

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.

Eigenvalues (λ_i)	Interpretation
$Re(\lambda_i) < 0$ for all i	Stable node
$Re(\lambda_i) < 0$ for some i	Saddle node
$Re(\lambda_i) > 0$ for all i	Unstable node
$Re(\lambda_i) = 0$ for all i	Neutrally stable
$Im(\lambda_i) = 0$ for all i	No oscillations
$Im(\lambda_i) \neq 0$ for some i	Oscillations

Lotka-Volterra Predator-Prey model

Resource is explicit: C - Consumer & R - Resource

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

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



Step 1: 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.

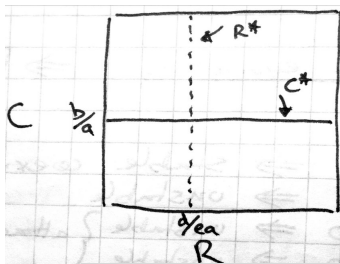
Isoclines

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

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

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

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



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

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

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

\Rightarrow dependence on initial conditions. Locked phase cycle.

Stability of LV-Pred-Prey model

Q: Is steady state stable or unstable?

Step 2: 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

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

Substitute $C^* = \frac{b}{a}$ 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 3: Evaluate eigenvalues of \mathbf{A}

\Rightarrow R-demonstration

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

Note absence of self-limitation (positive or negative) in either species.

\Rightarrow 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!

But remember that matching data is not necessarily the point of a model!

Assumptions so far include:

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

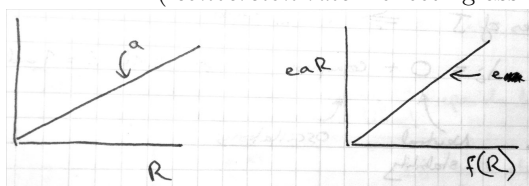
Functional vs. Numerical Response

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

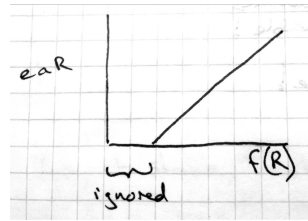
a - 'attack rate' - per capita rate at which prey are encountered

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

('conversion rate' reflecting assimilation and production rates)



\Rightarrow 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?

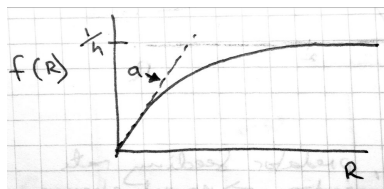
Capture rate subsumed into attack rate (a)

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

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

Assuming attacking (searching) and handling are *mutually-exclusive* activities:

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



SLIDE

\Rightarrow Saturation at high prey densities

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

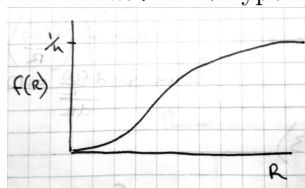
Multi-species extension:

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

Extension to Holling 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 $m = 1$ & $h = 0$

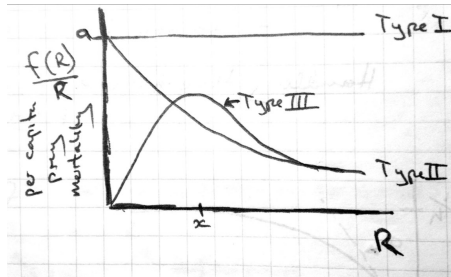
Phenomenological model of prey switching where consumer ignores focal prey at low prey densities.

e.g., Let $a = \hat{a}R$ (preference increases with density), then get $f(R) = \frac{\hat{a}R^2}{1 + \hat{a}hR^2}$.

Many more functional response models exist! SLIDE

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

Type II: Prey per capita mortality rate 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: $\frac{d\frac{f(R)}{R}}{dR}$!

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

⇒ Mathematica



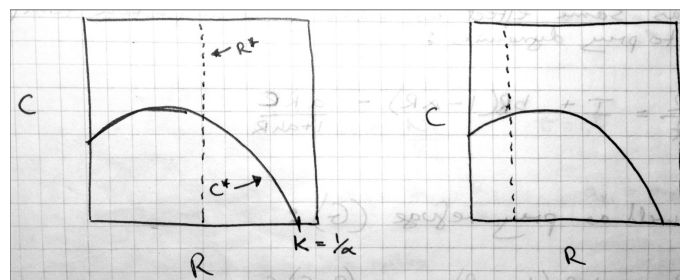
Remember from LV-model:

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

For MacArthur-Rosenzweig model:

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

⇒ Prey isocline C^* depends on R



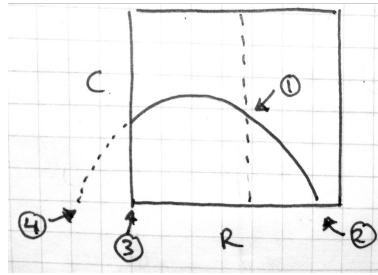
When isoclines intersect to the *right* of hump ⇒ stable fixed point equilibrium

When isoclines intersect to the *left* of hump ⇒ 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

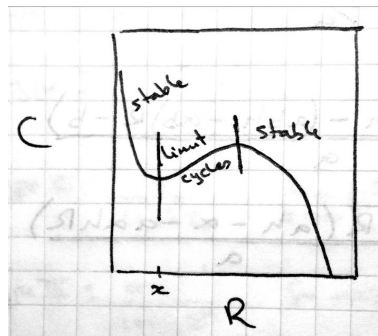
$\left. \begin{array}{l} \text{decreasing } d \\ \text{increasing } e \\ \text{increasing } a \end{array} \right\} \text{ moves } R^* \text{ to left } \Rightarrow \text{ limit cycles}$

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

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 similar refuge-inducing effect as adding prey immigration (I):

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

Also similar to the effect of adding an explicit prey refuge (R'):

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

Note mixed use of lower and upper-case parameters, Latin and Greek parameters.
 Such usage is ill-advised!