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QBIO 482
Spring 2025
Homework 3

Question 1

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1. In the wild, turkeys compete for habitat and resources with the California quail. A competition model between turkeys (T) and quail (Q) can be described by:

$$T' = 24T - 2T^2 - 3TQ$$
$$Q' = 15Q - Q^2 - 3TQ$$

a. Describe in words the meaning of each of the terms in the equations.

<u>For the Turkey equation:</u>

T': refers to the rate of change of turkey population

24T: represents the natural exponential growth of the turkey population without constraints (at a per capita rate of 24)

$-2T^2$: represents the intraspecific competition among turkeys; as the turkey population grows, competition for food, space, and other resources increases, reducing the growth rate

-3TQ: represents interspecific competition with quail; the presence of quail negatively affects the turkey population due to competition for shared resources

<u>For the quail population:</u>

Q': refers to the rate of change of the quail population

15Q: represents the natural exponential growth of the quail population without constraints (at a per capita rate of 15)

$-Q^2$: represents intraspecific competition among quail; as the quail population increases, competition among quail individuals reduces their growth rate

-3TQ: represents interspecific competition with turkeys; the presence of turkeys negatively affects the quail population due to competition for shared resource

b. Find the nullclines of this system and plot them.

Find nullclines by setting each equation equal to 0:

$T' = 24T - 2T^2 - 3TQ = 0$

$T(24 - 2T - 3Q) = 0 \rightarrow T = 0, \quad (24 - 2T - 3Q) = 0$

$(24 - 2T) = 3Q \rightarrow Q = \frac{24-2T}{3}$

$T = 0, \quad Q = \frac{24-2T}{3}$

$Q' = 15Q - Q^2 - 3TQ = 0$

$Q(15 - Q - 3T) = 0 \rightarrow Q = 0, (15 - Q - 3T) = 0$

$(15 - 3T) = Q$

$Q = 0, Q = 15 - 3T$

The turkey nullcline consists of:

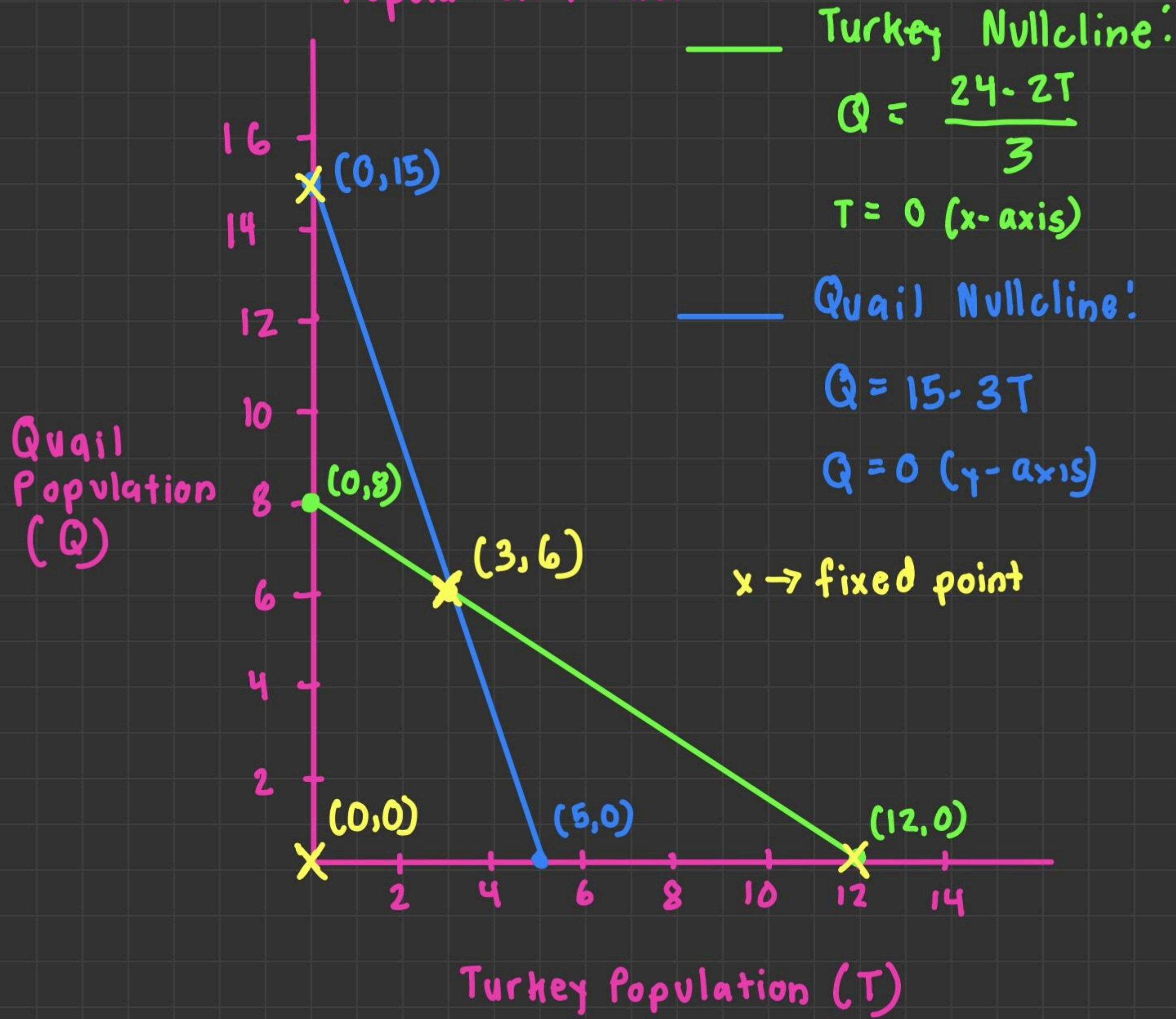
- $T = 0\ (x - axis)$
- $Q = \frac{24-2T}{3}$

The quail nullcline consists of:

- $Q = 0\ (y - axis)$
- $Q = 15 - 3T$

The plot of the nullclines is on the next page ↓

Nullclines of the Turkey-Quail Population Model



Find Turkey Nullcline intercepts

$$Q = \frac{24-2T}{3}$$

$$0 = 24-2T$$

$$2T = 24$$

$$T = 12$$

$(12, 0)$

$$Q = \frac{24}{3} = 8$$

$(0, 8)$

Find Quail Nullcline intercepts:

$$Q = 15-3T$$

$$0 = 15-3T$$

$$3T = 15$$

$$T = 5$$

$(5, 0)$

$$Q = 15-3(0)$$

$$Q = 15$$

c. Use the nullclines (or algebra) to find the fixed points of the system

Using the factored equations from part b:

$If\ T = 0,\ then\ Q(15 - Q - 3T) = 0 \rightarrow Q(15 - Q) = 0$

$Q = 0, Q = 15$

So two fixed points are (0, 0) and (0, 15)

$If\ Q = 0,\ then\ T(24 - 2T - 3Q) = 0 \rightarrow T(24 - 2T) = 0$

$T = 0, T = 12$

So another fixed point is (12, 0).

Then set the turkey and quail nullcline equations equal to each other:

Turkey nullcline: $Q = \frac{24-2T}{3}$

Quail nullcline: $Q = 15 - 3T$

$15 - 3T = \frac{24-2T}{3} \rightarrow 15 - 3T - 8 + \frac{2T}{3} = 0 \rightarrow 7 - 3T + \frac{2T}{3} = 0$

$21 - 9T + 2T = 0 \rightarrow 21 - 7T = 0 \rightarrow T = 3$

$Q = \frac{24-2T}{3} = \frac{24-2(3)}{3} = \frac{18}{3} = 6$

Thus the last fixed point is (3, 6). This is shown in the plot from part b: this point is the intersection of the turkey and quail nullclines.

Hence, there are four fixed points: (0, 0), (0, 15), (12, 0), (3, 6)

d. Sketch the direction of the vector field along each of the nullclines. Use your intuition, plus additional few test points as needed, to fill in the vector field of the plot around the nullclines.

$T' = 24T - 2T^2 - 3TQ = 0$

$Q' = 15Q - Q^2 - 3TQ = 0$

Region where T, Q > 0: example point (5, 10)

$T' = 24(5) - 2(5)^2 - 3(5)(10) = 120 - 50 - 150 = -80 \rightarrow leftward$

$Q' = 15(10) - 10^2 - 3(5)(10) = 150 - 100 - 150 = -100 \rightarrow downward$

Region where T and Q are small: example point (1, 1)

$T' = 24 - 2 - 3 = 19 \rightarrow rightward$

$Q' = 15 - 1 - 1 = 13 \rightarrow upward$

Region where T is large and Q is small: example point (10, 2)

$T' = 24(10) - 2(10)^2 - 3(10)(2) = 240 - 200 - 60 = -20 \rightarrow leftward$

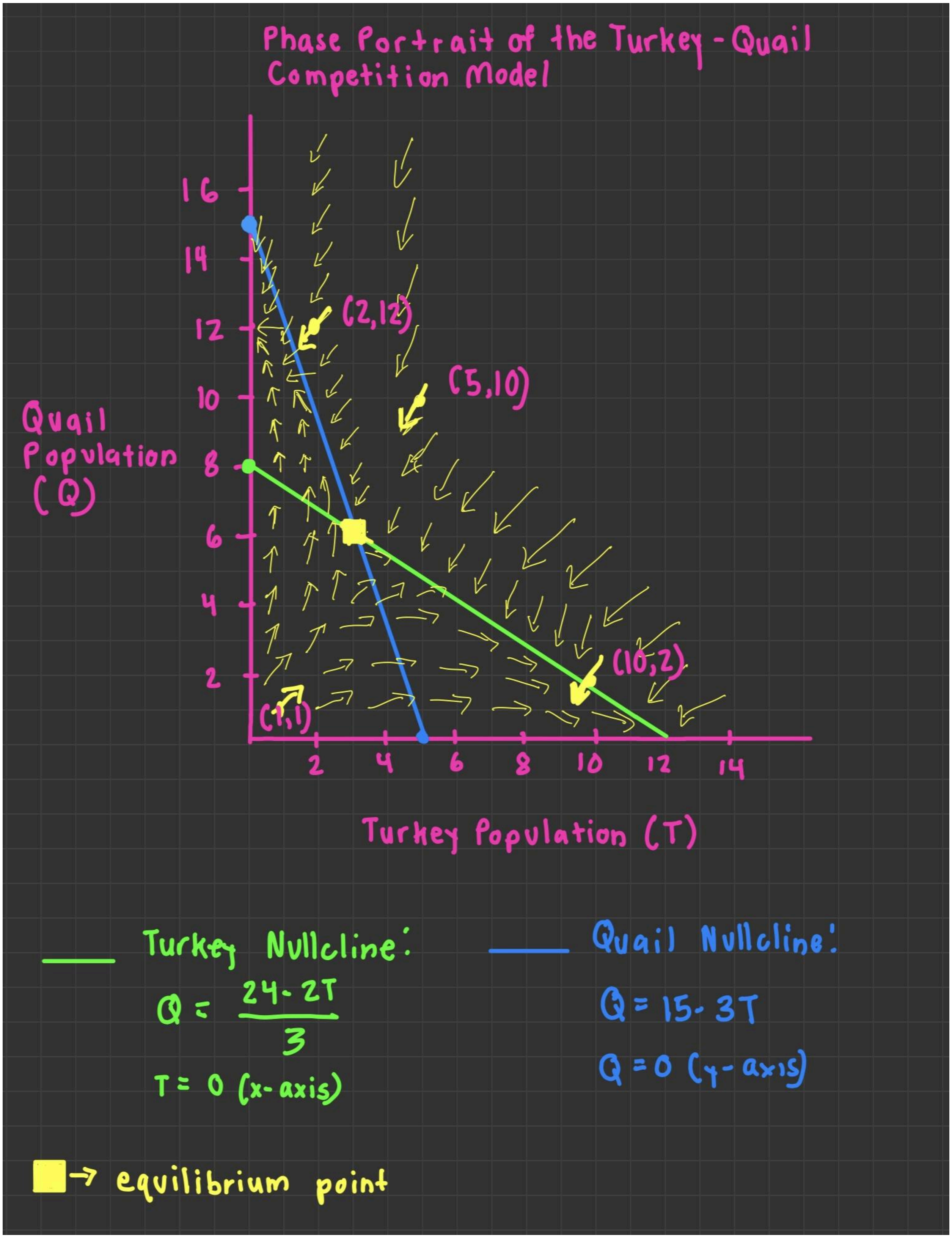
$Q' = 15(2) - 2^2 - 3(10)(2) = 30 - 4 - 60 = -34 \rightarrow downward$

Region where T is small and Q is large: example point (2, 12)

$T' = 24(2) - 2(2)^2 - 3(12)(2) = 48 - 8 - 72 = -32 \rightarrow leftward$

$Q' = 15(12) - 12^2 - 3(12)(2) = 180 - 144 - 72 = -36 \rightarrow downward$

Vector field of the plot of nullclines is on the next page.



Phase Portrait of the Turkey-Quail Competition Model
Quail Population (Q)
Turkey Population (T)
16
14
12
10
8
6
4
2
2
4
6
8
10
12
14
(2,12)
(5,10)
(10,2)
(1,1)
Turkey Nullcline:
$Q = \frac{24-2T}{3}$
T = 0 (x-axis)
Quail Nullcline:
Q = 15-3T
Q = 0 (y-axis)
→ equilibrium point

e. How many stable equilibria are there? Describe in words the biological behaviors of this system.

Compute the Jacobian:

$f(T, Q) \ = \ 24T \ - \ 2T^2 \ - \ 3TQ, \qquad g(T, Q) \ = \ 15Q \ - \ Q^2 \ - \ 3TQ$

$\frac{df}{dT} = \frac{d}{dT}(24T \ - \ 2T^2 \ - \ 3TQ) \ = \ 24 \ - \ 4T \ - \ 3Q$

$\frac{df}{dQ} = \frac{d}{dQ}(24T \ - \ 2T^2 \ - \ 3TQ) \ = \ - \ 3T$

$\frac{dg}{dT} = \frac{d}{dQ}(15Q \ - \ Q^2 \ - \ 3TQ) \ = \ - \ 3Q$

$\frac{dg}{dQ} = \frac{d}{dQ}(15Q \ - \ Q^2 \ - \ 3TQ) \ = \ 15 \ - \ 2Q \ - \ 3T$

$J \ = \begin{bmatrix} \frac{df}{dC} & \frac{df}{dS} \\ \frac{dg}{dC} & \frac{dg}{dS} \end{bmatrix} = \begin{bmatrix} 24-4T-3Q & -3T \\ -3Q & 15-2Q-3T \end{bmatrix}$

Evaluate Jacobian at each fixed point:

At (0, 0): extinction

$J \ = \begin{bmatrix} 24 & 0 \\ 0 & 15 \end{bmatrix}, \ so \ \lambda_1 \ = \ 24, \ and \ \lambda_2 \ = \ 15$

Thus, the point (0, 0) is an unstable fixed point because both eigenvalues are positive.

At (0, 15): quail only

$J \ = \begin{bmatrix} 24-3(15) & 0 \\ -3(15) & 15-2(15) \end{bmatrix} = J \ = \begin{bmatrix} -21 & 0 \\ -45 & -15 \end{bmatrix}, \ so \ \lambda_1 = \ - \ 21, \ and \ \lambda_2 = \ - \ 15$

Since both eigenvalues are negative, (0, 15) is a stable fixed point.

At (12, 0): turkey only

$J \ = \begin{bmatrix} 24-4(12) & -3(12) \\ 0 & 15-3(12) \end{bmatrix} = \begin{bmatrix} -24 & -36 \\ 0 & -21 \end{bmatrix}, \ so \ \lambda_1 = \ - \ 24, \ and \ \lambda_2 = \ - \ 21$

Since both eigenvalues are negative, (12, 0) is a stable fixed point.

At (3, 6): coexistence equilibrium

$$J = \begin{bmatrix} 24-4(3)-3(6) & -3(3) \\ -3(6) & 15-2(6)-3(3) \end{bmatrix} = \begin{bmatrix} -6 & -9 \\ -18 & -6 \end{bmatrix}$$

$$Solve\ for\ det(J - \lambda I) = 0$$

$$(J - \lambda I) = \begin{bmatrix} -6-\lambda & -9 \\ -18 & -6-\lambda \end{bmatrix}$$

$$det(J - \lambda I) = 0 = (-6 - \lambda)(-6 - \lambda) - (-9)(-18)$$

$$0 = (\lambda + 6)^2 - 162 \rightarrow 162 = (\lambda + 6)^2$$

$$\lambda + 6 = \pm\sqrt{162} \rightarrow \lambda = -6 \pm \sqrt{162}$$

This will result in one positive λ value and one negative λ value. Thus, (3, 6) is not a stable fixed point.

<u>Overall, there are two stable equilibria:</u> (0, 15) and (12, 0).

<u>Describe in words the biological behaviors of this system:</u>

At (0, 0), the turkey and quail populations are both extinct. This fixed point is unstable.

At (0, 15), there are only quail and no turkey. This means if turkeys go extinct, the quail population settles at 15. This fixed point is stable.

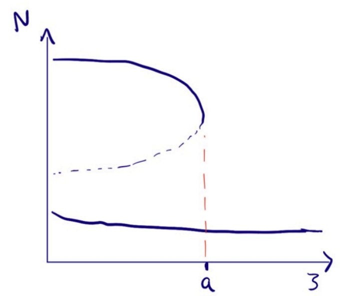
At (12, 0) there are only turkey and no quail. This means if quails go extinct, the turkey population settles at 12. This fixed point is stable.

At (3, 6), the turkey and quail populations coexist. This fixed point is unstable, thus one species will eventually dominate.

Overall, the system exhibits competitive exclusion. If both populations start near equilibrium, one species will dominate eventually. The winner depends on which species starts with a large enough advantage. If turkeys start with a large enough advantage, their population reaches 12; if quail start with the bigger advantage, their population will reach 15. Moreover, small populations of one species cannot invade the other's stable equilibrium.

Question 2

2. Consider a population of humans, N(t), which can be modeled via an ODE model (not given) that includes an interaction term ζ. This term encapsulates the role of an interaction between the humans and an invading alien population. The bifurcation diagram of N with respect to ζ is given below, for the range $\zeta \geq 0$.



a. Describe mathematically the model behavior for $\zeta > a$ and $\zeta < a$.

<u>$\zeta > a$ (Monostable Region):</u> When $\zeta > a$, the upper stable equilibrium disappears due to the bifurcation. In this region, the system now has only one stable equilibrium at a low population level. Mathematically, there is only fixed point:

$$f(N,\ \zeta)\ =\ 0,\ \frac{df}{dN} <\ 0$$

<u>$\zeta < a$ (Bistable Region):</u> When $\zeta < a$, there are two stable equilibria (the solid lines) and one unstable equilibrium (the dashed line). Mathematically, this means the system has three fixed points, where the unstable equilibrium satisfy:

$f(N,\ \zeta)\ =\ 0,\ \frac{df}{dN} >\ 0$ and the two stable equilibrium satisfy: $f(N,\ \zeta)\ =\ 0,\ \frac{df}{dN} <\ 0.$

b. Describe in words what is happening biologically in this system in the two regions above and below a. What happens at a?

<u>$\zeta > a$ (Monostable Region):</u> In this region, the system only has one stable equilibrium at a low population level. Thus, the population will eventually decline to this low, stable equilibrium.

<u>$\zeta < a$ (Bistable Region):</u> When $\zeta < a$, the human population, N, can either be at a high stable state (the upper solid line) or a low stable state (the lower solid line). The unstable equilibrium (dashed line) acts as a boundary: if the initial population is above this boundary, it converges to the high stable state, and if the initial is below this boundary, it declines to the low stable state.

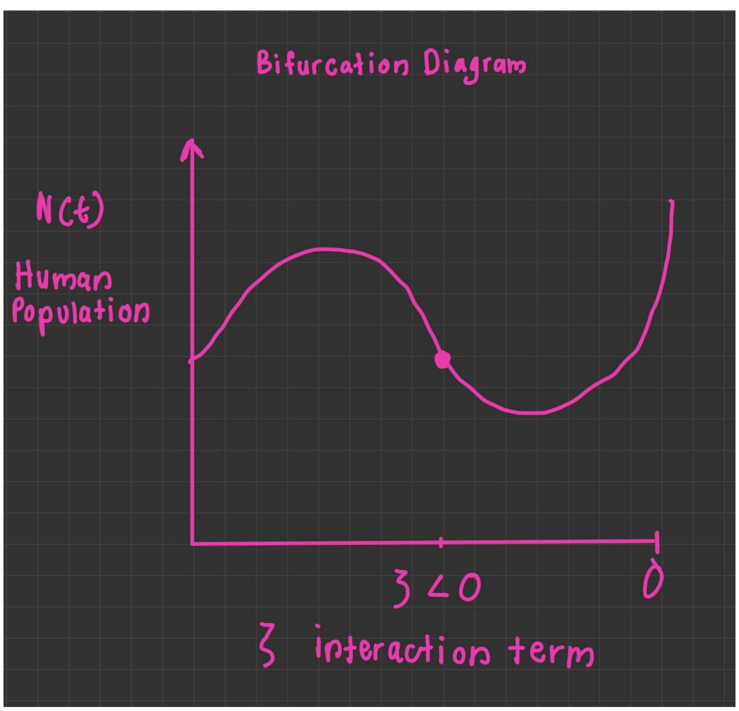
$\zeta = a$ (Bifurcation): At $\zeta = a$, a saddle-node bifurcation occurs, where the upper stable equilibrium and the unstable equilibrium collide and annihilate each other. This instance marks the point at which the population collapses to a lower state.

c. The point on the curve at the value of $\zeta = a$ is called a saddle point. There is one other saddle point for the bifurcation diagram shown but it is not in the plotted region. What change to the model should occur for the second saddle point to enter the plotted region? What would be the implications for the humans in this case?

For the second saddle point to appear in the plotted region, the model parameters must be changed in a way that extends the bistable region, shifting the bifurcation points. Some ways to change the parameters include altering the interaction term, changing the carrying capacity, or introducing an allele effect.

If a second saddle-node bifurcation enters the plotted region, humans would have a larger range of values of ζ where the population remains bistable. This means that if ζ increases slightly, the population might still persist at a higher level. Although, if ζ increases beyond the new upper bifurcation point, the collapse will be happen even quicker. This means that once the threshold is crossed, human extinction (or near-extinction) becomes inevitable. There is potential for population recovery, however, if ζ were to decrease again. Then, the human population could possibly recover from the lower equilibrium.

d. Redraw the bifurcation diagram for N in terms of ζ in the case where $a < 0$. Describe what has happened and discuss the implications for the human population.



In the redrawn diagram, the human population is more resilient, there is no tipping point in the plotted region (tipping point was previously at the bifurcation line), and the saddle-node bifurcation moved out of the domain. This means that for the human population, survival is guaranteed, the human population dynamics become less sensitive to alien invasion, and the system exhibits a single, stable equilibrium.

Question 3

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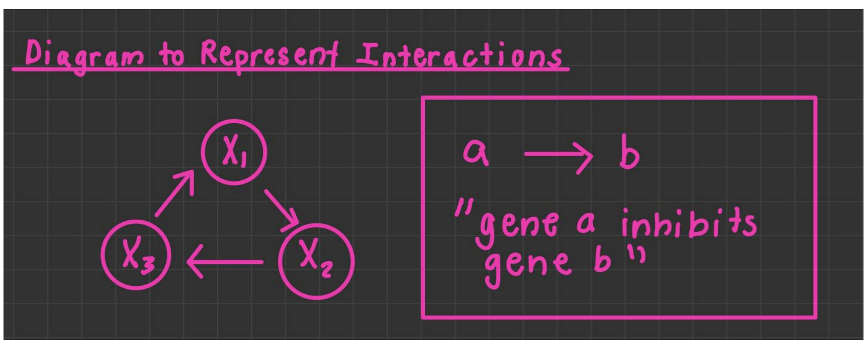
3. The repressilator is a gene regulatory network model of three mutually inhibiting gene products. (Analogous to the outcomes in a game of rock-paper-scissors.) In bacteria for example, this network is achieved by the lac operon consisting of TetR, cI, and LacI (see e.g. Potvin-Trottier et al. *Nature* 2016). For the purposes of our model, consider three genes, $x1$ $x2$ and $x3$, where x1 inhibits $x2$, $x2$ inhibits $x3$, and $x3$ inhibits $x1$. The dynamics of this system can be given by:

$$\frac{dx_i}{dt} = \beta . \frac{1}{1 + x_j^n} - \gamma x_i$$

where there are three possible pairs of (i, j): (1,3), (2,1) and (3,2).

a. Draw a diagram to represent the interactions in this model.



b. Describe under what conditions you would model this system using deterministic equations (ODEs) vs stochastic methods.

<u>You would model this system using ODEs for the following circumstances:</u>

- The number of molecules is large (like in the hundreds or thousands)
- The gene expression dynamics are smooth and predictable
- The repression and degradation terms are continuous and differentiable
- You are looking for the average behavior rather than single-cell variability
- A mean-field approach is appropriate (short-term fluctuations average out)

You would model this system using Stochastic Methods for the following circumstances:

- The number of molecules is low (in the range of 1-100)
- Gene expression is highly variable
- Discrete transcription events leads to stochasticity
- You want to capture single-cell variability
- The system operates in an environment where noise can induce qualitative changes
- You want to model how fluctuations affect synchronization or desynchronization

c. Derive an SDE model for this system, assuming multiplicative noise, parameterized by δ for species $x1$ and $x2$ and by λ for species $x3$. Explain all the terms of the model.

The stochastic version of the system is:

$$dx_i = f_i(x)dt \; + \; g_i(x)dW_i$$

where:

- $f_i(x)$ represents the deterministic part
- $g_i(x)$ represents the noise intensity function
- dW_i is a Wiener process (white noise term)

Since we assume multiplicative noise, the noise term should depend on the state variables. Then, we introduce parameters **δ** for species $x_1, \; x_2, \; and \, \lambda \, for \; x_3$ controlling the noise strength. So the SDE system becomes:

$$dx_1 = [\, \beta\left(\frac{1}{1+x_3^n} - \gamma x_1\right)]dt \; + \; \delta x_1 dW_i$$

$$dx_2 = [\, \beta\left(\frac{1}{1+x_1^n} - \gamma x_1\right)]dt \; + \; \delta x_2 dW_2$$

$$dx_3 = [\, \beta\left(\frac{1}{1+x_2^n} - \gamma x_1\right)]dt \; + \; \lambda x_3 dW_3$$

Deterministic Terms

- $\frac{1}{1+x_j^n}$ is the activation term, which accounts for the repression of gene i by gene j
- $-\;\gamma x_1$ is the degradation term, ensuring the natural decay of the gene product

Stochastic Terms

- $\delta x_i dW_i$ models multiplicative noise for x_1 and x_2
- $\lambda x_3 dW_3$ models multiplicative noise at a different noise strength for x_3

Wiener Terms

- dW_i is a Gaussian white noise process with mean zero and variance dt

The remaining questions are answered in the qbio-482-hw3-part2.pdf file. This file contains the code and answers to questions 3d, 3e, and all of 4 in the format of a jupyter notebook.