

UNIVERSITY OF TORONTO

Faculty of Arts and Science
Department of Ecology and Evolutionary Biology



**Mathematical modeling in ecology and evolution
(EEB314/1430)**

Test 2 – October 15, 2025

Available Time: 50m

Permitted Materials: Pen/pencil

Question 1 (9/9 points) Related individuals may share alleles inherited from the same ancestors. We say such alleles are identical by descent. When related individuals mate there is then a chance that their offspring have loci with alleles that are identical by descent. We call these loci autozygous (homozygous by descent). The inbreeding coefficient of an individual is the fraction of its loci that are autozygous, which is determined by the relatedness of the parents. In particular, the inbreeding coefficient of an offspring is the probability that two alleles chosen at random, one from the same locus in each parent, are identical by descent. This measure of relatedness is called the coefficient of consanguinity. Given a particular mating structure (pedigree), we can write down recursions for the inbreeding coefficients and coefficients of consanguinity.

Take for example the extreme case of full-sib mating, where offspring from the same parents mate every generation. All individuals in a given generation t have the same inbreeding coefficient, $f(t)$, which is the coefficient of consanguinity of their parents, $g(t - 1)$. The coefficient of consanguinity for full-sibs, $g(t)$, can be broken down into the probability the two randomly chosen alleles come from the same parent ($1/2$) and are the same ($1/2 + f(t - 1)/2$) plus the probability the two random alleles come from different parents ($1/2$) but are still the same ($g(t - 1)$). This creates a system of linear recursion equations,

$$\begin{aligned}f(t+1) &= g(t) \\g(t+1) &= \frac{1+f(t)}{4} + \frac{g(t)}{2}.\end{aligned}$$

- (a) (1 points) This system of recursion equations can be written in matrix form, $\vec{x}(t+1) = \mathbf{M}\vec{x}(t) + \vec{m}$, where $\vec{x}(t) = \begin{pmatrix} f(t) \\ g(t) \end{pmatrix}$ and \mathbf{M} and \vec{m} do not contain variables. Specify the entries of \mathbf{M} and \vec{m} .

Answer

$$\mathbf{M} = \begin{pmatrix} 0 & 1 \\ 1/4 & 1/2 \end{pmatrix}$$

$$\vec{m} = \begin{pmatrix} 0 \\ 1/4 \end{pmatrix}$$

- (b) (2 points) Show how to solve for the equilibrium, $\hat{\vec{x}} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$. In a sentence, describe what $g = 1$ means in terms of autozygosity.

Answer

We set $\vec{x}(t+1) = \vec{x}(t) = \hat{\vec{x}}$ and solve,

$$\begin{aligned}\hat{\vec{x}} &= \mathbf{M}\hat{\vec{x}} + \vec{m} \\ -\vec{m} &= \mathbf{M}\hat{\vec{x}} - \hat{\vec{x}} \\ -\vec{m} &= (\mathbf{M} - \mathbf{I})\hat{\vec{x}} \\ -(\mathbf{M} - \mathbf{I})^{-1}\vec{m} &= \hat{\vec{x}}.\end{aligned}$$

The inverse is

$$\begin{aligned}-(\mathbf{M} - \mathbf{I})^{-1} &= -\begin{pmatrix} -1 & 1 \\ 1/4 & -1/2 \end{pmatrix}^{-1} \\ &= -\frac{1}{1/4} \begin{pmatrix} -1/2 & -1 \\ -1/4 & -1 \end{pmatrix} \\ &= \begin{pmatrix} 2 & 4 \\ 1 & 4 \end{pmatrix}.\end{aligned}$$

And we do the final multiplication to get

$$\begin{aligned}-(\mathbf{M} - \mathbf{I})^{-1}\vec{m} &= \begin{pmatrix} 2 & 4 \\ 1 & 4 \end{pmatrix} \begin{pmatrix} 0 \\ 1/4 \end{pmatrix} \\ &= \begin{pmatrix} 1 \\ 1 \end{pmatrix}.\end{aligned}$$

In biological terms, $g = 1$ means that every locus in every individual is autozygous, i.e., every individual is completely inbred.

- (c) (2 points) Show how to derive the eigenvalues, $\lambda = \frac{1 \pm \sqrt{5}}{4}$, which are roughly 0.8 and -0.3 . Is the equilibrium stable?

Answer

We need to solve the characteristic polynomial, $|\mathbf{M} - \lambda\mathbf{I}| = 0$. In the 2x2 case we know the solutions are

$$\lambda = \frac{\text{Tr}(\mathbf{M}) \pm \sqrt{\text{Tr}(\mathbf{M})^2 - 4|\mathbf{M}|}}{2}.$$

Here $\text{Tr}(\mathbf{M}) = 1/2$ and $|\mathbf{M}| = -1/4$. So

$$\begin{aligned}\lambda &= \frac{\text{Tr}(\mathbf{M}) \pm \sqrt{\text{Tr}(\mathbf{M})^2 - 4|\mathbf{M}|}}{2} \\ &= \frac{1/2 \pm \sqrt{5/4}}{2} \\ &= \frac{1 \pm \sqrt{5}}{4}.\end{aligned}$$

In discrete time stability requires all $|\lambda| < 1$, so yes, the equilibrium is stable.

- (d) (2 points) Show how to derive the right eigenvector associated with the leading eigenvalue, $\lambda_1 = \frac{1+\sqrt{5}}{4}$, which is $\vec{v}_1 = \begin{pmatrix} 1 \\ \lambda_1 \end{pmatrix}$.

Answer

The right eigenvector equation is

$$\begin{aligned} \mathbf{M}\vec{v}_1 &= \lambda_1\vec{v}_1 \\ \begin{pmatrix} 0 & 1 \\ 1/4 & 1/2 \end{pmatrix} \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} &= \lambda_1 \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} \\ \begin{pmatrix} v_2 \\ v_1/4 + v_2/2 \end{pmatrix} &= \begin{pmatrix} \lambda_1 v_1 \\ \lambda_1 v_2 \end{pmatrix} \end{aligned}$$

One element of \vec{v}_1 is arbitrary, so choose $v_1 = 1$. The first row of the above equation then says $v_2 = \lambda_1$, giving $\vec{v}_1 = \begin{pmatrix} 1 \\ \lambda_1 \end{pmatrix}$.

- (e) (1 points) The deviation from the equilibrium is $\vec{y}(t) = \begin{pmatrix} 1 - f(t) \\ 1 - g(t) \end{pmatrix}$, which describes the fraction of loci within an individual that are not autozygous and the probability two alleles chosen at random, one from the same locus in each parent, are not identical by descent. The recursion for these variables is $\vec{y}(t+1) = \mathbf{M}\vec{y}(t)$, with the same \mathbf{M} as above.

Given the appropriately scaled left eigenvector associated with λ_1 is $\vec{u}_1 = \begin{pmatrix} \frac{1}{1+4\lambda_1^2} & \frac{4\lambda_1}{1+4\lambda_1^2} \end{pmatrix}$ and initial condition $\vec{y}(0) = \begin{pmatrix} h_0 \\ k_0 \end{pmatrix}$, show that in the long term we have

$$\vec{y}(t) \approx \begin{pmatrix} \lambda_1^t \\ \lambda_1^{t+1} \end{pmatrix} \frac{h_0 + 4\lambda_1 k_0}{1 + 4\lambda_1^2}.$$

Answer

The long term approximation is

$$\begin{aligned} \vec{y}(t) &\approx \lambda_1^t \vec{v}_1 \vec{u}_1 \vec{y}(0) \\ &= \lambda_1^t \begin{pmatrix} 1 \\ \lambda_1 \end{pmatrix} \begin{pmatrix} \frac{1}{1+4\lambda_1^2} & \frac{4\lambda_1}{1+4\lambda_1^2} \end{pmatrix} \begin{pmatrix} h_0 \\ k_0 \end{pmatrix} \\ &= \begin{pmatrix} \lambda_1^t \\ \lambda_1^{t+1} \end{pmatrix} \frac{h_0 + 4\lambda_1 k_0}{1 + 4\lambda_1^2}. \end{aligned}$$

- (f) (1 points) If we wanted to reduce autozygosity in some distant generation t and could decrease either the inbreeding coefficient or the coefficient of consanguinity of the founders, $f(0)$ or $g(0)$, by the same small amount, why should we decrease $g(0)$?

Answer

We are trying to maximize the long term value of $\vec{y}(t)$, the deviation from the fully autozygous equilibrium, by changing the initial conditions. Since the initial conditions have no effect on λ_1 the only part of the long term approximation we can affect is $h_0 + 4\lambda_1 k_0 = (1 - f(0)) + 4\lambda_1(1 - g(0))$. Since $4\lambda_1 > 1$, decreasing $g(0)$ causes a larger increase than decreasing $f(0)$. So, to reduce autozygosity in some distant generation t we would rather decrease the initial coefficient of consanguinity, ie how related the founders are, then their inbreeding coefficients.

———— *End of Exam* ———