BMSE247/EEMB247 Local Stability Analysis

What we do when we do local stability analysis is we:
1. calculate the equilibrium
2. Use Taylor's theorem to linearize the differential equation near equilibrium.
3. Solve the linear differential equation describing the dynamics of a small perturbation from equilibrium.

Taylor's theorem says:

$$f(N_2) \cong f(N_1) + \frac{f'(N_1)(N_2 - N_1)}{1!} + \frac{f''(N_1)(N_2 - N_1)^2}{2!} + \cdots + \frac{f^{(n)}(N_1)(N_2 - N_1)^n}{n!} + \cdots$$

What this says is, if we know the value of a function at any one point, we can approximate the value at any later point by using the derivative of the function at that point.
If the difference between N_1 and N_2 is very small, then we can say that something very small squared is extremely small, so we can ignore second order and higher terms, and approximate f(N_2) by:

$$f(N_2) \cong f(N_1) + f'(N_1)(N_2 - N_1)$$

Here's what this means graphically:
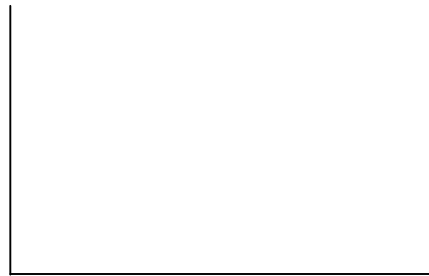
We know the value at N1 and we want to know the value at N2, so we take the value at N1 and the slope of the function at N1 and use that to calculate the value at N2.
a) The approximation is worse as N2 is further away from N1.
b) The approximation is worse the more non-linear f(N) is. This is why we only look at solutions close to equilibrium → local stability analysis.

How does this apply to linearization of differential equations?
Well, we can take N1 to be the equilibrium, and n to be a small perturbation from equilibrium, then:

$$f(N^* + n) \cong f(N^*) + f'(N^*)n$$

The way that we make use of this is that f(N) is the right hand side of a differential equation:
dN/dt = f(N).

For example, the Logistic model:

$$f(N) = \frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

First step is to calculate the equilibria:

dN/dt = 0 => N = 0 or N = K

Let's look first at the N = 0 equilibrium:

We move the population a small distance from equilibrium, and ask what happens to this perturbation.

Does the population return to the equilibrium, or does it diverge away from equilibrium?

N = N* + n

Taylor's theorem says:

$$f(N^* + n) \cong f(N^*) + f'(N^*)n$$

So we need to calculate f'(N*):

f'(N) = r – 2rN*/K = r (if N* = 0)

Therefore

$$\frac{d(N^* + n)}{dt} = \frac{dn}{dt} = 0 + rn$$

$$\frac{dn}{dt} = rn$$ is the equation for the dynamics of a small perturbation from equilibrium.

We know the solution to this linear equation. It's the equation for exponential growth, so the population will diverge away from the trivial equilibrium, N* = 0. This is an unstable equilibrium.

Next let's look at the more interesting equilibrium, N* = K

f'(N) = r – 2rN*/K = r – 2r = -r (if N* = K)

f(N*) = r K (1-K/K) = 0 This is always true, the rate of change of N at the equilibrium value will always be zero.

$$\frac{d(N^* + n)}{dt} = \frac{dn}{dt} = 0 - rn$$

$$\frac{dn}{dt} = -rn$$ This linear version of the model is the equation for exponential decay. It has

the solution n(t) = $n_0 e^{-rt}$

Therefore the perturbation from equilibrium will decrease through time, and the population will return to its stable equilibrium.

We can look at what we are doing graphically:

This process is called "linearizing about the equilibrium".
So, a) the approximation is good near the equilibrium
b) approx is bad far away, but for this model always gets the sign right.

Remember that all that local stability analysis does is tell if a small perturbation from equilibrium will return to equation, or will diverge away from equilibrium. If it finds that the equilibrium is unstable, it cannot tell you how Nt is going to behave.
dn/dt is just a local linear approx to dN/dt, and as it gets far away from equilibrium it's not a good guide.

If the equilibrium is locally unstable, the actual dynamics could be exponential divergence, or it could be cycles that diverge exponentially, or it could be truly cyclic dynamics.

This type of analysis suggests a type of experiment that you could do to tell of a population is regulated.
Perturbation experiments: If you have a population that is at some sort of equilibrium, you could perturb the population by adding or removing some fraction of the population to see fi the population returns to equilibrium.

This type of experiment has been done in the field with marine invertebrates, and with insects. Often they find that the population eventually returns to their pre-perturbation densities.

Taylor's Theorem can be generalized to systems with any number of state variables:

$$\frac{dX_1}{dt} = f_1(X_1, X_2, \cdots, Xn)$$

$$\frac{dX_2}{dt} = f_2(X_1, X_2, \cdots, Xn)$$

$$\vdots$$

$$\frac{dX_n}{dt} = f_n(X_1, X_2, \cdots, Xn)$$

calculate the equilibria: X1*, X2*, ..., Xn*

define a small perturbation from equilibrium:
$X_1 = X_1{}^* + x_1$
$X_2 = X_2{}^* + x_2$
$\vdots$
$X_n = X_n{}^* + x_n$

$$\frac{dx_1}{dt} = f_1(x_1, x_n, \cdots, x_n) \cong f_1(X_1{}^*, X_2{}^*, \cdots, X_n{}^*) + \left.\frac{\partial f_1}{\partial X_1}\right|_* x_1 + \left.\frac{\partial f_1}{\partial X_2}\right|_* x_2 + \cdots + \left.\frac{\partial f_1}{\partial X_n}\right|_* x_n$$

$$\frac{dx_2}{dt} \cong f_2(X_1{}^*, X_2{}^*, \cdots, X_n{}^*) + \left.\frac{\partial f_2}{\partial X_1}\right|_* x_1 + \left.\frac{\partial f_2}{\partial X_2}\right|_* x_2 + \cdots + \left.\frac{\partial f_2}{\partial X_n}\right|_* x_n$$

$$\vdots$$

$$\frac{dx_n}{dt} \cong f_n(X_1{}^*, X_2{}^*, \cdots, X_n{}^*) + \left.\frac{\partial f_n}{\partial X_1}\right|_* x_1 + \left.\frac{\partial f_n}{\partial X_2}\right|_* x_2 + \cdots + \left.\frac{\partial f_n}{\partial X_n}\right|_* x_n$$

This gives us the linearized equations for the small perturbations from equilibrium. We then can directly use the tools that we have learned form talking about systems of linear differential equations to determine the solution of these linearized equations. This will tell us if the solution will return to equilibrium, or diverge from equilibrium.

This is now in the form:

$$\begin{pmatrix} x_1{}' \\ x_2{}' \\ \vdots \\ x_n{}' \end{pmatrix} = \begin{pmatrix} \left.\frac{\partial f_1}{\partial X_1}\right|_* & \left.\frac{\partial f_1}{\partial X_2}\right|_* & \cdots & \left.\frac{\partial f_1}{\partial X_n}\right|_* \\ \left.\frac{\partial f_2}{\partial X_1}\right|_* & \left.\frac{\partial f_2}{\partial X_2}\right|_* & \cdots & \left.\frac{\partial f_2}{\partial X_n}\right|_* \\ \vdots & & & \\ \left.\frac{\partial f_n}{\partial X_1}\right|_* & \left.\frac{\partial f_n}{\partial X_2}\right|_* & \cdots & \left.\frac{\partial f_n}{\partial X_n}\right|_* \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_n \end{pmatrix}$$

x'(t) = A x(t)

where A is the Jacobean matrix.

We can then take the determinant of A- λI, and set it equal to zero to calculate the eigenvalues, λ, of the Jacobean matrix.

From this we can tell directly whether a peturbation will return to equilibrium or not.

Let's look at an example:
The Lotka-Volterra Predator-Prey equations.
We already know that the equilibrium is neutrally stable, but let's go through the steps.

prey: $\dfrac{dN}{dt} = f_1 = rN - aNP$

predators: $\dfrac{dP}{dt} = f_2 = caNP - dP$

The first step is to calculate the equilibria:
dN/dt = 0. This is true if N = 0 or if P* = r/a
dP/dt = 0. This is true if P = 0 or if N* = d/ca

Let's look only at the non-trivial, non-zero, equilibrium.

We are going to start with the system at its equilibrium value of prey and predators, and then slightly perturb the system, adding a few individuals of n and a few individuals of p. We'll then ask whether these perturbations decay to zero, or whether they increase in size.

From the Taylor's Theorem we know:
$$\frac{dn}{dt} = f_1(n,p) \cong f_1(N^*, P^*) + \left.\frac{\partial f_1}{\partial N}\right|_* n + \left.\frac{\partial f_1}{\partial P}\right|_* p$$
dN/dt @ eqm =0 + effect of adding   effect of adding
                      prey on prey   predators on prey rate
                      rate of increase   of increase

$$\frac{dp}{dt} = f_2(n,p) \cong f_2(N^*, P^*) + \left.\frac{\partial f_2}{\partial N}\right|_* n + \left.\frac{\partial f_2}{\partial P}\right|_* p$$
dN/dt @ eqm =0 + effect of adding   effect of adding
                      prey on pred   preds on pred rate
                      rate of increase   of increase

The next step is to calculate the elements of the Jacobean Matrix:

$$A_{11} = \frac{\partial f_1}{\partial N}\Big|_* = r - aP^* = r - ar/a = 0 \Rightarrow \text{no effect of prey on its own rate of increase}$$

$$A_{12} = \frac{\partial f_1}{\partial P}\Big|_* = -aN^* = -\frac{d}{c} \quad \Rightarrow \text{predators reduce prey rate of increase}$$

$$A_{21} = \frac{\partial f_2}{\partial N}\Big|_* = caP^* = cr \quad \Rightarrow \text{prey increase predator rate of increase}$$

$$A_{22} = \frac{\partial f_2}{\partial P}\Big|_* = caN^* - d = cad/(ca) - d = 0 \quad \Rightarrow \text{no effect of preds on its rate of increase}$$

So, the linearize equations look like:
dn/dt = 0 + 0 n – (d/c) p = (-d/c) p
dp/dt = 0 + (cr) n + 0 p = (cr) n

We know that the general solution to these linear equations is:

$$\begin{pmatrix} n_t \\ p_t \end{pmatrix} = c_1 \mathbf{v_1} e^{\lambda_1 t} + c_2 \mathbf{v_2} e^{\lambda_2 t}$$

We usually aren't that interested in the exact solution of the perturbation from equilibrium, so we don't usually bother with calculating the eigenvectors and constants, c's. All we are really interested in whether in the long term this perturbation will return to equilibrium, or diverge from equilibrium.
To know this, all we have to do is look at the **eigenvalues**, λ_1 and λ_2.

If these eigenvalues are both real, then if either one of them is greater than zero, then the solution will diverge away from equilibrium. Then the equilibrium will be unstable. Thus for a stable equilibrium, of the eigenvalues are real, we want both of them to be negative.

If the eigenvalues are complex: $\lambda_1 = \alpha + \beta i$, $\lambda_2 = \alpha - \beta i$ then we found that this will be something of the form: $n_t = e^{\alpha t} \sin(\beta t + \phi)$.
We found if $\alpha > 0$, then the solution will appear as diverging oscillations
if $\alpha = 0$, it will be neutrally-stable oscillations
if $\alpha < 0$, it will be converging oscillations.

Thus, with complex conjugate roots, we want the real part of any complex eigenvalues to be negative.

This in general, for both real and complex roots, for the equilibrium to be locally stable, the real part of all of the eigenvalues must be negative.

For the Lotka-Volterra predator-prey model, we can determine the eigenvalues by:

Det(**A**-λ**I**) = 0

$$Det\begin{pmatrix} -\lambda & -\frac{d}{c} \\ cr & -\lambda \end{pmatrix} = 0$$

$\lambda^2 + rd = 0$
$\lambda = \pm i\sqrt{rd}$

Thus we have complex conjugate roots. The real part is equal to zero, and the imaginary part is equal to the square root of rd.
Thus the equilibrium is not stable, it is neutrally stable.
A small perturbation will not return to equilibrium, it will cycle around equilibrium in a sinusoid, with a radian frequency of $\sqrt{rd}$. The period for a small perturbation is then $2\pi/\sqrt{rd}$.
The larger r and d, the shorter the period is. That is, the larger the prey rate of increase and the larger the predator death rate is, the shorter the period is.

The amplitude of the cycles will depend on the initial conditions. That is, it will depend on how large the initial perturbation was.

The phase difference between the trajectory for prey and the trajectory for predators will depend on the eigenvalues. If you calculate these, you'll find that the predators lag behind the prey by a quarter of a period.

General Solution for systems of 2 differential equations.

We can look at the solution in general for systems of 2 differential equations.
We will get the Jacobean matrix:

$$\begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix}$$

$Det(\mathbf{A} - \lambda\mathbf{I}) = 0$

$(A_{11} - \lambda)(A_{22} - \lambda) - A_{12}A_{21} = 0$

$\lambda^2 - \lambda(A_{11} + A_{22}) + (A_{11}A_{22} - A_{12}A_{21}) = 0$

The solution to this is:

$$\lambda = \underset{\alpha}{\underbrace{\frac{A_{11} + A_{22}}{2}}} \underset{\pm}{\pm} \underset{\beta}{\underbrace{\frac{\sqrt{(A_{11} + A_{22})^2 - 4(A_{11}A_{22} - A_{12}A_{21})}}{2}}}$$

For local stability, we need the real parts of all eigenvalues to be negative. In order for this to be met, the following conditions must be met:

(1) $(A11 + A22) < 0$ => Must be some self-damping = density-dependence
(2) $A_{11}A_{22} > A_{12}A_{21}$ => Collective self-damping must exceed strength of
                                             interspecific interactions

These are the Routh-Hurwitz Criteria for stability of a 2-species interaction.
They are a short-hand way of telling whether an equilibrium is locally stable or not.

For the Lotka-Volterra predator-prey model:

(1) $(A_{11} + A_{22}) = 0$, So not stable and not unstable
(2) $A_{11}A_{22} > A_{12}A_{21}$ -> YES.
But both of these must be true in order for the equilibrium to be stable.
In this case it is not, it's neutrally stable.

Let's go back to the Jacobean matrix to see if we can tell anything from it directly.
If we look at just the signs of the terms in the matrix:

$$\begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix} = \begin{pmatrix} 0 & - \\ + & 0 \end{pmatrix}$$

predators always have a negative effect on the prey rate of increase,
and prey always have a positive effect on the predators rate of increase.

These "off-diagonal" elements are here, and their product is always < 0.

$$\lambda = \frac{A_{11} + A_{22}}{2} \pm \frac{\sqrt{(A_{11} + A_{22})^2 - 4(A_{11}A_{22} - A_{12}A_{21})}}{2}$$

Therefore the stuff under the square root sign tends to be negative. So, it's a general property of predator-prey systems that they oscillate.

Another example:
Let's just add Logistic Growth to the Prey Population:
In the original Lotka-Volterra model, we assumed that in the absence of the predator, the prey could grow exponentially, without bounds.

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - aNP$$

$$\frac{dP}{dt} = caNP - dP$$

First step, calculate the equilibrium:
dP/dt = 0 => P* = 0, or N* = d/ca
dN/dt = 0 => If P* = 0, then N* = K
              IF N* = d/(ca), then P* = (r/a)(1-N*/K) = (r/a)(1-d/(Kca))
This equilibrium is only possible if P*>0 that is if (1-d/(Kca)) > 0
That is if K > d/(ca), that is, if the prey equilibrium in the absence of the predator is greater than the prey equilibrium in the presence of the predator.
If this condition is not true, then the predator cannot sustain itself on this prey population.
The addition of the predator must lead to a decrease in the equilibrium abundance of the prey.

Let's just look at the non-zero equilibrium:
N* = d/ca, P* = (r/a)(1-N*/K) = (r/a)(1-d/(Kca))

$$A_{11} = \left.\frac{\partial f_1}{\partial N}\right|^* = r - 2rN^*/K - aP^*$$

$$= r - 2rN^*/K - r + rN^*/K$$
$$= -(r/K)N^*$$
$$= -\frac{rd}{caK}$$

$$A_{12} = \left.\frac{\partial f_1}{\partial P}\right|^* = -aN^*$$

$$= -\frac{d}{c}$$

$$A_{21} = \frac{\partial f_2}{\partial N}\bigg|^* = caP^*$$

$$= cr\left(1 - \frac{d}{caK}\right)$$

$$A_{22} = \frac{\partial f_2}{\partial P}\bigg|^* = cN^* - d = 0$$

_____

Routh-Hurwitz Criteria:

(1) $A_{11} + A_{22} < 0$?
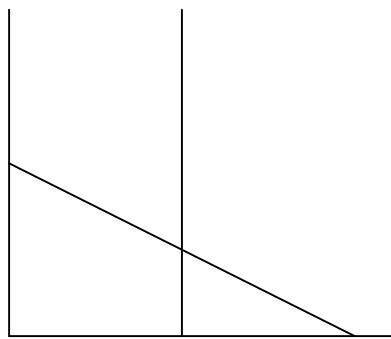
$$-\frac{rd}{caK} + 0 \ < 0 ?$$ YES!

(2) $A_{11}A_{22} > A_{12}\ A_{21}$?

$A_{11}A_{22} = 0$ => So we need: $A_{12}\ A_{21}\ < 0$

$$-\frac{d}{c}\ caP^* < 0$$

This is true as long as $P^* > 0$. That is, as long at the predator can persist in the system, the equilibrium is locally stable.

What does this look like on the phase plane, using the graphical methods that we learned last time?

Type II Functional Response.
What if instead of having a type 1 functional response, in which the number of prey eaten per predator per unit time increases linearly with increasing prey density, it levels off. This can occur either because at high prey densities the predators become saturated, or because there is a handling time. It takes a certain length of time for the predators to

handle each prey item that at high prey densities, the predators are spending most of their time handling prey, so they have limited time available for searching.
This can be expressed mathematically in one of two ways:

$$f(N) = \frac{aN}{1 + aT_h N}$$

$$f(N) = \frac{I_m N}{N_h + N}$$

where:
a = attack rate (search eff.) at low densities
T_h = handling time per prey item

I_m = maximum ingestion rate
N_h = half saturation prey density

prey: $\dfrac{dN}{dt} = rN - \left(\dfrac{aN}{1 + aT_h N} \right) P$

predators: $\dfrac{dP}{dt} = c\left(\dfrac{aN}{1 + aT_h N} \right) P - dP$

$dN/dt = 0$: $P^* = (r/a)(1 + a\, T_h\, N)$

$dP/dt = 0$: $N^* = \dfrac{d}{ac - adT_h}$

Find the elements of the Jacobean Matrix:

$A_{11} = \left. \dfrac{\partial f_1}{\partial N} \right|_* = rdT_h / c$

$A_{12} = \left. \dfrac{\partial f_1}{\partial P} \right|_* = -\dfrac{d}{c}$

$A_{21} = \left. \dfrac{\partial f_2}{\partial N} \right|_* = r(c - dTh)$

$A_{22} = \left. \dfrac{\partial f_2}{\partial P} \right|_* = 0$

Routh-Hurwitz Criteria:
(1) $A_{11} + A_{22} < 0$?

$-\dfrac{rdT_h}{c} + 0 \; < 0$?   NO!   Equilibrium is unstable.

Routh-Hurwitz Criteria for higher order systems.
There are equivalents for the Routh-Hurwitz Criteria for third and fourth order systems:
Another way of writing the criteria for the second order system is:
If you have the characteristic equation:
$\lambda^2 + a_1\lambda + a_2 = 0$
For local stability: $a_1 > 0$, $a_2 > 0$

For a third order system:
$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$
For local stability: $a_1 > 0$, $a_3 > 0$, $a_1a_2 > a_3$

$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0$
For local stability: $a_1 > 0$, $a_3 > 0$, $a_3 > 0$, $a_1a_2a_3 > a_3^2 + a_1^2a_4$

For systems higher than this they become unwieldy.

Example:
Models of disease. Infectious diseases are of two broad types:
Microparasites: things like viruses and bacteria where effectively an individual is either infected or uninfected. Models of this usually don't take into account the number of disease organisms in an infected host. Microparasites reproduce within the host and are usually transmitted directly form one host to another.

Macroparasites are things like worms, where how sick an individual is depends on how many parasite individuals are present within a host individual. Most macroparasites have complicated lifecycles and often have secondary hosts or carries. – Things like malaria or schistosomiasis.

Let's look at some classic models for microparasite infections, because they are a lot easier to deal with than macroparasites.

Consider a disease like measles.
SIRS model:

susceptibles   infecteds   recovered
                                 resistant
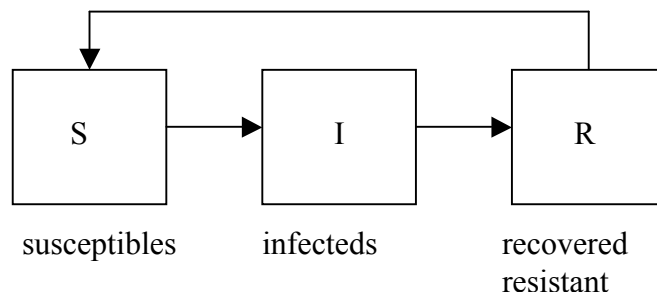
$$\frac{dS}{dt} = -\beta SI + \gamma R$$

$$\frac{dI}{dt} = \beta SI - \nu I$$

$$\frac{dR}{dt} = \nu I - \gamma R$$

Individuals become infected by coming into contact with infected individuals. The model assumes random mixing within the population. Individuals are removed from the infected class at a rate νI, which means that the average duration of the infected stage is $1/\nu$ days. Similarly, resistant individuals loose their resistance at a rate γ. These individuals reenter the susceptible class.

This model assumes that the disease does not affect the total human population size. Few diseases have had a real impact on the human population size, except the plague. This means that $N = S + I + R$ is constant.

We can solve for the equilibrium:
There are two possible equilibrium:
$S* = N$, $I* = 0$, $R* = 0$. In this case the whole population is healthy, and the disease is eradicated.
or

$$S* = \frac{\nu}{\beta} \qquad I* = \frac{\gamma(N - S*)}{(\gamma + \nu)} \qquad R = \frac{\nu I *}{\gamma}$$

For the infected class to be positive, N must be greater than $S*=\nu/\beta$.

This leads to the conclusion that the disease will be established in the population provided that total population N exceeds some threshold ν/β, which can be rewritten: $N\beta/\nu > 1$.
The ratio, b/n has a meaningful interpretation.
Since the removal rate from the infected class is ν, the average period of infectivity is $1/\nu$.
Thus, β/ν is the fraction of the population that comes into contact with an infective individual during its period of infectiousness.

The quantity $R_0 = N\beta/\nu$ is the intrinsic reproductive rate of the disease, or the average number of secondary infections caused by introducing a single infected individual into a host population of N susceptibles.
The threshold result is then written as $R_0 > 1$ for the disease to become established.

Since the total population is constant, we can get rid of the equation for R, so that we have a system of only 2 equations.
$R = N-S-I$

$dS/dt = -\beta SI + \gamma(N - S - I) = f_1$
$dI/dt = \beta S I - \nu I$

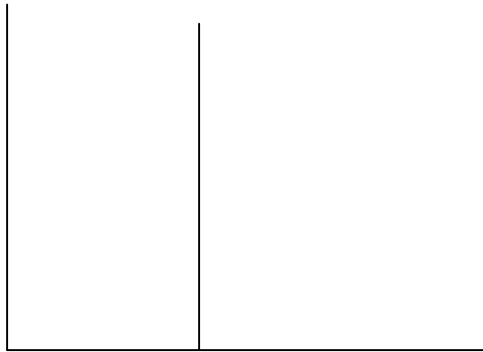We then have the zero-growth isoclines:

$dI/dt = 0$ for $I = 0$ and $S = \nu/\beta$

$dS/dt = 0$ for $\beta\,S\,I = \gamma\,(N - S - I)$

$$I = I = \frac{\gamma(N - S)}{(\beta S + \gamma)}$$

This curve intersects the axes at $(N,0)$ and $(0,N)$.

Steady States:

$(S, I) = (N,0)$

$$(S, I) = \left(\frac{\nu}{\beta}, \frac{N - (\nu/\beta)}{\nu + \gamma} \right)$$

Jacobean:

$$J = \begin{pmatrix} -(\beta I* + \gamma) & -(\beta S* + \gamma) \\ \beta I* & \beta S* - \nu \end{pmatrix}$$

For stability:

(1) $A_{11} + A_{22} < 0$?

$-(\beta\,I* + \gamma) + 0\ \ < 0$?   YES!

(2) $A_{11}A_{22} > A_{12}\,A_{21}$?

$0 > -(\beta\,S* + \gamma)\beta I*$ Yes!

Always locally stable.