# Lecture 14 – Ruth-Hurwitz Criteria

**Concepts:**

- Determinant, Traces & Routh-Hurwitz criteria
- Paper discussion

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**Back to Biology: Classifying steady states**

For 2x2 system:

$$\lambda^2 - \underbrace{(A_{11} + A_{22})}_{\text{Trace}}\lambda + \underbrace{A_{11}A_{22} - A_{12}A_{21}}_{\text{Determinant}}$$

**Routh-Hurwitz stabiliy criteria**

Provide *biological insight* (far more challenging using just $\lambda$'s)
Unfortunately, the simplicity of the following applies only to 2 x 2 systems.

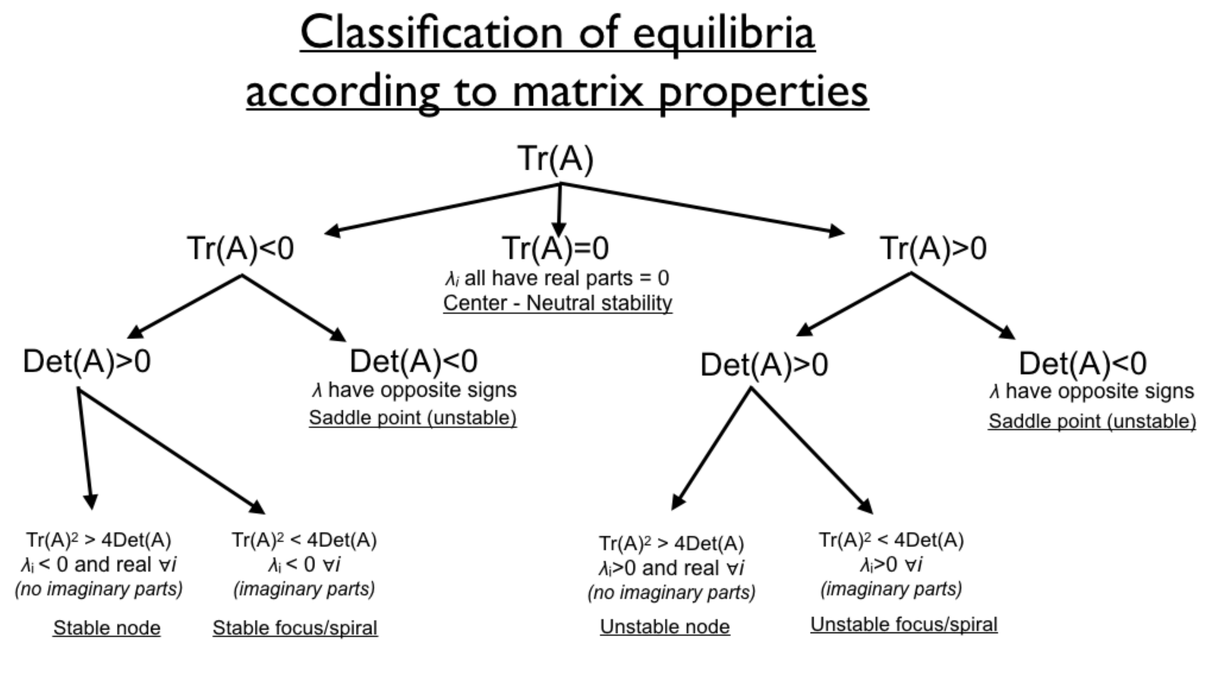
$\mathrm{Tr}(\mathbf{A}) < 0 \quad \Rightarrow \quad A_{11} + A_{22} < 0$ is necessary for stability
$\Rightarrow$ *At least some species must be strongly self-limiting for stability* $\Leftarrow$

$\mathrm{Det}(\mathbf{A}) > 0 \quad \Rightarrow \quad A_{11}A_{22} - A_{12}A_{21} > 0$ is necessary for stability
$\Rightarrow$ *Overall self-limitation must be stronger then interspecific effects for stability* $\Leftarrow$
$\Rightarrow$ *Intra > inter-specific effects* $\Leftarrow$

Each condition by itself is *necessary, but not sufficient.*

$$\lambda = \tfrac{1}{2}\mathrm{Tr}(\mathbf{A}) \pm \tfrac{1}{2}\sqrt{(-\mathrm{Tr}(\mathbf{A}))^2 - 4 \cdot \mathrm{Det}(\mathbf{A})}$$

Whichever parts of $\sqrt{\ }$ is bigger determines with or without oscillations.
Bifurcation occurs at $(-\mathrm{Tr}(\mathbf{A}))^2 = 4 \cdot \mathrm{Det}(\mathbf{A})$.

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**Rosenzweig-MacArthur paradox of enrichment model - revisited**

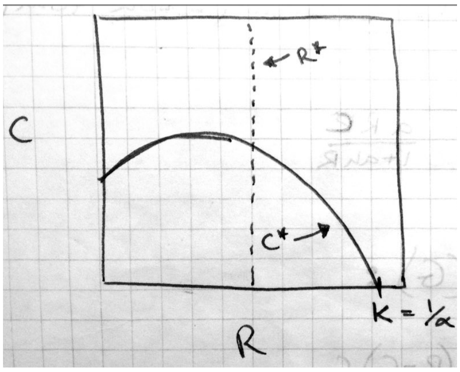
$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{aRC}{1+ahR} \qquad\qquad \frac{dC}{dt} = \frac{eaRC}{1+ahR} - dC$$

Prey isocline:

$$\frac{dR}{dt} = 0 \quad \Rightarrow \quad C^* = \frac{r(K-R)(1-ahR)}{aK}$$

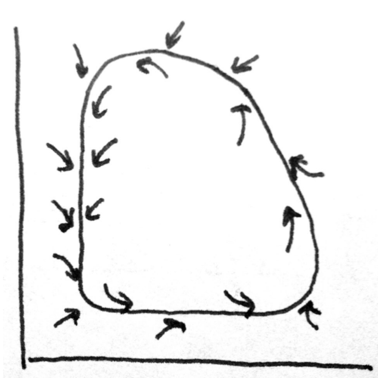
Predator isocline:

$$\frac{dC}{dt} = 0 \quad \Rightarrow \quad R^* = \frac{d}{a(e-dh)}$$



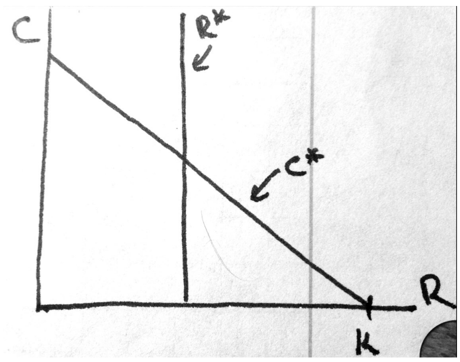

When $R* > K \Rightarrow$ predator extinct
Increasing $K$ shifts $C^*$ to right

When $R^* > \max C^* \Rightarrow$ stable fixed point
When $R^* < \max C^* \Rightarrow$ stable limit cycle
= *Hopf bifurcation*



**Key control parameters:**
As $K$ increases, oscillation amplitude increases $\Rightarrow$ Risk of extinction
$h$ influences position of $R^*$ and how hump-shaped $C^*$ is.

Note: If $h = 0 \Rightarrow C^* = \frac{r(K-R)}{aK}$, just like LV but with logistic prey:




Other parameters are less interesting for today.

**Formal stability analysis**

**Step 1:** Solve for steady state equilibria: *Mathematica*

Three solutions:

$$(R^*, C^*) = \begin{cases} 0 & 0 \\ K & 0 \\ \frac{d}{a(e-dh)} & \frac{er(aeK-d-adhK)}{Ka^2(e-dh)^2} \end{cases}$$

**Step 2:** Evaluate Jacobian at steady state(s)

Interested only in coexistence, so focus on 3rd

$$\mathbf{A}|_{R^*,C^*} = \begin{bmatrix} r - \frac{2rR^*}{K} - \frac{aC^*}{(1+ahR^*)^2} & \frac{-aR^*}{1+ahR^*} \\ \frac{eaC^*}{(1+ahR^*)^2} & \frac{eaR^*}{1+ahR} - d \end{bmatrix}$$

$$= \begin{bmatrix} \frac{-dr(e+dh+ahK(dh-e))}{eaK(e-dh)} & \frac{-d}{e} \\ r\left(e - dh - \frac{d}{aK}\right) & 0 \end{bmatrix} = \begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{bmatrix}$$

Note that for this model:

$A_{21}$ will always be positive (look at first matrix) - *prey effect on pred*

$A_{12}$ will always be negative - *pred effect on prey*

$A_{11}$ can be positive or negative depending on $R^*$ and $C^*$

Q: How can $A_{11} > 0$? A: If $R^*$ and $C^*$ are small, or $K$ is large and $a$ is small.

Q: Why is $A_{22} = 0$? A: Consumer has no self-limitation (look back at model)

**Step 3:** Assess stability using eigenvalues or Routh-Hurwitz Criteria

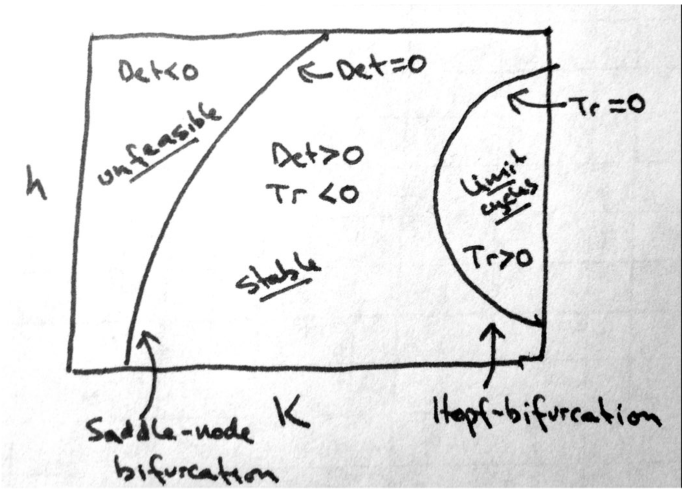
$\lambda_i < 0 \; \forall i \Rightarrow$ Stable fixed point

$Tr(\mathbf{A}) < 0$ & $Det(\mathbf{A}) > 0 \quad \Rightarrow \quad$ Stable fixed point

Graphical analysis:

Set $Tr(\mathbf{A})$ & $Det(\mathbf{A}) = 0$ and plot as functions of $K$ and $h$:

Or plot $Tr(\mathbf{A}) = Det(\mathbf{A})$



**Summary**: Two transitions between stability to local 'instability' (two bifurcation types)

$$\lambda = \tfrac{1}{2}\mathrm{Tr}(\mathbf{A}) \pm \tfrac{1}{2}\sqrt{(-\mathrm{Tr}(\mathbf{A}))^2 - 4 \cdot \mathrm{Det}(\mathbf{A})}$$

**Extinction of consumer:**

$\lambda$ has only real part

$\mathrm{Tr}(\mathbf{A})^2 > 4 \cdot \mathrm{Det}(\mathbf{A})$

Transition at:

$\lambda = 0$

$Det(\mathbf{A}) = 0$

$Tr(\mathbf{A})$ can be $<$ or $> 0$

**Emergence of limit cycle**

$\lambda$ is complex

$\mathrm{Tr}(\mathbf{A})^2 < 4 \cdot \mathrm{Det}(\mathbf{A})$

Transition at:

$\lambda = 0 \pm i\sqrt{\#}$

$Det(\mathbf{A}) > 0$

$Tr(\mathbf{A}) = 0$

**Result:**
Qualitative change in type of steady-state.
Disappearance of fixed point equilibrium.
Appearance of new (boundary) equilibrium.

$\Rightarrow$ *Saddle-node bifurcation* $\Leftarrow$

**Result:**
Transition between damped oscillations
to sustained oscillations.
Equilibrium doesn't disappear.

$\Rightarrow$ *Hopf bifurcation* $\Leftarrow$