

# Numerical Solutions to Differential Equations

## Lecture Notes #5 $\frac{1}{2}$ — Application of RK Methods to Lotka-Volterra Models

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### Introduction

The Lotka<sup>[1]</sup>-Volterra<sup>[2]</sup> predator-prey model was introduced by Lotka in 1910 (for chemical reactions), and extended by Volterra in 1920 to model organic systems; the equation form famous today was introduced in 1925.



Google scholar returns 18,400 hits for the search “lotka volterra” with the restriction “since 2000.”

We will examine mathematical models and Runge-Kutta based simulations for two species that are intertwined in a predator-prey or host-parasite relationship.

The discussion will be fairly complete, but we will gloss over (some) theoretical details that are not the focal point of *this class*.

[1] Alfred James Lotka (March 2, 1880 – December 5, 1949)

[2] Vito Volterra (3 May 1860 – 11 October 1940)

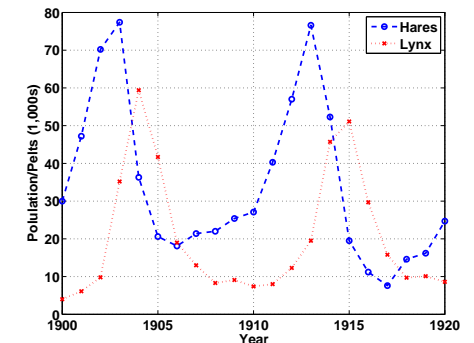
### Outline

- 1 Lotka Volterra Predator-Prey Models
  - Introduction; Modeling
  - Equilibrium Analysis
- 2 Modeling and Fitting with Real Data...
  - The Data Set
  - Initializing
  - Finding Optimal Parameters

**Acknowledgment:** This lecture adopted from Joe Mahaffy's notes from *Math 636: Mathematical Modeling*.

### Classical Example: The Lynx & The Hare

The Lynx-Hare system has been extensively studied, mainly because the Hudson Bay company kept careful records of all furs from the early 1800s into the 1900s<sup>[1]</sup>. [RIGHT] Graph of the partial data-set, 1900-1920.



[1] Charles Elton and Mary Nicholson, *The Ten-Year Cycle in Numbers of the Lynx in Canada*, *Journal of Animal Ecology*, Vol. 11, No. 2 (Nov., 1942), pp. 215-244.

## The Model: Hares

Let  $H(t)$  be the population of hares, and  $L(t)$  be the population of lynx.

The rate of change in a population is equal to the net increase (births) into the population minus the net decrease (deaths) of the population.

In a naive model we have: (1) The primary growth in the hare population is Malthusian (the population grows in proportion to its own population)  $a_1 H(t)$ . (2) Predation, being the only reason for hare population decline, modeled by assuming random Lynx-Hare contact,  $-a_2 H(t)L(t)$ ; so

$$\frac{dH(t)}{dt} = a_1 H(t) - a_2 H(t)L(t).$$

## Equilibria &amp; Jacobian

$$\begin{aligned}\frac{dH(t)}{dt} &= a_1 H(t) - a_2 H(t)L(t) \\ \frac{dL(t)}{dt} &= -b_1 L(t) + b_2 H(t)L(t).\end{aligned}$$

By inspection we see that we have equilibria for the cases

$$(H, L) \in \{(0, 0), (b_1/b_2, a_1/a_2)\}.$$

These equilibria do not help explain the oscillatory behavior of the lynx and snowshoe hare. We examine the stability of these solutions, by computing the **Jacobian**:

$$J(H, L) = \begin{bmatrix} a_1 - a_2 L(t) & -a_2 H(t) \\ b_2 L(t) & -b_1 + b_2 H(t) \end{bmatrix}.$$

## The Model: Lynx

Assuming that hares are the main food source for lynx: the growth of the lynx population is similar to the death rate for the hare population with a different constant of proportionality:  $b_2 H(t)L(t)$ .

The loss of lynx is presumed to be a type of reverse Malthusian growth. That is, in the absence of hares, the lynx population declines in proportion to their own population, which mathematically is given by the negative modeling term,  $-b_1 L(t)$ ;  
so

$$\frac{dL(t)}{dt} = -b_1 L(t) + b_2 H(t)L(t).$$

**Note:** The model ignores the role of climate variation and the interactions of other species, including human disturbance. Other significant factors that are ignored in this modeling effort are the ages of the animals and the spatial distribution.

## Stationary Points &amp; Behavior

We find

$$J(0, 0) = \begin{bmatrix} a_1 & 0 \\ 0 & -b_1 \end{bmatrix}, \quad \lambda_1 = a_1, \quad \xi_1 = \begin{bmatrix} 1 \\ 0 \end{bmatrix}, \quad \lambda_2 = -b_1, \quad \xi_2 = \begin{bmatrix} 0 \\ 1 \end{bmatrix}$$

Which shows that  $(0, 0)$  is a saddle node, with exponential growth along the  $Hare(t)$  axis, and decay along the  $Lynx(t)$  axis.

4 nanoseconds of thought confirms that's what we should expect!

$$J(b_1/b_2, a_1/a_2) = \begin{bmatrix} 0 & -a_2 b_1 \\ a_1 b_2 & 0 \end{bmatrix}, \quad \lambda_{1,2} = \pm i \sqrt{a_1 b_1} = \pm i \omega$$

To **linear order** this generates periodic solutions

$$\begin{bmatrix} H_L(t) \\ L_L(t) \end{bmatrix} = c_1 \begin{bmatrix} \cos(\omega t) \\ A \sin(\omega t) \end{bmatrix} + c_2 \begin{bmatrix} \sin(\omega t) \\ -A \cos(\omega t) \end{bmatrix}, \quad A = \frac{b_2}{a_2} \sqrt{\frac{a_1}{b_1}}.$$

## Periodic Solutions

The linear solution produces a structurally unstable model, because small perturbations from the nonlinear terms result in the solution either spiraling toward or away from the equilibrium.

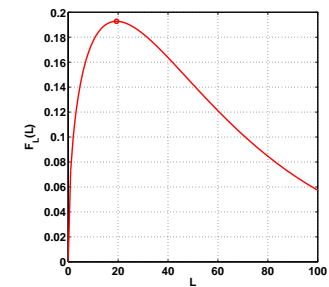
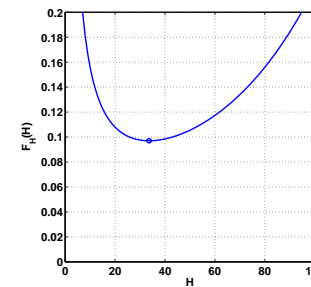
However, there are periodic **limit cycles** for all initial conditions in the 1<sup>st</sup> quadrant: formally divide the equations (taking time out of the picture)

$$\frac{dH}{dL} = \frac{a_1 H - a_2 H L}{-b_1 L + b_2 H L}$$

which has the implicit solution

$$\underbrace{H^{-b_1} e^{b_2 H}}_{F_H(H)} = \underbrace{C L^{a_1} e^{-a_2 L}}_{F_L(L)}.$$

## Characterizing the Solution



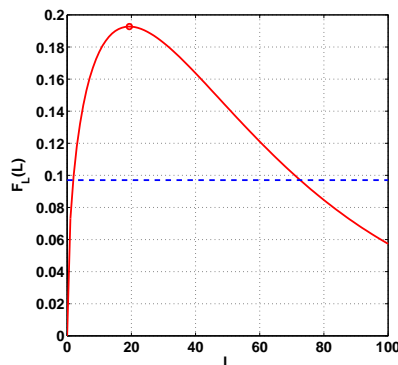
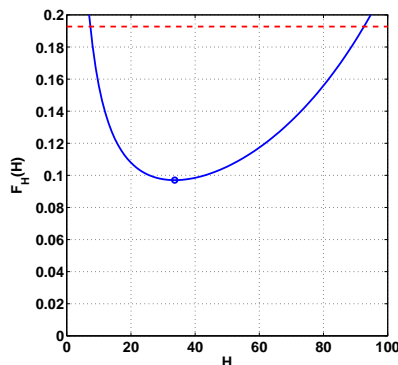
$$F_H(H) = H^{-b_1} e^{b_2 H}, \quad F'_H(H) = H^{-b_1-1} e^{b_2 H} (b_2 H - b_1),$$

$$F_L(L) = C L^{a_1} e^{-a_2 L}, \quad F'_L(L) = C L^{a_1-1} e^{-a_2 L} (a_1 - a_2 L).$$

$F_H(H)$  has a vertical asymptote at  $H = 0$ ,  $\lim_{H \rightarrow 0} F_H(H) = \infty$ , and a minimum at  $H_{\min} = b_1/b_2$ .

$F_L(L)$  has a maximum at  $F_{\max} = a_1/a_2$ ,  $F_L(0) = 0$ , and  $\lim_{L \rightarrow \infty} F_L(L) = 0$ .

## Existence of Periodic Solutions

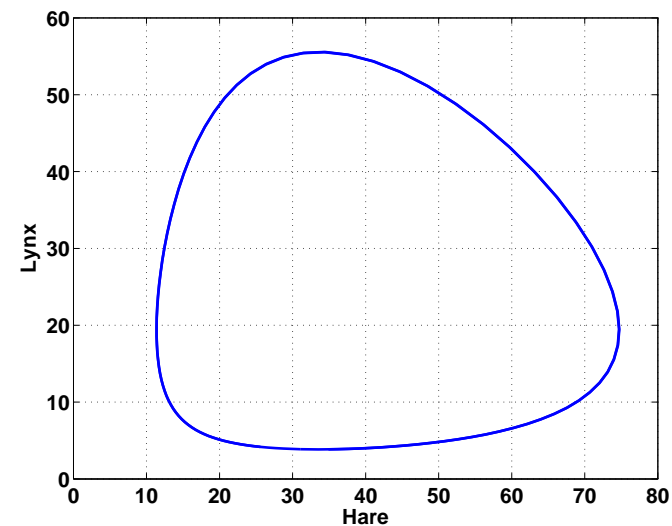


These functions are equal (with  $F_L(L)$  shifting depending on the integration constant,  $C$ .) This can only happen on the range

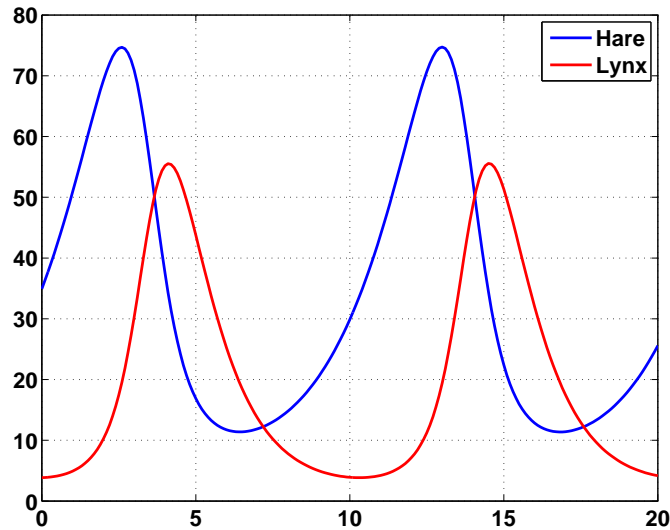
$$[\min F_H(H), \max F_L(L)].$$

Since  $F_L(L)/F_H(H)$  takes two values at the min/max of  $F_H(H)/F_L(L)$ , it follows that there must be a periodic orbit.

## Periodic Orbits



## Periodic Orbits



## Parameter Guesses

We set our initial conditions to  $H(0) = 30$ , and  $L(0) = 4$  (from the data).

By averaging the data over one period (eye-balled at about **12 years**), and looking at snapshots of **rapid growth/decay** in the populations, it is possible (see Math 636 for the real discussion) to come up with some useful estimates to get things going, e.g.

$$H_{\min} = \frac{b_1}{b_2} \approx H_{\text{mean}} \approx 34.6, \quad L_{\max} = \frac{a_1}{a_2} \approx L_{\text{mean}} \approx 22.1,$$

$$a_1 b_1 \approx \frac{\pi^2}{36} \approx 0.274,$$

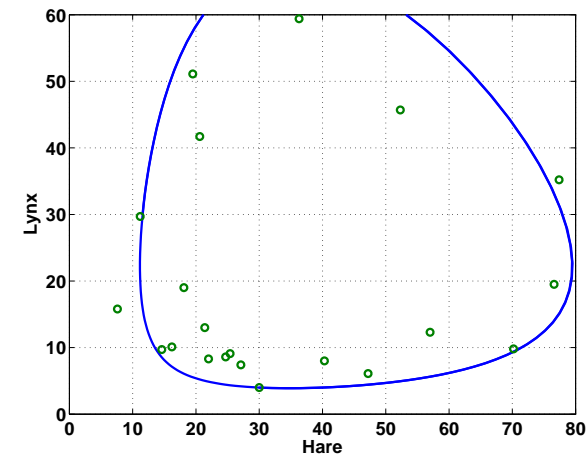
$$a_1 = 0.397, \quad b_1 = 0.786, \quad a_2 = 0.018, \quad b_2 = 0.023.$$

Given the partial data set

| Year | Hare (1,000) | Lynx (1,000) | Year | Hare (1,000) | Lynx (1,000) |
|------|--------------|--------------|------|--------------|--------------|
| 1900 | 30           | 4            | 1911 | 40.3         | 8            |
| 1901 | 47.2         | 6.1          | 1912 | 57           | 12.3         |
| 1902 | 70.2         | 9.8          | 1913 | 76.6         | 19.5         |
| 1903 | 77.4         | 35.2         | 1914 | 52.3         | 45.7         |
| 1904 | 36.3         | 59.4         | 1915 | 19.5         | 51.1         |
| 1905 | 20.6         | 41.7         | 1916 | 11.2         | 29.7         |
| 1906 | 18.1         | 19           | 1917 | 7.6          | 15.8         |
| 1907 | 21.4         | 13           | 1918 | 14.6         | 9.7          |
| 1908 | 22           | 8.3          | 1919 | 16.2         | 10.1         |
| 1909 | 25.4         | 9.1          | 1920 | 24.7         | 8.6          |
| 1910 | 27.1         | 7.4          |      |              |              |

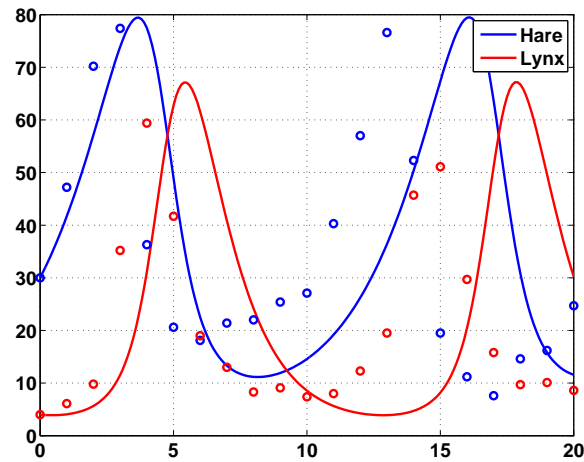
One might wonder what the parameters  $a_1$ ,  $a_2$ ,  $b_1$ , and  $b_2$  are???

## Periodic Orbits; Gussed Parameters



$$H(0) = 30, \quad L(0) = 4, \quad a_1 = 0.397, \quad a_2 = 0.018, \quad b_1 = 0.786, \quad b_2 = 0.023$$

## Periodic Orbits; Guessed Parameters



$$H(0) = 30, L(0) = 4, a_1 = 0.397, a_2 = 0.018, b_1 = 0.786, b_2 = 0.023$$

## Parameter Fitting

Using a bit of black-box technology (Matlab's `fminsearch`) related to Math 693a, and RKF45 (known as `ode45` in Matlab) we can set up a search for the optimal (as measured in the sum-of-squares-sense) parameters

$$H_0^*, L_0^*, a_1^*, a_2^*, b_1^*, b_2^*.$$

## Matlab Code: Fragment #1 — Initializing

```
function exitflag = lynx_hare

%Data and the initial guess.
td = [0:20];
yr = 1900:1920;
hare = [30 47.2 70.2 77.4 36.3 20.6 18.1 21.4 22 25.4 ...
        27.1 40.3 57 76.6 52.3 19.5 11.2 7.6 14.6 16.2 24.7];
lynx = [4 6.1 9.8 35.2 59.4 41.7 19 13 8.3 9.1 7.4 8 ...
        12.3 19.5 45.7 51.1 29.7 15.8 9.7 10.1 8.6];
p = [30 4 0.4 0.018 0.8 0.023];
```

## Parameter Fitting

## Matlab Code: Fragment #2 — Optimize

```
% This finds the min...
[p,fval,exitflag] = fminsearch(@leastcomp,p,[],td,hare,lynx);

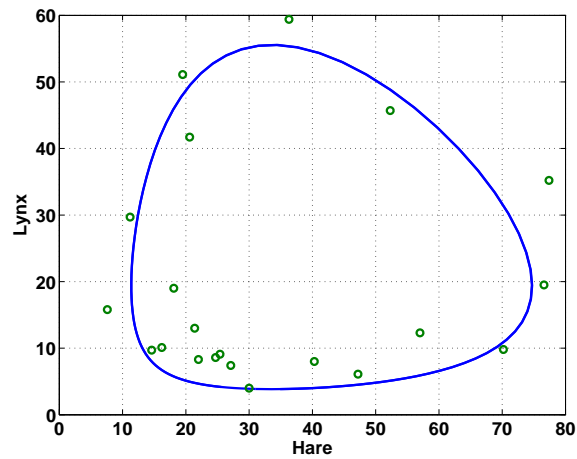
%Compute the least squares error of current guess
function J = leastcomp(p,tdata,xdata,ydata)
[t,y] = ode45(@lotvol,tdata,[p(1),p(2)],[],p(3),p(4),p(5),p(6));
errx = y(:,1) - xdata';
erry = y(:,2) - ydata';
J = sum(abs(errx).^2) + sum(abs(erry).^2);

% Predator and Prey ODE Model
function dydt = lotvol(t,y,a1,a2,b1,b2)
tmp1 = a1*y(1) - a2*y(1)*y(2);
tmp2 = -b1*y(2) + b2*y(1)*y(2);
dydt = [tmp1; tmp2];
```

## Action Slide!!!

⟨⟨ play with matlab code ⟩⟩

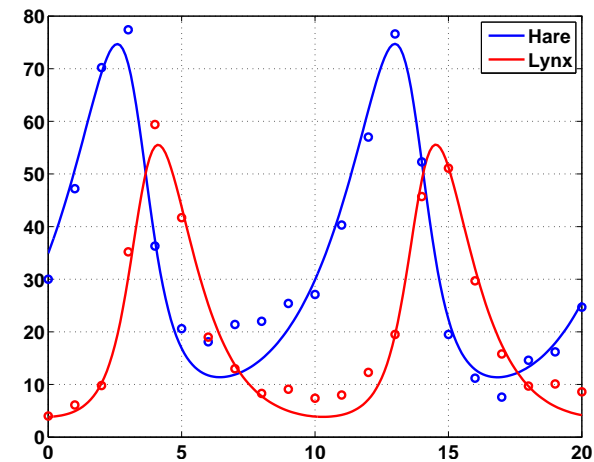
## Periodic Orbits; Optimal Parameters



$$H(0) = 34.91, L(0) = 3.857,$$

$$a_1 = 0.4807, a_2 = 0.02482, b_1 = 0.9272, b_2 = 0.02756$$

## Periodic Orbits; Optimal Parameters



$$H(0) = 34.91, L(0) = 3.857,$$

$$a_1 = 0.4807, a_2 = 0.02482, b_1 = 0.9272, b_2 = 0.02756$$

## Optimal Parameters: Curious Fact

Using ode23 (2nd-3rd order RK) we get

$$H(0) = 34.91, L(0) = 3.857,$$

$$a_1 = 0.4807, a_2 = 0.02482, b_1 = 0.9272, b_2 = 0.02756$$

with a sum-of-squares error of 594.9.

Using ode45 (4nd-5th order RK) we get

$$H(0) = 36.90, L(0) = 3.029,$$

$$a_1 = 0.4121, a_2 = 0.02249, b_1 = 1.089, b_2 = 0.03170$$

with a sum-of-squares error of 651.6.