Math 636 - Mathematical Modeling

Continuous Models
Lotka-Volterra

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Outline

Introduction

Introduction

- Studied *competition model for two species*.
- Analysis of the *system of differential equations* allowed an understanding of the dynamics of this model.
- *Phase portrait* gave qualititive behavior.
- *Least squares* allowed reasonable matching of experimental data.
- *Predator-prey* or *Host-parasite* interactions present a different ecological interaction to study with modeling.
- The two species are directly linked by interactions negatively affecting one species and positively affecting the other.
- Qualitative studies are performed for this new *system of differential equations*.
- A *predator-prey model* is fit to data, and the model behavior is analyzed.

Predator-Prey System

Predator-Prey System

- Examine two species that are intertwined in a predator-prey or host-parasite relationship.
- Most mammalian predators rely on a variety of prey.
- A few predators have become highly specialized and seek almost exclusively a single prey species.
  - A simplified predator-prey interaction is seen in Canadian northern forests.
  - Populations of the lynx and the snowshoe hare are intertwined in a life and death struggle.
  - There are good records of pelts of these species trappers brought to the Hudson Bay Company.
- This simplified system creates a good opportunity to create a *mathematical model*.

Lynx and Hare

Lynx and Hare: Specialized tightly linked predator and prey relationship.

Hudson Bay Company Pelt Data 1

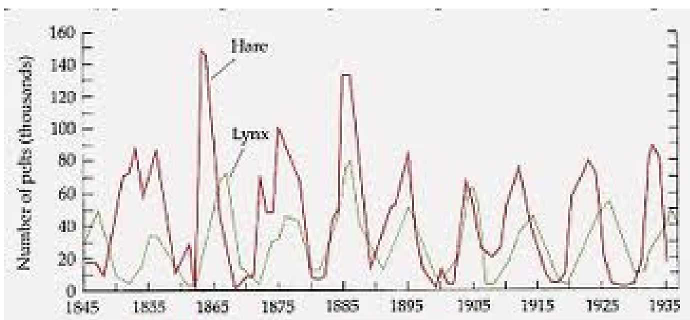
Hudson Bay Company Pelt Data: Detailed records on pelts collected over almost 100 years. Below is data from 1900-1920.

Year	Hares ($\times$1000)	Lynx ($\times$1000)	Year	Hares ($\times$1000)	Lynx ($\times$1000)
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			

- Many ecological texts use this selected set of the Hudson Bay Company data.
- Data from 1900-1920 show distinct rise of hares followed by a rise in lynx.
- Theory has predicted that following a rise of prey, then populations of predator increase
- Develop *Lotka-Volterra model* exhibiting this behavior

Hudson Bay Company Pelt Data 2

Hudson Bay Company Pelt Data over 100 years is shown below.



- Data over entire set show very complicated behavior.
- Do **NOT** show regular periodic behavior predicted by some ecological models.
- There exist models coupling economics to pelt harvesting that better match complete data set, while other models are improved with climate information.

Predator-Prey (Lotka-Volterra) Model 1

Lotka-Volterra Model: Classical model for interaction of ***predator*** and ***prey***.

- Alfred Lotka (1920), an American biologist and actuary, published the mathematical ***predator-prey model*** and its cyclical nature.
- It extended Lotka's work in autocatalysis in chemical reactions.
- Lotka originated many useful theories of stable populations, including the ***logistic model***.
- Vito Volterra (1925) proposed the same model to explain data from fish studies of his son-in-law Humberto D'Ancona on the fishing industry in Italy.
- The classical ***Lotka-Volterra predator-prey model*** for the dynamics of the populations of a predator and its prey species.

Predator-Prey (Lotka-Volterra) Model 2

Lotka-Volterra Model: Let $H(t)$ be the population of snowshoe 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.
- Modeling hare population growth assumes ***Malthusian growth***, where the population grows in proportion to its population, $a_1 H(t)$.
- Assume that the primary loss of hares is due to predation by lynx.
- Predation is often modeled by assuming random contact between the species in proportion to their populations with a fixed percentage of those contacts resulting in death of the prey species.
- This is modeled by a negative term, $-a_2 H(t)L(t)$.
- The growth model for the hare population is:

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

Predator-Prey (Lotka-Volterra) Model 3

Lotka-Volterra Model with $H(t)$ as the population of snowshoe hares and $L(t)$ as the population of lynx.

- The primary growth for the lynx population depends on sufficient food for raising lynx kittens, which implies an adequate nutrients from predation on hares.
- This growth rate is similar to the death rate for the hare population with a different constant of proportionality, $b_2 L(t)H(t)$.
- In the absence of hares, the lynx population declines in proportion to its own population, $-b_1 L(t)$.
- The growth model for the lynx population is:

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

Predator-Prey Model – Analysis 1

Predator-Prey Model – Analysis: The model satisfies the ***system of ODEs***:

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

The first step is finding ***equilibria***, (H_e, L_e), so want

$$\frac{dH(t)}{dt} = 0 \quad \text{and} \quad \frac{dL(t)}{dt} = 0,$$

which is equivalent to:

$$\begin{aligned}0 &= a_1 H_e - a_2 H_e L_e = H_e(a_1 - a_2 L_e),\\ 0 &= -b_1 L_e + b_2 L_e H_e = L_e(-b_1 + b_2 H_e).\end{aligned}$$

Predator-Prey Model – Analysis 2

Equilibrium Analysis: The ***equilibria*** satisfy:

$$\begin{aligned}H_e(a_1 - a_2 L_e) &= 0,\\ L_e(-b_1 + b_2 H_e) &= 0.\end{aligned}$$

The first equation gives either $H_e = 0$ or $L_e = \frac{a_1}{a_2}$.

If $H_e = 0$, then the only solution of the second equation is $L_e = 0$, which gives the ***extinction equilibrium***, $(H_e, L_e) = (0, 0)$.

If $L_e = \frac{a_1}{a_2}$, then the only solution of the second equation is $H_e = \frac{b_1}{b_2}$, which gives the ***coexistence equilibrium***, $(H_e, L_e) = (\frac{b_1}{b_2}, \frac{a_1}{a_2})$.

It follows that there are only ***2 equilibria***:

$$(H_e, L_e) = (0, 0) \quad \text{and} \quad (H_e, L_e) = \left(\frac{b_1}{b_2}, \frac{a_1}{a_2}\right),$$

which quite interestingly show that the ***equilibrium*** for the hares, H_e, depends only on the parameters governing the lynx population and the lynx equilibrium, L_e, depends only on the parameters governing the hare population.

Predator-Prey Model – Analysis 3

Linear Analysis: The nonlinear model satisfies the ***system of ODEs***:

$$\frac{dH(t)}{dt} = a_1 H - a_2 H L = F_1(H,L),$$
$$\frac{dL(t)}{dt} = -b_1 L + b_2 L H = F_2(H,L),$$

so it is ***linearized*** by making the change of variables be $h(t) = H(t) - H_e$ and $l(t) = L(t) - L_e$ and keeping only the ***linear terms***.

From before, the ***linearized system*** is written with the ***Jacobian matrix*** evaluated at the ***equilibria***:

$$\begin{pmatrix} \frac{dh(t)}{dt} \\ \frac{dl(t)}{dt} \end{pmatrix} = J(H_e, L_e) \begin{pmatrix} h(t) \\ l(t) \end{pmatrix} = \begin{pmatrix} \frac{\partial F_1(H_e,L_e)}{\partial H} & \frac{\partial F_1(H_e,L_e)}{\partial L} \\ \frac{\partial F_2(H_e,L_e)}{\partial H} & \frac{\partial F_2(H_e,L_e)}{\partial L} \end{pmatrix} \begin{pmatrix} h(t) \\ l(t) \end{pmatrix},$$

where

$$J(H_e, L_e) = \begin{pmatrix} a_1 - a_2 L_e & -a_2 H_e \\ b_2 L_e & -b_1 + b_2 H_e \end{pmatrix}.$$

Predator-Prey Model – Analysis 4

Linear Analysis (cont): Given the ***Jacobian matrix***:

$$J(H_e, L_e) = \begin{pmatrix} a_1 - a_2 L_e & -a_2 H_e \\ b_2 L_e & -b_1 + b_2 H_e \end{pmatrix},$$

at the equilibrium $(H_e, L_e) = (0, 0)$, we have:

$$J(0,0) = \begin{pmatrix} a_1 & 0 \\ 0 & -b_1 \end{pmatrix}$$

This matrix (**diagonal**) has the ***eigenvalues*** and ***associated eigenvectors***:

$$\lambda_1 = a_1, \quad \xi_1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \qquad \text{and} \qquad \lambda_2 = -b_1, \quad \xi_1 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}.$$

Thus, the equilibrium $(0, 0)$ is a ***saddle node*** with solutions exponentially growing along the H-axis and decaying along the L-axis, so

$$\begin{pmatrix} h(t) \\ l(t) \end{pmatrix} = c_1 \begin{pmatrix} 1 \\ 0 \end{pmatrix} e^{a_1 t} + c_2 \begin{pmatrix} 0 \\ 1 \end{pmatrix} e^{-b_1 t}.$$

Predator-Prey Model – Analysis 5

Linear Analysis (cont): At the ***equilibrium***, $(H_e, L_e) = \left(\frac{b_1}{b_2}, \frac{a_1}{a_2}\right)$, we have:

$$J\left(\frac{b_1}{b_2}, \frac{a_1}{a_2}\right) = \begin{pmatrix} 0 & -\frac{a_2 b_1}{b_2} \\ \frac{a_1 b_2}{a_2} & 0 \end{pmatrix}$$

This matrix has the ***purely imaginary eigenvalues***:

$$\lambda_{1,2} = \pm i\sqrt{a_1 b_1} \equiv \pm i\omega.$$

Thus, the equilibrium $\left(\frac{b_1}{b_2}, \frac{a_1}{a_2}\right)$ is a ***center***, which suggests that the solution cycles around for the predator-prey model. The ***linear solution*** satisfies:

$$\begin{pmatrix} h(t) \\ l(t) \end{pmatrix} = c_1 \begin{pmatrix} \cos(\omega t) \\ A \sin(\omega t) \end{pmatrix} + c_2 \begin{pmatrix} \sin(\omega t) \\ -A \cos(\omega t) \end{pmatrix},$$

where $A = \frac{b_2}{a_2}\sqrt{\frac{a_1}{b_1}}$.

This produces a ***structurally unstable model***.

The model is ***structurally unstable*** because small perturbations from the nonlinear terms could result in the solution either ***spiraling toward*** or ***away*** from the equilibrium or possibly a completely different trajectory.

Predator-Prey Model – Periodic Analysis 1

Predator-Prey Model – Periodic Analysis: The ***Lotka-Volterra model*** can be written:

$$\frac{1}{H}\frac{dH}{dt} = a_1 - a_2 L,$$
$$\frac{1}{L}\frac{dL}{dt} = -b_1 + b_2 H.$$

This formulation gives the modeling interpretation:

- In the absence of predators $(Y = 0)$ the per capita prey growth rate $\left(\frac{1}{H}\frac{dH}{dt}\right)$ of the prey population X was constant, but fell linearly as a function of predator population Y when predation was present $(Y > 0)$.
- In the absence of prey $(X = 0)$ the per capita growth rate of the predator $\left(\frac{1}{Y}\frac{dY}{dt}\right)$ was constant (and negative), and increased linearly with the prey population X when prey was present $(X > 0)$.

Predator-Prey Model – Periodic Analysis 2

With separation of variables, the ***Lotka-Volterra model*** can be written:

$$-\left(\frac{b_2 H - b_1}{H}\right)\frac{dH}{dt} + \left(\frac{a_1 - a_2 L}{L}\right)\frac{dL}{dt} = 0.$$

which can be written:

$$\frac{d}{dt}\left[b_1 \ln(H) - b_2 H + a_1 \ln(L) - a_2 L\right] = 0.$$

Integrate and let $Q : \mathbb{R}^+ \times \mathbb{R}^+ \to \mathbb{R}$ by

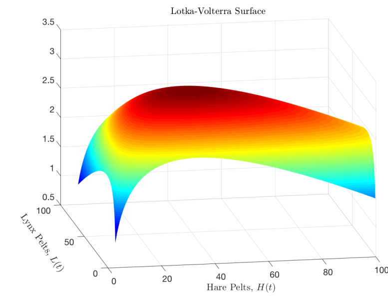
$$Q(H, L) = b_1 \ln(H) - b_2 H + a_1 \ln(L) - a_2 L = C,$$

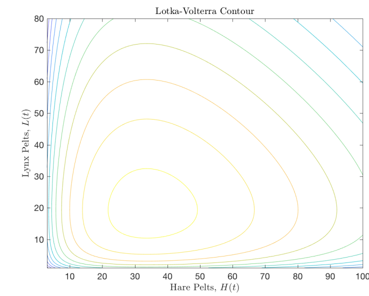
where C is a constant.

It follows that along a solution $(H(t), L(t))$ (for t where the solution exists, particularly all $t \geq 0$) the function Q is constant.

Predator-Prey Model – Periodic Analysis 3

Below we show graphs of the surface $Q(H, L)$ and the corresponding contour plot:





It is clear that the ***maximum*** occurs near the ***coexistence equilibrium***.

Predator-Prey Model – Periodic Analysis 4

We found the implicit solution:

$$Q(H(t), L(t)) = b_1 \ln(H(t)) - b_2 H(t) + a_1 \ln(L(t)) - a_2 L(t) = C.$$

Consider solutions for various initial conditions, $(H_0, L_0) = (H(0), L(0)) \in \mathbb{R}^+ \times \mathbb{R}^+$.

This initial condition gives $Q(H(0), L(0))$ is finite and all ***trajectories*** $(H(t), L(t))$ evolve so that

$$Q(H(t), L(t)) = Q(H(0), L(0)) = Q(H_0, L_0) = C,$$

for a specific constant C based on the initial condition.

From either the graph or taking two partial derivatives, it is clear that Q is ***strictly concave downward***, which implies there is a maximum.

Predator-Prey Model – Periodic Analysis 5

Moreover, $Q(H, L) \to -\infty$ as $|(H, L)| \to \infty$ or $HL \to 0$, which gives a ***unique maximum*** where $\nabla Q = 0$ or

$$\frac{b_1}{H_{max}} - b_2 = 0 \quad \text{and} \quad \frac{a_1}{L_{max}} - a_2 = 0,$$

so the ***unique maximum*** agrees with the ***equilibrium***

$$(H_{max}, L_{max}) = \left(\frac{b_2}{b_1}, \frac{a_2}{a_1}\right).$$

Since Q is strictly concave with a unique maximum in $\mathbb{R}^+ \times \mathbb{R}^+$, every trajectory with $H_0 > 0$, $L_0 > 0$ must be a ***closed curve*** (since it coincides with the projection onto $\mathbb{R}^+ \times \mathbb{R}^+$ of the curve formed from the intersection the graph the concave function Q and a horizontal plane)

This proves all ***solution trajectories***, $(H(t), L(t))$, starting from a positive initial condition are ***periodic***.

Predator-Prey Model – Periodic Analysis 6

Integrating about the Periodic Orbits: The orbits are ***periodic***, so we want to determine the ***average value of the solutions***.

Assume a period of T, the average population of hares and lynx satisfies:

$$\bar{H} = \frac{1}{T}\int_0^T H(t)dt \quad \text{and} \quad \bar{L} = \frac{1}{T}\int_0^T L(t)dt.$$

From the differential equations, we can write:

$$\begin{aligned} \frac{1}{T}\int_0^T \frac{H'(t)}{H(t)}dt &= \frac{1}{T}\int_0^T (a_1 - a_2L(t))\,dt, \\ \frac{1}{T}\ln(H(t))\Big|_0^T &= \frac{a_1 t}{T}\Big|_0^T - a_2\int_0^T L(t)dt, \\ 0 &= a_1 - \frac{a_2}{T}\int_0^T L(t)dt. \end{aligned}$$

The left hand side above is **zero** because $H(T) = H(0)$ from the assumption of periodicity.

Predator-Prey Model – Periodic Analysis 7

The right hand side is easily rearranged to give:

$$\frac{1}{T}\int_0^T L(t)dt = \bar{L} = \frac{a_1}{a_2}.$$

An almost identical argument gives:

$$\frac{1}{T}\int_0^T H(t)dt = \bar{H} = \frac{b_1}{b_2}.$$

It follows that the average population around any ***periodic orbit*** is given by the ***equilibrium*** value:

$$(\bar{H}, \bar{L}) = \left(\frac{b_2}{b_1}, \frac{a_2}{a_1}\right).$$

We noted before that the model is ***structurally unstable*** because of the ***center node***, however, the ***equilibrium*** is ***robust*** because all periodic orbits have the same mean (the equilibrium).

Fitting the Model to Parameters 1

Fitting the Model to Parameters: The data from the Hudson Bay Company on the lynx and hare pelts collected from 1900 to 1920 are used to find the best fitting ***predator-prey model***:

$$\begin{aligned} \frac{dH(t)}{dt} &= a_1H - a_2HL, \qquad H(0) = H_0, \\ \frac{dL(t)}{dt} &= -b_1L + b_2LH, \qquad L(0) = L_0, \end{aligned}$$

where we must find a_1, a_2, $H(0)$, b_1, b_2, and $L(0)$.

The initial estimates for $H(0) = 30$ and $L(0) = 4$ are from the actual data.

To avoid bias from an incomplete cycle it is best to take an average from a maximum to a maximum or minimum to minimum.

Averaging the hares from 1903 to 1913 and the lynx from 1904 to 1915 (omitting the last year) give:

$$H_e = \frac{b_1}{b_2} = 34.6 \quad \text{and} \quad L_e = \frac{a_1}{a_2} = 22.1.$$

Fitting the Model to Parameters 2

Fitting the Model to Parameters (cont): From before, this model produces a ***center*** with ***eigenvalues***, $\lambda = \pm i\omega = \pm i\sqrt{a_1b_1}$, which is the frequency of the period.

Using the maxima as a guide to the period, we find the period is around 10.5 years, so

$$T \approx 10.5 = \frac{2\pi}{\omega} \quad \text{or} \quad a_1b_1 = \omega^2 \approx 0.358,$$

which is low as the period increases as solutions move from the equilibrium.

Need one more relationship to estimate the system parameters, so look to the ***Malthusian growth*** of the hare when there is a low density of lynx.

The lowest density of lynx are the first two years (1900 and 1901), and the hare populations are 30 and 47.2, respectively.

Assuming locally the hare population satisfies:

$$H(t) = H_0e^{a_1t} \quad \text{or} \quad 47.2 = 30e^{a_1},$$

which gives an estimate of

$$a_1 \approx \ln\left(\tfrac{47.2}{30}\right) = 0.453.$$

Fitting the Model to Parameters 3

Fitting the Model to Parameters (cont): The results from above are combined to obtain reasonable estimates of the parameters; a_1, a_2, b_1, and b_2.

With $a_1 \approx 0.453$, we approximate a_2 from $L_e \approx 22.1$,

$$a_2 \approx \frac{a_1}{L_e} \approx 0.0205.$$

From $\omega^2 = a_1 b_1 \approx 0.358$, we obtain:

$$b_1 \approx \frac{\omega^2}{a_1} \approx 0.790.$$

Finally, from $H_e \approx 34.6$, we have

$$b_2 \approx \frac{b_1}{H_e} \approx 0.0229.$$

Fitting the Model to Parameters 4

Fitting the Model to Parameters (cont): The estimates above are used with `fminsearch` and a ***sum of square errors program*** in **MatLab** to find the best fitting parameters.

```
load lynxhare % Provides data (td,hare,lynx) and ...
    initial parameters (p0)
options = optimset('MaxFunEvals',5000);
[p,fval,exitflag] = ...
    fminsearch(@leastcomplv,p0,options,td,hare,lynx);
```

The ***ODE model*** is:

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


Fitting the Model to Parameters 5

The ***sum of square errors program*** is:

```
function J = leastcomplv(p,tdata,xdata,ydata)
%Create the least squares error function to be ...
    minimized.
[t,y] = ode23(@lotvol,tdata,[p(1),p(2)],[],...
    p(3),p(4),p(5),p(6));
errx = y(:,1)-xdata';
erry = y(:,2)-ydata';
J = errx'*errx + erry'*erry;
end
```

In fact, the **6** parameter estimate from above is not sufficiently close to the convergent values, so `fminsearch` must be run twice (or have its options adjusted) to obtain adequate convergence.

This means assign `p0` to the output value of p and rerun `fminsearch`.

Fitting the Model to Parameters 6

The ***best fitting parameters*** from **MatLab** are ***initial conditions***:

$$H(0) = 34.9134 \qquad \text{and} \qquad L(0) = 3.8566.$$

and parameters:

$$a_1 = 0.48069, \quad a_2 = 0.024822, \quad b_1 = 0.92718, \quad b_2 = 0.027564.$$

with the ***least sum of square errors*** being $J = 594.94$.

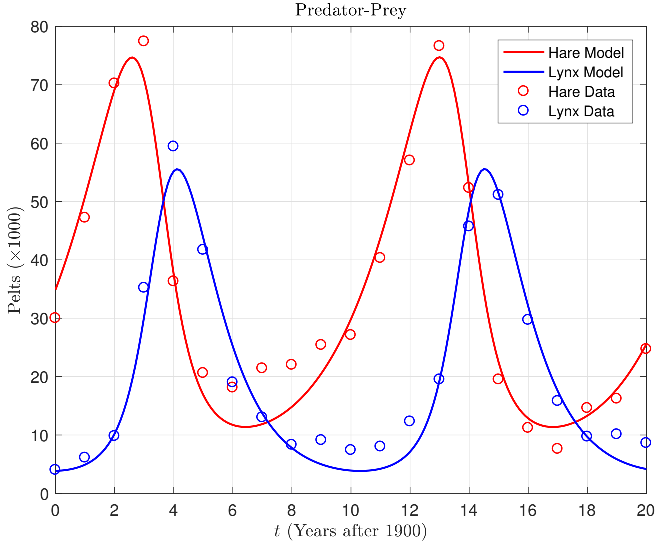
This results in the ***equilibrium***:

$$H_e = 33.637 \qquad \text{and} \qquad L_e = 19.365.$$

These parameters are used in the **MatLab** program `ode23` to create the graphs of the ***time series simulation*** and ***phase portrait***.

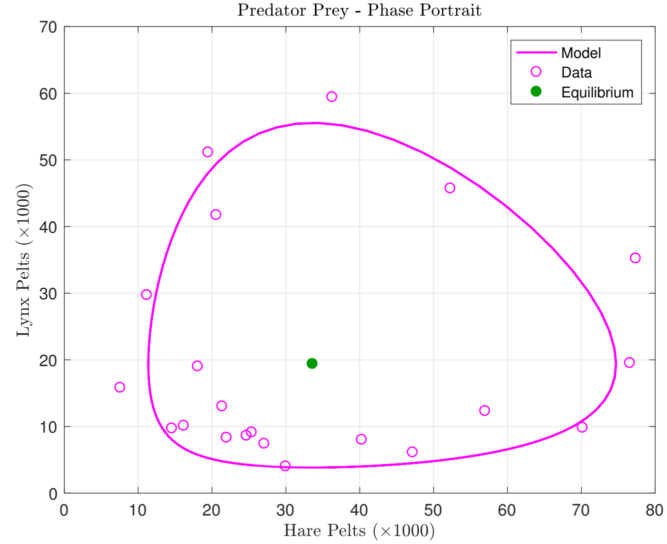
Fitting the Model to Parameters 7

The *graph* using the best fitting parameters of the ***Lynx/Hare Model***.



Fitting the Model to Parameters 8

The *phase portrait* using the best fitting parameters of the ***Lynx/Hare Model***.

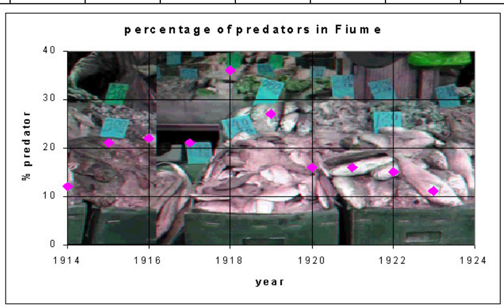


Modeling of Fishing 1

Data on Fishing: Interesting study in 1924 showed human fishing seriously impacts fish populations.

- In 1924, Humberto D'Ancona, an Italian biologist, completed a statistical study of fish populations in the Adriadic Sea.
- The study shows that the reduced fishing in World War I resulted in an increased percentage of predator fish, especially sharks and skates, in the markets.
- This increase in percentage of the predator fish declined after the war.

Year	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923
Predator	12%	21%	22%	21%	36%	27%	16%	16%	15%	11%



Modeling of Fishing 2

Model for Fishing: Volterra created a model to explain increases in predator population. Why should World War I affect the relative frequency of fish in Italian ports?

- D'Ancona asked Volterra (father-in-law) if there was a mathematical model to explain this observed relative change in the populations of fish species.
- Volterra produced a series of models for the interaction of two or more species.
- Data do not show oscillations, but a rise and fall in the percent of sharks and skates of the fish catch due to the war.
- A modification of the predator-prey model, using an equilibrium analysis, can explain the observed data.
- Volterra reasoned that the dangers of fishing during wartime and the loss of fishermen to fighting in the war, caused a significant decline in the amount of fishing.
- This decline in fishing is included in a modification of the predator-prey model.

Modified Predator Prey Model 1

Modified Predator Prey Model: Let $F(t)$ be the food fish or prey fish and $S(t)$ be the shark and skate population (less desirable catch in those times).

The Lotka-Volterra predator-prey model with fishing is written:

$$\frac{dF}{dt} = a_1F - a_2FS - a_3F,$$
$$\frac{dS}{dt} = -b_1S + b_2FS - b_3S,$$

where the coefficients a_1, a_2, b_1, and b_2 are the same as the previous predator-prey model, while a_3 and b_3 reflect the intensity of fishing by nets.

The analysis previously showed that the integral average around a cycle gives the ***equilibrium***.

Thus, if the ***predator-prey solution cycles*** have a sufficiently short period, then observed fish catches should reflect the ***equilibrium***.

Furthermore, the ***Lotka-Volterra model*** is a ***structurally unstable model***, so the oscillating solutions cannot be trusted. However, the ***equilibrium*** is **robust**.

Modified Predator Prey Model 2

The **Modified Predator Prey Model** is:

$$\frac{dF}{dt} = a_1F - a_2FS - a_3F,$$
$$\frac{dS}{dt} = -b_1S + b_2FS - b_3S,$$

so the ***equilibria*** satisfy:

$$a_1F_e - a_2F_eS_e - a_3F_e = F_e(a_1 - a_2S_e - a_3) = 0,$$
$$-b_1S_e + b_2F_eS_e - b_3S_e = S_e(-b_1 + b_2F_e - b_3) = 0,$$

where F_e and S_e are the ***equilibria***.

From an analysis similar to the one for the ***Lynx/Hare model***, it is easy to see there are ***two equilibria***:

$$(F_e, S_e) = (0,0) \quad \text{(Extinction)} \qquad \text{or} \qquad (F_e, S_e) = \left(\frac{b_1 + b_3}{b_2}, \frac{a_1 - a_3}{a_2}\right).$$

With no fishing ($a_3 = b_3 = 0$), this model has the same ***equilibria*** as the ***Lynx/Hare model***.

Modified Predator Prey Model 3

The nonzero ***equilibrium*** of the **modified Predator-Prey model** is:

$$(F_e, S_e) = \left(\frac{b_1 + b_3}{b_2}, \frac{a_1 - a_3}{a_2}\right),$$

where a_3 and b_3 reflect the fishing intensity from the linear process of netting fish proportional to their densities in the water.

- The equilibrium, F_e, increases as harvesting of their natural predator increases, b_3.
- The model shows that human harvesting of $F(t)$, seen in a_3 (at least when not too extreme), does not appear in the formula for F_e.
- Thus, fishing for the food fish has no effect on the food fish equilibrium, F_e, which is not so intuitive!
- The equilibrium of the sharks and skates, S_e, decreases as a_3 increases.
- This makes sense because the fisherman are in direct competition with the sharks and skates for this food source.
- Again the model shows that human harvesting of $S(t)$, seen in b_3 (at least when not too extreme), does not appear in the formula for S_e.
- Thus, fishing for $S(t)$ has no effect on the equilibrium, S_e, which is not so intuitive!

Modified Predator Prey Model 4

The ***equilibrium*** study of the **modified Predator-Prey model** agrees qualitatively with the data of D'Ancona.

Thus, as the level of fishing, a_3 and b_3, decreases then the ***equilibrium analysis*** gives support that the percent of the food fish, F, would increase over the percent selachians in the fish markets (though numbers of both would be lower).

There is insufficient data to obtain more than this gross qualitative overview of the effect of human fishing on the population dynamics.

More detailed studies of the data and the model would be required to obtain better qualitative and quantitative results.