# Domination & Hierarchy in Ecosystems

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# Introduction

- Universal characteristics of Ecosystems
  : in dominance/competition/hierarchy
- Behavioral choice with Preference
  : dynamics with two Time Scales
- Lotka-Volterra with Parametric Variation
- Prediction without hand waving

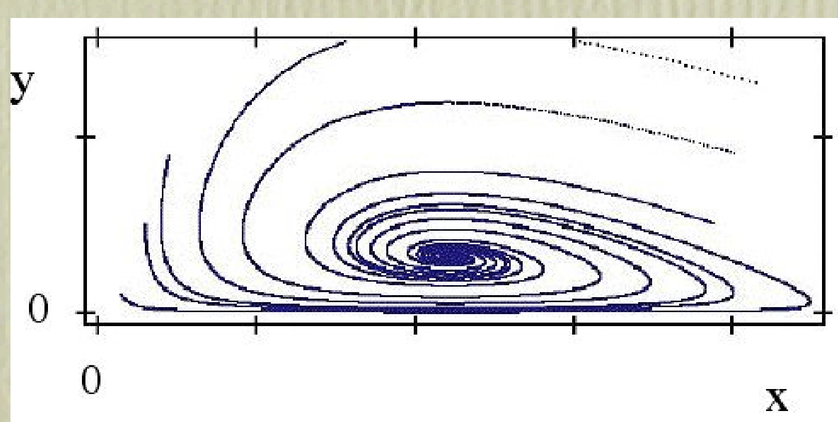
# Plan of the Talk

- Optimal aggression in prey-predator system
- N-species vertical food-chain :
  Elton's pyramid of number
- Two competitors with a master :
  Why are there boses?

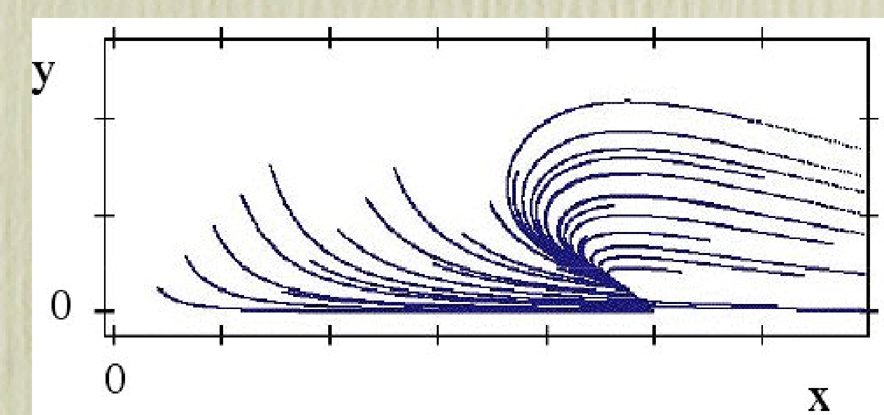
# Prey-Predator System

- Lotka-Volterra eq. for N=2 Food web
  $dx/dt = b\,x - a\,x^2 - R\,x\,y$
  $dy/dt = -d\,y + f\,R\,x\,y$
- ( a, b, d, f ) fixed parameters
- aggression {R} varies adiabatically to maximize predator y

# Fixed Point Solutions

- System evolves toward absorptive fixed point (X, Y) (when fRb>ad):
  - $0 = b - a X - R Y$
  - $0 = -d + f R X$
- 

“right” R

“wrong” R

# Evolution of Aggression

- Fixed point (X[R], Y[R])
  stability eigenvalues $<0$ ( $fRb \gg ad$ )
- Assume R addiabatically evolves
  to increase Y[R]
- A possible evolution equation ($M \gg 1$)
  $1/R \; dR/dt = -1/M \; dY[R]/dR$

# Optimal Aggression

- Irrespective to precise form of R evolution, it will evolve toward R* that maximize

$$Y\{R\} = -b/R + ad/fR^2$$

- Evol. stability at $R^* = 2ad/fb$

$$X^* = b/2a, \quad Y^* = b/2R^*$$

- half of natural population $X=b/a$ taken

# Tritrophic System

- N=3 Food web
  $dx/dt = b\,x - a\,x^2 - R_2\,x\,y$
  $dy/dt = -d_2\,y + f_2\,R_2\,x\,y - R_3\,y\,z$
  $dz/dt = -d_3\,z + f_3\,R_3\,y\,z$
- Fixed point (X,Y,Z)
- Maximize $Z[R_3]$, $Y[R_2]$ simultaneously

# Separation to 2 Systems

- $0 = b/2 - a(X - b/2a) - R_2 Y$
  $0 = -d_2/2 + f_2 R_2 (X - b/2a)$

- $0 = b_2 - a_2 Y - R_3 Z$ $\quad a_2 := f_2R_2\hat{}2/a$
  $0 = -d_3 + f_3 R_3 Y$ $\quad b_2 := f_2bR_2/a - d_2$

- $R_2^* = 2ad_2/f_2b,$ $\quad X^* = 3b/4a,$ $Y^* = b/2R_2^*$
  $R_3^* = 8ad_2d_3/f_2f_3b\hat{}2,$ $\quad Z^* = d_2/2R_3^*$

# Generalization to N species

- N Food chain

  $dx_1/dt = b\, x_1 - a\, x_1\hat{}2 - R_2\, x_2\, y_2$

  $dx_2/dt = -d_2\, x_2 + f_2\, R_2\, x_1\, x_2 - R_3\, x_2\, x_3$

  ...

  $dx_{N-1}/dt = -d_{N-1}\, x_{N-1} + f_{N-1} R_{N-1} x_{N-2}\, x_{N-1} - R_N x_{N-1}\, x_N$

  $dx_N/dt = -d_N\, x_N + f_N\, R_N\, x_{N-1}\, x_N$

- Maximize $X_N[R_N]\ldots X_2[R_2]$ simultaneously

# Slave & Master Forms

- For $n=1..N-1$
  - $= h_n b_n - a_n (X_n - h_{n+1} b_n / 2a_n) - R_{n+1} X_{n+1}$

    slave form
  - $= -h_n d_{n+1} + f_{n+1} R_{n+1} (X_n - h_{n+1} b_n / 2a_n)$

    master form

- $a_n := f_n R_n\hat{}2/a_{n-1}$, $b_n := f_n R_n b_{n-1}/a_{n-1} - d_n$

  $h_{n+1} := 2^{-2} h_n$ ; $h_{N-1} := 1$, $a_1 = a$, $b_1 = b$

# Pyramidal Hierarchy

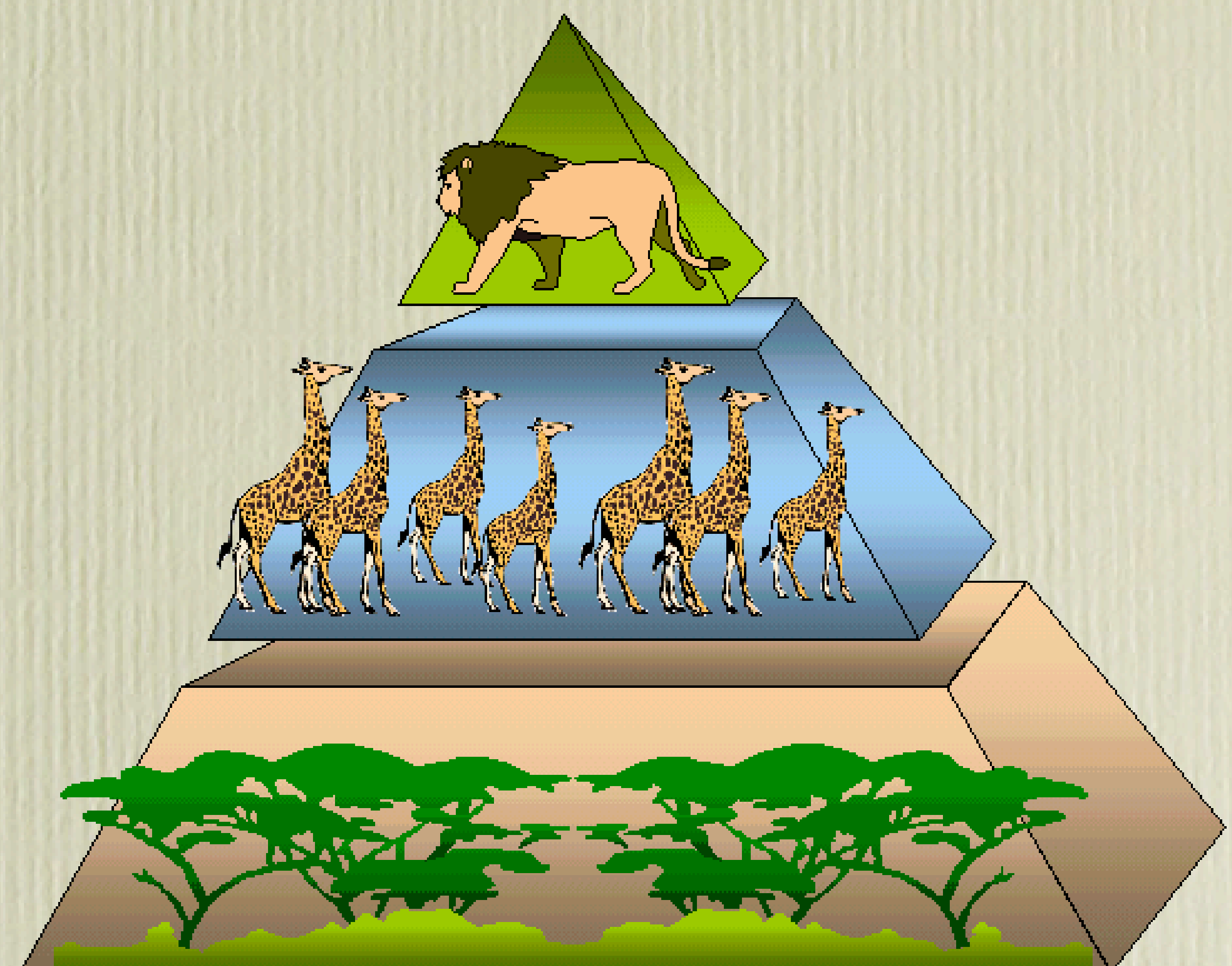
- $R_2^*=2ad_2 / f_2b$,  $R_2^*=8ad_2d_3 / f_2f_3b$, ...
  $R_N^*=2\hat{}(2N-3)ad_{N-1}d_N / f_2...f_Nb$

- $X_1^* = B_Nb / 2\hat{}(N-1)a$ ,
  $X_2^* = B_{N-1}f_2b\hat{}2 / 2\hat{}Nad_2$ ,  ...
  $X_N^* = B_1f_2...f_Nb\hat{}2 / 2\hat{}(2N-3)ad_N$

- $B_{N+2}=B_{n+1}+2B_n$ : A Fibonaci:
  : 1 1 3 5 11 21 43 ...

# Elton's Pyramid of Numbers

- N-trophic food chain $\{x_1, x_2, \ldots, x_N\}$
- Example N=5,
  $X_5^* \sim (1/256)\, X_1^*$
  $X_4^* \sim (1/128)\, X_1^*$
  $X_3^* \sim (3/64)\, X_1^*$
  $X_2^* \sim (5/32)\, X_1^*$
  $X_1^* = (11/16)\, b/a$

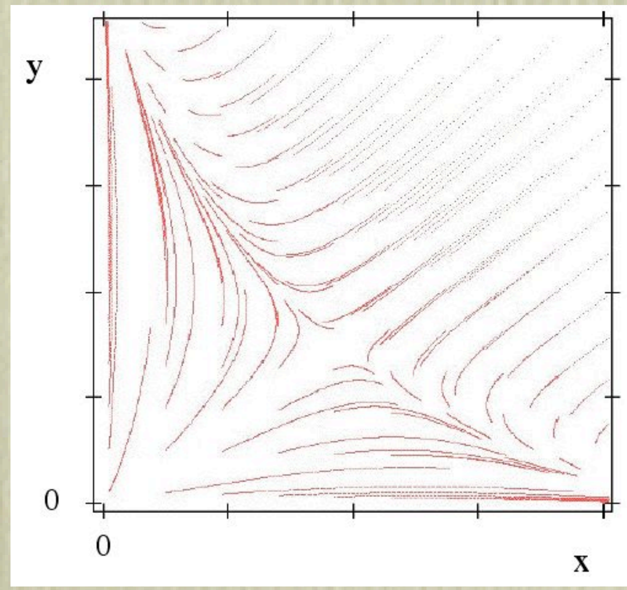


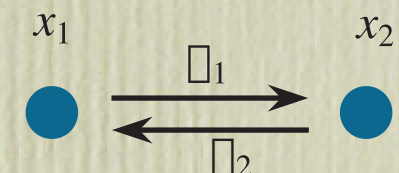
# Competition to Extinction

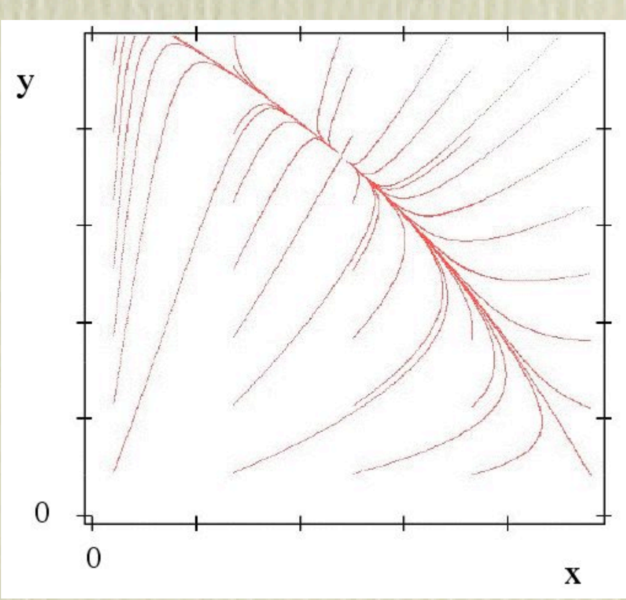
- Two competing species

  $dx_1/dt = b_1 x_1 - a_1 x_1\hat{}2 - R_2 x_1 x_2$

  $dx_2/dt = b_2 x_2 - a_2 x_2\hat{}2 - R_1 x_1 x_2$

- 

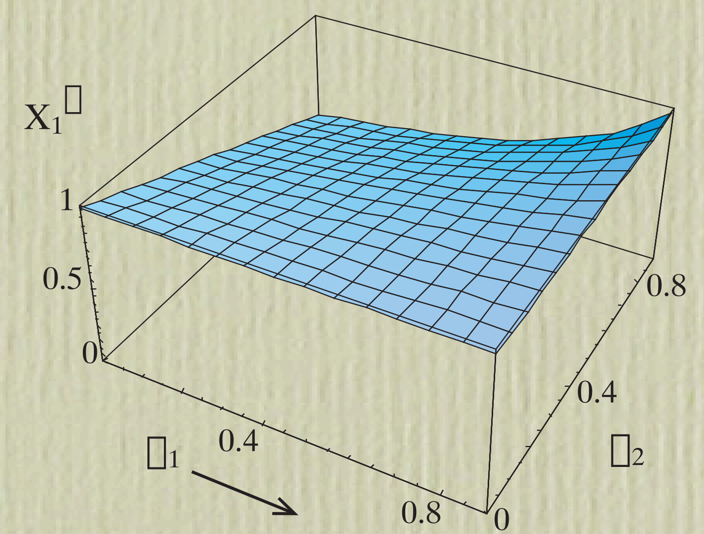


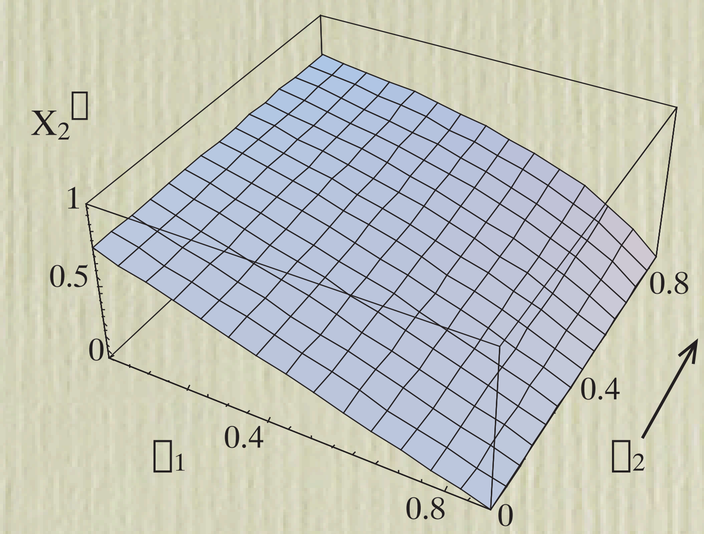



$(X_1,X_2)$ unstable if $R_1,R_2$ large        stable if $R_1,R_2$ small

# Escalation of Hostility

- Maximize $X_1[R_1]$, $X_2[R_2]$ but $X_i[R_1,R_2]$: Game



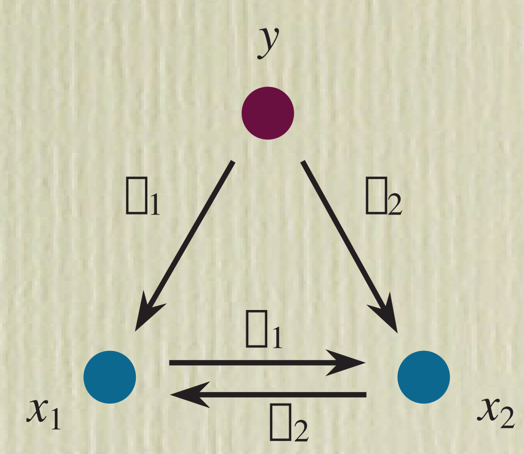




- Continuous variable prisoner's dilemma

discretized version:

| $R_1 \backslash R_2$ | dove | hawk |
|---|---|---|
| dove | +\+ | --\++ |
| hawk | ++\-- | -\- |

# Enters the Master



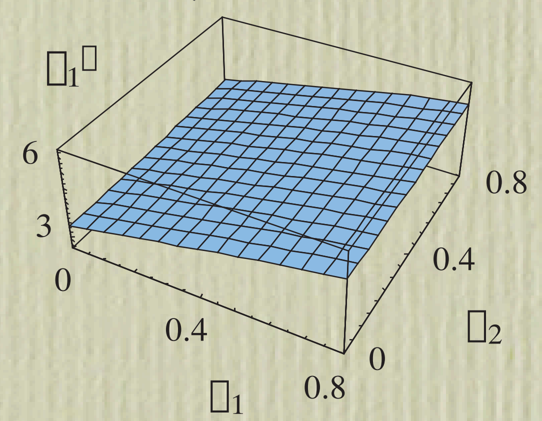

- An N=3 system : competition
  with apex predator

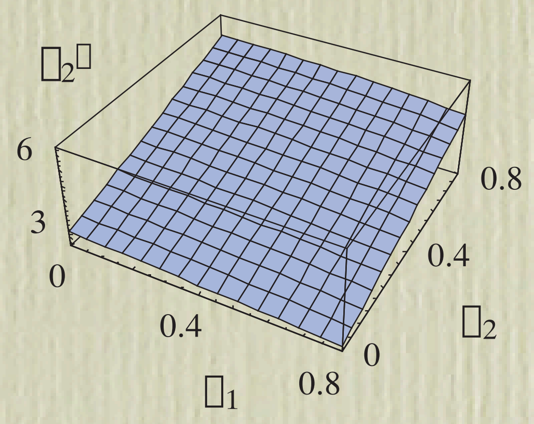
$$\frac{dx_1}{dt} = b_1x_1 - a_1x_1^2 - S_2x_1x_2 - R_1x_1y$$
$$\frac{dx_2}{dt} = b_2x_2 - a_2x_2^2 - S_1x_1x_2 - R_2x_2y$$
$$\frac{dy}{dt} = -d\,y + f\,R_1x_1y + f\,R_2x_2y$$

- Maximize fixed points $X_1[S_1]$, $X_2[S_2]$, $Y[R_1,R_2]$ simultaneously

# Suppression of Hostilities

- Optimal apex predator aggression $R_1^*$, $R_2^*$ ($dR_1 \backslash dY = dR_2 \backslash dY = 0$)




- This leads to

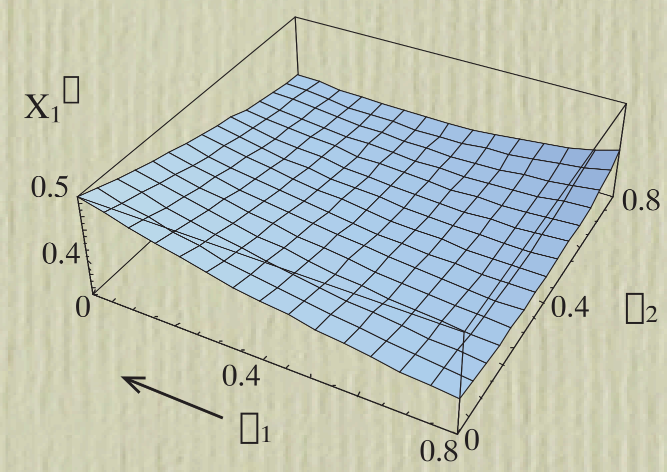
$$X_1^* = [2a_2b_1 - b_2S_+]/[4a_1a_2 - S_+^2]$$

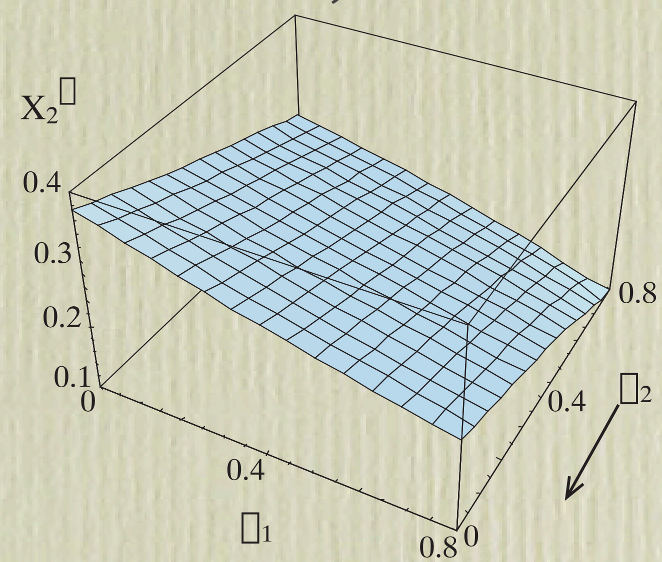
$$X_2^* = [2a_1b_2 - b_1S_+]/[4a_1a_2 - S_+^2]$$

$$S_+ := S_1 + S_2$$

# Coexistence under the Boss

- Maximize $X_1[R_1]$, $X_2[R_2]$ ($X_i[R_1,R_2]$)




- dilemma solved

discretized version:

| $R_1 \setminus R_2$ | dove | hawk |
|---|---|---|
| dove | +\+ | -\- |
| hawk | -\- | --\-- |

# Shape of Ecosystems

- Multidimensional Lotka-Volterra equation with adiabatic parameter shift
- Partial explanation of Elton's Universal Pyramid
- Extensions to multi-species in a trophic level : Stabilization by Dominance

# References


- T. Cheon, “Evolutionary stability of ecological hierarchy”, Phys. Rev. Lett. 90 (2003) 258105.
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- T. Cheon and S. Ohta, “Suppression of ecological competition by apex predator”, arXiv.org cond-mat/0305351 (2003).
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