UNIVERSITY OF TORONTO

Faculty of Arts and Science
Department of Ecology and Evolutionary Biology

Mathematical modeling in ecology and evolution

(EEB314/1430)

Midterm Exam – October 9, 2024

Available Time: 1h 50m

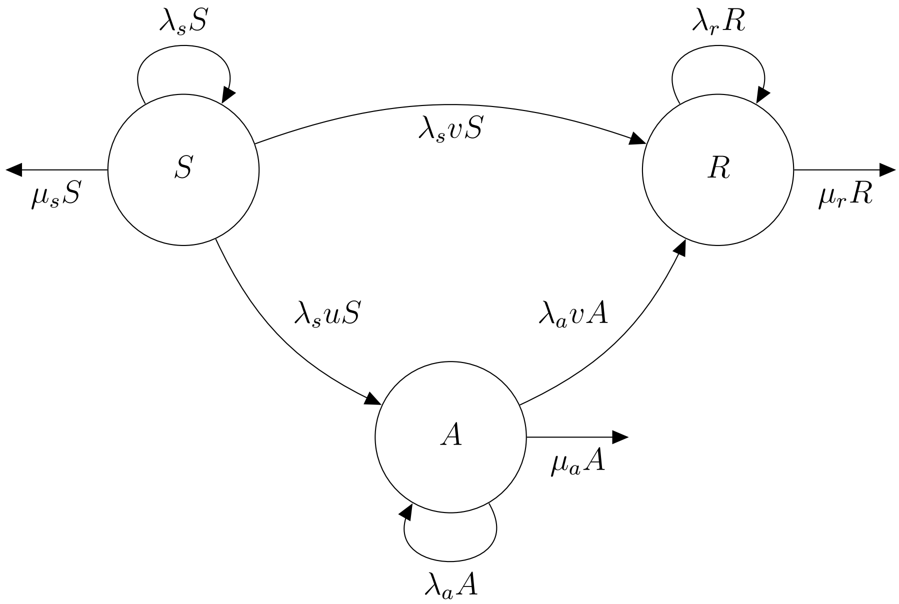
Permitted Materials: Pen/pencil

Guidelines:

1. The front page lists the materials you can use during this exam. Any other materials are not allowed. This includes calculators and phones.
2. Write your name and student number on the booklet provided, answer the questions in the booklet, and hand the booklet in at the end of the exam.
3. Please write clearly.

NB. This is an individual exam. Good luck!

Question 1 [5/20 points] Stana *et al.* (2024) study the evolution of drug resistance in cancer. They are particularly concerned about aneuploidy (cells with unusual numbers of chromosomes) contributing to resistance. The issue is that there is a high mutation rate to aneuploidy and aneuploidy may offer partial drug resistance, facilitating full resistance via further mutation. To understand the impact of aneuploid cells on resistance they build a mathematical model describing the number of sensitive cells (S), the number of aneuploid cells (A), and the number of resistant cells (R). They use the following flow diagram to describe their model.



a. [3 points] Write down the differential equations corresponding to this flow diagram.

b. [2 points] Here the λ_i are cell division rates, the μ_i are cell death rates, and the u and v are the fraction of daughter cells that mutate. The authors assume $u > v$ and $\mu_a < \mu_s$ in the presence of the drug. What do these two assumptions mean, biologically?

Question 2 [8/20 points] The Beverton-Holt model (Beverton & Holt 1957),

$$n(t+1) = \frac{Rn(t)}{1+cn(t)},$$

describes density-dependent population growth. Here R is the number of offspring per individual when the population size is small and c describes the impact of competition.

a. [2 points] Show that $n(t) = 0$ and $n(t) = (R-1)/c$ are the two equilibria of this model.

b. [1 points] When is $n(t) = (R-1)/c$ biologically valid? Assume both R and c are positive.

c. [4 points] Determine when each equilibrium is stable.

d. [1 points] What does the last line in the following Python code do?

```
from sympy import * #import symbolic tools
R,n,c = var('R,n,c') #define parameters and variables
f = R*n/(1 + c*n) #define recursion equation
eqs = solve(f-n,n) #solve for equilibria
fprime = diff(f,n).simplify() #slope of recursion with respect
                               to variable
[fprime.subs(n,i) for i in eqs]
```

Question 3 [7/20 points] Chris Carlson is studying evolution in mutualisms. He is interested in how the mean trait values in two interacting species evolve when an individual has higher fitness when it has a slightly larger trait value than its mutualistic partner. For example, a flower may want to hide its nectar a little deeper than the pollinator's proboscis can reach and the pollinator may want to easily reach the nectar at the bottom of a flower. Let individuals do best when their trait value is δ larger than the trait value of their partner. And let $\Delta z = \bar{z}_1 - \bar{z}_2$ be the mean trait value of the first species minus the mean trait value of the second species. Then this trait difference evolves like

$$\frac{\mathrm{d}\Delta z}{\mathrm{d}t} = G_1(\delta - \Delta z) - G_2(\Delta z + \delta),$$

where G_i is the amount of genetic variance times the strength of selection in species i.

a. [1 points] Show that $\Delta z = (G_1 - G_2)\delta/(G_1 + G_2)$ is an equilibrium.

b. [2 points] Show that this equilibrium is always stable (assuming $G_i > 0$).

c. [3 points] This is a linear differential equation, so we can find the general solution. The deviation from the equilibrium, $\epsilon(t) = \Delta z(t) - \widehat{\Delta z}$, has solution $\epsilon(t) = \epsilon(0)\exp(-(G_1 + G_2)t)$, where $\widehat{\Delta z}$ is the equilibrium. Use this to derive the general solution for $\Delta z(t)$ in terms of $\Delta z(0)$, t, and the parameters.

d. [1 points] What must be true about the parameters for species 1 to be "winning" the evolutionary race, i.e., to have a larger mean trait value than species 2, in the long-run?

——— *End of Exam* ———