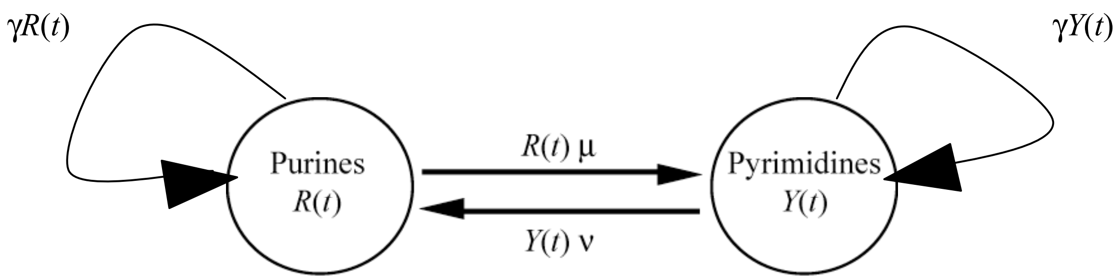
Biomathematics 301 Midterm 2008

Name:____________________ **Signature:**_______________________

Question 1 [20 points]: In an earlier homework assignment, you modeled the number of purine nucleotides (adenine and guanine) and pyrimidine nucleotides (cytosine and thymine) over time in the presence of mutation. Here we consider the continuous time model based on the flow diagram:



(a) Modify the flow diagram to account for gene duplications that copy nucleotides of each type at a rate γ, causing the genome to grow in size. Add arrows with flow rates. [Assume that purines and pyrimidines are copied in proportion to their current levels.]

(b) Write down differential equations for your altered model to account for these duplications:

$$\frac{dR}{dt} = (\gamma - \mu)\, R(t) + \nu\, Y(t)$$

$$\frac{dY}{dt} = (\gamma - \nu)\, Y(t) + \mu\, R(t)$$

Question 2 [50 points]: The savannahs of Kenya are dotted by a single species of acacia tree, *Acacia drepanolobium*, which are protected from browsing by ants. The acacia trees provide nourishment (sugar solution at nectaries) and housing (enlarged hollow thorns called "domatia") for the ants, and a single tree can support hundreds of thousands of ants. Each tree is inhabited by a single species of ant, but different trees can house different ant species. In this question, we explore what processes could maintain coexistence of two ant species within the savannah. *(Photo: Todd Palmer)*

We start by assuming that a tree inhabited by species 1 becomes vacant with probability e_1 per time step and a tree inhabited by species 2 becomes vacant with probability e_2. Can both ant species co-exist if species 1 is more likely to be lost from a tree ($e_1 > e_2$) but is more likely to colonize a tree (by a factor α)? This question can be addressed using a recursion for the proportion of trees inhabited by species 1:

$$p[t+1] = \underbrace{p[t]\left(1-e_1\right)}_{\text{Species 1 persists on tree}} + \underbrace{\left(p[t]\,e_1 + \left(1-p[t]\right)e_2\right)}_{\text{Vacated trees}} \underbrace{\frac{\alpha\, p[t]}{\alpha\, p[t] + \left(1-p[t]\right)}}_{\text{Colonized by species 1}}. \qquad (1)$$

We will assume throughout that $\alpha > 1$ and $0 < e_2 < e_1 < 1$.

(a) What are all of the possible equilibria of this model? Show your work.

Solve $\hat{p} = \hat{p}\left(1-e_1\right) + \left(\hat{p}\, e_1 + \left(1-\hat{p}\right) e_2\right) \dfrac{\alpha\, \hat{p}}{\alpha\, \hat{p} + \left(1-\hat{p}\right)}$

All terms contain a $\hat{p}$, so we may divide both sides by $\hat{p}$, implying that $\hat{p}$ = 0 is an equilibrium and leaving:

$$1 = \left(1-e_1\right) + \left(\hat{p}\, e_1 + \left(1-\hat{p}\right) e_2\right) \frac{\alpha}{\alpha\, \hat{p} + \left(1-\hat{p}\right)}$$

subtracting 1 from both sides:

$$0 = \left(-e_1\right) + \left(\hat{p}\, e_1 + \left(1-\hat{p}\right) e_2\right) \frac{\alpha}{\alpha\, \hat{p} + \left(1-\hat{p}\right)}$$

placing over a common denominator:

$$0=\frac{(-e_1)\left(\alpha\,\hat{p}+(1-\hat{p})\right)+\left(\hat{p}\,e_1+(1-\hat{p})\,e_2\right)\alpha}{\alpha\,\hat{p}+(1-\hat{p})}$$

$$0=\frac{-\alpha\,\hat{p}\,e_1-e_1+\hat{p}\,e_1+\alpha\,\hat{p}\,e_1+\alpha\,e_2-\alpha\,\hat{p}\,e_2}{\alpha\,\hat{p}+(1-\hat{p})}$$

For the numerator to equal 0 requires that:

$$-\hat{p}\,e_1+\alpha\,\hat{p}\,e_2=-e_1+\alpha\,e_2$$

$$\hat{p}=\frac{-e_1+\alpha\,e_2}{-e_1+\alpha\,e_2}=1$$

Thus, $\hat{p}$ *= 1 and* $\hat{p}$ *= 0 are the two equilibria.*

(b) Imagine that only one species is initially present and the other species is introduced. To determine whether the other ant species can invade, you perform a stability analysis of equation (1) and find that:

$$\left.\frac{\mathrm{d}f}{\mathrm{d}p}\right|_{p=0} = 1 - e_1 + \alpha\, e_2 \tag{2a}$$

$$\left.\frac{\mathrm{d}f}{\mathrm{d}p}\right|_{p=1} = 1 + \frac{e_1}{\alpha} - e_2 \tag{2b}$$

where f is the recursion equation (1) and p is the fraction of trees inhabited by species 1.

<u>When can species 1 invade if it is initially rare?</u> [Specify when the equilibrium $p = 0$ is locally stable or unstable and whether or not you expect oscillatory behavior. Simplify as much as possible.]

Note that $\lambda = \left.\frac{\mathrm{d}f}{\mathrm{d}p}\right|_{p=0} = 1 - e_1 + \alpha\, e_2$ *must be positive under the assumptions listed before (because* $1 - e_1$ *is positive as is* $\alpha\, e_2$*). Thus, there cannot be oscillations. The system will be unstable and species 1 can invade if and only if* $\lambda > 1$*, that is,* $1 - e_1 + \alpha\, e_2 > 1$ *(we don't have to worry about* $\lambda < -1$ *because* λ *cannot be negative). Rearranging, we get invasion if* $\alpha\, e_2 > e_1$ *or placing the extinction terms together* $\alpha > e_1 / e_2$.

Points were taken off if the restrictions on the parameters were not used (e.g., if it was said that oscillations were possible).

<u>Verbal interpretation:</u>

Species 1 can invade if its advantage in terms of colonization rate (α*) is larger than its relative risk of extinction (*e_1 / e_2*).*

Points were not given if the result was not interpreted but just restated. That is, if you said in the first part that instability required $\alpha\, e_2 > e_1$*, you would not get points here if you just wrote that species 1 would invade if* $\alpha\, e_2 > e_1$*.*

<u>When can species 2 invade if it is initially rare?</u> [Specify when the equilibrium $p = 1$ is locally stable or unstable and whether or not you expect oscillatory behavior. Simplify as much as possible.]

Note that $\lambda = \left.\frac{\mathrm{d}f}{\mathrm{d}p}\right|_{p=1} = 1 + \frac{e_1}{\alpha} - e_2$ *must be positive under the assumptions listed before (because* $1 - e_2$ *is positive as is* e_1/α*). Thus, there cannot be oscillations. The system will be unstable and species 2 can invade if and only if* $\lambda > 1$*, that is,* $1 + \frac{e_1}{\alpha} - e_2 > 1$ *(we don't have to worry about* $\lambda < -1$ *because* λ *cannot be negative). Rearranging, we get invasion if* $\frac{e_1}{\alpha} > e_2$ *or placing the extinction terms together* $e_1/e_2 > \alpha$ *(the opposite of what was seen for the other equilibrium).*

Points were taken off if the restrictions on the parameters were not used (e.g., if it was said that oscillations were possible).

<u>Verbal interpretation:</u>

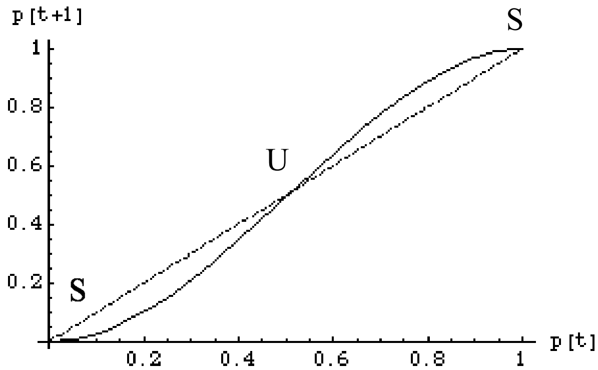
Species 2 can invade if the colonization advantage of species 1 (α*) is not larger than the relative risk of extinction of species 1 (*e_1/e_2*).*

Points were not given if the result was not interpreted but just restated.

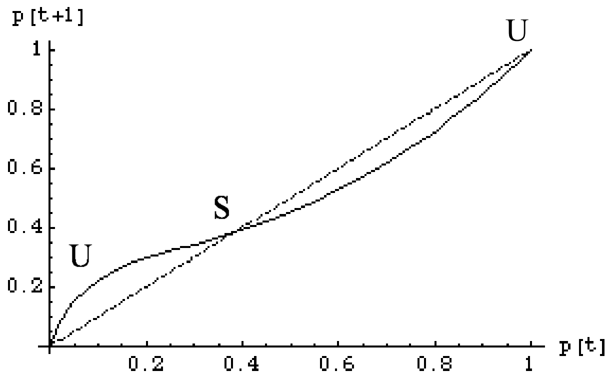
(c) Is it possible to maintain two ant species in the savannah if one species is more likely to vacate trees but is also more likely to colonize vacant trees? [Justify your results in the context of the previous sections, as appropriate.]

No, there is no valid equilibrium that contains both species (see answer to part a). According to part b, either $\alpha > e_1/e_2$*, in which case species 1 invades or* $e_1/e_2 > \alpha$ *in which case species 2 invades. There is no parameter condition under which both species can invade when rare, which would allow both to be maintained.*

(d) When branches from two trees cross, the ants from one tree displace ants from the other tree, literally fighting to the death. Equation (1) was altered to consider whether it was easier or harder to maintain both species with this direct competition. Depending on the case considered, plots of $p[t+1]$ versus $p[t]$ had the following shapes (solid curves; diagonal dashed lines are provided for comparison). **Label all stable equilibria with an S and all unstable equilibria with a U.**



Case 1: Species 1 *more* often wins battles but is more prone to vacating isolated trees ($e_1 > e_2$) [with equal colonization ability; $\alpha = 1$]



Case 2: Species 1 *less* often wins battles but is more likely to colonize vacant trees ($\alpha > 1$) [with equal probability of loss from trees; $e_1 = e_2$]

Based on the above graphs, circle the correct answers:

True or False: A trade-off between competitive ability and persistence on isolated trees [Case 1] can maintain both species in this simple model.

True or False: A trade-off between competitive ability and colonization ability [Case 2] can maintain both species in this simple model.

Question 4 [20 points]: Habitat degradation can cause the growth of a population to decline over time. Here we modify the exponential growth model in continuous time to allow the growth factor, r, to decline exponentially over time at rate δ from r_0 at time $t = 0$:

$$\frac{\mathrm{d}n}{\mathrm{d}t} = r_0\, e^{-\delta\, t}\; n \tag{3}$$

(a) Name one check that you could perform on equation (3) and perform it. Does (3) pass your check?

There were several correct answers for this, such as checking that if δ=0 we have the exponential model. Marks were deducted mainly for stated checks not matching the test carried out, or stated checks not being valid (such as "when t=0 we should have n[0], or when t->infinity the population goes extinct, which is not true for this model because a positive growth rate that decays exponentially never becomes negative and so there is no population decline)

(b) Begin to perform a separation of variables by rewriting equation (3) with the variables separated:

$$\int \frac{1}{n}\mathrm{d}n \quad = \int r_0\, e^{-\delta\, t}\mathrm{d}t$$

(c) Integrate both sides of your answer to part (b). [You can stop right after integrating both sides, you do not have to solve for n explicitly.]

$$\ln(n) = -\frac{r_0\, e^{-\delta\, t}}{\delta} + C$$

Question 5 [10 points]: Match up the following *Mathematica* inputs to outputs for the case where **`f[x_] = x^2/3`** (note that one of the inputs contains an error – *the last one because of the ( )*):

INPUT:	OUTPUT:
`Table[N[f[x]], {x, 0, 2}]`	`{f, f, f}`
`Table[f[x], {x, 0, 2}]`	`{0, 1/3, 4/3}`
`Table[Evaluate[D[f[x], x]], {x, 0, 2}]`	`{0, 2/3, 4/3}`
`Table[Evaluate[D[f(x), x]], {x, 0, 2}]`	`{0., 0.333333, 1.33333}`