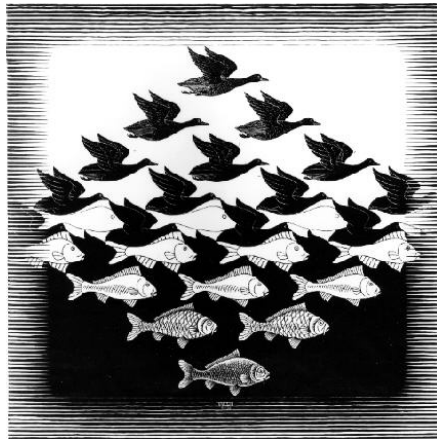# UNIVERSITY OF TORONTO

Faculty of Arts and Science
Ecology and Evolutionary Biology

Mathematical modeling in ecology and evolution
(EEB430/1430)

Midterm Exam – November 3, 2021

Available Time: Two hours

Permitted Materials: Pen/pencil

Guidelines:

1. Write your name and student number on the bottom of this page and hand this document at the end of the exam. Your exam will not be graded if you fail to return this question form.

2. The front page lists the materials you can use during this exam. Any other materials are not allowed. This includes mobile devices.

3. When asked, elaborate your answers by providing the equations used or listing the assumptions made. If you need more space for your answers please raise your hand and ask for more paper.

4. Please write clearly.

NB. This is an individual exam. Good luck!

Name: _____ Student number: _____

Question 1 [4/23 points] Below is a flow diagram describing the rate of change in the number of individuals who are susceptible to and infected with a pesky virus named 2-VoC-SRAS.
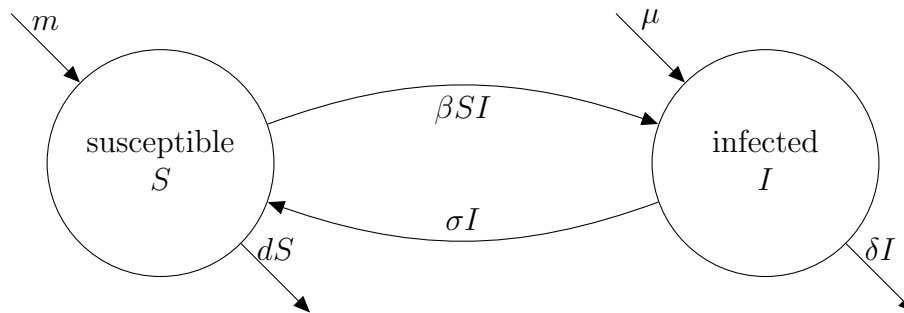
a. [1 points] Explain how a hypothetical new more contagious variant of the virus would affect the parameters.

> **Answer**
>
> If the new variant is more *contagious* then it would increase the *rate of transmission*, β.

b. [3 points] Imagine a vaccine is invented that reduces (but does not eliminate) the chance of being infected. Assume that the effect of the vaccine wears off with time and that recovering from infection does not provide protection from future infection. Add a new variable to the flow diagram above to represent this and label the arrows (including new parameters). Describe in words what each added arrow represents.

> **Answer**
>
> - Draw a new node, V, for vaccinated individuals.
> - Let susceptibles get vaccinated at some rate, e.g., aS (could be more complicated, e.g., peer-pressure).
> - Let vaccinateds die at some rate, e.g., dV (same per capita rate as susceptibles).
> - Let vaccinateds become infected at some rate, e.g., bIV ($b < \beta$, i.e., the vaccine reduces transmission).
> - Let vaccinateds become susceptible at some rate, e.g., θV (this models the vaccine effectiveness wearing off).
> - Let infecteds get vaccinated at some rate, e.g., bI (optional; note this also

Question 2 [10/23 points] The model of logistic growth incorporates competition by assuming the number of surviving individuals per parent, R, declines linearly with the size of the population, $R(n) = 1 + r(1 - n/k)$. This increases as the number of individuals, n, declines to 0. But in some populations offspring production may be impaired when there are too few individuals, e.g., when it is difficult to find mates (this is called an Allee effect). To model an Allee effect we can write the number of surviving individuals per parent as $R(n) = 1 + r(1 - n/k)(n - a)/(k - a)$, with $0 < a < k$. The recursion equation for the size of the population is $n(t + 1) = R(n)n(t)$.

a. [3 points] Find the equilibrium values of n.

> **Answer**
>
> Letting $n(t + 1) = n(t) = \hat{n}$ the equilibria are the solutions to $\hat{n} = R(\hat{n})\hat{n}$. Therefore one solution is $\hat{n} = 0$ and the others are determined by
>
> $$1 = R(\hat{n})$$
> $$1 = 1 + r(1 - \hat{n}/k)(\hat{n} - a)/(k - a)$$
> $$0 = r(1 - \hat{n}/k)(\hat{n} - a)/(k - a)$$
>
> giving $\hat{n} = a$ and $\hat{n} = k$.

b. [6 points] Determine the stability of each equilibrium assuming $r > 0$.

> **Answer**
>
> Let $f(n(t)) = n(t + 1) = R(n(t))n(t)$. Then stability is determined by the derivative $f'(n)$. Using the product rule this is $f'(n) = R'(n)n + R(n)$, with $R'(n) = r((-1/k)(n - a)/(k - a) + (1 - n/k)(1/(k - a)))$ (again using the product rule). It will be more convenient to keep the structure of the original equations rather than expanding this out.
>
> We need $|f'(n)| < 1$ for stability since this is a discrete-time model.
>
> When $\hat{n} = 0$ we have $f'(0) = R'(0)0 + R(0) = R(0) = 1 + r(-a/(k - a))$. Given $0 < k < a$ and $r > 0$ we have $f'(0) < 1$ and therefore we need $f'(0) > -1$ for stability. The latter is true when $r(-a/(k - a)) > -2$ or, dividing by -1 (and reversing the inequality), when $ra/(k - a) < 2$ (i.e., small r and a, large k). But note that given that we have defined $R(n)$ as the number of surviving individuals per parent, we should always have $R(n) >= 0$, and therefore $f'(0) = R(0) > 0$, which places the a stricter bound on our parameters, $ra/(k - a) < 1$. This also implies there is no cycling around $\hat{n} = 0$ (which wouldn't make sense biologically because the population size would become negative).

c. [1 points] Assume that a population of woodland caribou follows these dynamics. If this population disappeared from an area and we wanted to re-introduce them, what is the minimum population size we should start with?

Question 3 [9/23 points] Historically, we've typically assumed populations are well adapted to their environments. That is, we've assumed they have trait values that closely match the trait values that optimize fitness. With climate change this may no longer be the case, and an important question is how well populations can evolutionarily track changes in optimal trait values. A simple, and common, model for a population evolving in a changing environment is

$$\frac{\mathrm{d}z}{\mathrm{d}t} = v\gamma(o - z) \tag{1}$$

$$\frac{\mathrm{d}o}{\mathrm{d}t} = k \tag{2}$$

where z is the population mean trait value, o is the optimal trait value, v is the amount of genetic variance in the trait (assumed constant), γ is the strength of selection on the trait (assumed constant), and k is the rate of environmental change (assumed constant).

This is a multivariate model (two variables, z and o), but we can make it univariate by switching our perspective to think about the lag of the mean trait value behind the optimal with a transformation, $L = o - z$.

a. [1 points] Write the differential equation for the change in lag, L, in terms of L alone (i.e., there should be no o or z in this equation).

Answer

We use the fact that the derivative of a sum is the sum of the derivatives

$$\frac{\mathrm{d}L}{\mathrm{d}t} = \frac{\mathrm{d}(o - z)}{\mathrm{d}t}$$

$$\frac{\mathrm{d}L}{\mathrm{d}t} = \frac{\mathrm{d}o}{\mathrm{d}t} - \frac{\mathrm{d}z}{\mathrm{d}t}$$

$$\frac{\mathrm{d}L}{\mathrm{d}t} = k - v\gamma(o - z)$$

$$\frac{\mathrm{d}L}{\mathrm{d}t} = k - v\gamma L$$

b. [1 points] What is the equilibrium lag?

Answer

We set the change in L to zero and solve for $\hat{L}$

$$0 = k - v\gamma\hat{L}$$
$$\hat{L} = k/(v\gamma)$$

c. [2 points] Determine the stability of the equilibrium (assume all parameters are positive).

Answer

Let $f(L) = \frac{\mathrm{d}L}{\mathrm{d}t} = k - v\gamma L$. Stability is determined by the derivative $f'(L) = -v\gamma$.

Since this is continuous-time model we need $f'(L) < 0$ for stability, which is guaranteed as long as v and γ have the same sign (and given v is a variance, which is always positive, we need both to be positive – when $\gamma > 0$ we have what is called stabilizing selection).

d. [1 points] Assuming the population goes extinct when the equilibrium lag is greater than some critical value, L_c, what is the fastest rate of environmental change a population can persist under?

Answer

Here we set the equilibrium lag equal to the critical lag and solve for the so-called critical rate of environmental change, k_c.

$k_c/(v\gamma) = L_c \implies k_c = L_c v\gamma$

(Note, in a more realistic model the critical lag L_c will depend on the amount of genetic variance in the population and the strength of selection, both of which positively contribute to something called variance load, which reduces fitness

and thus the critical lag.)

e. [3 points] Use separation of variables to find the lag as a function of time, $L(t)$, assuming the population is initially perfectly adapted, $L(0) = 0$. [Hint, the integral of $1/(a - bx)$ with respect to x is $-\ln(a - bx)/b$.]

Answer

$$\frac{\mathrm{d}L}{\mathrm{d}t} = k - v\gamma L$$

$$\frac{\mathrm{d}L}{k - v\gamma L} = \mathrm{d}t$$

$$\int \frac{\mathrm{d}L}{k - v\gamma L} = \int \mathrm{d}t$$

$$-\ln(k - v\gamma L)/(v\gamma) = t + c$$

$$\ln(k - v\gamma L) = -v\gamma(t + c)$$

$$k - v\gamma L = e^{-v\gamma(t+c)}$$

$$L = \frac{k - e^{-v\gamma(t+c)}}{v\gamma}$$

Now using $L(0) = 0$ we see $0 = k - e^{v\gamma c} \implies e^{v\gamma c} = k$ so that $e^{-v\gamma(t+c)} = e^{-v\gamma t}e^{-v\gamma c} = e^{-v\gamma t}k$. Subbing this in to the above and simplifying we get

$$L(t) = \frac{k(1 - e^{-v\gamma t})}{v\gamma}$$

f. [1 points] Check your answer in (e) by comparing what happens as t goes to infinity to your answer in (b).

Answer

As $t \to \infty$ we have $e^{-v\gamma t} \to 0$ (given $v\gamma > 0$) so that $\lim_{t\to\infty} L(t) = k/(v\gamma) = \hat{L}$.

————— *End of Exam* —————