# Nonlinear Systems of ODE: Examples and Parameter Estimation 

MATH 469, Texas A\&M University

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## Overview

As we discussed while talking about nonlinear systems of difference equations, nonlinearities typically arise from interactions between individuals in the same population (e.g., carrying capacity terms) or interactions between individuals in different populations (e.g., predation terms).

These nonlinearities generally take the same form for differential equations as for difference equations, so all of the models we talked about during our study of difference equations have counterparts for differential equations.

Let's start by looking at some of these.

## The Lotka-Volterra Predator-Prey System

We set

$$
\begin{aligned}
& y_{1}(t)=\# \text { of prey at time } t \\
& y_{2}(t)=\# \text { of predators at time } t
\end{aligned}
$$

The Lotka-Volterra predator-prey model is

$$
\begin{aligned}
& \frac{d y_{1}}{d t}=a y_{1}-b y_{1} y_{2} ; \quad y_{1}(0)=y_{1_{0}} \\
& \frac{d y_{2}}{d t}=-r y_{2}+c y_{1} y_{2} ; \quad y_{2}(0)=y_{2_{0}}
\end{aligned}
$$

We often make adjustments to the right-hand side precisely as we did for the Lotka-Volterra difference system. For example, we might add a (GSSM) carrying capacity to the prey equation, along with a half-saturation constant to the predator equation to obtain the system on the next slide.

The Lotka-Volterra Predator-Prey System
We get:

$$
\begin{aligned}
\frac{d y_{1}}{d t} & =\frac{a}{\alpha} y_{1}\left(1-\left(\frac{y_{1}}{K_{1}}\right)^{\alpha}\right)-b y_{1} y_{2} ; \quad y_{1}(0)=y_{1_{0}} \\
\frac{d y_{2}}{d t} & =-r y_{2}+\frac{c y_{1} y_{2}}{M+y_{1}} ; \quad y_{2}(0)=y_{2_{0}} .
\end{aligned}
$$

## Competition Models

Recall that for competition models, we consider two or more species that are competing for the same resources. If we have two species with populations $y_{1}(t)$ and $y_{2}(t)$, a natural competition model is

$$
\begin{array}{ll}
\frac{d y_{1}}{d t}=r_{1} y_{1}\left(1-\frac{y_{1}+s_{1} y_{2}}{K_{1}}\right) ; & y_{1}(0)=y_{1_{0}} \\
\frac{d y_{2}}{d t}=r_{2} y_{2}\left(1-\frac{s_{2} y_{1}+y_{2}}{K_{2}}\right) ; & y_{2}(0)=y_{2_{0}} .
\end{array}
$$

## Mutualistic Models

Mutualistic models arise when two or more species mutually benefit one another. If we have two species with populations $y_{1}(t)$ and $y_{2}(t)$, a natural mutualistic model is

$$
\begin{array}{ll}
\frac{d y_{1}}{d t}=r_{1} y_{1}\left(1-\frac{y_{1}}{K_{1}}\right)+b_{1} y_{1} y_{2} ; & y_{1}(0)=y_{1_{0}} \\
\frac{d y_{2}}{d t}=r_{2} y_{2}\left(1-\frac{y_{2}}{K_{2}}\right)+b_{2} y_{1} y_{2} ; & y_{2}(0)=y_{2_{0}}
\end{array}
$$

## The SIR Model

Recall that the SIR epidemic model involves the following three populations:
$y_{1}(t)=\#$ of susceptible individuals in the population at time $t$ $y_{2}(t)=\#$ of infected/infective individuals in the population at time $t$ $y_{3}(t)=\#$ of recovered/removed individuals in the population at time $t$. The SIR model is

$$
\begin{aligned}
& \frac{d y_{1}}{d t}=-a y_{1} y_{2} ; \quad y_{1}(0)=y_{1_{0}} \\
& \frac{d y_{2}}{d t}=a y_{1} y_{2}-b y_{2} ; \quad y_{2}(0)=y_{2_{0}} \\
& \frac{d y_{3}}{d t}=b y_{2} ; \quad y_{3}(0)=y_{3_{0}} .
\end{aligned}
$$

As in the case of difference equations, the first two equations form a closed system (i.e., $y_{3}(t)$ doesn't appear in either of them).

## Restoration Ecology and Conservation Biology

This example is taken from the paper, "Hopes for the future: restoration ecology and conservation biology," by A. P. Dobson, A. D. Bradshaw, and A. J. M. Baker, in Science 277 (1997) 515-522.

The idea here is to model the progression in which forested land is taken over for agriculture. Generally speaking, we start with an initial area of (mostly) uninhabited forest, which gets cleared for agricultural purposes. Subsequently, when the soil's nutrients are depleted and the land becomes difficult to work, it is abandoned. Eventually, one of three things typically happens to the abandoned land: (1) it reverts back to forest; (2) with time, its soil recovers, and it can be used again for agriculture; or (3) it gets converted to industrial use.

In this article, the authors focus on the first two possibilities.

## Restoration Ecology and Conservation Biology

The variables are as follows:
$F(t)=$ area of forest land at time $t$
$A(t)=$ area of agricultural land at time $t$
$U(t)=$ area of unused (not forest, not agricultural) land at time $t$
$P(t)=$ (local) human population at time $t$

## Restoration Ecology and Conservation Biology

The model is as follows:

$$
\begin{array}{ll}
\frac{d F}{d t}=-a F P+b U ; & F(0)=F_{0} \\
\frac{d A}{d t}=a F P+c U-f A ; & A(0)=A_{0} \\
\frac{d U}{d t}=f A-(b+c) U ; & U(0)=U_{0} \\
\frac{d P}{d t}=r P\left(1-\frac{P}{K(A)}\right) ; & P(0)=P_{0},
\end{array}
$$

where $K(A)=\frac{A}{h}$, with $h$ denoting the amount of agricultural land required to sustain a single individual. I.e., the equation for the human population can be expressed as

$$
\frac{d P}{d t}=r P\left(1-\frac{h P}{A}\right) ; \quad P(0)=P_{0}
$$

## Restoration Ecology and Conservation Biology

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$$
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\frac{d A}{d t}=a F P+c U-f A ; & A(0)=A_{0} \\
\frac{d U}{d t}=f A-(b+c) U ; & U(0)=U_{0} \\
\frac{d P}{d t}=r P\left(1-\frac{P}{K(A)}\right) ; & P(0)=P_{0} .
\end{array}
$$

First equation: The term -aFP corresponds with conversion of the land for agricultural purposes. The term bU corresponds with unused land converting back to its forested state.

Second equation: The term $c U$ corresponds with unused land re-claimed for agricultural purposes. The term - $f A$ corresponds with abandoned agricultural land.

## Parameter Estimation

As an example of parameter estimation, we'll fit the Lotka-Volterra model

$$
\begin{aligned}
& \frac{d y_{1}}{d t}=a y_{1}-b y_{1} y_{2} ; \quad y_{1}(0)=y_{1_{0}} \\
& \frac{d y_{2}}{d t}=-r y_{2}+c y_{1} y_{2} ; \quad y_{2}(0)=y_{2_{0}}
\end{aligned}
$$

to the same set of hare-lynx data we used earlier for a version of the Lotka-Volterra difference system. In this case, we won't incorporate a carrying capacity into the prey equation, primarily because we don't need it in order to get a good fit to the data. We recall the data on the next slide.

## Parameter Estimation

| Year | 1900 | 1901 | 1902 | 1903 | 1904 | 1905 | 1906 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| \# Hare | 30.0 | 47.2 | 70.2 | 77.4 | 36.3 | 20.6 | 18.1 |
| \# Lynx | 4.0 | 6.1 | 9.8 | 35.2 | 59.4 | 41.7 | 19.0 |
| Year | 1907 | 1908 | 1909 | 1910 | 1911 | 1912 | 1913 |
| \# Hare | 21.4 | 22.0 | 25.4 | 27.1 | 40.3 | 57.0 | 76.6 |
| \# Lynx | 13.0 | 8.3 | 9.1 | 7.4 | 8.0 | 12.3 | 19.5 |
| Year | 1914 | 1915 | 1916 | 1917 | 1918 | 1919 | 1920 |
| \# Hare | 52.3 | 19.5 | 11.2 | 7.6 | 14.6 | 16.2 | 24.7 |
| \# Lynx | 45.7 | 51.1 | 29.7 | 15.8 | 9.7 | 10.1 | 8.6 |

Table: Hare and Lynx Populations in thousands, 1900-1920.

## Parameter Estimation

As usual, we need to begin the process by identifying a relationship among the variables that's linear in the parameters. Looking first at the prey equation, we can divide by $y_{1}$ to obtain

$$
\frac{1}{y_{1}} \frac{d y_{1}}{d t}=a-b y_{2}
$$

Similarly as when we were fitting the logistic model to US population growth, we would like to plot values of $\frac{1}{y_{1}} \frac{d y_{1}}{d t}$ against values of $y_{2}$, and fit the values to a regression line.
We can obtain values for $\frac{d y_{1}}{d t}$ with derivative approximation. In this case, our data has the form $\left\{\left(t_{k}, H_{k}, L_{k}\right)\right\}_{k=1}^{21}$, corresponding with the years 1900-1920.

We'll take $t_{1}=0$ to correspond with 1900, so that our times are $t_{1}=0, t_{2}=1, t_{3}=2, \ldots, t_{21}=20$.

## Parameter Estimation

Correspondingly, we have the data values $\left(H_{1}, L_{1}\right)=(30,4)$, $\left(H_{2}, L_{2}\right)=(47.2,6.1),\left(H_{3}, L_{3}\right)=(70.2,9.8)$, $\left(H_{4}, L_{4}\right)=(77.4,35.2) \ldots,\left(H_{19}, L_{19}\right)=(14.6,9.7)$, $\left(H_{20}, L_{20}\right)=(16.2,10.2),\left(H_{21}, L_{21}\right)=(24.7,8.6)$.

We'll use the central difference derivative approximation, so we'll only have 19 data points for our derivatives. For these, we compute

$$
\begin{aligned}
\left(\frac{d y_{1}}{d t}\right)_{1} & =\frac{y_{1}\left(t_{2}+h\right)-y_{1}\left(t_{2}-h\right)}{2 h}=\frac{70.2-30}{2}=20.1 \\
\left(\frac{d y_{1}}{d t}\right)_{2} & =\frac{77.4-47.2}{2}=15.1 \\
& \vdots \\
\left(\frac{d y_{1}}{d t}\right)_{19} & =\frac{24.7-14.6}{2}=5.05 .
\end{aligned}
$$

## Parameter Estimation

Keeping in mind that our relation is

$$
\frac{1}{y_{1}} \frac{d y_{1}}{d t}=a-b y_{2}
$$

a few points are as follows:

$$
\begin{aligned}
\left(L_{2}, \frac{1}{H_{2}}\left(\frac{d y_{1}}{d t}\right)_{1}\right) & =(6.1, .4258) \\
\left(L_{3}, \frac{1}{H_{3}}\left(\frac{d y_{1}}{d t}\right)_{2}\right) & =(9.8, .2151) \\
& \vdots \\
\left(L_{20}, \frac{1}{H_{20}}\left(\frac{d y_{1}}{d t}\right)_{19}\right) & =(10.2, .3117) .
\end{aligned}
$$

The plot associated with these values is given on the next slide. We find $a=.4732$ and $b=.0240$.


## Parameter Estimation

For the predator equation, we have

$$
\frac{d y_{2}}{d t}=-r y_{2}+c y_{1} y_{2} .
$$

In this case, we divide by $y_{2}$ to obtain the relation

$$
\frac{1}{y_{2}} \frac{d y_{2}}{d t}=-r+c y_{1}
$$

Proceeding similarly as for the prey equation, we obtain the plot given on the next slide. We find $c=.0234$ and $r=.7647$.

We now have values for our four parameters, so we can numerically solve the Lotka-Volterra model and plot the result along with our hare-lynx data. This plot is given following the plot of our fit for the predator equation.


Prey population, model and data


Predator population, model and data


## Parameter Estimation

The values we obtained from our linear fits are $a=.4732$, $b=.0240, c=.0234$, and $r=.7646$.

We now use these as initial values to carry out the nonlinear regression. As usual, MATLAB will do most of the work for our nonlinear regression, so let's just be clear about what it's doing.

Given the initial values $y_{1}(0)=30$ and $y_{2}(0)=4$, we can numerically solve the Lotka-Volterra system

$$
\begin{aligned}
& \frac{d y_{1}}{d t}=a y_{1}-b y_{1} y_{2} ; \quad y_{1}(0)=y_{1_{0}} \\
& \frac{d y_{2}}{d t}=-r y_{2}+c y_{1} y_{2} ; \quad y_{2}(0)=y_{2_{0}}
\end{aligned}
$$

for any set of parameter values $a, b, c$, and $r$.

## Parameter Estimation

In order to emphasize the role of the parameters, let's denote the solution to this system

$$
\vec{y}(t ; a, b, c, r)=\binom{y_{1}(t ; a, b, c, r)}{y_{2}(t ; a, b, c, r)} .
$$

Let's also denote our data values $\vec{y}_{k}=\left(H_{k}, L_{k}\right)$, for $k=1,2, \ldots, 21$.

For the nonlinear regression, we minimize the SSR

$$
E(a, b, c, r)=\sum_{k=1}^{21}\left|\vec{y}\left(t_{k} ; a, b, c, r\right)-\vec{y}_{k}\right|^{2}
$$

We find $a=.5482, b=.0283, c=.0265$, and $r=.8369$. A plot of our model with these values along with the original data is given on the next slide. As a reminder, the fit we obtained using difference equations is given on the subsequent slide.

Prey population, model and data


Predator population, model and data



Predator population, model and data


