Lecture 12 – 2D Stability – Consumer-Resource Intxs

Overview: Will use same tools we learned for LV-competition to study LV-predation. Both describe species interaction strengths as linear functional forms. Then extend to non-nonlinear species interaction by studying the effects of alternative predator functional responses on dynamics and stability.

Lotka-Volterra Predator-Prey model

Resource is explicit: C - Consumer & R - Resource

$$f_R(R,C) = \frac{dR}{dt} = \underbrace{b \cdot R}_{\text{growth}} - \underbrace{a \cdot R \cdot C}_{\text{feeding rate}}$$

$$f_C(R,C) = \frac{dC}{dt} = \underbrace{e \cdot a \cdot R \cdot C}_{\text{conversion of prey to preds}} - \underbrace{d \cdot C}_{\text{death rate}}$$

What are the equilibria?

Prey exhibits exponential growth in absence of predators

Predator exhibits exponential decay in absence of prey

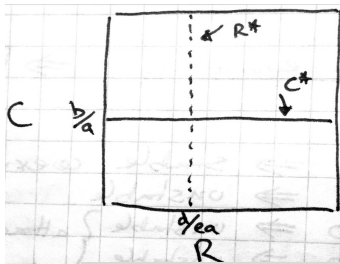Thus only 2: Trivial and non-trivial (coexistence) steady state.

Isoclines

Set $f_i = 0$. Solve for j...

$$\frac{dR}{dt} = bR - aRC = 0 \quad \Rightarrow \quad bR = aRC \quad \Rightarrow \quad C^* = \frac{b}{a}$$

$$\frac{dC}{dt} = eaRC - dC = 0 \quad \Rightarrow \quad eaRC = dC \quad \Rightarrow \quad R^* = \frac{d}{ea}$$

Notice that both isoclines are independent of density $\Rightarrow$ straight lines!

$$\left.\begin{array}{r}\text{If birth rate increases} \\ \text{or attack rate decreases}\end{array}\right\} C^* \text{ increases}$$

$$\left.\begin{array}{r}\text{If death rate increases} \\ \text{or attack rate decreases} \\ \text{or conversion efficiency decreases}\end{array}\right\} R^* \text{ increases}$$

R-demonstration varying $R(0)$ and $C(0)$

$\Rightarrow$ dependence on initial conditions. Locked phase cycle. SLIDE

Stability of LV-Pred-Prey model
Q: Are cycles stable or unstable?
Step 1: Construct Jacobian and evaluate at (R^*, C^*).

$$\mathbf{A} = \begin{bmatrix} \dfrac{\partial f_R}{\partial R} & \dfrac{\partial f_R}{\partial C} \\[2mm] \dfrac{\partial f_C}{\partial R} & \dfrac{\partial f_C}{\partial C} \end{bmatrix}$$

$$A_{11} = \frac{\partial(bR - aRC)}{\partial R} = b - aC$$

$$A_{12} = \frac{\partial(bR - aRC)}{\partial C} = -aR$$

$$A_{12} = \frac{\partial(eaRC - dC)}{\partial R} = eaC$$

$$A_{22} = \frac{\partial(eaRC - dC)}{\partial C} = eaR - d$$

Thus

$$\mathbf{A} = \begin{bmatrix} b - aC^* & -aR^* \\[2mm] eaC^* & eaR^* - d \end{bmatrix}\Bigg|_{R^*, C^*}$$

Then, since $C^* = \frac{b}{a}$ and $R^* = \frac{d}{ae}$...

$$\mathbf{A} = \begin{bmatrix} b - a\frac{b}{a} & -a\frac{d}{ae} \\[2mm] ea\frac{b}{a} & ea\frac{d}{ae} - d \end{bmatrix} = \begin{bmatrix} 0 & -\frac{d}{e} \\[2mm] eb & 0 \end{bmatrix}$$

Step 2: Determine eigenvalues of $\mathbf{A}$
$\Rightarrow$ R-demonstration
R-output: In this case $\quad \lambda_i = \underbrace{\text{Real part} = 0}_{\text{neutral stability}} \;+\; \underbrace{\text{complex part} \neq 0}_{\text{oscillations}} \quad$ for both $i = 1$ and 2

$\Rightarrow$ *The LV pred-prey model is 'pathalogical'* $\Leftarrow$
Like a pendulum swinging with no air or joint resistance.
SLIDE Applicability to Lynx-Hare dynamics extremely questionable.
Some Lynx-Hare cycles are clockwise!

Assumptions so far include:

- Exponential prey growth $\rightarrow$ *use logistic instead*
- Exponential predator decays $\rightarrow$ *okay*
- Linear functional response
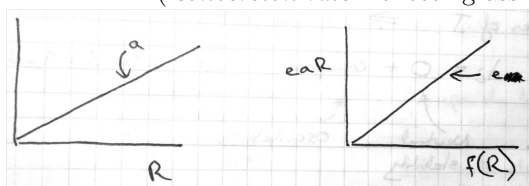- Linear numerical response

Functional vs. Numerical Response
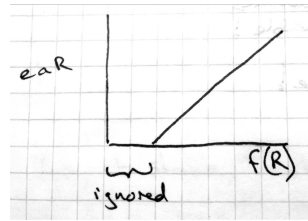In Lotka-Volterra model: $\quad e \cdot a \cdot R \cdot C$
$\quad a$ - '*attack rate*' - per capita rate at which prey are encountered
$\quad e$ - rate at which consumed prey are converted to new predator numbers
$\quad\quad$ ('*conversion rate*' reflecting assimilation and production rates)

$\Rightarrow$ Feeding rate depends only on $R \Rightarrow f(R)$

Lawton, Hassell & Beddington (1975) SLIDE

Linearity assumption of e probably okay (but rarely tested!)

$$f(R) = aR \quad \Rightarrow \quad \text{Type I functional response.}$$
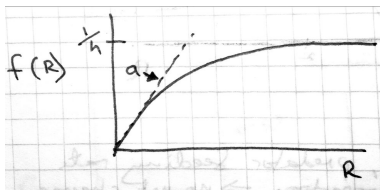
Type II

Is unlimited feeding rate defensible? What limits feeding rate?

Capture rate subsumed into attack rate (a)

- ability to search and find prey item (includes failed capture attempts)

Handling time (h) - time required to consume a successfully captured prey individual

$$f(R) = \frac{aR}{1 + ahR} \quad \Rightarrow \quad \text{Type II functional response}$$

SLIDE

$\Rightarrow$ Saturation at high prey densities
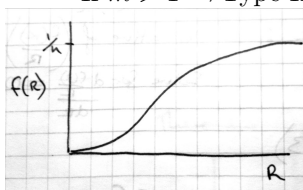$\Rightarrow$ Reduces to Type I if $h = 0$

Multi-species extension:

$$f(R_1, R_2) = \frac{a_1 R_1 + a_2 R_2}{1 + \sum_{i=1}^{2} a_i h_i R_i}$$

Extension to Type III

$$f(R) = \frac{aR^m}{1 + ahR^m}$$

If $m > 1 \Rightarrow$ Type II functional response.

$\Rightarrow$ Saturation at high prey densities
$\Rightarrow$ Accelerating feeding rate at low prey densities
$\Rightarrow$ Reduces to Type II if $m = 1$
$\Rightarrow$ Reduces to Type I if $m = 1$ & $h = 0$

'Phenomenological' model of prey switching where consumer ignores focal prey at low prey densities.
e.g., Let $a = \hat{a}R$ (preference increases with density), then get $f(R) = \frac{aR^2}{1 + ahR^2}$.

NOTE: Many more functional response models exist!

Effects of alternative functional responses on prey's *per capita* mortality rate (i.e. $\frac{f(R)}{R}$)

$$\text{Type I: } \frac{f(R)}{R} = \frac{aR}{R} = a$$

$$\text{Type II: } \frac{a}{1 + ahR} \qquad \text{Note: } \lim_{R \to \infty} \frac{a}{1 + ahR} = 0$$

$$\text{Type III: } \frac{aR^{m-1}}{1 + ahR^m} \qquad \text{For } m = 2: \quad \frac{aR}{1 + ahR^2}$$
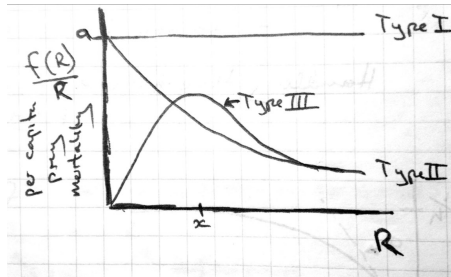
Type I: Neutral response
  As prey increases, predator feeding rate increases in constant proportion $\Rightarrow$ no net change.
Type II: Prey per capita mortality rate increases as R increases/ decreases as R increases.
Type III: Prey experiences refuge at low $R < x$

$$\frac{aR}{1 + ahR^2}$$

  Numerator dominates for $R < x$
  Denominator dominates for $R > x$

Q: How would you find value of x? A: Solve for x in derivative: $\dfrac{d\frac{f(R)}{R}}{dR}$!

MacArthur-Rosenzweig Model (1963) (a.k.a. Paradox of enrichment model)

$$\frac{dR}{dt} = bR(1 - \alpha R) - \frac{aRC}{1 + ahR} \qquad \frac{dC}{dt} = \frac{eaRC}{1 + ahR} - dC$$
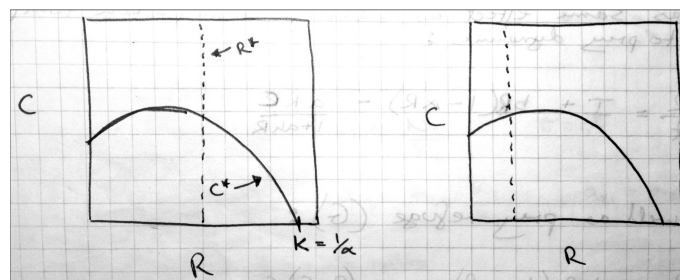

Isoclines
  $\Rightarrow$ Mathematica

Remember from LV-model:

$$R^* = \frac{d}{ae} \qquad\qquad C^* = \frac{b}{a}$$

For MacArthur-Rosenzweig model:

$$R^* = \frac{d}{ae - adh} \qquad\qquad C^* = \frac{b}{a} + \frac{bR(ah - \alpha - a\alpha hR)}{a}$$

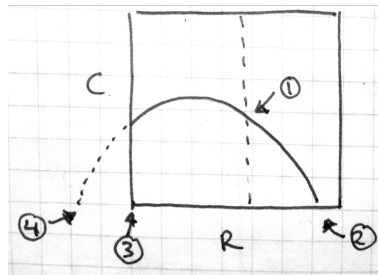$$\Rightarrow C^* \text{ depends on } R.$$

When isoclines intersect to the *right* of hump $\Rightarrow$ stable fixed point equilibrium
When isoclines intersect to the *left* of hump $\Rightarrow$ stable limit cycles (= "locally unstable")

Find equilibria
    ⇒ Mathematica
Sometimes may be given *four* equilibria !?!?!

① $R^* > 0, C^* > 0$ coexistence
② $R^* = K, C^* = 0$ boundary (invasible)
③ $R^* = 0, C^* = 0$ trivial
④ $R^* < 0, C^* = 0$ unfeasible

Study isoclines

$$\left.\begin{array}{l}\text{decreasing } d \\ \text{increasing } e \\ \text{increasing } a\end{array}\right\} \text{ moves } R^* \text{ to left } \Rightarrow \text{ limit cycles}$$

$$\left.\begin{array}{l}\text{increasing } a \\ \text{increasing } h \\ \text{increasing } b \\ \text{decreasing } \alpha\end{array}\right\} \uparrow \text{ steepness and moves hump to right } \Rightarrow \text{ limit cycles}$$

SLIDE:
    Luckinbill (1973) experiment manipulated $a \Rightarrow$ cycles or extinction
    Decreasing α (i.e. increasing K) $\Rightarrow$ 'Paradox of enrichment'

Isoclines of Type III (Problem set #6)
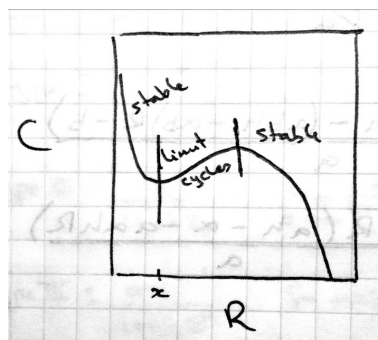
Type III has same effect as adding Immigration term (I) to prey growth...

$$\frac{dR}{dt} = I + bR(1 - \alpha R) - \frac{aRC}{1 + ahR}$$

...as well as the effect of adding a prey refuge (R')...

$$\frac{dR}{dt} = bR(1 - \alpha R) - \frac{a(R - R')C}{1 + ah(R - R')} \qquad \frac{dC}{dt} = \frac{ea(R - R')C}{1 + ah(R - R')} - dC$$