School of Mathematics & Applied Statistics
MATH11: Mathematical Modelling 1
Assignment Week 12

--- Solutions

Spring 2004

1. The transmission dynamics of a disease in a population is represented by the equation

\[ \frac{dI}{dt} = \beta I \left(1 - \frac{I}{K}\right) - \alpha I, \]

where \( I \) is the number of infectious individuals in the population, \( \beta \) denotes the transmission coefficient, \( K \) is the total population size and \( \alpha \) the recovery rate. Assume that \( K > 0, \alpha > 0 \) and \( \beta > 0 \).

(a) Find the steady-state solutions of this model and determine their stability as a function of the recovery rate \( \alpha \).

\textbf{Answer} The steady-state solutions of the differential equation

\[ \frac{dI}{dt} = f(I) \]

are found by solving the equation

\[ f(P) = 0, \]

Here we have the equation

\[ f(P) = \beta P \left(1 - \frac{P}{K}\right) - \alpha P \]

\[ = \beta \left[ 1 - \frac{P}{K} \right] \frac{P}{K} - \alpha \]

\[ = \beta \left( \frac{P^2}{K} - \frac{P}{K} \right) \]

\[ = \beta \frac{P^2}{K} - \beta \frac{P}{K} - \alpha P \]

\[ = \beta \left( \frac{1}{K} - \frac{1}{K} \right) P - \alpha P \]

Thus the steady-state solutions are

\[ P^* = 0 \quad \text{and} \quad P^* = \frac{K}{\beta} (\beta - \alpha). \]

Suppose that \( P^* \) is a steady-state solution of the differential equation

\[ \frac{dI}{dt} = f(I), \]

Then the associated eigenvalue is given by

\[ \lambda (P^*) = f'(P^*). \]

Here we have

\[ \lambda (P^*) = \beta \left(1 - \frac{2P^*}{K}\right) - \alpha, \]

The eigenvalue for the steady-state solution \( P^* = 0 \) is

\[ \lambda (P^*) = \beta - \alpha, \]

\( P^* \) is stable if

\[ \lambda (P^*) < 0 \quad \Rightarrow \quad \beta < \alpha, \]

The eigenvalue for the steady-state solution \( P^* = \frac{K}{\beta} (\beta - \alpha) \) is

\[ \lambda (P^*) = \beta \left[ 1 - \frac{2K (\beta - \alpha)}{\beta (\beta - \alpha)} \right] - \alpha \]

\[ = \beta \left( \frac{1}{\beta} - \frac{\beta}{\beta - \alpha} \right) \]

\[ = \beta - \frac{\beta}{\beta - \alpha} \]

\[ = \alpha - \beta, \]

\( P^* \) is stable if

\[ \lambda (P^*) < 0 \quad \Rightarrow \quad \alpha < \beta. \]

(b) Hence, or otherwise, determine the condition for the disease to be eradicated.

\textbf{Answer} The steady-state \( P^* \) represents eradication of the disease whilst the steady-state \( P^* \) represents an endemic disease. For the disease to be eradicated we need \( P^* \) to be stable and \( P^* \) to be unique.

Thus the condition for the disease to be eradicated is

\[ \alpha > \beta. \]

This result is unsurprising: biologically it means that the recovery rate must be higher than transmission coefficient.

(c) Draw a steady-state diagram for this model treating the recovery rate, \( \alpha \), as the control parameter. Indicate stable and unstable steady-state solutions using solid and dashed lines respectively.

\textbf{Answer} See figure 1

2. (a) A population is governed by the differential equation

\[ x' = x \left( e^x - x - 1 \right). \]

Find all steady-state solutions and determine their stability.

\textbf{Answer} The steady-state solutions to the differential equation

\[ \frac{dz}{dt} = f(z) \]

are found by solving the equation

\[ f(z^*) = 0, \]

Here we have

\[ \frac{dz}{dt} = z \left( e^z - z - 1 \right) \]

and the steady-state solutions are found by solving the equation

\[ z^* \left( e^{z^*} - z^* - 1 \right) = 0, \]
When $x^* = 0$ we have

$$\lambda = e^3 - 1 > 0,$$

When $x^* = 3$ we have

$$\lambda = 3,$$

Thus the steady-state solution $x^* = 0$ is **unstable** whilst the steady-state solution $x^* = 3$ is **stable**.

(b) A fraction $p \ (0 < p < 1)$ of the population in part (a) is removed in unit time so that the population size is governed by the differential equation

$$x' = x \left( e^3 - 1 - p \right),$$

For what values of $p$ is there a stable positive equilibrium?

**Answer** The steady-state solutions of the new model are given by

$$x^* \left( e^3 - 1 - p \right) = 0$$

Thus $x^*_1 = 0$ or

$$e^3 x^*_1 = 1 - p = 0$$

$$3 = x^*_1 = \ln (1 + p)$$

Note that the steady-state solution $x^*_1 = 0$ is not positive. The steady-state solution $x^*_2$ is positive if

$$3 > \ln (1 + p)$$

$$e^3 > 1 + p$$

$$p < e^3 - 1,$$

We are asked to find for what values of $p$ there is a stable positive equilibrium. We now know that there is a positive equilibrium if $p < e^3 - 1$. We therefore need to check the stability of the steady-state solution $x^*_2$. We have

$$f(x) = x \left( e^3 - 1 - p \right)$$

so that the eigenvalue equation is

$$\lambda = (1 - x^*) e^3 x^* - (1 + p),$$

Note from equation (1) that

$$e^3 x^*_2 = 1 + p$$

and the eigenvalue equation becomes

$$\lambda = (1 - x^*_2) (1 + p) - (1 + p)$$

$$= (1 + p) (1 - x^*_2 - 1)$$

$$= (1 + p) x^*_2$$

$$< 0 \text{ if } x^*_2 > 0,$$

The steady-state solution $x^*_2$ is therefore stable when it is positive and unstable when it is negative. Thus there is a stable positive equilibrium when $p < e^3 - 1$. 

---

**Figure 1**: Steady-state diagram showing how the number of infectives in the population ($I^*$) depends upon the recovery rate ($\alpha$).
3. A population of sandhill cranes (*Grus canadensis*) has been modelled by a logistic equation with carrying capacity of 194,600 members and intrinsic growth rate 0.0987 year$^{-1}$. Find the critical harvest rate for which constant yield harvesting will drive the population to extinction, and find the equilibrium population size under constant yield harvesting of 3000 birds per year. You may quote appropriate results from your lecture notes.

**Answer** The differential equation for this question is

$$\frac{dx}{dt} = rz \left(1 - \frac{x}{K}\right) = H,$$

where $K = 194,600$ members and $r = 0.0987$ year$^{-1}$.

From the lecture notes the critical value of the harvesting parameter is given by

$$H_c = \frac{rK}{4} = 4801.755 \text{ members},$$

We are now asked to find the equilibrium population size when $H = 3000$ members year$^{-1}$. The first step is to find the steady-state solutions of the differential equation

$$\frac{dx}{dt} = rz \left(1 - \frac{x}{K}\right) = H.$$

These are given by

$$r x^* \left(1 - \frac{x^*}{K}\right) = H = 0,$$

$$r x^* - \frac{x^*}{K} = 0,$$

$$r K x^* = r x^* + H = 0,$$

$$r K x^* = r K x^* + H K = 0,$$

$$\Rightarrow x^* = \frac{r K \pm \sqrt{r^2 K^2 - 4 H K}}{2r} = \frac{r K \pm \sqrt{r K (r K - 4 H)}}{2r}.$$

The second step is to calculate the eigenvalue for each steady-state solution. This is given by

$$\lambda = r \left(1 - \frac{2 x^*}{K}\right),$$

For $x^*$ we have

$$\lambda (x^*) = 0.086,$$

For $x_1$ we have

$$\lambda (x_1) = 0.066,$$

Thus the steady-state solutions $x^*$ and $x_1$ are unstable and stable respectively. Thus the equilibrium population size under constant yield harvesting of 3000 birds per year is 156,901.983.

4. (Tricky) Consider the model (Smith, 1963)

$$x' = \frac{r x (K - x)}{K + a x}$$

subjected to constant yield harvesting

$$x' = \frac{r x (K - x)}{K + a x} = h,$$

(a) Consider the equation

$$dx' + e x + f = 0, \quad d > 0 \quad f > 0,$$

Explain why the roots of this equation, should they exist, are positive if and only if $e < 0$. 

**Answer** The roots of the equation are

$$x = \frac{-e \pm \sqrt{e^2 - 4df}}{2d}.$$

We assume that the roots are real, i.e., $e^2 - 4df > 0$.

Suppose that $e > 0$, Clearly

$$x = \frac{-e \pm \sqrt{e^2 - 4df}}{2d} < 0,$$

We know that $d > 0$ and $f > 0$. Thus

$$-e > 0,$$

$$e^2 - 4df < 0,$$

$$\sqrt{e^2 - 4df} < \sqrt{e^2} = e,$$

$$-e \pm \sqrt{e^2 - 4df} < 0.$$ 

Thus if $e > 0$ both roots are negative, 

Suppose that $e < 0$. Clearly

$$x = \frac{-e \pm \sqrt{e^2 - 4df}}{2d} > 0,$$

We know that $d > 0$ and $f > 0$. Thus

$$-e < 0,$$

$$e^2 - 4df < 0,$$

$$\sqrt{e^2 - 4df} < \sqrt{e^2} = e,$$

$$-e \pm \sqrt{e^2 - 4df} > 0,$$

$$\Rightarrow x = \frac{-e \pm \sqrt{e^2 - 4df}}{2d} > 0.$$

Thus the roots of this equation, should they exist, are positive if and only if $e < 0$.

(b) Show that the steady-states of equation (2) are given by

$$r x^* + (ah - r K) x^* + h K = 0$$

Explain why harvesting is only sustainable if

- $ah < r K < 0$,
- $a^2 h^2 - 2r (a + 2) K h + r^2 K^2 \geq 0$. 

Answer We know from the previous question that the roots of the equation
\[ dx^3 + cx + f = 0, \quad d > 0 \quad f > 0 \]
are positive, should they exist, if and only if \( c > 0 \). Comparing this equation to
\[ r x^3 + (a - r K) x^2 + h K = 0 \]
we have \( d = r > 0 \) and \( f = h K > 0 \). Thus we require
\[ c = ah - rk < 0, \]
We also require that the discriminant of the equation be greater than, or equal to, zero, else the roots are complex:
\[ (ah - rk)^2 - 4rhK \geq 0 \]
\[ \implies a^2h^2 - 2a(9a + 2)rK + r^2K^2 \geq 0, \]
\[ \Box \]
(c) Suppose that \( r = K = 1 \) and \( a = 2 \). Find the maximum sustainable value of the harvesting parameter \( h \).

From the previous question we require \( h \) to satisfy two inequalities. The first is
\[ ah - rk < 0 \]
\[ \implies 2h - 1 < 0 \]
\[ \implies h < \frac{1}{2} \]
The second inequality is
\[ a^2h^2 - 2a(9a + 2)rK + r^2K^2 \geq 0 \]
\[ \implies 4h^2 - 8h + 1 \geq 0, \]
This quadratic is equal to zero when
\[ h = 1 \pm \frac{\sqrt{3}}{2}. \]
Observe that when \( h = 0 \) we have
\[ 4h^2 - 8h + 1 = 1 > 0 \]
and that when \( h \geq 1 \)
\[ 4h^2 - 8h + 1 \geq 4h^2 > 0, \]
Thus
\[ 4h^2 - 8h + 1 \geq 0 \]
if
\[ h \in \left( -\infty, 1 - \frac{\sqrt{3}}{2} \right) \]
or
\[ h \in \left[ 1 + \frac{\sqrt{3}}{2} \right), \]
We are only interested in \( h \geq 0 \). Combining our two results harvesting is only sustainable if
\[ h < \frac{1}{2} \]
and
\[ h \in \left[ 0, 1 - \frac{\sqrt{3}}{2} \right] \quad \text{or} \quad h \in \left[ 1 + \frac{\sqrt{3}}{2} \right). \]

Now
\[ 1 - \frac{\sqrt{3}}{2} \approx 0.133 \]
\[ 1 + \frac{\sqrt{3}}{2} \approx 1.866 \]
from which we conclude that harvesting is only sustainable if
\[ h \in \left[ 0, 1 - \frac{\sqrt{3}}{2} \right] \]
Thus the maximum sustainable rate of harvesting is
\[ h = 1 - \frac{\sqrt{3}}{2}. \]