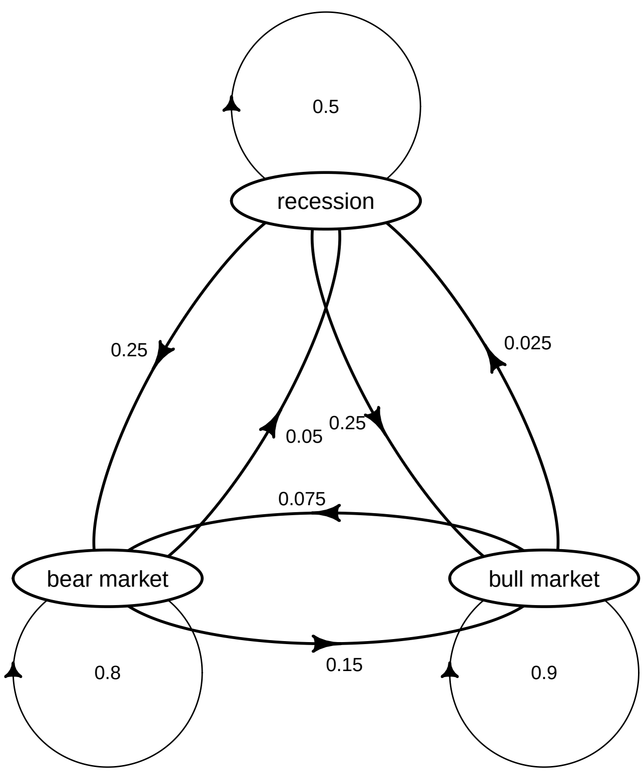
The intensity is a function, $f(d) = 1/d^2$, of distance. Its first and second derivatives are $f'(d) = -2/d^3$ and $f''(d) = 6/d^4$. At the mean these quantities are $f(10) = 1/10^2$, $f'(10) = -2/10^3$ and $f''(10) = 6/10^4$. Therefore the approximations are $E(I) \approx 10^{-2} + 3 \times 10^{-3}$ and $Var(I) \approx 4 \times 10{-}5$

3 Markov models

Given the following stock market diagram (from `http://en.wikipedia.org/wiki/Markov_chain`):



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Is this a regular or absorbing Markov chain, or neither? Write down two ways, one using a `for` loop and the other using the `eigen` function, to find the long-term fraction of the time the economy will spend in recession.

regular

```
dn <- c("bull market","bear market","recession")
(M <- matrix(c(0.9,0.075,0.025,
               0.15,0.8,0.05,
               0.25,0.25,0.5),nrow=3,
             dimnames=list(dn,dn)))

##             bull market bear market recession
## bull market       0.900        0.15      0.25
## bear market       0.075        0.80      0.25
## recession         0.025        0.05      0.50

X <- c(1,0,0)
for (i in 1:100) X <- M %*% X
X

##                [,1]
## bull market 0.6250
## bear market 0.3125
## recession   0.0625

e1 <- Re(eigen(M)$vectors[,1])
e1/sum(e1)

## [1] 0.6250 0.3125 0.0625
```

Consider a Markov model represented by the following transition diagram:

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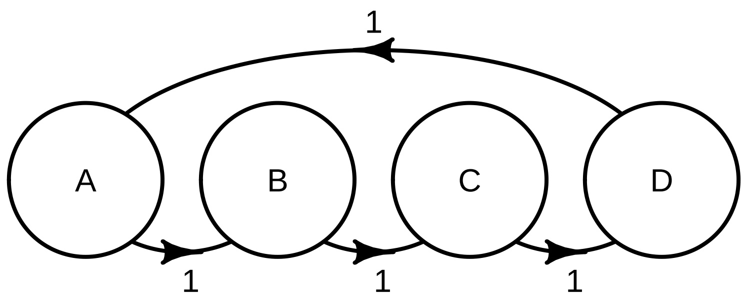

Is the corresponding transition matrix absorbing, regular, or neither? How do you know? Write down a transition matrix for the model (you can use 1.0 for all of the non-zero entries). If both of these properties are not true, how could you change the transition matrix to make one of them true?

The transition matrix M is

$$\begin{pmatrix} 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix}.$$

M^2 is

$$\begin{pmatrix} 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \end{pmatrix}$$

and M^3 is

$$\begin{pmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \end{pmatrix}$$

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and M^4 is

$$\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}$$

and M^5 is

$$\begin{pmatrix} 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix}$$

which is the same as the original M. Therefore, all of these matrices are the only possible matrix powers. None of them have all positive entries and so the chain is therefore not regular. The chain is also not absorbing however, because the transition matrix cannot be put into a form where the lower right block is an identity matrix and the upper right block is all zeros. In other words, we cannot change the order of the states as they appear in the transition matrix so that we obtain such a form.

4 Equilibria and stability of 1-D continuous-time systems

Consider a population growing according to the continuous logistic equation, $dN/dt = rN(1-N/K)$. Find the equilibria and characterize their stability. Now suppose that the non-zero equilibrium is stable, but add constant-effort harvesting (i.e., subtract a term eN from the population growth rate). Find the new equilibria. Is there more than one non-zero equilibrium? Under what conditions is it/are they stable? What is the yield (eN) when the system is at equilibrium? What harvesting effort e gives the maximum yield?

Logistic equation: equilibria 0 and K, non-zero equilibrium is unstable and zero equilibrium is stable if $r > 0$. With harvesting we have $-rX^2/K + (r-e)X = 0$. $X^* = 0$ or $X^* = K(1-e/r)$. Stable if $r - e - 2rX^*/K < 0$, or $X^* > K/2(1-e/r)$: always true. Yield $= eX^* = eK(1-e/r)$; maximum when $e = r/2$.

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Consider an SI (susceptible-infected) model of an epidemic,

$$\begin{aligned} \frac{dS}{dt} &= -\beta SI \\ \frac{dI}{dt} &= \beta SI \end{aligned} \tag{2}$$

where β is an infection rate. Because $N = S + I$ is a constant of motion (i.e. $\frac{dN}{dt} = 0$), this is in fact a one dimensional model,

$$\frac{dS}{dt} = -\beta S(N - S) \tag{3}$$

Assuming that $N > 0$, find the fixed points of this model and evaluate its stability.
$\frac{dS}{dt} = 0 = -\beta S(N - S)$. If $\beta = 0$, every S is a fixed point. If $\beta \neq 0$, $S = 0, N$ are fixed points. The derivative of $\frac{dS}{dt}$ with respect to S is $-\beta(N - 2S)$. Therefore the general stability condition is $0 < -\beta(N-2S)$, which reduces to $N < 2S$. Therefore $S = 0$ is always unstable, given that N is negative, and $S = N$ is always stable given that N is positive.

5 Equilibria and stability of 1-D discrete-time systems

$$x(t+1) = f(x(t)) \tag{4}$$

where $f(x) = x - a + e^{-bx}$ and $a, b > 0$.
A fixed point obeys $f(x) = x$, so $-a + e^{-bx} = 0$ and $e^{-bx} = a$, which leads to $-bx = \log(a)$ and there $x = -\frac{\log(a)}{b}$ is a fixed point. The derivative of $f(x)$ is $f'(x) = 1 - be^{-bx}$. At the fixed point this derivative becomes $1-ab$. Therefore the stability condition is $-1 < 1-ab < 1$ or $2 > ab > 0$.

Now assume that $f(x) = x - a + \frac{1}{1+x}$ and analyze stability.
The fixed point condition is $a = \frac{1}{1+x}$, which leads to $x = \frac{1-a}{a}$. The derivative of $f(x)$ is $f'(x) = 1 - \frac{1}{(1+x)^2}$, which at the fixed point is $f'(x) = 1 - \frac{1}{(1+\frac{1-a}{a})^2}$, which leads to $f'(x) = 1 - a^2$. Therefore the stability criterion is $-1 < 1 - a^2 < 1$, or $2 > a^2 > 0$. Because it must be that $a^2 > 0$, this criterion reduces to $a^2 < 2$, or $-\sqrt{2} < a < \sqrt{2}$.

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6 Equilibria and stability of 2-D continuous systems

Consider the SIR epidemic model with equal birth and death rates:

$$\frac{dS}{dt} = \mu N - \beta S I - \mu S$$
$$\frac{dI}{dt} = \beta S I - (\mu + \gamma) I$$
$$\frac{dR}{dt} = \gamma I - \mu R$$

If $N = S + I + R$, prove that the population size is constant (i.e., $dN/dt = 0$). If this is true, then we don't need to keep track of R. Find the equilibria of the system for S and I alone (treating N as a constant) and evaluate their stability. When can an epidemic take off?

Prove $dN/dt = 0$ by adding $dS/dt + dI/dt + dR/dt$ and showing the sum is zero.

Equilibria: from I equation, $I^* = 0$ or $S^* = (\mu+\gamma)/\beta$. Substituting in to S equation gives $S^* = N$ or

$$\mu(N - S^*) = \beta S^* I^*$$
$$\mu(N - (\mu+\gamma)/\beta) = (\mu+\gamma) I^*$$
$$\mu/(\mu+\gamma) N - \mu/\beta = I^*$$

Jacobian:

$$\begin{pmatrix} -\beta I^* - \mu & -\beta S^* \\ \beta I^* & \beta S^* - (\mu+\gamma) \end{pmatrix}$$

At $S^* = N$ equilibrium:

$$\begin{pmatrix} -\mu & -\beta N \\ 0 & \beta N - (\mu+\gamma) \end{pmatrix}$$

$T = \beta N - 2\mu - \gamma$, positive if $\beta N/(2\mu+\gamma) > 1$. $\Delta = -\mu(\beta N - (\mu+\gamma))$, < 0 if $\beta N/(\mu+\gamma) > 1$ ($\Delta > T$, so Δ is always > 0 if $T > 0$). Alternatively, we could just look at the matrix and see that the eigenvalues are $-\mu$, $\beta N - (\mu+\gamma) \ldots$)

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At positive equilibrium:

$$\begin{pmatrix} -\beta\mu N/(\mu+\gamma)+\mu & -(\mu+\gamma) \\ \beta\mu N/(\mu+\gamma)-\mu & 0 \end{pmatrix}$$

$T = -\beta\mu N/(\mu+\gamma)+\mu$, < 0 if $\beta N/(\mu+\gamma) > 1$.

$\Delta = \beta\mu N - \mu(\mu+\gamma)$, > 0 if $\beta N/(\mu+\gamma) > 1$.

Stable if $\beta N/(\mu+\gamma) > 1$.

Consider following special case of the Lotka-Volterra competition model:

$$\frac{dx}{dt} = rx\left(1-\frac{x}{K}-\alpha y\right)$$
$$\frac{dy}{dt} = ry\left(1-\frac{y}{K}\right)$$

Find a fixed point (other than $\{x=0, y=0\}$) and evaluate its stability. Assume all parameters are positive. Hint: recall that the eigenvalues of an upper-triangular matrix are on the diagonal.
The y equation is logistic and doesn't depend on x, so $y = K$ is an equilibrium. Subbing into the x equation gives $x = K(1-\alpha K)$. The Jaccobian is,

$$\begin{pmatrix} r(1-(2x/K)-\alpha y) & -r\alpha x \\ 0 & r(1-(2y/K)) \end{pmatrix}$$

which at the fixed point is,

$$\begin{pmatrix} r(1-2+2\alpha K-\alpha K) & -r\alpha K(1-\alpha K) \\ 0 & -r \end{pmatrix}$$

which reduces to,

$$\begin{pmatrix} r(\alpha K-1) & -r\alpha K(1-\alpha K) \\ 0 & -r \end{pmatrix}$$

Therefore, the two eigenvalues are $r(\alpha K-1)$ and $-r$. The second one is always negative so the stability condition is not violated by the second eigenvalue. The first one is negative whenever $\alpha K < 1$. Therefore, we have stability whenever $\alpha < \frac{1}{K}$.

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7 Equilibria and stability of 2-D discrete-time systems

Find a non-zero fixed point and analyze its stability under the following model. Hint: you will only require the determinant condition.

$$\begin{aligned} N(t+1) &= RN(t)e^{-aP(t)} \\ P(t+1) &= aN(t)(1-e^{-aP(t)}) \end{aligned} \tag{5}$$

For the N equation we have the conditions for the P coordinate of a fixed point,

$$1 = Re^{-aP} \tag{6}$$

which reduces to,

$$P = \frac{\log(R)}{a} \tag{7}$$

The P equation gives the coordinate for N,

$$N = \frac{R\log(R)}{a^2(R-1)} \tag{8}$$

The Jacobian in terms of state variables is,

$$\begin{bmatrix} Re^{-aP} & -aRNe^{-aP} \\ a(1-e^{-aP}) & a^2Ne^{-aP} \end{bmatrix} \tag{9}$$

which after subbing in fixed points becomes,

$$\begin{bmatrix} 1 & \frac{-R\log(R)}{a(R-1)} \\ \frac{a}{R}(R-1) & \frac{\log(R)}{R-1} \end{bmatrix} \tag{10}$$

which yields the determinant,

$$\delta = \frac{\log(R)}{R-1} + \frac{R\log(R)}{a(R-1)}\frac{a(R-1)}{R} \tag{11}$$

which simplifies to,

$$\delta = \log(R)\frac{R}{R-1} \tag{12}$$

For a positive fixed point we must have $R > 1$. But when $R > 1$, $\delta > 1$. Therefore, there are no positive and stable fixed points.

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8 Time-dependent solutions

How long would it take a population, x, growing acording to the following model to double?

$$\frac{dx}{dt} = 1.1x \tag{13}$$

The time dependent solution is,

$$x(t) = x(0)e^{1.1t} \tag{14}$$

The population doubles in time t_d if,

$$\frac{x(t_d)}{x(0)} = e^{1.1t_d} = 2 \tag{15}$$

Therefore, the doubling time is,

$$t_d = \frac{\log(2)}{1.1} \tag{16}$$

Find the time-dependent solution of the following model of a population that grows logistically from time $t = 0$ to $t = 1$, at which point all of its food is removed and a 'linear predator' is added.

$$\frac{dx}{dt} = \begin{cases} x(1-x), & t < 1 \\ -x, & t \geq 1 \end{cases}$$

and $x(0) = 0.5$. Hint: recall the partial fractions trick: $\frac{1}{x(1-x)} = \frac{1}{x} + \frac{1}{1-x}$. Suggestion: if you can't find the solution for $0 \leq t < 1$, try to do it for $t \geq 1$ only.
For $t < 1$, $\frac{dx}{dt} = x(1-x)$, which yields $\int_{0.5}^{x} \frac{dx}{x(1-x)} = \int_0^t dt$. Using partial fractions: $\int_{0.5}^{x} \frac{dx}{x} + \int_{0.5}^{x} \frac{dx}{1-x} = t$, which yields $\log(x) - \log(0.5) - \log(1-x) + \log(0.5) = t$. Exponentiating gives $\frac{x}{1-x} = e^t$, and rearranging gives $x = 1/(1+e^{-t})$. Now for $t \geq 1$. The initial conditions are x at $t = 1$ in the first condition: $x(1) = 1/(1+e^{-1})$. Therefore, for $e^{-t}/(1+e)$, $\int_{1/(1+e^{-1})}^{x} \frac{dx}{x} = -\int_1^t dt$. This yields, $\log(x) + log(1+e^{-1}) =$

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$1 - t$. Exponentiating gives $x(1 + e^{-1}) = e^{1-t}$ and finally $x = \frac{e^{1-t}}{1+e^{-1}}$. So the final solution is,

$$x(t) = \begin{cases} \frac{1}{1+e^{-t}}, & t < 1 \\ \frac{e^{1-t}}{1+e^{-1}}, & t \geq 1 \end{cases}$$

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