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,

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

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 $\hat{n} = (b - c^2/(2v^2\gamma))/d$.

Answer

We start with the lag equation, as it does not depend on population size,

$$\begin{aligned}
\frac{\mathrm{d}\ell}{\mathrm{d}t} &= 0 \\
c - v\gamma\hat{\ell} &= 0 \\
\hat{\ell} &= \frac{c}{v\gamma}.
\end{aligned} \tag{1}$$

Now we can sub this into the population size equation and solve,

$$
\begin{aligned}
\frac{\mathrm{d}n}{\mathrm{d}t} &= 0 \\
\hat{n}(b - \gamma\hat{\ell}^2/2 - d\hat{n}) &= 0 \\
\hat{n}\left(b - \gamma\left(\frac{c}{v\gamma}\right)^2/2 - d\hat{n}\right) &= 0 \\
\hat{n}\left(b - \frac{c^2}{2v^2\gamma} - d\hat{n}\right) &= 0.
\end{aligned} \tag{2}
$$

So either $\hat{n} = 0$ or we can divide by $\hat{n}$ to find

$$
\begin{aligned}
&b - \frac{c^2}{2v^2\gamma} - d\hat{n} = 0 \\
&\left(b - \frac{c^2}{2v^2\gamma}\right)/d = \hat{n}.
\end{aligned} \tag{3}
$$

(**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 $\hat{n} > 0$.

Answer

The Jacobian is

$$
\begin{aligned}
\mathbf{J} &= \begin{pmatrix} \frac{\partial}{\partial n}\frac{\mathrm{d}n}{\mathrm{d}t} & \frac{\partial}{\partial \ell}\frac{\mathrm{d}n}{\mathrm{d}t} \\ \frac{\partial}{\partial n}\frac{\mathrm{d}\ell}{\mathrm{d}t} & \frac{\partial}{\partial \ell}\frac{\mathrm{d}\ell}{\mathrm{d}t} \end{pmatrix} \\
\mathbf{J} &= \begin{pmatrix} b - \gamma\ell^2/2 - 2dn & -n\gamma\ell \\ 0 & -v\gamma \end{pmatrix}.
\end{aligned} \tag{4}
$$

Evaluating at the $\hat{n} > 0$ equilibrium,

$$
\mathbf{J}\big|_{n=\hat{n}>0,\ell=\hat{\ell}} = \begin{pmatrix} -\left(b - \frac{c^2}{2v^2\gamma}\right) & -\left(b - \frac{c^2}{2v^2\gamma}\right)\frac{c}{v} \\ 0 & -v\gamma \end{pmatrix}. \tag{5}
$$

This is a triangular matrix, and so the eigenvalues are along the diagonal,

$$
\begin{aligned}
\lambda_1 &= -\left(b - \frac{c^2}{2v^2\gamma}\right) \\
\lambda_2 &= -v\gamma.
\end{aligned} \tag{6}
$$

The second is never positive and the first is negative as long as $\hat{n} > 0$ (since we see that we can write $\hat{n} = -\lambda_1/d$).

(**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.

Answer

We have persistence as long as $\hat{n} > 0$, and so we can find the critical rate by solving

$$\begin{aligned}
\hat{n} &= 0 \\
\left(b - \frac{c^2}{2v^2\gamma}\right)/d &= 0 \\
b - \frac{c^2}{2v^2\gamma} &= 0 \\
c^2 &= 2bv^2\gamma \\
c &= v\sqrt{2b\gamma}.
\end{aligned} \tag{7}$$

(**b**) Now consider a scenario where selection and density-dependence interact, e.g., when death depends on both trait value and population size,

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

(**i**) (1 points) Show how to determine that at equilibrium, $\hat{\ell} = c/(v\gamma\hat{n})$, with $\hat{n} = (b \pm \sqrt{b^2 - 2dc^2/(v^2\gamma)})/(2d)$.

Answer

We start with the lag equation,

$$\begin{aligned}
\frac{\mathrm{d}\ell}{\mathrm{d}t} &= 0 \\
c - v\gamma\hat{\ell}\hat{n} &= 0 \\
\hat{\ell} &= \frac{c}{v\gamma\hat{n}}.
\end{aligned} \tag{8}$$

Now we can sub this into the population size equation and solve,

$$\begin{aligned}
\frac{\mathrm{d}n}{\mathrm{d}t} &= 0 \\
\hat{n}(b - (d + \gamma\hat{\ell}^2/2)\hat{n}) &= 0 \\
\hat{n}\left(b - \left(d + \gamma\left(\frac{c}{v\gamma\hat{n}}\right)^2/2\right)\hat{n}\right) &= 0 \\
\hat{n}\left(b - \left(d + \frac{c^2}{2v^2\gamma\hat{n}^2}\right)\hat{n}\right) &= 0.
\end{aligned} \tag{9}$$

So either $\hat{n} = 0$ or we can divide by $\hat{n}$ to find

$$\begin{aligned} b - \left(d + \frac{c^2}{2v^2\gamma\hat{n}^2}\right)\hat{n} &= 0 \\ b - d\hat{n} - \frac{c^2}{2v^2\gamma\hat{n}} &= 0 \\ -d\hat{n}^2 + b\hat{n} - \frac{c^2}{2v^2\gamma} &= 0 \\ \hat{n} &= \frac{b \pm \sqrt{b^2 - 2dc^2/(v^2\gamma)}}{2d}, \end{aligned} \tag{10}$$

where we used the quadratic equation in the last step.

(ii) (1 points) Explain why, mathematically, these two equilibria are biologically invalid when $b^2v^2\gamma < 2dc^2$.

Answer

The equilibrium population size has an imaginary part when the term inside the square root becomes negative,

$$\begin{aligned} b^2 - 2dc^2/(v^2\gamma) &< 0 \\ b^2 &< 2dc^2/(v^2\gamma) \\ b^2v^2\gamma &< 2dc^2. \end{aligned} \tag{11}$$

Since, $\hat{\ell} = c/(v\gamma\hat{n})$, the lag will then also have an imaginary part.

(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

$$\begin{aligned} \mathrm{Tr}(\mathbf{J}) &= -\frac{b(2d + v\gamma) + \sqrt{\gamma(b^2v^2\gamma - 2dc^2)}}{2d} \\ \mathrm{Det}(\mathbf{J}) &= \frac{b^2v\gamma - 2dc^2/v + \sqrt{\gamma(b^2v^2\gamma - 2dc^2)}}{2d}. \end{aligned}$$

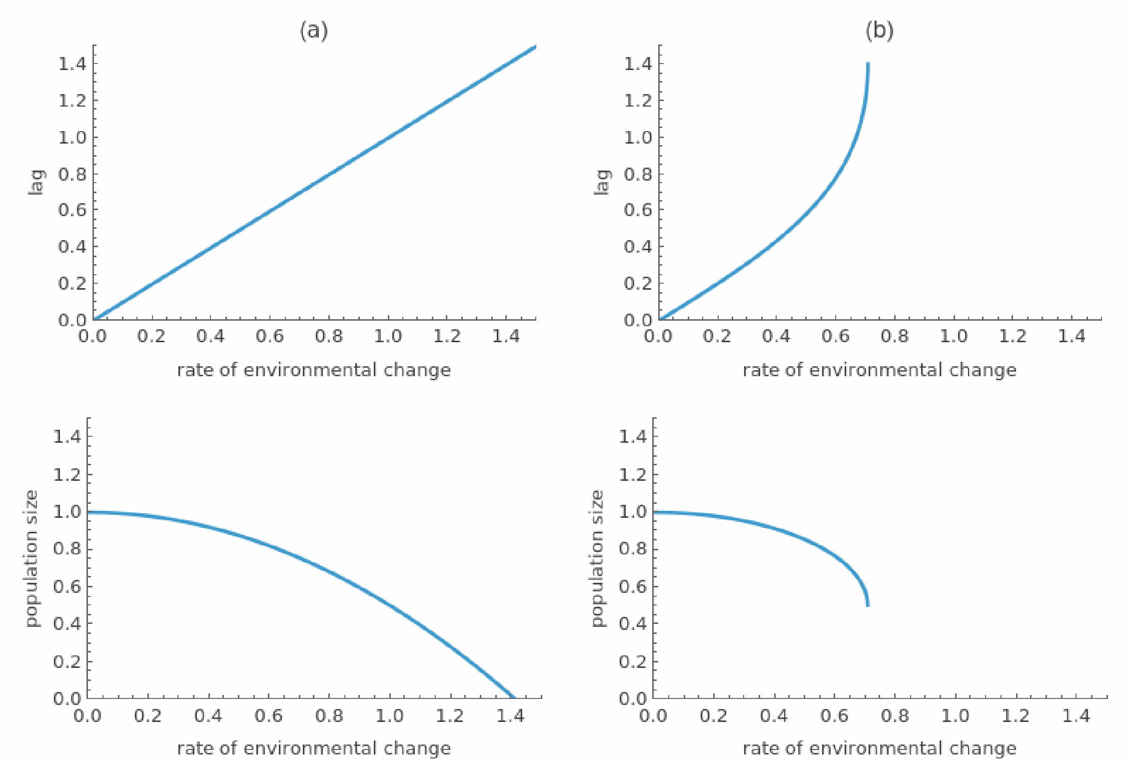
Explain why we can conclude that this equilibrium is stable when $b^2v^2\gamma > 2dc^2$. It turns out the other equilibrium is unstable under these conditions.

Answer

By the Routh-Hurwitz criteria for a 2x2 Jacobian in continuous-time, stability requires a negative trace and positive determinant. We can see that the trace is always negative. And given $b^2v^2\gamma > 2dc^2$, the determinant is positive.

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 equilibium 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.



Answer

In both models, death rates increase with density, meaning that when the population size is large there are lots of deaths. In the second model, death is also where selection happens, meaning evolution happens faster in larger populations. There is therefore a positive feedback between population size and adaptive evolution in the second model – from which the tipping point arises.

——— *End of Exam* ———