

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-linear 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.

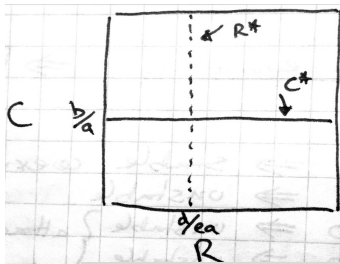
Isoclines

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

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

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

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



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

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

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^*) .

$$\mathbf{A} = \begin{bmatrix} \frac{\partial f_R}{\partial R} & \frac{\partial f_R}{\partial C} \\ \frac{\partial f_C}{\partial R} & \frac{\partial f_C}{\partial C} \end{bmatrix}$$

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

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

$$A_{21} = \frac{\partial(eaRC - dC)}{\partial R} = eaC$$

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

Thus

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

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

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

Step 2: Determine eigenvalues of \mathbf{A}

⇒ R-demonstration

R-output: In this case $\lambda_i = \underbrace{\text{Real part} = 0}_{\text{neutral stability}} + \underbrace{\text{complex part} \neq 0}_{\text{oscillations}}$ for both $i = 1$ and 2

⇒ The LV pred-prey model is 'pathological' ⇔

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 → use logistic instead
- Exponential predator decays → okay
- Linear functional response
- Linear numerical response

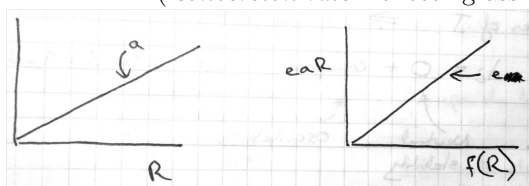
Functional vs. Numerical Response

In Lotka-Volterra model: $e \cdot a \cdot R \cdot C$

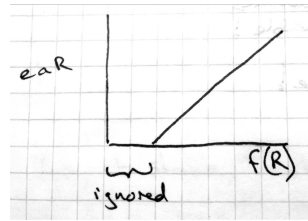
a - 'attack rate' - per capita rate at which prey are encountered

e - rate at which consumed prey are converted to new predator numbers

('conversion rate' reflecting assimilation and production rates)



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



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

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

Type II

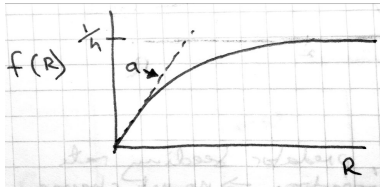
Is unlimited feeding rate defensible? What limits feeding rate?

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

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



SLIDE

\Rightarrow Saturation at high prey densities

\Rightarrow Reduces to Type I if $h = 0$

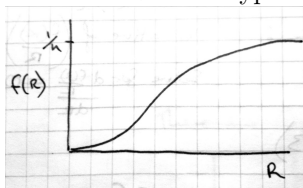
Multi-species extension:

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

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 $m = 1$

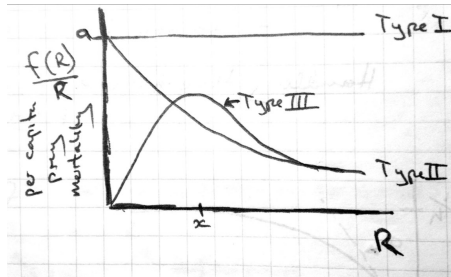
\Rightarrow Reduces to Type I if $m = 1$ & $h = 0$

‘Phenomenological’ model of prey switching where consumer ignores focal prey at low prey densities.
e.g., Let $\hat{a} = aR$ (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. $\frac{f(R)}{R}$)

Type I: $\frac{f(R)}{R} = \frac{aR}{R} = a$
 Type II: $\frac{a}{1 + ahR}$ Note: $\lim_{R \rightarrow \infty} \frac{a}{1 + ahR} = 0$
 Type III: $\frac{aR^{m-1}}{1 + ahR^m}$ For $m = 2$: $\frac{aR}{1 + ahR^2}$



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 $R < x$

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

Numerator dominates for $R < x$

Denominator dominates for $R > x$

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

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

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

Isoclines

\Rightarrow Mathematica



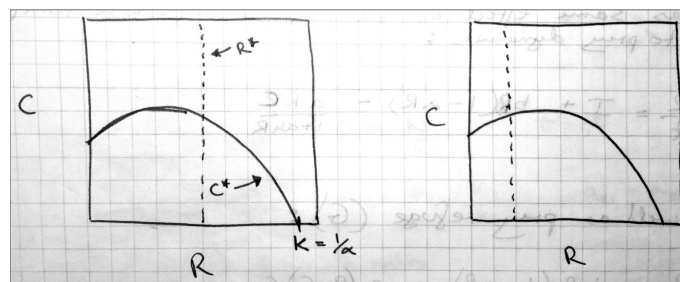
Remember from LV-model:

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

For MacArthur-Rosenzweig model:

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

$\Rightarrow C^*$ depends on R .



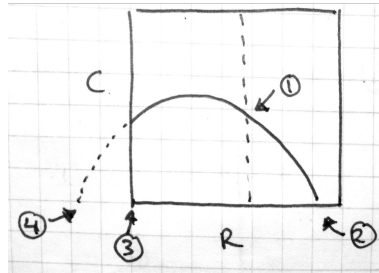
When isoclines intersect to the *right* of hump \Rightarrow fixed point equilibrium

When isoclines intersect to the *left* of hump \Rightarrow limit cycles

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

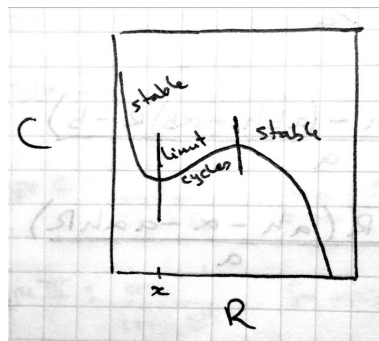
$\left. \begin{array}{l} \text{decreasing } d \\ \text{increasing } e \\ \text{increasing } a \end{array} \right\} \text{ moves } R^* \text{ to left } \Rightarrow \text{ limit cycles}$

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

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')...

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