Modeling a Fox Population in which Rabies is Present

Submitted to:

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Applied Modeling/Advance Modeling Project

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A system of first-order nonlinear ordinary differential equations is solved by using Mathcad and examining the results. Four nonlinear systems of differential equations are used to model a fox population in which rabies is present.

The Four Nonlinear Systems are as follows:

\[
\frac{dX}{dt} = rX - \gamma XN - \beta XY
\]

\[
\frac{dI}{dt} = \beta XY - (\sigma + b + \gamma N)I
\]

\[
\frac{dY}{dt} = \sigma I - (\alpha + \beta + \gamma N)Y
\]

\[
\frac{dN}{dt} = aX - (b + \gamma N)N - \alpha Y
\]

The parameters are as follows:

\(X(t)\) represents the population of fox susceptible to rabies at time \(t\).

\(I(t)\) represents the population that has contracted the rabies virus but is not yet ill.

\(Y(t)\) represents the population that has developed rabies.

\(N(t)\) represents the total population of foxes.

The parameters \(a, b, r, \gamma, \sigma, \alpha, \text{ and } \beta\) represent constants and are described in the following table.
<table>
<thead>
<tr>
<th>Constant</th>
<th>Description</th>
<th>Typical Value(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a$</td>
<td>$a$ represents the average per capita birth rate of foxes.</td>
<td>1</td>
</tr>
<tr>
<td>$b$</td>
<td>$1/b$ denotes fox life expectancy (without resource limitations), which is typically in the range of 1.5 to 2.7 years.</td>
<td>0.5</td>
</tr>
<tr>
<td>$r$</td>
<td>$r=a-b$ represents the intrinsic per capita population growth rate.</td>
<td>0.5</td>
</tr>
<tr>
<td>$K$</td>
<td>$K=r/\gamma$ represents the fox carrying capacity of the defined area, which is typically in the range of 0.1 to 4 foxes per km$^2$. We will compute $K$ and $r$ and then approximate $\gamma$.</td>
<td>Varies</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>$1/\sigma$ represents the average latent period. This represents the average time (in years) that a fox can carry the rabies virus but not actually be ill with rabies. Typically, $1/\sigma$ is between 28 and 30 days.</td>
<td>12.1667</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>$\alpha$ represents the death rate of foxes with rabies. $1/\alpha$ is the life expectancy (in years) of a fox with rabies and is typically between 3 and 10 days.</td>
<td>73</td>
</tr>
<tr>
<td>$\beta$</td>
<td>$\beta$ represents a transmission coefficient. Typically, $1/\beta$ is between 4 and 6 days.</td>
<td>80</td>
</tr>
</tbody>
</table>


1. Generating a numerical solution to the system that satisfies the initial conditions $X(0)=0.93$, $I(0)=0.035$, $Y(0)=0.035$ and $N(0)=1.0$ valid for

$$0 \text{ years } \leq t \leq 40 \text{ years}$$

using the values given in the previous table if $K=1,2,3,4,$ and 8. In each case, graph $X(t)$, $I(t)$, $Y(t)$, and $N(t)$ for

$$0 \text{ years } \leq t \leq 40 \text{ years}$$

The Format in Mathcad 2000 is the following:

Let $X(t)=Y_0$, $I(t)=Y_1$, $Y(t)=Y_2$, and $N(t)=Y_3$. As required for solving the equations, the system of equations modeling the fox populations are already written with the derivative on the left side only. Applying the substitutions to the dependent variable of each equation and placing them alongside their set of initial conditions results in the following system:
\[ \frac{dY_0}{dt} = rY_0 - \gamma Y_0 Y_3 - \beta Y_0 Y_2 \quad Y_0(0) = 0.93 \]
\[ \frac{dY_1}{dt} = \beta Y_0 Y_2 - (\sigma + b + \gamma Y_3)Y_1 \quad Y_1(0) = 0.035 \]
\[ \frac{dY_2}{dt} = \sigma Y_1 - (\alpha + \beta + \gamma Y_3)Y_2 \quad Y_2(0) = 0.035 \]
\[ \frac{dY_3}{dt} = aY_0 - (b + \gamma Y_3)Y_3 - \alpha Y_2 \quad Y_3(0) = 1.0 \]

The System with Table Constants are as follows:

\[ \frac{dY_0}{dt} = 0.5 \cdot Y_0 - \gamma Y_0 Y_3 - 80 \cdot Y_0 Y_2 \]
\[ \frac{dY_1}{dt} = 80 \cdot Y_0 Y_2 - (12.1667 + 0.5 + \gamma Y_3)Y_1 \]
\[ \frac{dY_2}{dt} = 12.1667 \cdot Y_1 - (73 + 80 + \gamma Y_3)Y_2 \]
\[ \frac{dY_3}{dt} = 1 \cdot Y_0 - (0.5 + \gamma Y_3)Y_3 - 73 \cdot Y_2 \]

The constant \( \gamma \) varies and for this problem, the values of \( K \) and \( r \) are given such that \( \gamma \) can be calculated as shown:
\[ K = 1 \quad \gamma = \frac{r}{K} = \frac{0.5}{1} = 0.5 \]

\[ K = 2 \quad \gamma = \frac{r}{K} = \frac{0.5}{2} = 0.25 \]

\[ K = 3 \quad \gamma = \frac{r}{K} = \frac{0.5}{3} = 0.1667 \]

\[ K = 4 \quad \gamma = \frac{r}{K} = \frac{0.5}{4} = 0.125 \]

\[ K = 8 \quad \gamma = \frac{r}{K} = \frac{0.5}{8} = 0.0625 \]

Each value of \( \gamma \) will be substituted into the equations along with the other constants to provide a solution set to the system of equations as specified by problem statement one. Beginning by substituting the \( \gamma \) corresponding to \( K=1 \) results in:

For \( K=1 \)

A function that determines a vector of derivative values at any solution point \((t,Y)\):

Additional arguments for the ODE solver as specified by the problem statement number one:

- Initial value of independent variable
- Terminal value of independent variable
- Vector of initial function values
- Number of solution values on \([0, t_1]\)
Graphs For $K=1$

Population of foxes susceptible to rabies begins close to 0.95, drops and levels off close to 1 after 10 years because fewer fox to spread rabies.

Population that has contracted the rabies virus but is not yet ill begins close to 0.04 and then drops to zero fast.

Population that has developed rabies begins close to 0.04 and then drops to zero fast.

Total population of foxes begins at 1, drops and then levels off at 1 after 10 years.

Graphs For $K=2$

Population of foxes susceptible to rabies begins close to 1, rises close to 2 where it levels off after 10 years because there are 2 fox per km$^2$.

Population that has contracted the rabies virus but is not yet ill begins close to 0.04 and then drops to zero fast.

Population that has developed rabies begins close to 0.04 and then drops to zero fast.

Total population of foxes begins at 1, rises close to 2 where it levels off after 10 years.
Graphs For K=3

Population of foxes susceptible to rabies dampens over time. This population cycles every 7 years.

Population that has contracted the rabies virus but is not yet ill dampens over time. This population cycles every 7 years.

Population that has developed rabies dampens over time. This population cycles every 7 years.

Total population of foxes dampens over time. This population cycles every 7 years.

Graphs For K=4

Population of foxes susceptible to rabies dampens over time. This population rises at 10 years.

Population that has contracted the rabies virus but is not yet ill dampens over time. This population drops at 10 years.

Population that has developed rabies dampens over time. This population drops at 10 years.

Total population of foxes dampens over time. This population rises at 10 years.
2. Generating a numerical solution to the system that satisfies the initial conditions $X(0)=0.93$, $I(0)=0.02$, $Y(0)=0.05$ and $N(0)=2.0$ valid for

- $0 \text{ years} \leq t \leq 40 \text{ years}$

using the values given in the previous table if $K=1,2,3,4,$ and 8. In each case, graph $X(t)$, $I(t)$, $Y(t)$, and $N(t)$ for

- $0 \text{ years} \leq t \leq 40 \text{ years}$

The Format in Mathcad 2000 is the following:

Let $X(t)=Y_0$, $I(t)=Y_1$, $Y(t)=Y_2$, and $N(t)=Y_3$. As required for solving the equations, the system of equations modeling the fox populations are already written with the derivative on the left side only. Applying the substitutions to the dependent variable of each equation and placing them alongside their set of initial conditions results in the following system:
\[
\begin{align*}
\frac{dY_0}{dt} &= rY_0 - \gamma Y_0 Y_3 - \beta Y_0 Y_2 & Y_0(0) &= 0.93 \\
\frac{dY_1}{dt} &= \beta Y_0 Y_2 - (\sigma + b + \gamma Y_3)Y_1 & Y_1(0) &= 0.02 \\
\frac{dY_2}{dt} &= \sigma Y_1 - (\alpha + \beta + \gamma Y_3)Y_2 & Y_2(0) &= 0.05 \\
\frac{dY_3}{dt} &= aY_0 - (b + \gamma Y_3)Y_3 - \alpha Y_2 & Y_3(0) &= 2.0
\end{align*}
\]

Each value of \(\gamma\) will be substituted into the equations along with the other constants to provide a solution set to the system of equations as specified by problem statement one. Beginning by substituting the \(\gamma\) corresponding to \(K=1\) results in:

\[K=1\]

A function that determines a vector of derivative values at any solution point \((t,Y)\):

Additional arguments for the ODE solver as specified by the problem statement number one:

<table>
<thead>
<tr>
<th>Argument</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td>Initial value of independent variable</td>
</tr>
<tr>
<td>(b)</td>
<td>Terminal value of independent variable</td>
</tr>
<tr>
<td>(x_0)</td>
<td>Vector of initial function values</td>
</tr>
<tr>
<td>(x_1)</td>
<td>Number of solution values on ([0, t_1])</td>
</tr>
</tbody>
</table>
Graphs For $K=1$

Population of foxes susceptible to rabies begins close to 0.95, drops and levels off close to 1 after 10 years because fewer fox to spread rabies.

Population that has contracted the rabies virus but is not yet ill begins close to 0.03 and then drops to zero fast.

Population that has developed rabies begins at 0.05 and then drops to zero fast.

Total population of foxes begins at 2, drops below 1 and then levels off at 1 after 10 years.

Graphs For $K=2$

Population of foxes susceptible to rabies begins close to 1, rises close to 2 where it levels off after 10 years because there are 2 fox per km$^2$.

Population that has contracted the rabies virus but is not yet ill begins close to 0.03 and then drops to zero fast.

Population that has developed rabies begins close to 0.05 and then drops to zero fast.

Total population of foxes begins at 2, drops below 1.5, and rises back to 2 where it levels off after 10 years.
Graphs For K=3

Population of foxes susceptible to rabies dampens over time. This population cycles every 7 years.

Population that has contracted the rabies virus but is not yet ill dampens over time. This population cycles every 7 years.

Population that has developed rabies dampens over time. This population cycles every 7 years.

Total population of foxes dampens over time. This population cycles every 7 years.

Graphs For K=4

Population of foxes susceptible to rabies dampens over time. This population rises at 10 years.

Population that has contracted the rabies virus but is not yet ill dampens over time. This population drops at 10 years.

Population that has developed rabies dampens over time. This population drops at 10 years.

Total population of foxes dampens over time. This population rises at 10 years.
Graphs For K=8

Population of foxes susceptible to rabies has less dampening over time compared to smaller populations.

Population that has contracted the rabies virus but is not yet ill has less dampening over time compared to smaller populations.

Population that has developed rabies has less dampening over time compared to smaller populations.

Total population of foxes has less dampening over time compared to smaller populations.

3. For both problems, the estimation for the smallest value of K, say $K_T$, so that $Y(t)$ is a periodic function is the following.

The smallest value of K where $Y(t)$ is a periodic function is found by increasing K until the graph becomes sinusoidal.

For part 1, the smallest estimated value is $K = 20$.

For part 2, the smallest estimated value is $K = 21$. 
Graphs For $K = 20$

Population of foxes susceptible to rabies is higher because fox habitat is large.

Population that has contracted the rabies virus but is not yet ill is higher because fox habitat is large.

Population that has developed rabies is higher because fox habitat is large.

Total population of foxes is higher because fox habitat is large.

Graphs For $K = 21$

Population of foxes susceptible to rabies is higher because fox habitat is large.

Population that has contracted the rabies virus but is not yet ill is higher because fox habitat is large.

Population that has developed rabies is higher because fox habitat is large.

Total population of foxes is higher because fox habitat is large.
4. What happens to \( Y(t) \) and \( N(t) \) for \( K < K_T \)?

The population that has developed rabies \( [Y(t)] \) will become a damping function and the fox population \( [N(t)] \) will settle to its disease-free equilibrium density \( K \).

**Explanation of why this result makes sense.**

These variables form a dynamical system and they interact with one another.

\( Y(t) \) will eventually reach an equilibrium level.

5. Defining the basic reproductive rate \( R \) to be

\[
R = \frac{\sigma\beta K}{(\sigma + a)(\alpha + a)}
\]

and

\[
K_T = \frac{(\sigma + a)(\alpha + a)}{\sigma\beta}
\]

If \( R > 1 \) then \( K > K_T \) and if \( R < 1 \) then \( K < K_T \) is proven below.

\[
R = \frac{\sigma\beta K}{(\sigma + a)(\alpha + a)} > 1
\]

\[
\sigma\beta K > (\sigma + a)(\alpha + a)
\]

\[
K > \frac{(\sigma + a)(\alpha + a)}{\sigma\beta}
\]

\[
K > K_T
\]
\[ R = \frac{\sigma\beta K}{(\sigma + a)(\alpha + a)} < 1 \]

\[ \sigma\beta K < (\sigma + a)(\alpha + a) \]

\[ K < \frac{(\sigma + a)(\alpha + a)}{\sigma\beta} \]

\[ K < K_T \]

6. Using the values in the table to calculate

\[ K_T = \frac{(\sigma + a)(\alpha + a)}{\sigma\beta} \]

Comparing the results to the approximations in part 3.

Comparing them.

\[ K_T = \frac{(\sigma + a)(\alpha + a)}{\sigma\beta} \]

\[ = \frac{(12.1667+1)(73+1)}{12.1667(80)} \]

\[ = \frac{(13.1667)(74)}{973.336} \]

\[ = 1 \]
Comparing the results to the approximations in part 3.
In part 3: the smallest estimated value is $K_{p1} = 20$ for part 1
the smallest estimated value is $K_{p2} = 21$ for part 2

Comparing them.
$K_p$ in part 3 is much larger than $K_T$.
The $K_p$ values in part 3 are where $Y(t)$’s start to become
periodic functions, whereas $K_T$ in part 6 is the threshold value for
the maintenance of rabies in the fox population. Therefore, $Y(t)$
does not have to be periodic in this case.

7. Predict how the solutions would change if the transmission
coefficient $\beta$ were decreased or the death rate $\alpha$ were increased.

The disease-free form of the solution happens when $K < K_T$, in which $X(t)$
and $N(t)$ reach the equilibrium level of the total number of foxes in the
population, whereas the incubated fox population and the infectious
population - $I(t)$ and $Y(t)$ - will die out to the equilibrium level of zero
(Similar to $K=1$ in problem 1).

The derivatives of all the dependent variables $X$, $Y$, $I$, and $N$ converge to
zero as $t$ grows very large.

When we decrease $\beta$ or increase $\alpha$, $K_T$ increases, and all values of
$K < K_T$ will produce solutions of the disease-free model form. Therefore,
some lower values of $K$ which had the non-disease-free form before the
change will now have the disease-free form if they become smaller than
$K_T$. On the other hand, the threshold periodic $K_p$ is also raised
accordingly.
$\beta$ Decreased to 35

$K = 1$

$K = 2$
$\beta$ Decreased to 35

$K = 3$

$K = 4$
$\beta$ Decreased to 35

$K = 8$

$K = 34$
\( \alpha \) Increased to 120

\[ K = 1 \]

\[ y_0 \]

\[ y_1 \]

\[ y_2 \]

\[ y_3 \]

\[ \text{ } \]

\[ K = 2 \]

\[ y_0 \]

\[ y_1 \]

\[ y_2 \]

\[ y_3 \]
Increased to 120

$\alpha$

$K = 3$

$K = 4$
$\alpha$ Increased to 120

$K = 8$

$y_0$

$y_1$

$y_2$

$y_3$

$K = 35$

$y_0$

$y_1$

$y_2$

$y_3$

$t$
What if the average latent period $\sigma$ were increased? $K_T$ can be rewritten as follows:

\[
K_T = \frac{(\sigma + a)(\alpha + a)}{\sigma \beta}
\]

\[
K_T = \frac{(\sigma / \sigma + a / \sigma)(\alpha + a)}{\beta}
\]

\[
K_T = \frac{(1 + a / \sigma)(\alpha + a)}{\beta}
\]

Notice that $a / \sigma$ is a very small number nearly equal to 1/12 (from the values in the table). As $\sigma$ increases this ratio will approach zero very fast. Therefore, it will only decrease $K_T$ by a minimal amount. $K_T$ will become slightly less than 1 so any $K \geq 1$ will produce a solution of the non-disease free form.
σ Increased to 24

\[ K = 1 \]

\[ K = 2 \]
$\sigma$ Increased to 24

\[ K = 3 \]

\[ K = 4 \]
\( \sigma \) Increased to 24

\( K = 8 \)

\( K = 12 \)
Increased to $83$, $K = 4$

Population of foxes susceptible to rabies increases as the death rate increases.

Population that has contracted the rabies virus but is not yet ill have shorter life span as death rate increases because foxes die sooner and do not have as much opportunity to infect healthy foxes.

Population that has developed rabies have shorter life span as death rate increases because foxes die sooner and do not have as much opportunity to infect healthy foxes. The graph dampens faster.

Total population of foxes increases as the death rate increases.
\( \alpha \) increased to 123, \( K = 4 \)

Population of foxes susceptible to rabies increases as the death rate increases.

Population that has contracted the rabies virus but is not yet ill takes longer to contract as death rate increases foxes die sooner and do not have as much opportunity to infect healthy foxes. The graph dampens faster.

Population that has developed rabies takes longer to contract as death rate increases because foxes die sooner and do not have as much opportunity to infect healthy foxes. The graph dampens faster.

Total population of foxes increases as the death rate increases.
Average Latent Period Increased \( \sigma = 30 \)

Population of foxes susceptible to rabies dampens with more cycles as the latent period increases. More chance to infect other foxes.

Population that has contracted the rabies virus but is not yet ill decreases as the latent period increases.

Population that has developed rabies increases as the latent period increases.

Total population of foxes dampens with more cycles as the latent period increases. More chance to infect other foxes.
Average Latent Period Increased $\sigma = 50$

Population of foxes susceptible to rabies dampens with more cycles as the latent period increases. More chance to infect other foxes.

Population that has contracted the rabies virus but is not yet ill decreases as the latent period increases.

Population that has developed rabies increases as the latent period increases.

Total population of foxes dampens with more cycles as the latent period increases. More chance to infect other foxes.
Conclusions

- Rabies will be maintained within fox population provided \( R > 1 \). \( R \) is the expected number of secondary cases produced during a life span of an infectious fox introduced into a population of \( K \) susceptible animals.

- Endemic maintenance equivalently expressed as requirement fox population exceed a "threshold density" \( K > K_T \).

- Epidemiological evidence suggests \( K_T \) approximately equals 1.0 foxes per kilometer squared as most frequently reported value in Europe.

- Model predicts prevalence of rabies higher in favorable fox habitats (large \( K \)) which is consistent with German epidemiological evidence.

- In absence of rabies, fox populations seem to increase up to some characteristic density, \( K \), determined be carrying capacity of habitat within Europe, \( 0.1 < K < 4 \).
Bibliography

Population dynamics of fox rabies in Europe;
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Anthony M. Smith;
Zoology Department and Centre for Environmental Technology,
Imperial College, London University, London, UK;
WHO Collaborating Centre for Rabies Surveillance and Research,
Federal Research Institute for Animal Virus Diseases, Tubingen;
Biology Department, Princeton University, New Jersey, USA