Spotlight on Modeling: The Possum Plague

Reference: Sections 2.6, 7.2 and 7.3.

The ecological balance in New Zealand has been disturbed by the introduction of the Australian possum, a marsupial the size of a domestic cat with the proper name *Trichosurus vulpecula*. The animal was introduced in the 1830s for a planned fur trade. But there are no natural predators in the forests of New Zealand and the possum population rapidly increased. Today the estimated population is 70 million and only a few areas are possum-free. The animals have become a reservoir of a type of tuberculosis with about half of the possum population infected. This poses a threat of transfer of the disease to the livestock that form an important part of the New Zealand economy. An intense effort is underway to understand possum ecology and the disease. This effort includes the construction of mathematical models for the possum/disease dynamics. The simplest of these models is treated here. Our approach will be somewhat telegraphic, and we leave the detailed analysis to the reader.¹³

Modeling the Population/Disease Dynamics

Suppose that $P$ is the population of possums and $I$ is the subpopulation of infected possums, both measured in units of tens of millions. Note that $P \geq I$ and that the population of healthy possums is $P - I$. A dynamical model for $P(t)$ and $I(t)$ is

\[
\begin{align*}
P' &= (a - b)P - \alpha I \\
I' &= \beta I(P - I) - (\alpha + b)I
\end{align*}
\]  

(1)

where time $t$ is measured in years, $a$ and $b$ are the respective natural birth and death rate coefficients measured in units of year$^{-1}$, and $\alpha$ is the disease-induced death rate coefficient in year$^{-1}$ units. The number $\beta$ [measured in units of $(10^7 \cdot \text{year}^{-1})$] is the mass action coefficient that measures the effectiveness of interactions in transmitting the disease from the population $I$ of the diseased to the population $P - I$ of healthy animals. Once a possum contracts tuberculosis, it never recovers, so there is no subpopulation of “recovered.”

This model is only a crude approximation to reality and neglects such factors as patchiness (i.e., spatial variations in the population levels) and differences due to age

¹³This spotlight is adapted from the note “Percy Possum Plunders” by Graeme Wake, Professor of Applied Mathematics at the University of Auckland, New Zealand. The note appeared in the newsletter CODEE (Winter 1995). A detailed paper, “Thresholds and Stability Analysis of Models for the Spatial Spread of a Fatal Disease,” that includes other mathematical models of the possum population dynamics, was written by Wake and his colleagues K. Louie and M. G. Roberts and appeared in *IMA Journal for Mathematics Applied to Medicine and Biology* 10, (1993), pp. 207–226. Wake is a distinguished mathematician who enjoys applying mathematics to “real” problems like the possum plague discussed here. He uses mathematical techniques to help untangle the mysteries of why piles of wool being shipped overseas frequently begin to smolder in the holds of the ships, and why fish-and-chips shops in Australia suddenly catch fire. An excellent general reference on mathematical models for the spread of disease is an article by another distinguished applied mathematician, H. W. Hethcote, “Qualitative Analysis of Communicable Disease Models,” *Math. Biosci.* 28 (1976), pp. 335–356.
structure in the possum population. But the model is surprisingly effective in giving
a macroscopic picture of the situation and in giving some indication of how much
effort is going to be needed to change the long-term outcome. Nonconstant solutions
of system (1) can’t be expressed in terms of elementary functions, so we must rely on
mathematical theory and computer simulation to understand solution behavior.

Scaling the Variables, Population Equilibrium Levels

System (1) has four parameters, \( a, b, \alpha, \) and \( \beta. \) We can scale the populations \( P \) and \( I \)
and time \( t \) to reduce the number of parameters before we do computer simulations:

\[
P = hx, \quad I = jy, \quad t = ks
\]

where \( h, j, \) and \( k \) are positive scaling constants which are to be determined. From
system (1), the relations in (2), and the Chain Rule we have

\[
\begin{align*}
\frac{dP}{dt} &= \frac{dP}{dx} \frac{dx}{ds} \frac{ds}{dt} = \frac{h \, dx}{k \, ds} = (a - b)hx - \alpha jy \\
\frac{dI}{dt} &= \frac{dI}{dy} \frac{dy}{ds} \frac{ds}{dt} = \frac{j \, dy}{k \, ds} = \beta jy(hx - jy) - (\alpha + b) jy
\end{align*}
\]

The scaling constants will be chosen to focus attention on the coefficients of the \( x \)-term
in the first ODE of system (3) and the \( y \)-term in the second. If we set

\[
h = j = \alpha/\beta, \quad k = 1/\alpha, \quad c = (a - b)/\alpha, \quad r = (\alpha + b)/\alpha
\]

then system (1) becomes a system in dimensionless variables and parameters:

\[
\begin{align*}
\frac{dx}{ds} &= cx - y \\
\frac{dy}{ds} &= y(x - y) - ry = (x - y - r)y
\end{align*}
\]

There is a reason for focusing on the parameters \( c \) and \( r. \) The most likely way to reduce
the possum population is to reduce its birth rate or raise its natural death rate, that is,
alter \( a \) or \( b \) in the formulas in (4), and so change \( c \) and \( r. \)

Let’s look at the region \( R, \) \( 0 \leq y \leq x; \) because the scaled number \( y \) of infected
animals cannot exceed the entire scaled population \( x. \) By requiring that \( c + r \geq 1, \) we
can ensure that if \( 0 \leq y_0 \leq x_0, \) then the orbit starting at \( (x_0, y_0) \) stays in the region
\( 0 \leq y \leq x \) as time increases (see Problem 8).

The equilibrium points of system (5) are the intersection points of the nullclines
\( cx - y = 0 \) and \( (x - y - r)y = 0. \) The equilibrium points are the origin and a point
whose coordinates are

\[
x = r/(1 - c), \quad y = cr/(1 - c)
\]

The latter equilibrium point disappears if \( c = 1. \) If \( c = 0, \) then \( (x, 0) \) is an equilibrium
point in the region \( R \) for each \( x \geq 0. \)
Computer Simulations

One goal of the computer simulation is to determine whether the population orbits $x = x(s), \ y = y(s)$ of system (5) tend to an equilibrium point or become unbounded as $s$ increases. We can accomplish this by a study of the orbits of the system for various values of $c$ and $r$.

**EXAMPLE 1**

**From Extinction to Explosion**

Set $r = 2$ in system (5) and plot orbits in the region $R$ for $c = -1, 0, 1.5, \text{ and } 0.25$. Figures 1–4 show the results. In Figure 1, $c = -1$ and all orbits in $R$ tend to the origin; that is, as $s$ advances, the possums die out (and the disease, presumably, with them). Despite appearances, the orbits in Figure 2 (where $c = 0$) are not all asymptotic to a single equilibrium state $(x, 0)$. Zooming on the region near $(1, 0)$ will show that the seven orbits tend to seven different equilibrium points. Each equilibrium point models a disease-free possum population.

Figure 3 ($c = 1.5$) shows a disastrous situation. Figure 4 ($c = 0.25$) shows the intriguing scenario where the possum population and its diseased subpopulation approach an equilibrium state. This may be interpreted in terms of the disease becoming endemic and the healthy and diseased populations at equilibrium.

Figures 5 and 6 show an oscillating orbit, its approach to another endemic equilibrium $(22/19, 11/190)$ and the corresponding component graphs in the case $c = 0.05$ and $r = 1.1$ (somewhat more realistic than the values $c = 0.25, \ r = 2$ of Figure 4). But the time between successive population maxima is so large that it would take years of observation before one could decide whether the data support the validity of a model like this.
\[ \frac{dx}{ds} = 1.5x - y, \quad \frac{dy}{ds} = y(x - y) - 2y \]

FIGURE 3  The nightmare of explosive growth: \( c = 1.5, \ r = 2 \).

\[ \frac{dx}{ds} = 0.25x - y, \quad \frac{dy}{ds} = y(x - y) - 2y \]

FIGURE 4  Healthy and infected populations stabilize: \( c = 0.25, \ r = 2 \).

\[ \frac{dx}{ds} = 0.05x - y, \quad \frac{dy}{ds} = y(x - y) - 1.1y \]

\( x(0) = 7, \quad y(0) = 3.5 \)

FIGURE 5  Approach to stable equilibrium where disease is endemic at low population levels: \( c = 0.05, \ r = 1.1 \).

\[ \frac{dx}{ds} = 0.05x - y, \quad \frac{dy}{ds} = y(x - y) - 1.1y \]

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FIGURE 6  Population bursts during approach to low population levels \( x = 22/19 \approx 1.16 \) and \( y = 11/190 \approx 0.06 \): \( c = 0.05, \ r = 1.1 \).

**Looking Ahead**

This possum model is a model in the making. It isn’t yet known whether this or some other model will provide the breakthrough in understanding the dynamics of the situation and how the basic problem can be resolved. Any ideas?

The possum/tuberculosis model is one of a large number of disease models proposed over the last seventy-five years to understand the dynamics of the spread of disease (see Problems 1–5).
PROBLEMS

Modeling the Outbreak of an Epidemic: Kermack–McKendrick SIR Model. We may model the evolution of an epidemic in a fixed population by dividing the population into three distinct classes:

\[ S = \text{Susceptibles} \text{ are those who have never had the illness and can catch it} \]
\[ I = \text{Infectives} \text{ are those who are infected and are contagious} \]
\[ R = \text{Recovered} \text{ are those who had the illness and have recovered} \]

Assume that the disease is mild (everyone eventually recovers), that the disease confers immunity on the recovered, and that the diseased are infective until they recover.

1. **The SIR Model** Argue that the evolution of the epidemic may be modeled by the nonlinear system of first-order ODEs, \( S' = -aSI, \; I' = aSI - bI, \; R' = bI \), where the parameter \( b \) represents the reciprocal of the period of infection and \( a \) represents the reciprocal of the level of exposure of a typical person. [\textit{Hint: Compare with models for predator-prey interaction in Section 7.3.}] 

2. **Onset of Epidemic** Show that an epidemic can only occur if the susceptible population is large enough. Specifically, find the threshold value for \( S \) above which more people are infected each day than recover.

3. **German Measles** Suppose that German measles lasts for four days. Suppose also that the typical susceptible person meets 0.3% of the infected population each day and that the disease is transmitted in 1 out of every 6 contacts with an infected person. Find the values of the parameters \( a \) and \( b \) in the SIR model. How small must the susceptible population be for this illness to fade away without becoming an epidemic? Verify by plotting the component graph for \( I(t) \) for your choice of \( I(0) \) and for values of \( S(0) \) that are 50% above and 50% below the threshold value found in problem 2. Plot over \( 0 \leq t \leq 30 \) and discuss what you see.

4. **Dependence on \( S(0) \)** Suppose that another illness has parameter values \( a = 0.001 \) and \( b = 0.08 \), and suppose that 100 infected individuals are introduced into a population. Investigate how the spread of the infection depends on the size of the population by plotting \( S \), \( I \), and \( R \)-component graphs for \( 0 \leq t \leq 50 \), \( I(0) = 100 \), \( R(0) = 0 \), and values of \( S(0) \) ranging from 0 to 2000 in increments of 500. How does the value of \( S(0) \) affect the speed with which the epidemic runs its course?

5. **\( I \) as a function of \( S \)** Using \( a = 0.001 \) and \( b = 0.08 \), find \( I \) as a function of \( S \), \( I_0 \) and \( S_0 \). Plot \( I(t) \) against \( S(t) \) for various values of \( S_0 \) and \( I_0 \), \( 0 < S_0 < 1600 \), \( 0 < I_0 < 1250 \). Zooming near the origin, look at the long-term behavior. Interpret your graphs in terms of the model. [\textit{Hint: }\frac{dI}{dS} = -1 + b(aS)^{-1}.]

The Possum Plague Model.

6. **Scaling the Possum Plague** Suppose that the possum populations \( P \) and \( I \) are measured in millions and that time is measured in years. Show that if the scale constants \( h \) and \( j, k \) of (2) and (4) are measured, respectively, in units of \( 10^{-7} \) and \( (\text{years})^{-1} \), then \( x, y, \) and \( s \) are dimensionless variables.

7. **Write the possum model in terms of the susceptibles**. Suppose that the possum populations \( P \) and \( I \) are measured in millions and that time is measured in years. Show that if the scale constants \( h \) and \( j, k \) of (2) and (4) are measured, respectively, in units of \( 10^{-7} \) and \( (\text{years})^{-1} \), then \( x, y, \) and \( s \) are dimensionless variables. Then introduce scaled variables \( z = x - y, \; y, \; \text{and } s \) (where \( x, y, \) and \( s \) are as in the text), write the \( z \) and \( y \) ODEs, find the equilibria, and plot orbits for \( z \geq 0, \; y \geq 0 \) with the values of \( c \) and \( r \) as given in Figures 1–5. Interpret your graphs (zoom if necessary).

8. **Suppose that \( R \) is the region in the first quadrant bounded by the lines \( y = x \) and \( y = 0 \) (\( R \) includes its boundaries). Show that if \( c + r \geq 1 \), then orbits of system (5) that originate in \( R \) stay in \( R \) as \( t \) increases.

9. **Parameter Study** Make a parameter study of the possum plague model, using parameters of your choice. Relate your conclusions to an assessment of the situation in New Zealand.