Math 669: Math Bio Seminar Notes

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1 Day 1: Jan. 19, 2022

1.1 Simpson's Paradox

Real life: Data from Kidney stones treatments: Treatment A and B. (A is serious, B is mild.)

	Treatment A	Treatment B
Small	81/87 = 93%	234/ 270 = 87%
Big	192/263 = 73%	55/80 = 69%
Both	273/ 450 = 78%	289/350 = 83%

Simpson's Paradox: In each category, A is better, but overall, B is better. WHY?!

- Could be conditional probability/ hidden variable
- Experimental design
- Numbers vs. percentages (weights)

1.2 Chapter 1 of Murray

- Historically, math bio was about population models. (Foundation)
  - Could have any number of species.
  - Time-dependent (Continuous or discrete).
  - Start in 1 species, continuous model.
  - Many other axes
- Start in 1 species, continuous model.
- Example 1: Exponential Growth
  - $N(t)$ = population size at time t.
  - Rate of change: $\frac{dN}{dt}$ = births + deaths + migration
  - Example: $\frac{dN}{dt} = bN - dN + 0$; $b, d > 0$, birth and death rate with $N_0 = N(0)$.
  - Solution: $N(t) = N_0 e^{(b-d)t}$.
- Example 2: Logistic Growth/ Model
  - $\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$
  - K = "carrying capacity"
  - Where are the steady states?
  - Solution: $N = K,\ N = 0$.

- Q: Does the above analysis depend on K and r? No; only a shift and squish.
- Example 3: General case
  - $\frac{dN}{dt} = f(N)$ (usually nonlinear)
  - Prop: Let N be a steady state. If $f'(N) < 0$, then it is stable, if $f'(N) > 0$ unstable, if $f'(N) = 0$, indeterminate.
- Example 4: Parameters
  - $\frac{dN}{dt} = N^2 + DN + C$,$D, C \in \mathbb{R}$. The model now depends on the parameters.

2 Day 2: Jan 24, 2022

2.1 $\frac{dN}{dt} = f(N)$ again, a big example

- How could such a model get more interesting?
  - Add parameters ($\frac{dN}{dt} = N^2 + bN + c$
  - Biology
- Example: (Spruce Budworm; 1978)
  - Spruce is a tree (... duh?)
  - Budworm is something that hurts the tree (starts as larvae, become a bug); eats the foliage on the tree; birds eat the worms
  - $N(t)$ = population size of worms;
  - Model: $\frac{dN}{dt} = r_B N(\frac{K_B - N)}{K_B)} - \frac{BN^2}{A^2+N^2}$ $K_B =$; carrying capacity- measured in "worms"; r_B = birth rate- measured in $1/t$; second term is the predation rate of the bird; B = parameter- measured in N/t; A =parameter-measured in N;
  - (Important) Step 0: Nondimensionalize the model. Reasons; we want fewer parameters, and want to get rid of units ("meausred in")
  - New model: $\frac{dN}{dt} = r_B Au(\frac{K_B/A - u}{K_B/A} - B\frac{u^2}{1+u^2}$ $u = N/A$; now take $q = K_B/A$.
  - New model (again) $\frac{du}{dt} = \frac{1}{A}\frac{dN}{dt} = r_B Au(\frac{q-u}{q}) - \frac{B}{A}\left(\frac{u^2}{1+u^2}\right)$
  - To get ride of one more parameter, $\tau =$
  - New model: $\frac{du}{d\tau} = \frac{du}{dt}\frac{dt}{d\tau} = \frac{A}{B} r_B u(\frac{q-u}{q} - \frac{u^2}{1+u^2}$; take $r = r_B \frac{A}{B}$ (no units)
  - New mode: $\frac{du}{d\tau} = ru(\frac{q-u}{q}) - \frac{u^2}{1+u^2}$
  - Now to analyze:
  - Steady state: $u = 0$ (what's dead stays dead)
  - $\frac{du}{d\tau} = u\left[r\frac{q-u}{q} - \frac{u}{1+u^2}\right] = 0$. (Observing the powers, we see potentially three steady states.)
  - (This is the "art" of modeling: how to simplify the model is arbitrary from a math point of view, but has practical uses)
  - We analyzed the derivative, found the stable steady states.
  - Question: Why is "outbreak" worse than you might think?
  - Answer: Start r at 0, you'll stay along the steady the first one (the good one), but once you pass through the area with 3 steady states, you'll jump to the bad steady state. Now, if you start above the second steady state, you have to bring the rate all the way down to where we only have one steady state do we jump back down to the good steady state. This property is called **Hysterssis**; you tend to stay where you started (dynamically); "intetia"-like; "memory"

- Question: In real life, what to do to q and r to avoid outbreaks (or the bad steady state)? ($q = K_B/a, \quad r = r_B \frac{A}{B}$.
- Answer: Keeping r small is good (smaller reproduction is good), and keeping q small is also good (nature keeps the carrying capacity down, so helps the population stay low).
- Last thing: $\frac{dN}{dt} = f(N)$. Can we have any periodic solutions to the model? Depends on the source. In 1D, with no time-dependence, no parameter dependence, the answer is no: how would you be able to pass through a point positively, but somehow loop back negatively?
- Question: How to get periodic solution?
- Answer: One answer is to insist on some time dependence in the ODE. Another option is to involve *delays*.

2.2 Delays

- $\frac{dN}{dt} = f(N(t), N(t+T))$, ie, what were things like time T ago?
- Example: $\frac{dN}{dt} = rN(t)\frac{K-N(t-T)}{K}$.

3 Day 3: Jan. 26, 2022

3.1 Delayed logistic model (cont.)

- $\frac{dN}{dt} = rN(t)\left[\frac{k-N(t-T)}{k}\right]$.
- Would expect a period of about $4T$.
  - Step 0: Nondimensionalize
  - New Model: $\tau = rt$, $\hat{T} = rT$, $y(\tau) = N(t)/k$: $\frac{dy(\tau)}{d\tau} = y(\tau)\left[1 - y(\tau - \hat{R})\right]$.
  - Step 1: Steady States: (Solutions to $N* = N(t)$ for $t \geq 0$.
  - Set $0 = \frac{dy(\tau)}{d\tau}$. State 1: $y(\tau) = 0$ (this is trivial). Suppose y^* is a steady state (ie, $y(\tau) = y(\tau - \hat{T}) = 0$, so $y^* = 0$ or $y^* = 1$.
  - Step 2: Stability (and how they depend on parameters – in this case $\hat{T}$): $y^* = 0$) .
  - $y^* = 0$: is unstable (if you start a little bit away from 0), you will grow.
  - $y^* = 1$: Let $u(\tau) = y(\tau) - 1$, and find steady solutions near $u^* = 0$. Then $\frac{du(\tau)}{d\tau} = \frac{du(\tau)}{d\tau} = (u(\tau)+1)\left[-u(\tau - \hat{T})\right] \approx -u(\tau - \hat{T})$. So look at $\frac{du(\tau)}{d\tau} = -u(\tau - \hat{T})$. Which values of t yield 0 being stable?
  - Theory: Analyze by assuming solutions have the form $u(\tau) = e^{\lambda\tau}$. Examine the eigenvalues $\lambda \in \mathbb{C}$. Look at the real part of λ. If there exists an eigenvalue with negative real part, then $u^* = 0$ is stable. If the real part is real, then $u^* = 0$ is unstable.
  - Case 1: All eigenvalues λ are real. $\frac{du}{d\tau} = -u(\tau - \hat{T}) = \lambda e^{\lambda\tau} = -e^{\lambda(\tau - \hat{T})}$. So $\lambda = -e^{-\lambda\hat{T}}$. In this case, 0 will be stable (look at the graph of λ and the $-e^{-\lambda\hat{T}}$.

4 Day 4: Jan. 31, 2022

4.1 Stability (better)

Definition 1. Let $\bar{x} = (x_1, ..., x_n)$ be a steady state of and ODE system $\frac{dx_1}{dt} = f_1(x_1, ..., x_n)$;... $\frac{dx_n}{dt} = f_n(x_1, ..., x_n)$. This steady state is:

1. Locally stable if for all $\epsilon > 0$ there exists a $\delta > 0$ such that for every trajectory $x(t)$ for this system, $|x(0) - \bar{x}| < \delta \implies |x(t) - \bar{x}| < \epsilon$ for all $t > 0$. (Start near, then stay near)

2. Locally asymptotically stable if If $\bar{x}$ is locally stable and there exists a $\delta > 0$ such that $|x(0) - \bar{x}| < \delta$ then $\lim_{t\to\infty} |x(t) - \bar{x}| = 0$. (Start near, then converge) *An example of locally stable but not locally asymptotically stable would be orbits around a stead state point.*

3. Globally asymptotically stable if locally stable and every trajectory converges.

4. Global attractor if every trajectory converges to the steady state.

4.2 Delayed Logistic (cont.)

- Model: $\frac{dN}{dt} = fN(t)\left[\frac{K-N(t-T)}{K}\right]$; T =length of delay; K = carrying capacity.

Theorem 1. *For this model, there are two steady states: (1) $N^* = 0$, which is always unstable; (2) $N^* = K$ which is: locally asymptotically stable if $0 < T < \frac{\pi}{2r}$, and unstable if $T > \frac{\pi}{2r}$. Furthermore, at the bifurcation, from stable to unstable, oscillations are generated with period about $4T$.*

Proof. (1) Last class (2) We reduce to the case for which $\hat{T}(= rT)$ there exists $\lambda = a + bi$ with $a > 0$ (unstable) for which $\lambda = -e^{-\lambda\hat{T}}$. So $a + bi = -e^{-(a+bi)\hat{T}} = e^{-a\hat{T}}e^{-bi\hat{T}} = -e^{a\hat{T}}\left[\cos(b\hat{T}) - i\sin(b\hat{T})\right]$. Thus, $a = e^{-a\hat{T}}\cos(b\hat{T})$, $b = -e^{-a\hat{T}}\sin(b\hat{T})$. Using graphing techniques, we see that we move from stable to unstable at about $\hat{T} = 1.5$, where $\lambda = \pm i$. (Better analysis actually gives $\hat{T} = \pi/2$.) When $\hat{T} = \frac{\pi}{2} + \epsilon$, $\epsilon > 0$. The eigenvalues were near $\pm i$, so $\lambda = \delta + (1+\sigma)i$, $\delta > 0, \sigma$ small $(0 < |\sigma| << 1)$. Hence, $y(\tau) \approx 1 + ce^{\lambda t} = 1 + ce^{\delta\tau}e^{(1+\sigma)i\tau}$. Thus, the period is approximately $2\pi/(1+\sigma) \approx 2\pi$. This translates to period of $4T$ for the original system. ☐

(Brief aside:) We have local asymptotically stable when $0 < T < \frac{\pi}{2r}$. It is global when T is a little bit less than $\pi/(2r)$ (has been shown), but there's still a gap (active research).

5 Day 5: Feb. 2, 2022

5.1 Harvesting

5.2 Discrete Time

Fish harvesting: we want to maximize (sustainable) yield w/ least effort.
Example: ("constant effort") $\frac{dN}{dt} = rN(\frac{K-N}{K} - EN$ (E is some "effort" parameter), EN is the yield per unit time.

- $r, K, E > 0$
- What about steady states? $N = 0$ (as usual); $N = K(1 - \frac{E}{r})$. Want $E < r$. 0 is unstable and the second is stable (locally asymptotically stable).
- If $E > r$, then 0 is stable (insofar as a positive population will go to 0). In this case, it's no good: too much harvesting.
- At the second steady state, the yield is $EN^{**} = EK(1 - \frac{E}{r})$. We can maximize this with $0 < E < r$; max is at $E^* = r/2$. Then yield is $rK/4$. The steady state value is $N^{**} = K(1 - 1/2) = K/2$.

Proposition 2. For the constant effort model, max yield $= \frac{rk}{4}$ is realized at $E = r/2$ and the corresponding population size is $N^* = K/2$.

Another example: (Constant yield)

- $\frac{dN}{dt} = rN(\frac{K-N}{K}) - y_0$; y_0 =constant.

- Now there's NO steady state at 0. Still have a parabola. When $0 < y_0 < \frac{rK}{4}$, we have a "good" situation because we have a stable steady state. Max (actually sup) occurs at $rk/4 - \epsilon$.
- Question: Which of these two strategies is better? Model 1, because you have a much larger margin of error (the stable region is much larger) than in the second model, where a small perturbation can lead to an unstable situation.

5.3 Discrete Time

Here are working with 1 species, N_t at times $t = 1, 2, 3, ...$ The big question: relation between continuous time models and discrete time models? Often these are given by a recurrence relation; $N_{t+1} = f(N_t)$
Example: $N_{t+1} = rN_t$.

- We begin with some initial value N_0
- The solution becomes $N_{t+1} = r^t N_0$.
- Mathematically, what is a steady state of a recurrent relation: $N_{t+1} = f(N_t)$?
- Answer: N^* such that $N^* = f(N^*)$.

Example: $N_{t+1} = f(N_t)$

- SUPPOSE steady states are $0, K$ for some $K > 0$.
- Visually, K is stable, as is K.

Cobwebbing (for discrete models):

1. Draw the graph of f
2. Draw the $y = x$ line. (Intersection points are steady states)
3. Plot some initial point N_0.
4. Draw vertical line from $(N_0, N_1) \to (N_0, N_1)$
5. Draw horizontal line from $(N_0, N_1) \to (N_1, N_1)$
6. Repeat until limit found

Example: $N_{t+1} = rN_t$.

- This time allow negative r, $N_t < 0$.
- Suppose $-\infty < r < -1$. Then the limit does not exist (0 is unstable)
- When $r = -1$, you oscillate. (Locally stable, but NOT asymptotically stable)
- When $-1 < r < 0$, we will spiral to 0 (so 0 is stable asymptotically)
- When $r = 1$, we are stable.
- When $0 < r < 1$, 0 is asymptotically stable
- When $r > 1$, 0 is unstable

Theorem 3. *Stability Criterion: Let N be a steady state of a recursion $N_{t+1} = f(N_t)$. If $|f'(N)| < 1$ then N^* is locally asymptotically stable. Moreover, if $f'(N) < 1$, then solutions approach N with oscillations. If positive, then same thing but no oscillations. If $|f'(N)| > 1$, then N is unstable. If $|f'(N)| = 1$, we conclude nothing.*

6 Day 6: Feb. 7, 2022

6.1 Discrete Logistic Model

Brief summary from last class: Harvesting; cobwebbing; stability theorem.

- Model: $x_{t+1} = rx_t(1 - x_t)$. (Nondimensionalize form); discrete logistic model
- Downward parabola with roots at $x = 0, 1$. The max value is $r/4$.
- We want $0 \leq r/4 \leq 1$, so consider want $0 \leq r \leq 4$.
- Steady states: there's a possibility for 2. We have $f(x) = rx(1 - x)$, so $f'(x) = r(1 - 2x)$. When $f'(0) = 1$, we have only one steady state, so when $f'(0) = r = 1$. When $r > 1$, we have two steady states.
- Solving: $rx(1 - x) = x$, ($x = 0$ is trivial). Then, $x = 1 - \frac{1}{r}$.
- For $0 < r \leq 1$, there is only one steady state $x = 0$; when $1 < r \leq 4$, we have two steady states, with the other being $x = 1 - \frac{1}{r}$.
- Stability: When $r < 1$, we apply the theorem and the above calculation to deduce that $x = 0$ is stable. When $r > 1$, $x = 0$ is unstable. For $x = 1 - \frac{1}{r}$, we have $f'(x) = r(-1 + \frac{2}{r}) = 2 - r$. When $1 < r < 3$, we have stability; when $r > 3$, we have unstable.
- Remaining questions: When are these steady states actually globally stable? And what is the behavior when both stead states are unstable?

Proposition 4. Assume $f : [0, a) \to [0, a)$ is a continuous function such that $0 < f(x) < x$ for all $x \in (0, a)$. Then, consider the recursion $N_{t+1} = f(N_t)$; we have 0 is globally asymptotically stable.

Proof. Let x_0 be an initial condition. Then $0 < ... < f(f(x_0)) < x_0$. Therefore, we have a strictly monotonically decreasing sequence bounded below, thus converges. Let $y = \inf\{f(x_n)\}$. We claim $y = 0$. Assume for contradiction that $y > 0$ (not zero). Since f is continuous, $\lim_{t\to\infty} f(x_t) = f(y) < y$. But y was an infimum, and therefore have a contradiction. □

- Therefore, when $r < 1$, 0 is globally stable.
- For question 2: Yes, GAS "proof" by cobwebbing.

Definition 2. Let $f : I \to I$, where $I \subset \mathbb{R}$. This has an $m-$cycle if there exists some $x \in I$ such that $f^m(x) = x$ and $f^i(x) \neq x$ for $i = 1, ..., m - 1$.

Theorem 5. *Assume $f : [0, a) \to [0, a)$ is continuous such that: $f(0) = 0$, $f(x_0) = x_0$ for some x_0, $f(x) > x$ for if $0 < x < x_0$, $f(x) > x$ for $x_0 < x < a$, if f has a maximum at some x_m in $(0, x_0)$, then f is decreasing afterwards from x_m to a. Then for $N_{t+1} = f(N_t)$, x_0 is globally asymptotically stable iff there are no 2-cycles.*

- Checking the graph, the answer to 2 is yes, the second steady state is globally stable.

7 Day 7: Feb. 9, 2022

7.1 m-cycles

- Recall: $m - cycle$ of form $x_1 \to^f x_2 \to^f \cdots \to^f x_m$, and this is the smallest such that this happens.
- Ex: $N_{t+1} = -N_t$. So every point is a 2-cycle.
- Question: if you have a two cycle, are they locally stable (ie, given $\epsilon > 0$ there exists a $\delta > 0$ such that $|x_1 - \bar{x}| < \delta$, then $|x_{stuff} - \bar{x}_1| < \epsilon$... etc.)? What about locally asymptotically stable?

- Ex: $N_{t+1} = 1 - (N_t)^2$. Steady states: $\bar{x} = \frac{-1\pm\sqrt{5}}{2}$. Stability: $f'(x) = -2x$, so both are unstable. Are there any two cycles, ie, $1-(1-x^2)^2 = x$? So, $-x^4+2x^2-x = 0$; $-x(x^3-2x+1) = 0$; so $x-1$ is also a factor; $-x(x-1)(x^2+x-1) = 0$. So $x = 0$ and $x = 1$ are the two cycles. What about the stability of the two-cycle? (Look at the m-composition as a new function and apply previous theory to determine stability; also note that it suffices to test only one point in the path.)
- Observe that f being well defined that if x_1 is a two cycle, then we have another x_2 being a two-cycle for free. (Easily extended to m-cycles.)

7.2 Bifurcations

- Look at 4 types of bifurcations.
- Bifurcation diagrams.
- Saddle node: A stable and unstable steady state collide and vanish.
- Pitch fork: A steady steady splits into 3; 2 stable, 1 unstable.
- Transcritical: A stable and unstable steady state collide and exchange stability.
- A stable steady state splits into a pair of 2-cycles and an unsteady state.

8 Day 8: Feb. 14, 2022

8.1 Continuous time (2+ species)

Set up:

- 2 species; linear
- Model:

$$\frac{dx}{dt} = a_{11}x + a_{12}y$$
$$\frac{dy}{dt} = a_{21}x + a_{22}y$$

- Can set $A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$
- Steady states: $(\hat{x}, \hat{x}) = (0, 0)$
- Would need to check rank of A to see if there are more.
- Solutions:

$$\begin{bmatrix} x(t) \\ y(t) \end{bmatrix} = \begin{bmatrix} x(0)e^{\lambda_1 t} \\ y(0)e^{\lambda_2 t} \end{bmatrix}, \quad \lambda_1 \neq \lambda_2, \in \mathbb{R}$$

- Question: When is the steady state$(0, 0)$ stable?

Proposition 6 (Stability criterion)**.** In the above set up, if all eigenvalues of A have negative real part, then $(0, 0)$ is (GA) stable. If eigenvalues have nonpositive real part, then $(0, 0)$ is locally stable. Otherwise, if at least one eigenvalue has strictly positive real part, $(0, 0)$ is unstable.

- How to tell from A itself? Sum of eigenvalues is the trace and the product is the determinant. Alternatively, look at the characteristic polynomial of A: $\det(A-\lambda I) = \lambda^2 - Tr(A)\lambda + \det(A)$. So solving $0 = r^2 + c_1 r + c_2$ and asking when all roots have negative real part.

Theorem 7 (Routh - Hurwitz Criterion)**.** *The roots of* $0 = r^n + c_1 r^{n-1} + ... + c_n$ *all have negative real parts iff the determinants of the following Hurwitz matrices are positive:*

1. $H_1 = \begin{bmatrix} c_1 \end{bmatrix}$ $\quad H_1 = \begin{bmatrix} c_1 & 1 \\ c_3 & c_2 \end{bmatrix}$ $\quad H_3 = \begin{bmatrix} c_1 & 1 & 0 \\ c_3 & c_2 & c_1 \\ c_5 & c_4 & c_3 \end{bmatrix} \dots$ *where* $c_{n+1} := c_{n+i} := 0$ *if* $i \geq 1$.

- In the 2×2 case: if $c_1 > 0$ and $c_1 c_2 > 0$ (or $c_1 > 0$ and $c_2 > 0$). So I want $\det(A)$ and $tr(A) < 0$, then $(0,0)$ is (GA) stable.
- Summary: When $tr(A) < 0$ and $\det(A) > 0$, we have globally stability; when $tr(A) = 0$, $\det(A) > 0$, then $(0,0)$ is locally stable.
- Question: $\mathbb{R}$ vs $\mathbb{C}$ eigenvalues? Look at the discriminant: if $tr(A)^2 - 4\det(A) < 0$, then we have complex-valued eigenvalues.

9 Day 9: Feb. 16, 2022

9.1 Stability Criterion

- Linear case: $\begin{bmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{bmatrix} = A \begin{bmatrix} x \\ y \end{bmatrix}$.
- Now we move to nonlinear systems: $\begin{cases} \frac{dx_1}{dt} = f_1(x_1, ..., x_n) \\ \vdots \\ \frac{dx_n}{dt} = f_n(x_n, ..., x_n) \end{cases}$.
- We want to find and analyze steady states

Theorem 8 (Stability Criterion)**.** *Let* $\bar{x}$ *be a steady state for the nonlinear system of ODEs. Let* J *be the Jacobian matrix (so the matrix all the partial derivatives) for the system evaluated at* $\bar{x}$*. Then TFAE:*

1. *Every eigenvalue of* J *has negative real part.*
2. *The determinants of all the Hurwitz matrices of the characteristic polynomial of* J *are all positive.*

If either of these holds, then $\bar{x}$ *is locally asymptotically stable. Furthermore, if any of the eigenvalues are positive or if any of the determinants are negative, then* $\bar{x}$ *is unstable.*

9.2 Lotka-Volterra Predator-Prey

- Two species; prey (rabbits) and predators (fox/ wolves)
- Model:

$$\frac{dx}{dt} = x(a - by)$$
$$\frac{dy}{dt} = y(-c + ex).$$

- With no predators, prey has exponential growth
- With no prey, predators have exponential decay
- Let's nondimensionalize: let $u(t) = \frac{e}{c} x \frac{t}{a}$; $v(t) = \frac{b}{a} y \frac{t}{a}$.

- New model:

$$\frac{du}{dt} = u(1-v)$$
$$\frac{dv}{dt} = \frac{c}{a}v(u-1) := \alpha v(u-1).$$

- Steady states: $(0,0)$ and $(1,1)$.
- Stability: The Jacobian Matrix:

$$Jac = \begin{bmatrix} \frac{\partial f_1}{\partial u} & \frac{\partial f_1}{\partial v} \\ \frac{\partial f_2}{\partial u} & \frac{\partial f_2}{\partial v} \end{bmatrix} = \begin{bmatrix} 1-v & -u \\ \alpha v & \alpha(u-1) \end{bmatrix}.$$

- Then $Jac(0,0) = \begin{bmatrix} 1 & 0 \\ 0 & -\alpha \end{bmatrix}$; Then eigenvalues are 1 and $-\alpha$. Therefore, $(0,0)$ is unstable.
- $Jac(1,1) = \begin{bmatrix} 0 & -1 \\ \alpha & 0 \end{bmatrix}$. The characteristic polynomial is $\lambda^2 + \alpha = (\lambda + i\sqrt{\alpha})(\lambda - i\sqrt{\alpha})$. Stability is thus unclear (at this point).
- Aside: Consider the system:

$$\begin{bmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{bmatrix} = J \begin{bmatrix} x \\ y \end{bmatrix}$$

Then $\begin{bmatrix} x(t) \\ y(t) \end{bmatrix} = v_1 e^{i\sqrt{\alpha}t} + v_2 e^{-i\sqrt{\alpha}t}$. with $v_1,\ v_2$ eigenvectors with period $\frac{2\pi}{\sqrt{\alpha}}$. This give us:

Theorem 9. *Every solution of the Lotka-Volterra with initial condition $(u_0, v_0) \in \mathbb{R}^+ \setminus \{(1,1)\}$ is periodic.*

Proof. Use separation of variables: $\frac{dv}{du} = \frac{\alpha v(u-1)}{u(1-v)}$ becomes: $(1-v)\frac{dv}{v} = \alpha(u-1)\frac{du}{u}$. Integrate: $\int (1-v)\frac{dv}{v} = \int \alpha(u-1)\frac{du}{u} = \ln(v) - v = \alpha u - \alpha\ln(u) + C$, so $e^{\ln(v)}e^{-v} = e^{\alpha u}e^{-\alpha\ln(u)}\underbrace{e^C}_{K_1}$. Thus, $ve^{-v} = e^{\alpha u}u^{-\alpha}K_1$. We thus have:

$$\frac{v}{e^v}\frac{u^\alpha}{e^{\alpha u}} = K_1.$$

Let $h_1(v) = \frac{v}{e^v}$; $h_2(u) = \frac{u^\alpha}{e^{\alpha u}}$. Then, $\max_v = \frac{1}{e}$, $\max_u = \frac{1}{e^\alpha}$.

We now claim $0 < K_1 < \max_u \max_v$. The 0 bound is trivial because everything is positive (in particular, the initial condition). Furthermore, it is trivial that K_1 cannot exceed the product of the maxes. Suppose now that $K_1 = \max_v \max_u$. Maxes occur when $u = v = 1$, but this is not possible by assumption, and thus $K_1 < \max_u \max_v$.

If $u = 1$, then $h_1(v)h_2(u) = h_1(v)\max_u = K_1$, then $h_1(v) = K_1/\max_u < \max_v$. Thus there are two options for v: $v = v_1 < 1$ or $v = v_2 > 1$ (see the graph for h_1). For all other values of u (up to the min/max argument for v), again, $h_1(v) = K_1/h_2(u)$. So we have two options for v (same argument via graph). A symmetric-like argument for v shows that we have a closed curve solution. ∎

10 Day 10: Feb. 21, 2022

10.1 Better Model

- Model:

$$\begin{cases} \frac{dN}{dt} = N\left[r\left(\frac{K-N}{K}\right) - \frac{kP}{N+D}\right] \\ \frac{dP}{dt} = P\left[s\left(\frac{\frac{N}{h} - P}{\frac{N}{h}}\right)\right] \end{cases}$$

- Nondimensionalized model: $\tau = rt$; $u(\tau) = \frac{N(t)}{K}$; $v(\tau) = \frac{hP(t)}{K}$; $a = \frac{k}{hr}$; $b = \frac{s}{r}$; $d + \frac{D}{k}$.

$$\begin{cases} \frac{du}{d\tau} = u(1-u) - \frac{auv}{u+d} \\ \frac{dv}{d\tau} = bv(1 - \frac{v}{u}). \end{cases}$$

- Steady states: For second equation, $v = 0,\ v = u$. First equation (use the fact that $u = v$ is a steady state from the first equation). To solve, we could use the quadratic formula; could also use Descartes Rule of signs: . There is always 1 (nonzero) steady steady $u = 0$,

- Aside: Descartes Rule of Signs: Let $c_x^n + c_{n-1}x^{n-1} + \cdots + c_0 \in \mathbb{R}[x]$. Let N denote the number of positive roots of the polynomial. Consider the sequence of the sign of the coefficients (any 0's deleted). Then, (1) $N \leq \#$ of sign changes; (2) $N-$ $\#$ of sign changes is congruent to $0(mod 2)$.

- Example of Descartes Rule of Signs: $0 = x^5 - 4x^3 + 2x - 7$. (+, -, +,+), and so by the rule of signs, the number of positive roots is either 0 or 2.

- (Back to problem) The signs are (-, ?, +). So there is one for sure sign change.

- What is the stability of $(u, v) = (u, u)$ steady state? To find, take $Jac()|_{u=v}$ and consider the characteristic polynomial: $\lambda^2 - Tr(J) + \det(J)$. We claim (without showing) that $\det(J) > 0$. Furthermore:

$$Tr(J) = u\left[\frac{au}{(u+d)^2} - 1\right] - b.$$

  We only need to check the sign of $Tr(J)$ to know the stability of the steady state.

- Question: if the steady state is unstable, do nearby solutions converge to a periodic orbit?

Definition 3. The ω-limit set of the solution $(x(t), y(t))$ consists of points (a, b) such that $\lim_{i\to\infty}(x(t_i), y(t_i)) = (a, b)$ for some sequence $\{t_i\}_{i\in\mathbb{N}}$.

Theorem 10 (Poincare-Bendixson Theorem)**.** *Let $\boldsymbol{x} = \boldsymbol{F}(\boldsymbol{x})$ be a 2D ODE system, where F_1, F_2 are differentiable and defined on an open subset of $\mathbb{R}^2$. If some solution $(x(t), y(t))$ has a nonempty and compact ω-limit set which does not contain any steady states, then it converges to a periodic orbit.*

Proposition 11. For the model, when (u, u) is unstable (or $Tr(J) > 0$), then solutions near the steady state do converge to a periodic orbit.

Proof. By the theorem, we just need to construct a compact set containing (u, u) in the interior that solutions never leave (forward invariant). (Idea, not from class: look at □

11 Day 11: Feb. 23, 2022

11.1 Hopf Bifurcations

- Last time, we saw that there are periodic orbits for 2D predator-prey model (by Poincare-Bendixson)

- What about 3+ dimensions? One answer is Hopf Bifurcations.

- Def: A *Hopf Bifurcation* is a bifurcation in which (for some steady state $\hat{x}$) a single pair of complex conjugate eigenvalues of the Jacobian matrix of the ODE system at the steady state $\hat{x}$ crosses the imaginary axis at nonzero speed and all the other eigenvalues remain with negative real part.

Theorem 12 (1942; Hopf Bifurcation Theorem, (Any dimension))**.** *Somewhere near a Hopf bifurcation $(\hat{x}, \hat{r})$, (r is the bifurcation parameter) , there is a periodic orbit near $\hat{x}$. (The orbit could be unstable.)*

Example 13.

$$\begin{bmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{bmatrix} = \underbrace{\begin{bmatrix} 0 & 1 \\ -1 & r \end{bmatrix}}_{A} \begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} y \\ -x + ry \end{bmatrix}.$$

Notice that $Jac(A) = A$. Then, the characteristic polynomial is $\lambda^2 - r\lambda + 1$. (Note there is only one steady state: $(0,0)$.) Bifurcation happens at $(\hat{x}, \hat{r} = \left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, 0 \right)$.

11.2 Biochemical Reaction Networks