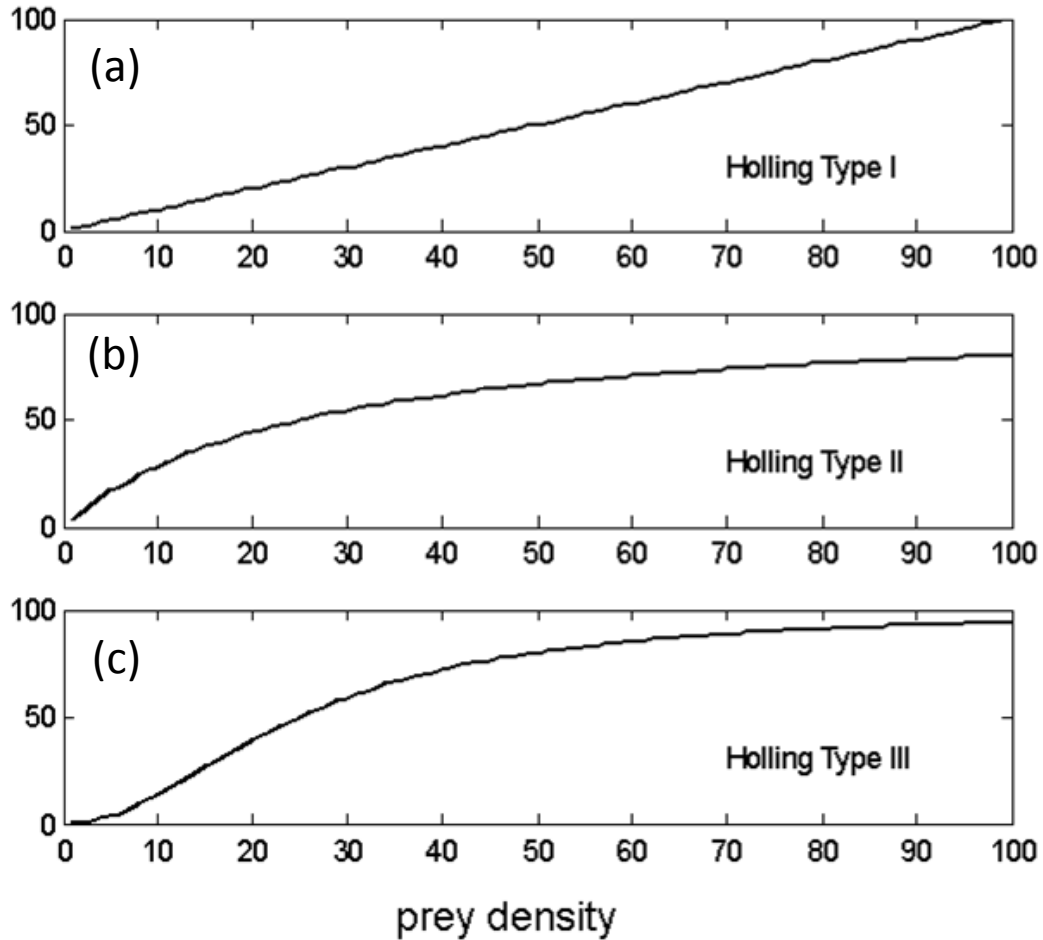
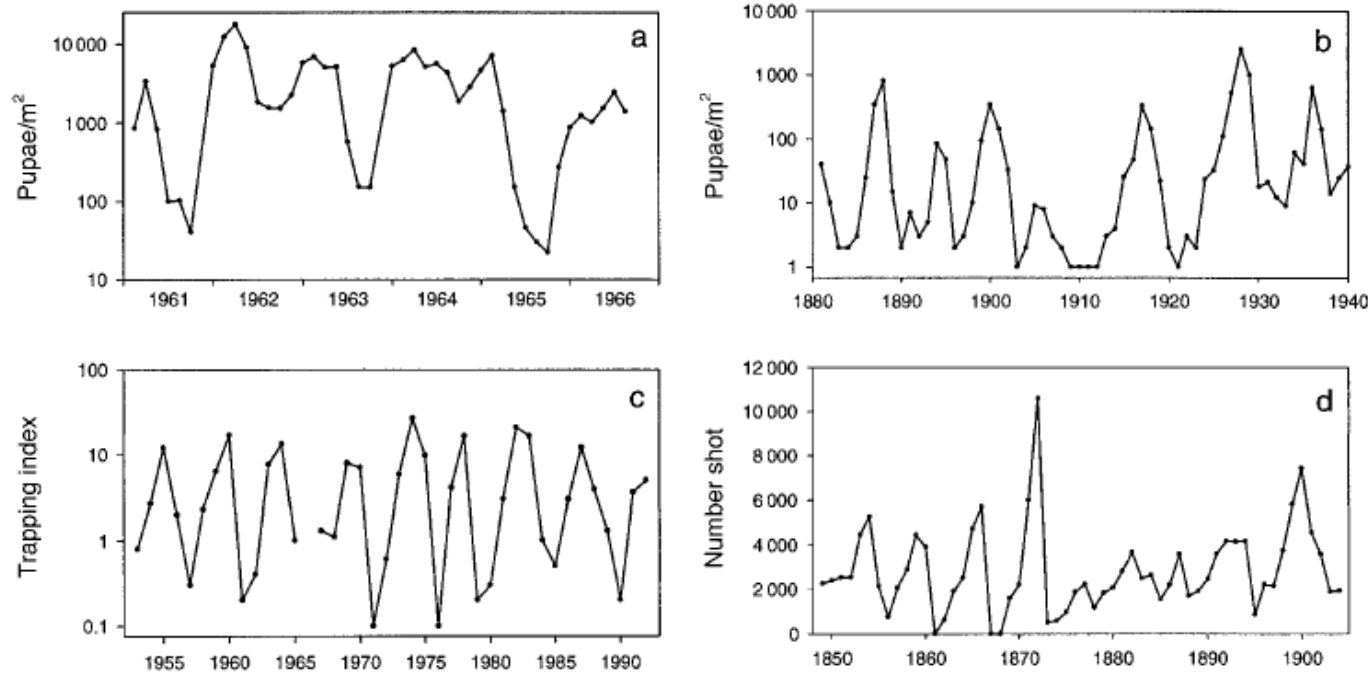


# Quiz



Which *functional response* is a result of search and handling of prey by predators?  
(a), (b), or (c)

# Frequency of Cyclical Dynamics

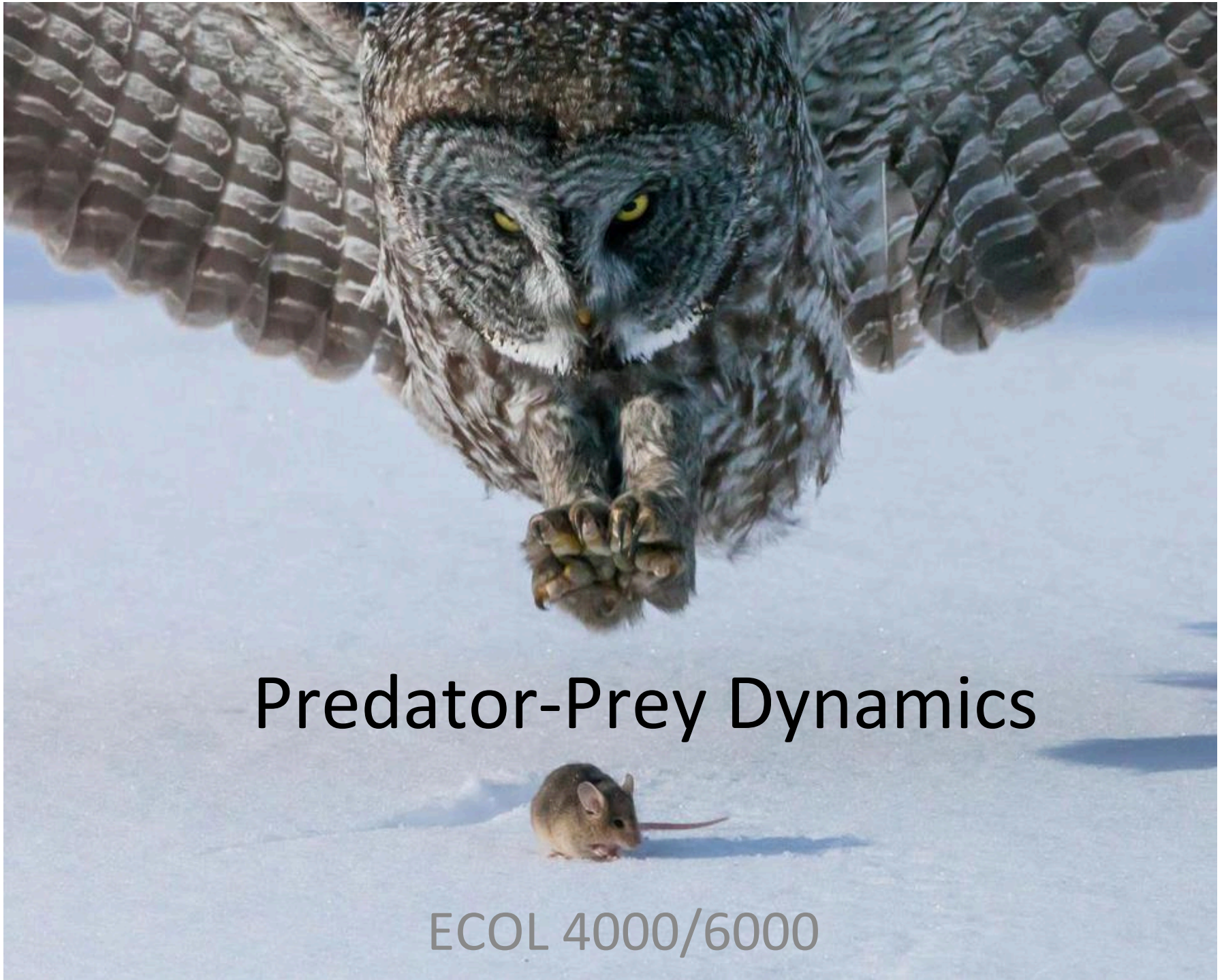


From Kendall et al. (1999) *Ecology* 80: 1789-1805.

30% of long term time series exhibit periodic oscillations



FIG. 1. Examples of cyclic population dynamics. (a) Coffee leaf-miners (*Leucoptera* spp.) at Lyamungu, Tanzania (Bigger 1973). (b) Pine looper (*Bupalus piniarius*) in Germany (Schwerdtfeger 1941). (c) Voles (*Microtus* and *Clethrionomys*) at Kilpisjärvi, northern Finland (Laine and Henttonen 1983, Hanski et al. 1993). (d) Red Grouse (*Lagopus lagopus scoticus*) in Scotland (Middleton 1934).



# Predator-Prey Dynamics

ECOL 4000/6000

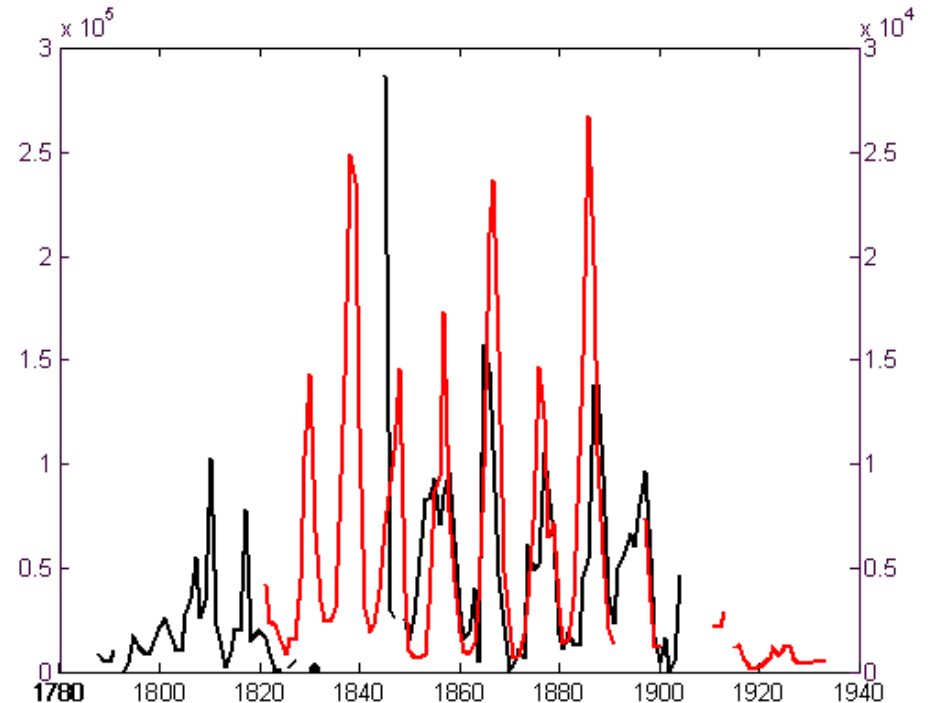
# Key points

- Recall two sources of predator-prey dynamics
- Identify basic components of predator-prey models (births, deaths, predation, other terms)
- Understand, write down, sketch functional responses 1,2,3 (recall sources for each of 2 and 3)
- Understand/identify key stabilizing and destabilizing mechanisms
- Translate predator-prey dynamics to phase plane (and vice-versa)
- Calculate straightforward coexistence equilibria
- Sketch null clines (ZNGIs) for key models
- Populate Jacobian matrix for certain predator-prey models (as in lecture/reading)
- Understand the principle of linearization and the meaning of the zones in a trace-determinant map
- Articulate the principle of the 'paradox of enrichment')

# Predator-Prey Dynamics

- A ubiquitous inter-specific interaction in nature
- A building block for understanding food webs
- An explanation for cyclical population dynamics

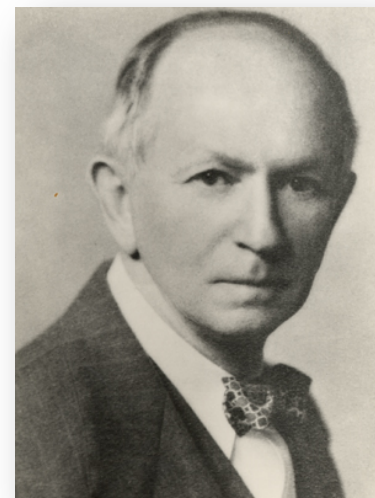
Hare-Lynx pelts from the Hudson's Bay Co.



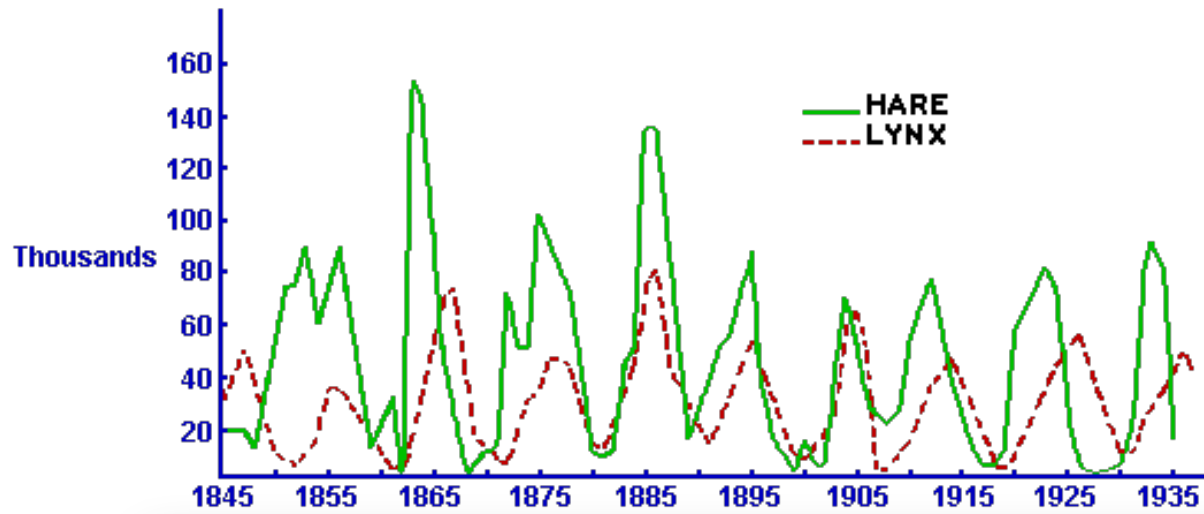
# Lotka-Volterra Model

(Predator-Prey)

- Vito Volterra (1860-1940)
  - Italian Mathematician
  - Studied these equations in 1926
- Alfred J. Lotka (1880-1949)
  - Statistician and actuarial demographer
  - Studied these equations in 1925



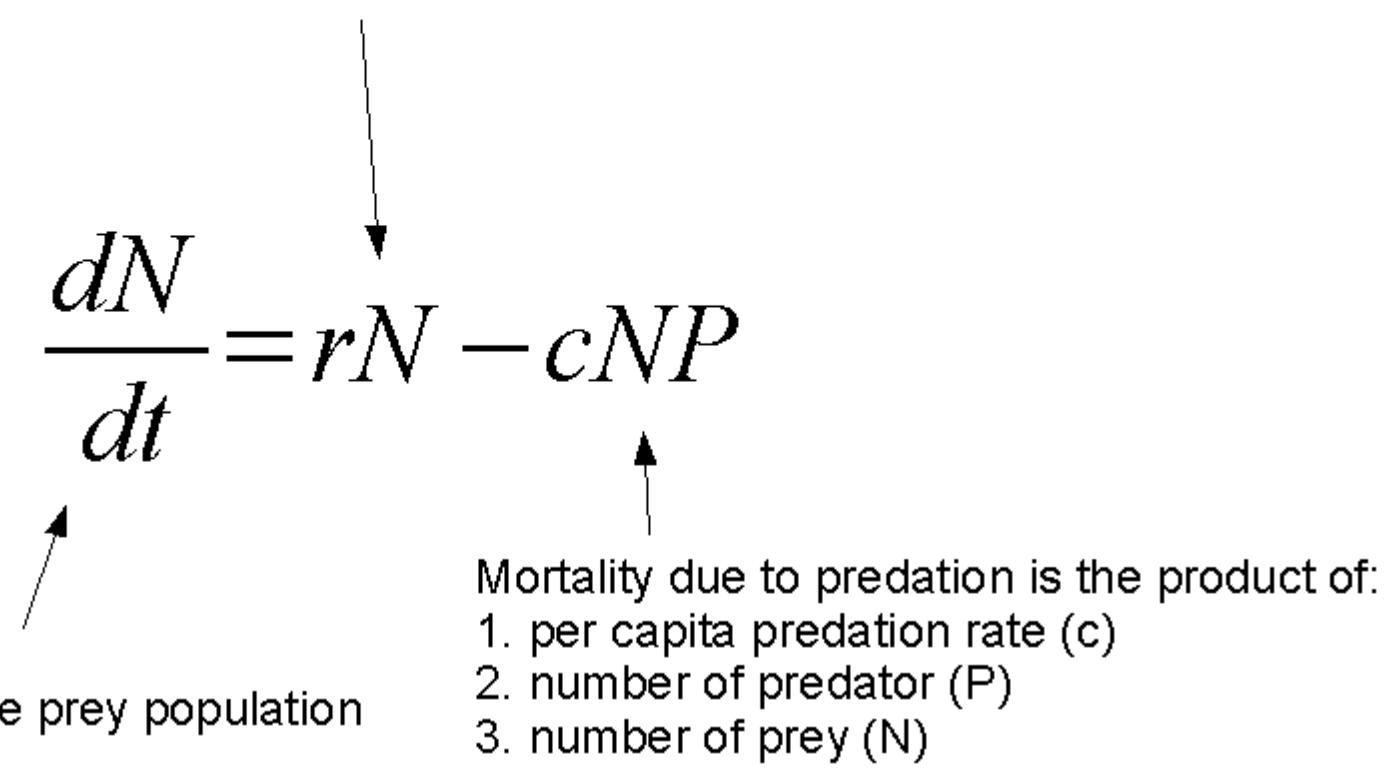
# Hare-Lynx Dynamics in Canada



# Lotka-Volterra Model

(Predator-Prey)

Population growth through reproduction and non-predator mortality


$$\frac{dN}{dt} = rN - cNP$$

The diagram features the equation  $\frac{dN}{dt} = rN - cNP$  centered on the page. A vertical arrow points downwards from the text 'Population growth through reproduction and non-predator mortality' to the term  $rN$ . Another vertical arrow points upwards from the text 'Mortality due to predation is the product of: 1. per capita predation rate (c) 2. number of predator (P) 3. number of prey (N)' to the term  $cNP$ . A diagonal arrow points upwards from the text 'Rate of change of the prey population' to the fraction  $\frac{dN}{dt}$ .

Rate of change of the prey population

Mortality due to predation is the product of:

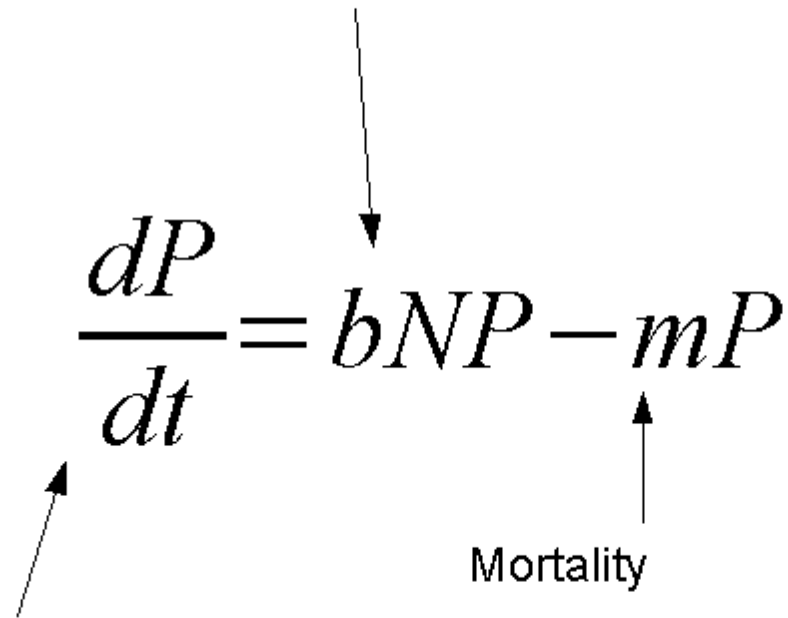
1. per capita predation rate ( $c$ )
2. number of predator ( $P$ )
3. number of prey ( $N$ )



# Lotka-Volterra Model

(Predator-Prey)

Population growth through “conversion” of prey



The diagram shows the differential equation  $\frac{dP}{dt} = bNP - mP$ . A vertical arrow points from the text 'Population growth through “conversion” of prey' down to the term  $bNP$ . Another vertical arrow points from the text 'Mortality' up to the term  $-mP$ . A diagonal arrow points from the text 'Rate of change of the predator population' up to the fraction  $\frac{dP}{dt}$ .

$$\frac{dP}{dt} = bNP - mP$$

Rate of change of the predator population

# Lotka-Volterra Model

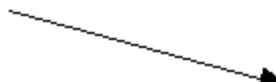
(Predator-Prey)

$$\frac{dN}{dt} = rN - cNP$$


$$\frac{dP}{dt} = bNP - mP$$

## Solution of a simple ODE

Diff'l eqn


$$\frac{dN}{dt} = rN$$

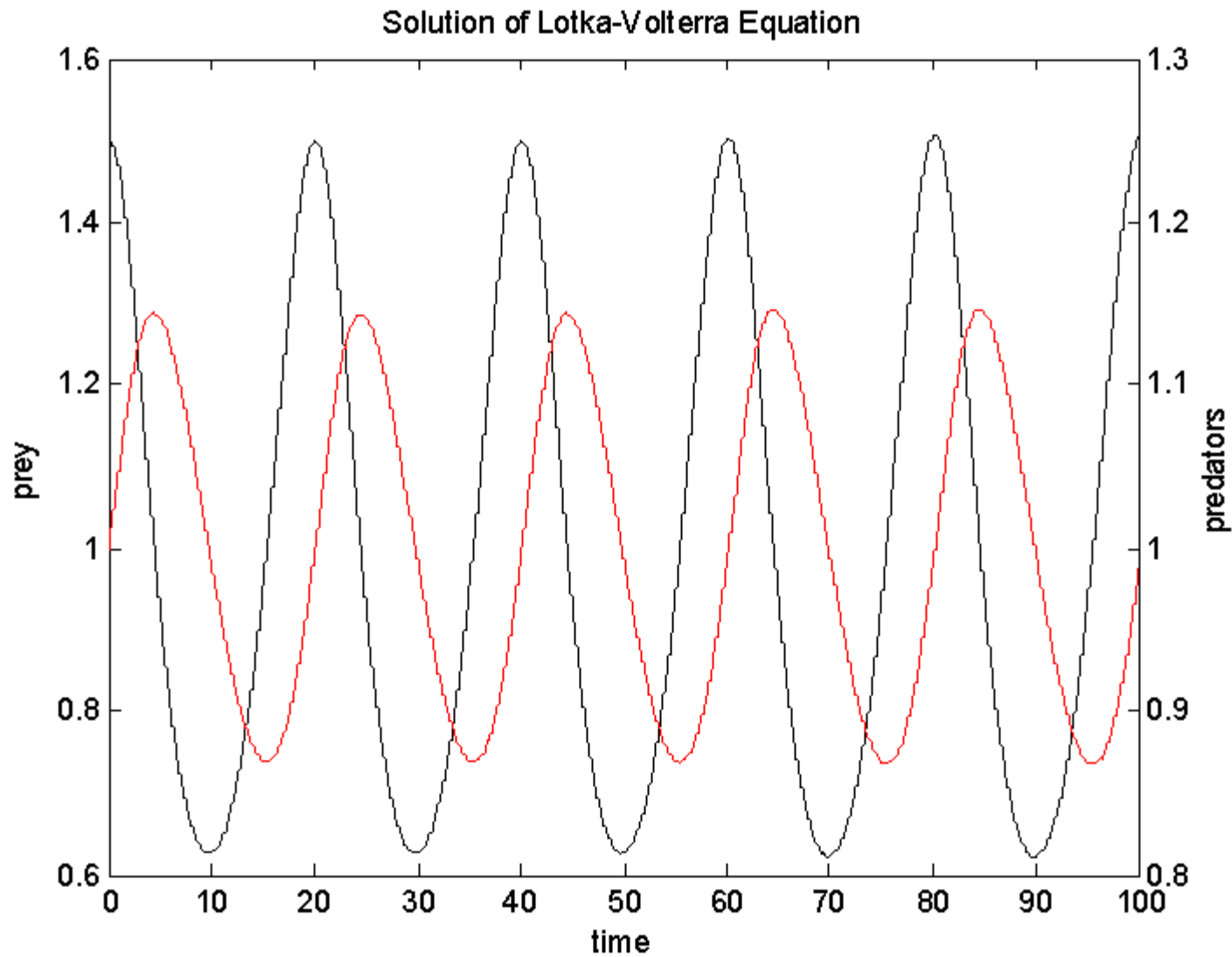
Solution


$$N_t = N_0 e^{rt}$$

# No simple solution: Alternative strategies needed to study this model

- Graphical Analysis
- Local stability analysis

# Graphical Analysis

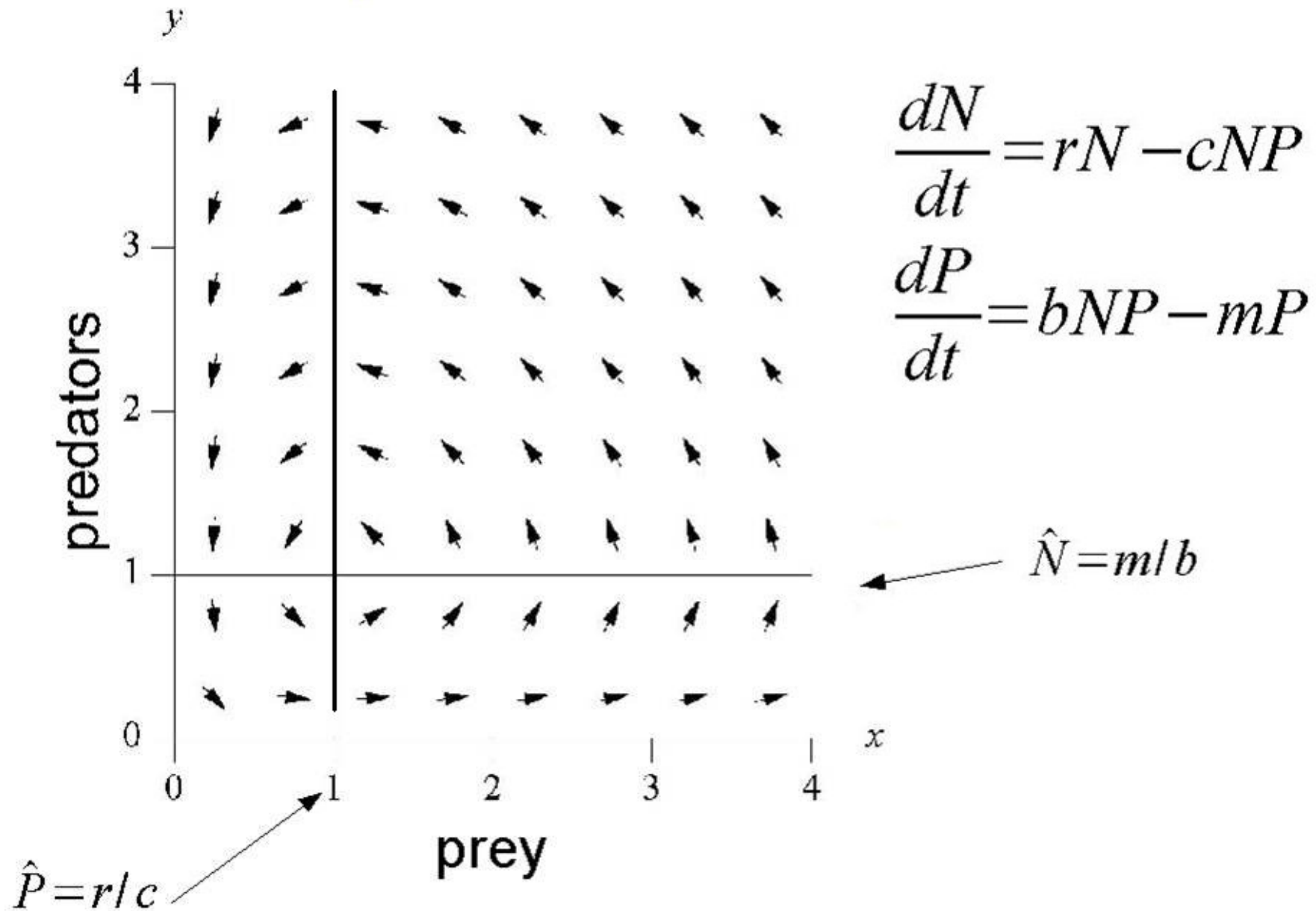


## Step 1: Find equilibria

$$\begin{array}{l} \frac{dN}{dt} = rN - cNP \\ \frac{dP}{dt} = bNP - mP \end{array} \longrightarrow \begin{array}{l} \frac{dN}{dt} = N(r - cP) \\ \frac{dP}{dt} = P(bN - m) \end{array}$$

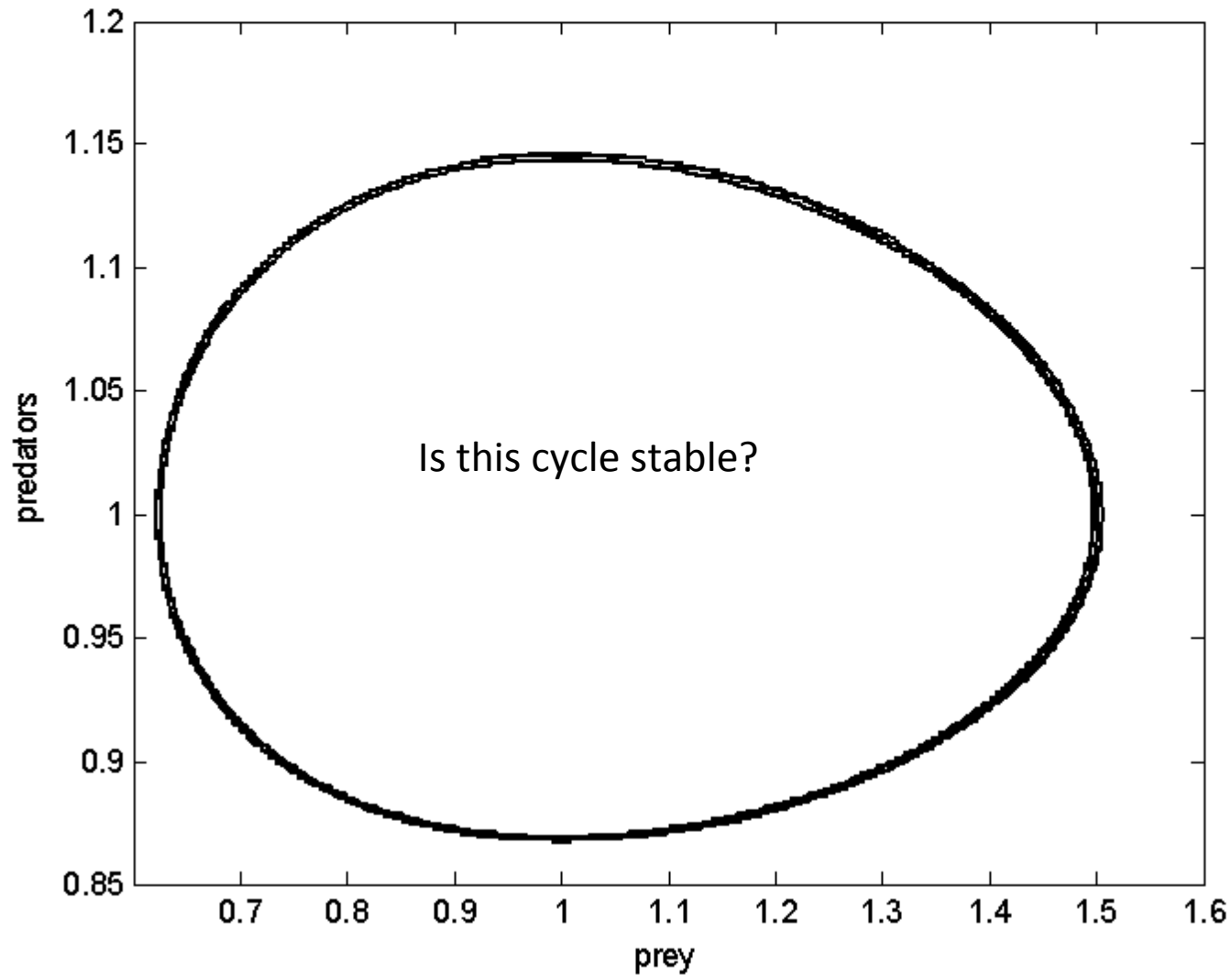
$$(N^*, P^*) = (0, 0), \left( \frac{m}{b}, \frac{r}{c} \right)$$

## Step 2: Sketch Null Clines



# Phase Portrait

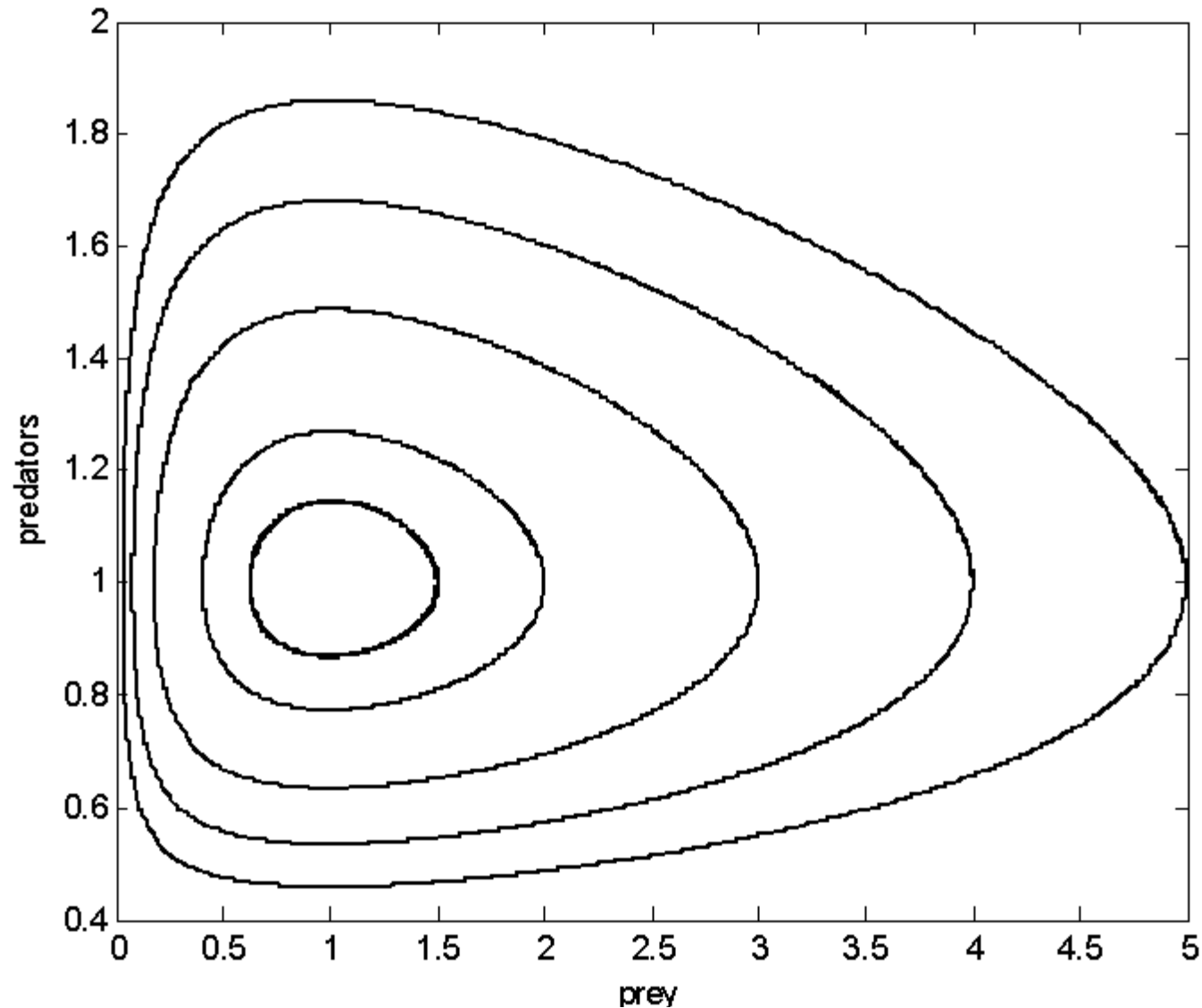
initial condition: prey=1.5 predators=1





# The L-V model is neutrally stable

initial condition: prey=[1.5, 2,3,4,5], predators=1



# Stabilizing Mechanisms

$$\frac{dN}{dt} = f(N) - g(N)P$$

$$\frac{dP}{dt} = h(g(N))P - m(P)$$

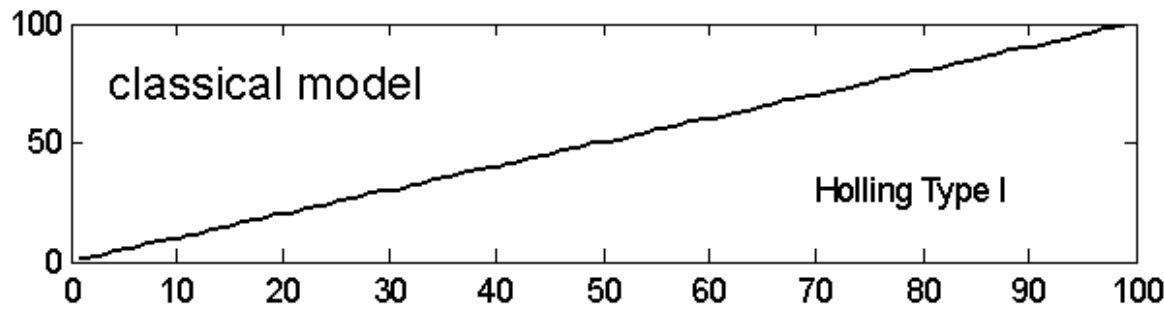
$f(x)$  – prey regulation

$g(x)$  – “functional response”

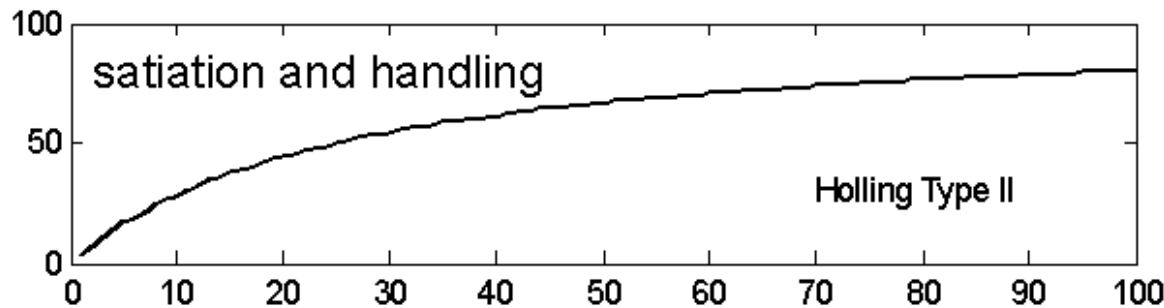
$h(x)$  – “numerical response”

$m(x)$  – predator mortality

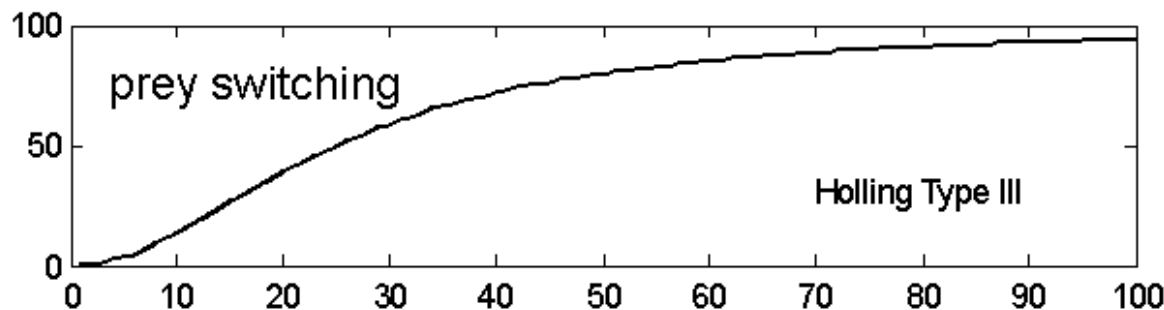
# Functional response



$$g(N) = cN$$



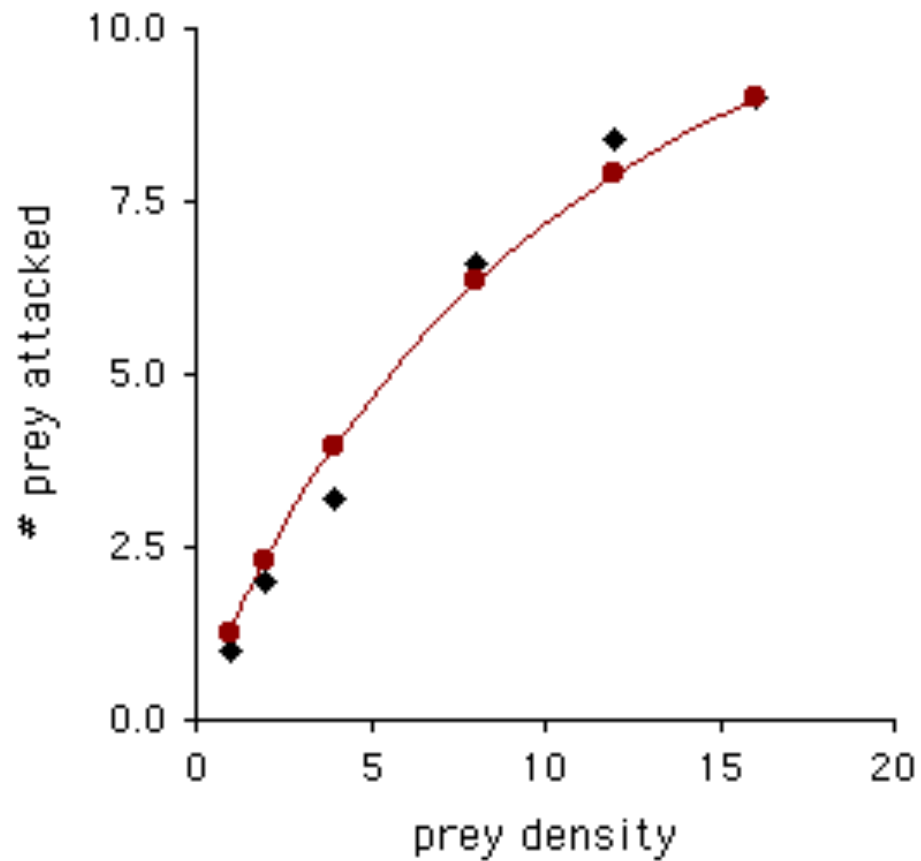
$$g(N) = \frac{\alpha N}{D + N}$$



$$g(N) = \frac{\alpha N^2}{D^2 + N^2}$$

prey density

# Type II Functional Response



Predator: Stinkbug  
(*Podisus maculiventris*)



Prey: Mexican Bean Beetle  
(*Epilachna varivestis*)

# Type II Functional Response

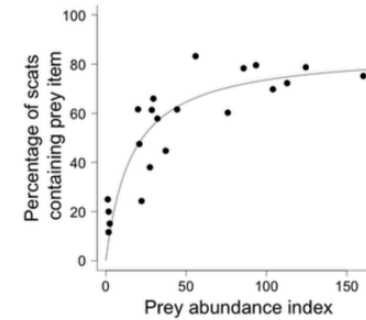
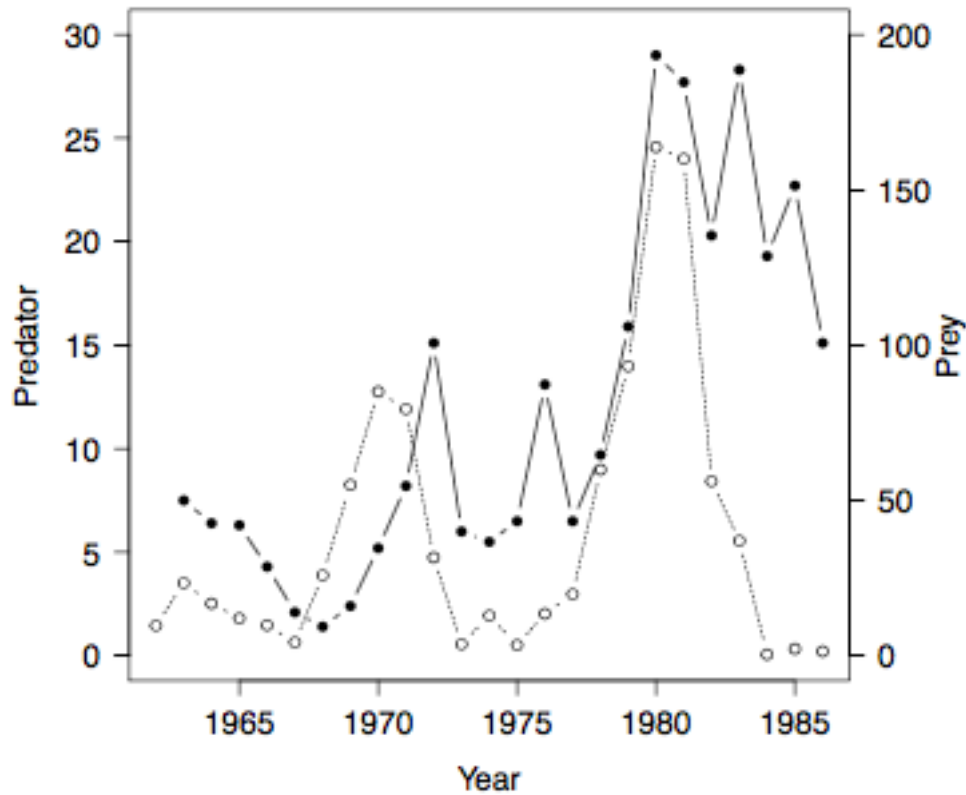
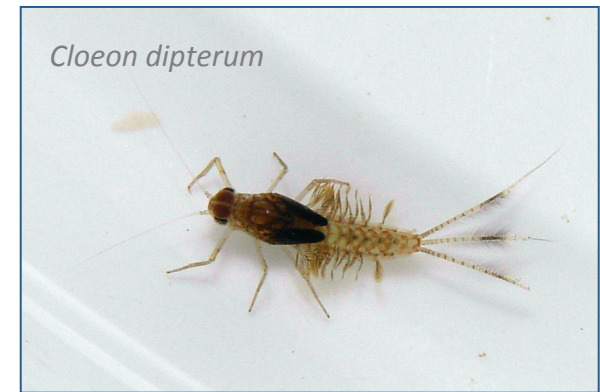
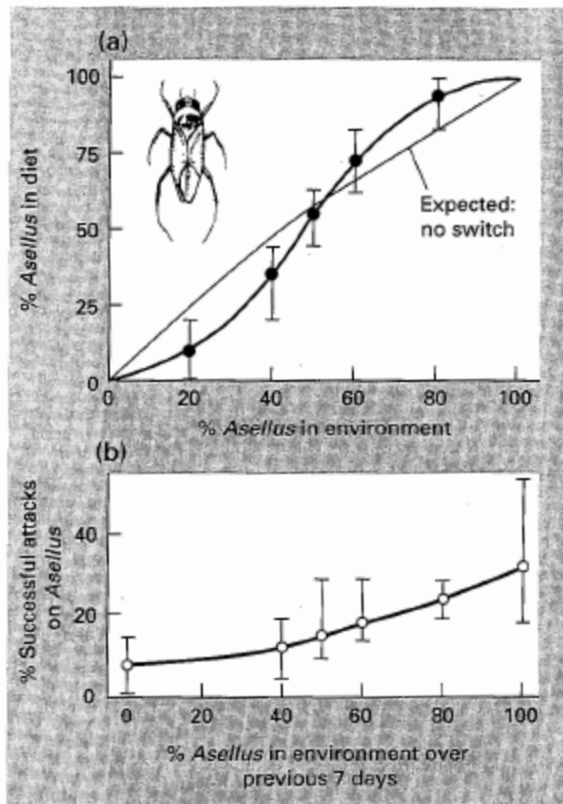


Figure 7: *C. latrans* functional feeding response to *L. californicus* abundance in Curlew Valley, Utah, 1977-1993. (Adapted from Bartel and Knowlton, 2005, *Canadian Journal of Zoology*)



Figure 1: Coyote (*Canis latrans*).

# Type III Functional Response



$$g(N) = \frac{\alpha N^2}{D^2 + N^2}$$

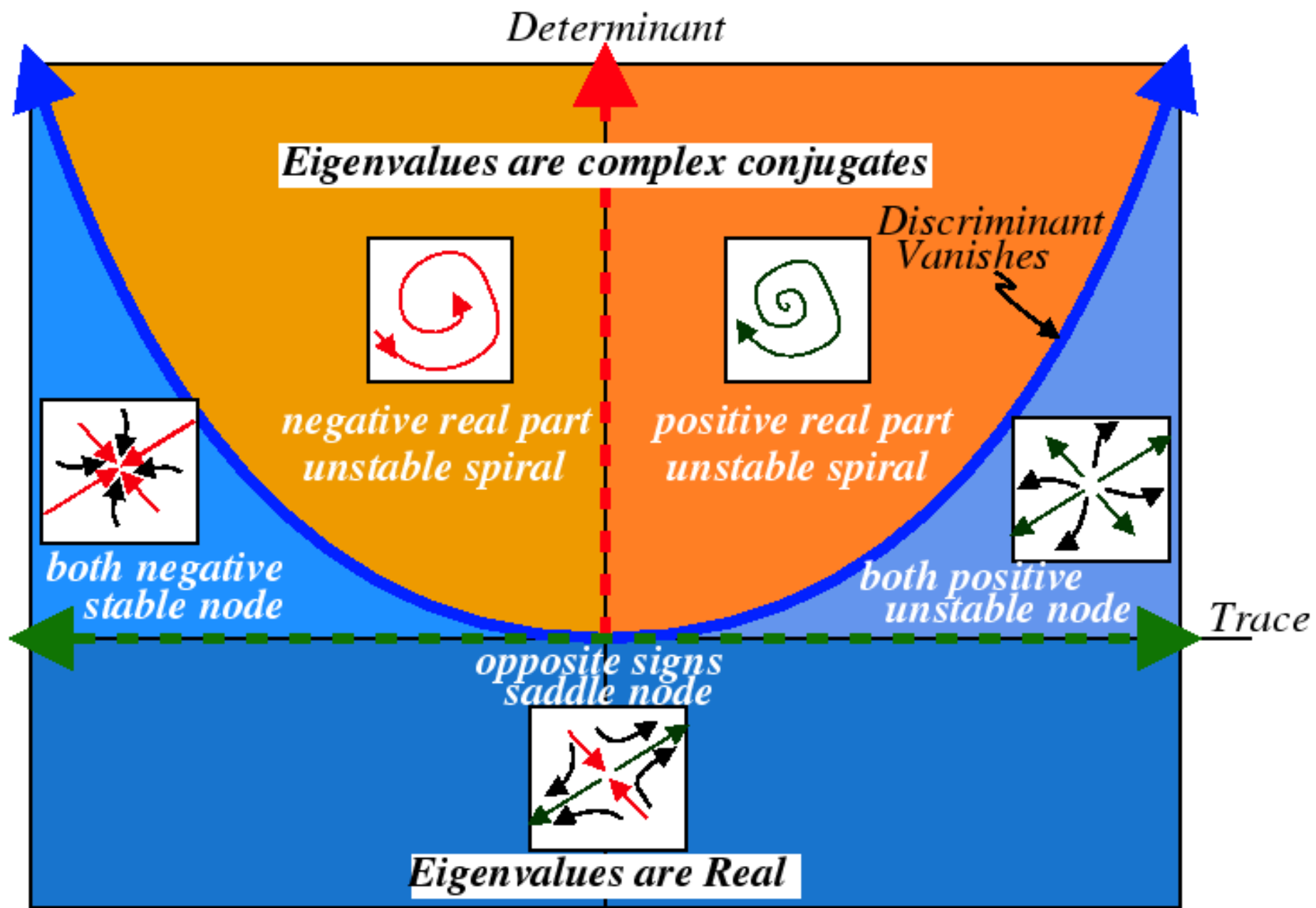
# Prey Equation

(Type II functional response)

$$\frac{dN}{dt} = rN - \frac{\alpha N P}{D + N}$$

$$N_{eq} = 0, \frac{\alpha P - rD}{r}$$

Effect of Type II functional response is *destabilizing*





# Stabilizing Mechanisms

- Basic L-V model is neutrally stable
- Type II (predator satiation) is **destabilizing**

# Stabilizing Mechanisms

- Basic L-V model is neutrally stable
- Type II (predator satiation) is **destabilizing**
- Prey regulation (logistic) is **stabilizing**
- Type III is **parameter dependent and initial condition dependent**
- Predator regulation (logistic) is **stabilizing**
- Prey refuge is **stabilizing**
- Predator immigration is **stabilizing**

# Explaining Persistent Cycles

- We started with a biological observation – evidently persistent cycles in hare and lynx
- We developed a model (L-V) to explain these cycles, but it was neutrally stable and therefore biologically unrealistic
- We enriched the theory with the concept of “stabilizing mechanisms”
- But, have we explained persistent cycles?

# Explaining Persistent Cycles

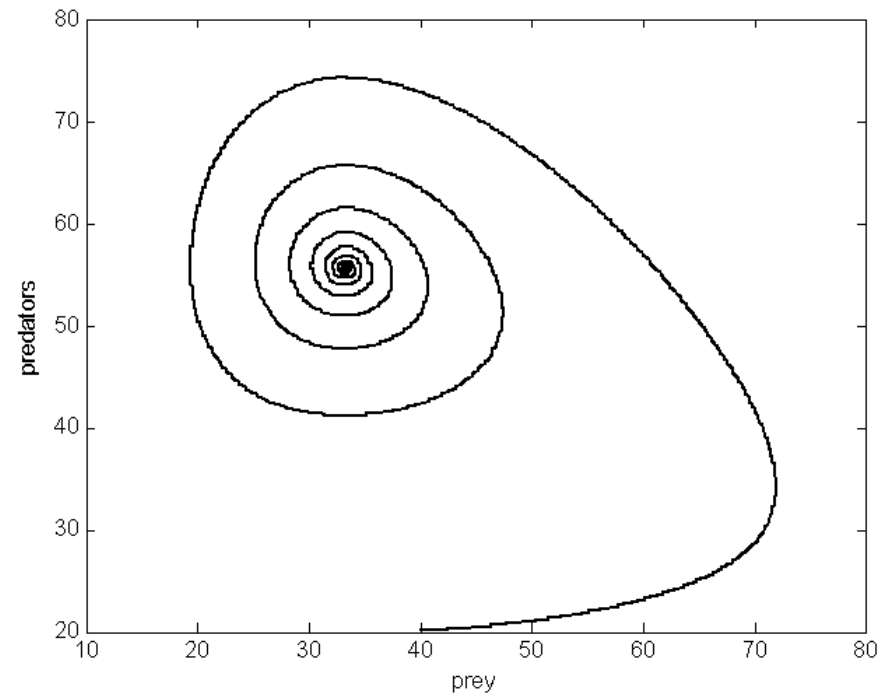
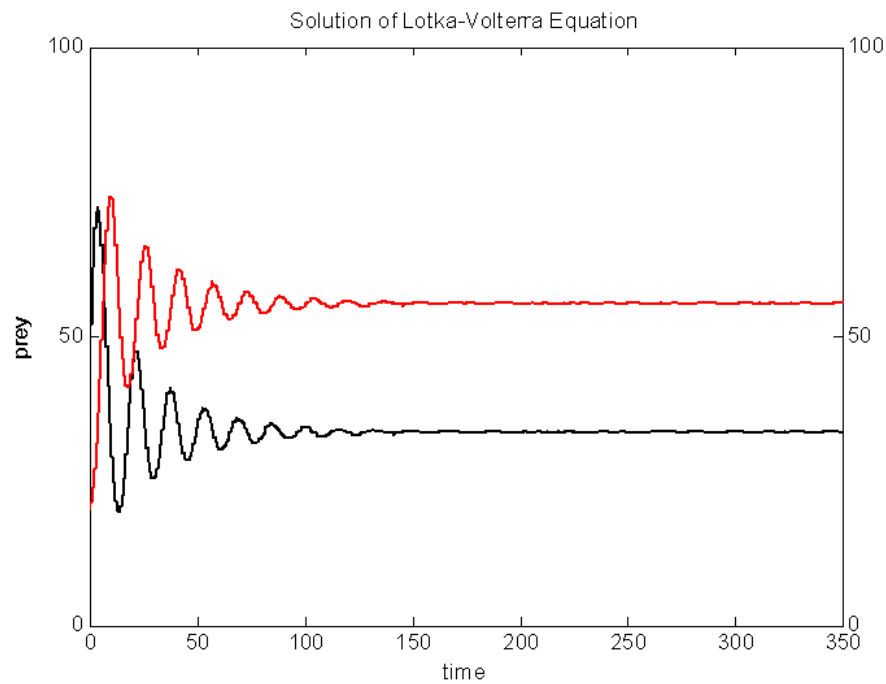
Combining stabilizing and destabilizing processes

The Rosenzweig-MacArthur Model

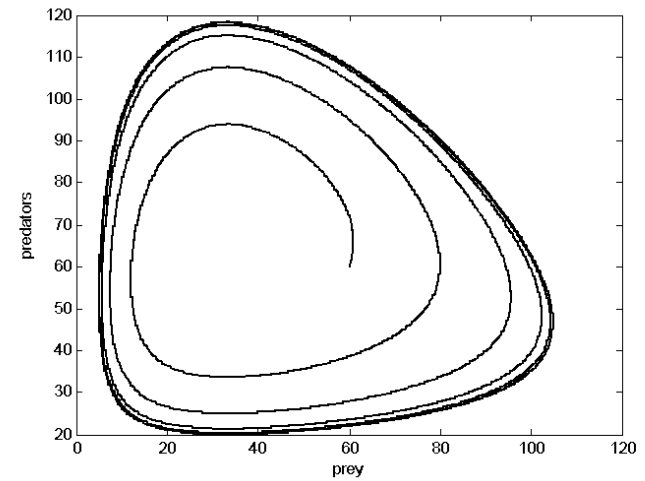
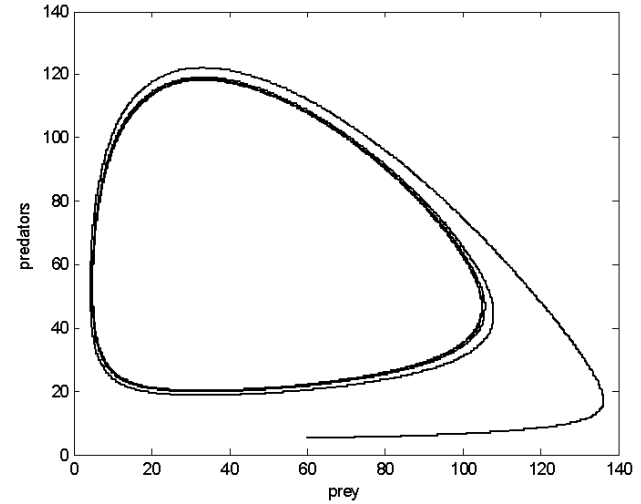
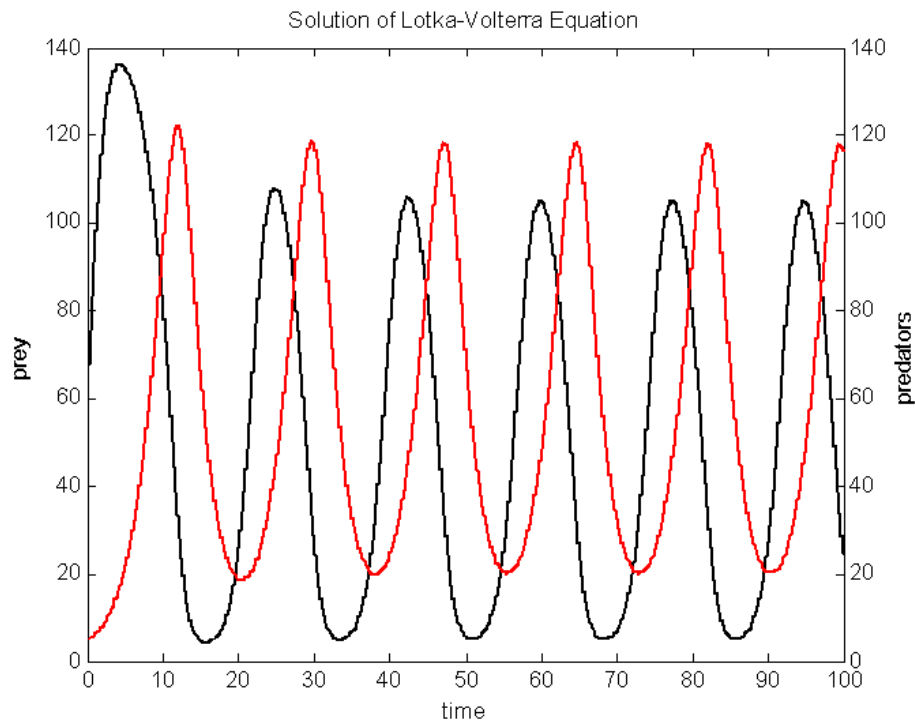
$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) - \frac{\alpha N P}{1 + \alpha T_h N}$$

$$\frac{dP}{dt} = b \frac{\alpha N P}{1 + \alpha T_h N} - mP$$

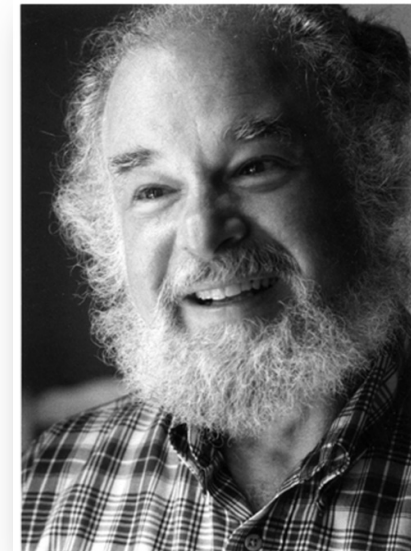
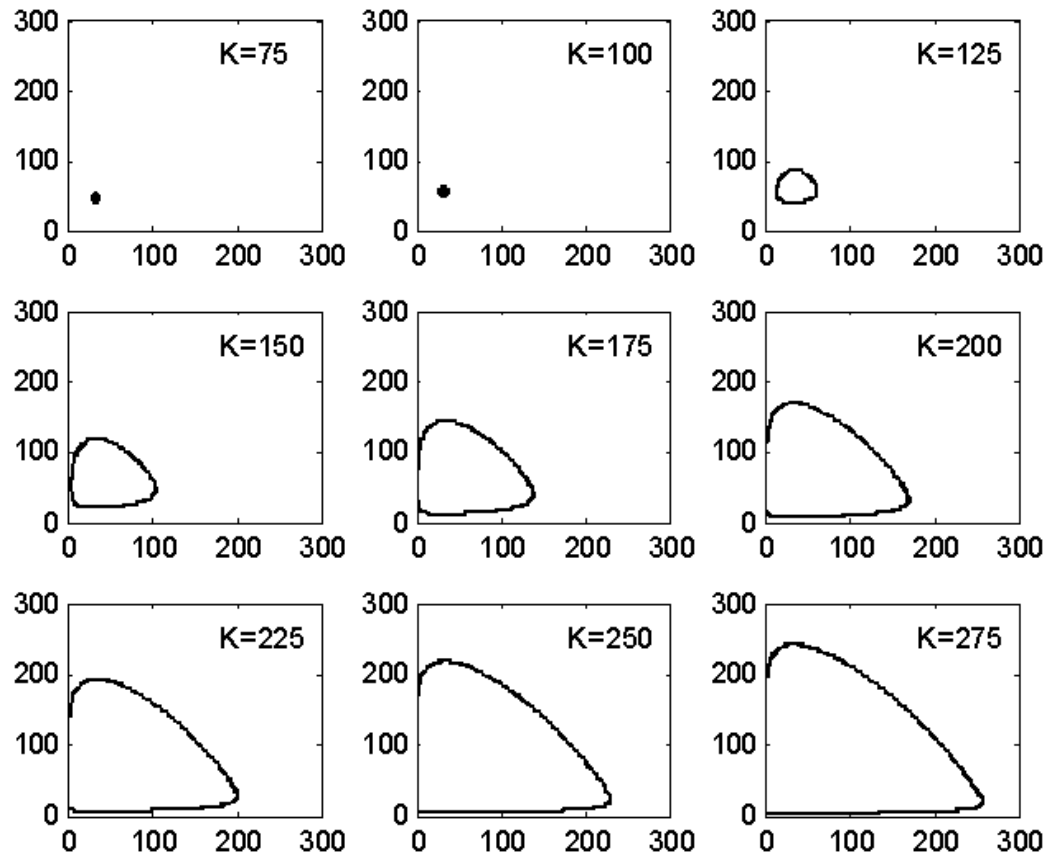
# Exhibits Damped Oscillations



# Or, Persistent Cycles



# The Paradox of Enrichment



# Conclusions

- Periodic population dynamics are common
- Periodicity appears most frequently among pairs of antagonistically interacting species
- Antagonistic interactions (i.e., predator-prey) are not sufficient to explain persistence, however, as revealed by the neutral stability of the Lotka-Volterra model
- Persistent periodic dynamics appear to result from the addition of both stabilizing and destabilizing mechanisms