

UNIVERSITY OF TORONTO

Faculty of Arts and Science
Department of Ecology and Evolutionary Biology



Mathematical modeling in ecology and evolution
(EEB314/1430)

Test 3 – November 12, 2025

Available Time: 50m

Permitted Materials: Pen/pencil

Question 1 (8/8 points) Many populations face continual environmental change, such as climate warming. Our understanding of how populations will respond to this type of environmental change is facilitated by so-called “moving optimum models”. In these models the environmentally-determined phenotype that maximizes fitness, θ , increases linearly at rate c . The mean phenotype of the population, \bar{z} , evolves to track this moving optimum, via selection to reduce the mean lag, $\ell = \theta - \bar{z}$. Persistence requires the equilibrium lag to not be too big. Here we’ll examine the effect of density-dependent population growth on the predictions of the moving optimum model, following Klausmeier et al. 2020 (Phil. Trans. B).

- (a) The simplest scenario is when selection and density-dependence do not interact. This occurs, for example, when birth depends on the mean lag and death depends on the population size, or vice-versa. We consider the former with the following model of population size, n , and mean lag, ℓ ,

$$\begin{aligned}\frac{dn}{dt} &= n(b - \gamma\ell^2/2 - dn) \\ \frac{d\ell}{dt} &= c - v\frac{\partial}{\partial\ell}\left(\frac{1}{n}\frac{dn}{dt}\right) = c - v\gamma\ell.\end{aligned}$$

Here the mean birth rate, $b - \gamma\ell^2/2$, is reduced by the lag and the death rate, dn , increases with population size. The dynamics of the mean lag, are then independent of population size, increasing due to environmental change, c , and decreasing by evolution, $v\gamma\ell$, where v is the amount of genetic variance in the trait and γ is the strength of selection.

- (i) (1 points) Show how to find the equilibrium lag, $\hat{\ell} = c/(v\gamma)$, and the two population size equilibria, $\hat{n} = 0$ and $\hat{n} = (b - c^2/(2v^2\gamma))/d$.
- (ii) (2 points) Show how to determine that the second equilibrium, $\hat{\ell} = c/(v\gamma)$ and $\hat{n} = (b - c^2/(2v^2\gamma))/d$, is stable when $\hat{n} > 0$.
- (iii) (1 points) Assuming, $\hat{n} = (b - c^2/(2v^2\gamma))/d$, is stable, what is the fastest rate of environmental change that allows long-term persistence? We call this the critical rate of environmental change.
- (b) Now consider a scenario where selection and density-dependence interact, e.g., when death depends on both trait value and population size,

$$\begin{aligned}\frac{dn}{dt} &= n(b - (d + \gamma\ell^2/2)n) \\ \frac{d\ell}{dt} &= c - v\frac{\partial}{\partial\ell}\left(\frac{1}{n}\frac{dn}{dt}\right) = c - v\gamma\ell n.\end{aligned}$$

- (i) (1 points) Show how to determine that at equilibrium, $\hat{\ell} = c/(v\gamma\hat{n})$, with $\hat{n} = (b \pm \sqrt{b^2 - 2dc^2/(v^2\gamma)})/(2d)$.
- (ii) (1 points) Explain why, mathematically, these two equilibria are biologically invalid when $b^2v^2\gamma < 2dc^2$.

(iii) (1 points) To determine stability we construct the Jacobian. Evaluating at $\hat{n} = (b + \sqrt{b^2 - 2dc^2/(v^2\gamma)})/(2d)$ we find that the trace and determinant are

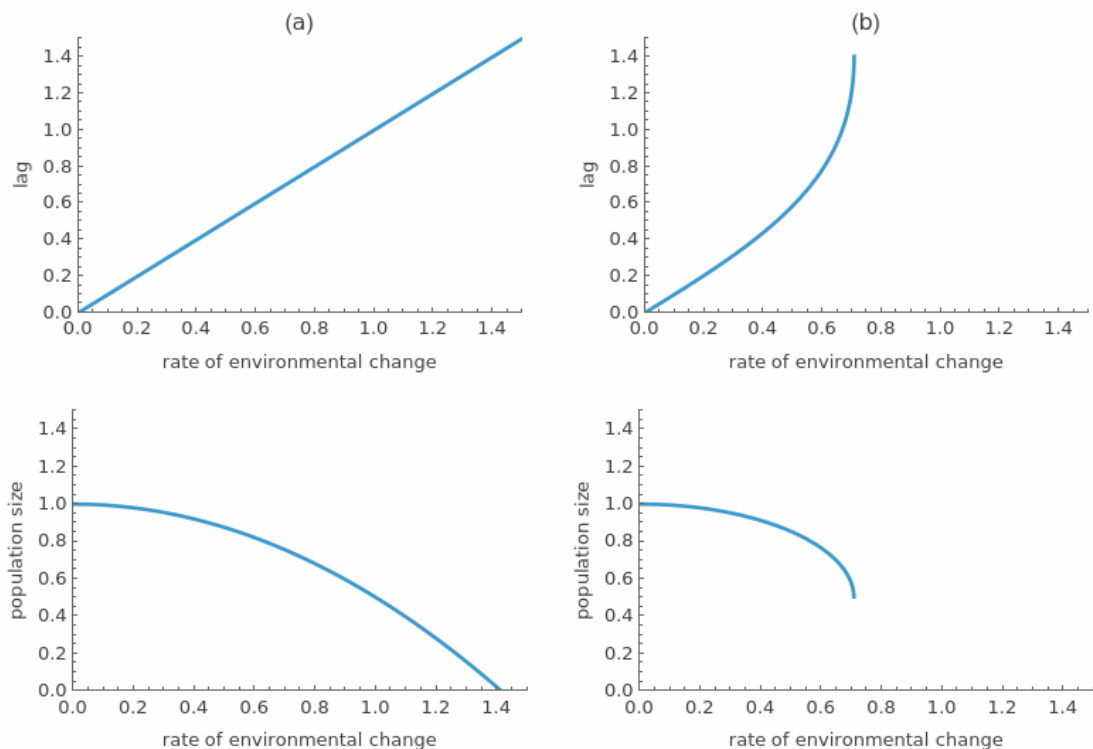
$$\text{Tr}(\mathbf{J}) = -\frac{b(2d + v\gamma) + \sqrt{\gamma(b^2v^2\gamma - 2dc^2)}}{2d}$$

$$\text{Det}(\mathbf{J}) = \frac{b^2v\gamma - 2dc^2/v + \sqrt{\gamma(b^2v^2\gamma - 2dc^2)}}{2d}.$$

Explain why we can conclude that this equilibrium is stable when $b^2v^2\gamma > 2dc^2$. It turns out the other equilibrium is unstable under these conditions.

Note that when $b^2v^2\gamma = 2dc^2$ the equilibrium population size is $\hat{n} = b/(2d) > 0$ but when we increase the rate of environmental change c a little further the equilibria become invalid – biologically, the rate of environmental change $c = bv\sqrt{\gamma/(2d)}$, is a tipping point beyond which populations suddenly go extinct.

- (c) (1 points) The stable equilibrium of each model (a and b) is plotted below as a function of the rate of environmental change. Only in the second model (b) do we see a tipping point (in the first model the equilibrium is a continuous function of c). Tipping points typically arise when there are positive feedbacks in a system. In 1-3 sentences, explain what the positive feedback in the second model is in biological terms.



————— *End of Exam* —————