

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,  $\theta$ , 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,  $\ell$ ,

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

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  $\gamma$  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

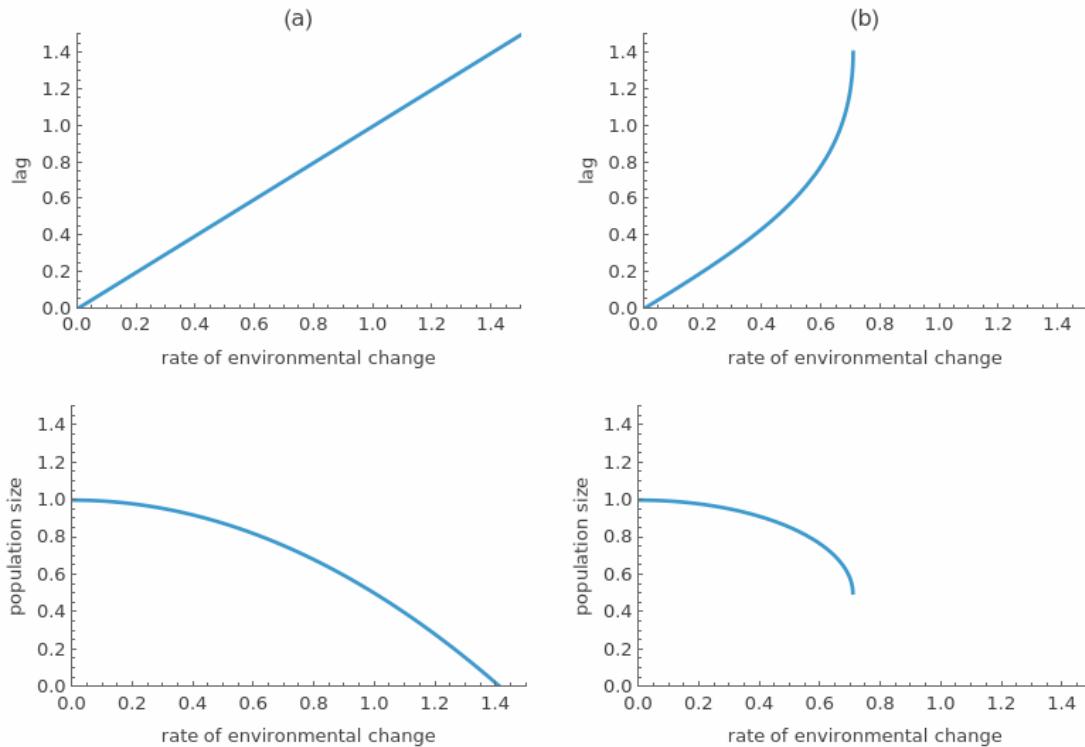
$$\text{Tr}(\mathbf{J}) = -\frac{b(2d + v\gamma) + \sqrt{(b^2v^2\gamma - 2dc^2)}}{2d}$$

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

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 ———