## UNIVERSITY OF TORONTO

Faculty of Arts and Science Ecology and Evolutionary Biology



## Mathematical modeling in ecology and evolution (EEB430/1430)

Midterm Exam - October 19, 2022

Available Time: Two hours 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 mobile devices.
- 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. Show/explain how you arrive at your answers.
- 4. Please write clearly.

## NB. This is an individual exam. Good luck!

**Question 1** [10/20 points] Puneeth Deraje is studying a phenomenon called "paramutation", where a "paramutable" allele (A) can be converted to another allele (B) when it pairs with a "paramutator" allele (a or B) in a heterozygote. This conversion is, however, unstable, causing the B allele to reset to the A allele over time. Puneeth also considers mutation from the a allele to the A allele. Below is a flow diagram for a continuous-time version of this model, tracking the frequencies of each allele in the absence of selection.



- **a.** [1 points] Write down the differential equations corresponding to this flow diagram.
- **b.** [3 points] At equilibrium  $p_a = 0$ . Since the frequencies sum to 1 we can write  $p_B = 1 p_A$  and reduce the above to a single differential equation in terms of  $p_A$

$$\frac{\mathrm{d}p_A}{\mathrm{d}t} = -mp_A(1-p_A) + r(1-p_A)$$

Solve for the equilibrium frequencies of the A allele.

- c. [1 points] Determine when the equilibrium  $\hat{p}_A = r/m$  is biologically valid.
- **d.** [3 points] Determine when the equilibrium  $\hat{p}_A = r/m$  is locally stable.
- e. [1 points] Explain what r < m means biologically.
- **f.** [ 1 points ] We could solve the differential equation for  $p_A$  using separation of variables and partial fractions, but instead we decide to just use Python. Briefly describe what each line below does.

```
from sympy import *
var('m,r,t')
p = Function('p')(t)
de = Eq(diff(p,t), (-m*p+r)*(1-p))
dsolve(de)
```

**Question 2** [10/20 points] Sydney Ackermann is studying population dynamics on a lattice, where individuals disperse and compete for vertices (intersections of lines in the diagram below, where filled dots represent occupied vertices and empty dots represent vacant vertices).



Here we'll consider an approximation of a simplified version of her discrete-time model, where, in each time step, 1) a fraction d of individuals die, 2) each survivor gives birth to b offspring, and 3) each offspring disperses to a randomly chosen vertex on a  $k \times k$  lattice (creating  $k^2$  vertices). She only allows one individual to exist at each vertex, and so when an offspring lands on an occupied vertex it either dies or displaces the resident. Taking a small enough time step, the expected population size in the next time step is

$$n_{t+1} = n_t \left( 1 + b \left( 1 - \frac{n_t}{k^2} \right) - d \right)$$

where  $1 - n_t/k^2$  is the fraction of vertices that are currently empty.

- **a.** [ 3 points ] Find the equilibria of this model.
- **b.** [1 points] Determine when the equilibrium  $\hat{n} = k^2(1 d/b)$  is biologically valid.
- **c.** [3 points] Determine when the equilibrium  $\hat{n} = k^2(1 d/b)$  is locally stable.
- **d.** [1 points] Explain why the population does not occupy all the vertices at equilibrium when d > 0 even when the birth rate is higher than the death rate, b > d.
- e. [1 points] We decide to simulate this recursion in Python. We start by defining a function to create a generator

```
def n(t0, n0, b, d, k, max=500):
    ''generator for lattice model'''
    t = t0
    nt = n0
    while t < max:
        yield nt
        t = t + 1
        nt = nt*(1 + b*(1-nt/k**2) - d)
```

and then supply parameter values of interest to make the generator

ns = n(0, 1, 0.1, 0.05)

at which point we get an error: n() missing 1 required positional argument: 'k'. How do we fix this error?

**f.** [ 1 points ] Now imagine that a fraction p of offspring disperse off the lattice, and die. Write down the recursion equation for this extended model.

-- End of Exam -