Question 1 (10/30) Chris Carlson is studying the effect of mutualism on adaptation to a changing environment. For concreteness, consider a population of plants and a population of pollinators in a warming world. We assume each individual has a trait value that affects both its ability to cope with temperature and the benefit it receives from mutualism. The optimum trait value for coping with temperature increases linearly with time, at rate c_x for plants and rate c_y for pollinators, and each species evolves in response to deviations from the optimum, at rate a_x for plants and rate a_y for pollinators. An individual receives the most benefit from mutualism when its trait value is d units bigger than its partners trait value and evolutionary responses to deviations from this maximum benefit occur at rates b_x for plants and rate b_y for pollinators. We can approximate the dynamics of the mean lag behind the optimal trait value for coping with temperature for each species, x and y, with the following two differential equations,

$$\frac{\mathrm{d}x}{\mathrm{d}t} = c_x - a_x x - b_x(d - (x - y))$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = c_y - a_y y - b_y(d - (y - x)).$$

For clarity, we assume all parameters are positive.

(a) (2/30) The pair of differential equations can be written in matrix form,

$$\begin{bmatrix} \frac{\mathrm{d}x}{\mathrm{d}t} \\ \frac{\mathrm{d}y}{\mathrm{d}t} \end{bmatrix} = \mathbf{M} \begin{bmatrix} x \\ y \end{bmatrix} + \vec{m},$$

where $\mathbf{M}$ and $\vec{m}$ are composed entirely of parameters. Determine the entries of $\mathbf{M}$ and $\vec{m}$.

> **Solution**
>
> It's perhaps easiest to start by grouping together the x and y terms
>
> $$\frac{\mathrm{d}x}{\mathrm{d}t} = (b_x - a_x)x - b_x y + c_x - b_x d$$
>
> $$\frac{\mathrm{d}y}{\mathrm{d}t} = -b_y x + (b_y - a_y)y + c_y - b_y d.$$
>
> We then use the coefficients of x and y to build the matrix,
>
> $$\mathbf{M} = \begin{bmatrix} b_x - a_x & -b_x \\ -b_y & b_y - a_y \end{bmatrix},$$
>
> and put the constants in the vector,
>
> $$\vec{m} = \begin{bmatrix} c_x - b_x d \\ c_y - b_y d \end{bmatrix}.$$

(b) (4/30) Find the equilibrium values of x and y, $\hat{x}$ and $\hat{y}$. If you like, you can check that the difference between them is

$$\hat{x} - \hat{y} = \frac{(a_x b_y - a_y b_x)d - a_x c_y + a_y c_x}{a_x a_y - a_x b_y - a_y b_x}.$$

1

Solution

This could be done by setting each differential equation to zero and solving for one variable at a time, but now that we have the pair of equations in matrix form we may as well solve for both variables at once. The equilibrium is found by setting the rate of change to zero and solving for our vector of variables,

$$\begin{bmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{bmatrix} = 0$$

$$\mathbf{M}\begin{bmatrix} \hat{x} \\ \hat{y} \end{bmatrix} + \vec{m} = 0$$

$$\mathbf{M}\begin{bmatrix} \hat{x} \\ \hat{y} \end{bmatrix} + \vec{m} = 0$$

$$\mathbf{M}\begin{bmatrix} \hat{x} \\ \hat{y} \end{bmatrix} = -\vec{m}$$

$$\begin{bmatrix} \hat{x} \\ \hat{y} \end{bmatrix} = -\mathbf{M}^{-1}\vec{m}$$

$$\begin{bmatrix} \hat{x} \\ \hat{y} \end{bmatrix} = -\frac{1}{|\mathbf{M}|}\begin{bmatrix} b_y - a_y & b_x \\ b_y & b_x - a_x \end{bmatrix}\begin{bmatrix} c_x - b_x d \\ c_y - b_y d \end{bmatrix}$$

$$\begin{bmatrix} \hat{x} \\ \hat{y} \end{bmatrix} = -\frac{1}{(b_x - a_x)(b_y - a_y) - b_x b_y}\begin{bmatrix} (b_y - a_y)(c_x - b_x d) + b_x(c_y - b_y d) \\ b_y(c_x - b_x d) + (b_x - a_x)(c_y - b_y d) \end{bmatrix}$$

$$\begin{bmatrix} \hat{x} \\ \hat{y} \end{bmatrix} = -\frac{1}{a_x a_y - a_x b_y - a_y b_x}\begin{bmatrix} (b_y - a_y)(c_x - b_x d) + b_x(c_y - b_y d) \\ b_y(c_x - b_x d) + (b_x - a_x)(c_y - b_y d) \end{bmatrix}$$

$$\begin{bmatrix} \hat{x} \\ \hat{y} \end{bmatrix} = \begin{bmatrix} \frac{(b_y - a_y)(b_x d - c_x) + b_x(b_y d - c_y)}{a_x a_y - a_x b_y - a_y b_x} \\ \frac{b_y(b_x d - c_y) + (b_x - a_x)(b_y d - c_y)}{a_x a_y - a_x b_y - a_y b_x} \end{bmatrix}$$

(c) (2/30) As in the univariate case, we can define the deviations of x and y from their equilibrium values, $\delta_x = x - \hat{x}$ and $\delta_y = y - \hat{y}$, and write a simpler equation for their dynamics,

$$\begin{bmatrix} \frac{d\delta_x}{dt} \\ \frac{d\delta_y}{dt} \end{bmatrix} = \mathbf{M}\begin{bmatrix} \delta_x \\ \delta_y \end{bmatrix},$$

where $\mathbf{M}$ is the same as in the previous question (you may also recognize $\mathbf{M}$ as the Jacobian!). Use the Routh-Hurwitz criteria (conditions on the determinant and trace) to determine what needs to be true about the parameter values for the equilibrium to be stable.

Solution

The Routh-Hurwitz criteria for a 2x2 matrix in continuous time are a positive determinant, $0 < |\mathbf{M}|$, and a negative trace, $\mathrm{Tr}(\mathbf{M}) < 0$. Starting with the determinant, which

2

we already calculated in the previous question,

$$0 < |\mathbf{M}|$$
$$0 < a_x a_y - a_x b_y - a_y b_x$$
$$a_x b_y + a_y b_x < a_x a_y.$$

For the trace we need
$$\mathrm{Tr}(\mathbf{M}) < 0$$
$$(b_x - a_x) + (b_y - a_y) < 0$$
$$b_x + b_y < a_x + a_y.$$

(d) (2/30) This is a linear system of equations and so we can write out the general solution for the deviations from equilibrium, $\vec{\delta}(t) = \begin{bmatrix} \delta_x(t) \\ \delta_y(t) \end{bmatrix}$, as $\vec{\delta}(t) = \mathbf{A}e^{\mathbf{D}t}\mathbf{A}^{-1}\vec{\delta}(0)$. Unfortunately the eigenvalues and eigenvectors are a little complicated, but given I told you the eigenvalues of $\mathbf{M}$ were λ_1 and λ_2 and their respective right eigenvectors were $\begin{bmatrix} u_{11} \\ u_{21} \end{bmatrix}$ and $\begin{bmatrix} u_{12} \\ u_{22} \end{bmatrix}$, write out the entries of $\mathbf{A}$ and $\mathbf{D}$.

Solution

The columns of $\mathbf{A}$ are the right eigenvectors,

$$\mathbf{A} = \begin{bmatrix} u_{11} & u_{12} \\ u_{21} & u_{22} \end{bmatrix},$$

and the diagonal elements of $\mathbf{D}$ are the respective eigenvalues,

$$\mathbf{D} = \begin{bmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{bmatrix}.$$

Question 2 (10/30) Sometimes selection acts differently on females and males. Because females and males share much of the same genome (besides some potential sex chromosomes), this can lead to evolutionary conflict between the sexes, which is called sexual antagonism. Here we look at a classic population genetic model of sexual antagonism (Kidwell *et al.*, 1977). To model this we need to keep track of the allele frequency in both females and males. We consider two alleles, A and a, and let p_f and p_m be the frequency of A in females and males, respectively. Let the fitnesses of AA, Aa, and aa genotypes in females be f_{AA}, f_{Aa}, and f_{aa}, with $0 < f_i$ for all i. Let the fitnesses of AA, Aa, and aa genotypes in males be m_{AA}, m_{Aa}, and m_{aa}, with $0 < m_i$ for all i. The allele frequency dynamics are then described by the following two recursion equations,

$$p_f(t+1) = \frac{f_{AA}p_f(t)p_m(t) + f_{Aa}[p_f(t)(1-p_m(t)) + (1-p_f(t))p_m(t)]/2}{\overline{F}(t)}$$

$$p_m(t+1) = \frac{m_{AA}p_f(t)p_m(t) + m_{Aa}[p_f(t)(1-p_m(t)) + (1-p_f(t))p_m(t)]/2}{\overline{M}(t)},$$

where the mean fitnesses in females and males are

$$\overline{F}(t) = f_{AA}p_f(t)p_m(t) + f_{Aa}[p_f(t)(1-p_m(t)) + (1-p_f(t))p_m(t)] + f_{aa}(1-p_f(t))(1-p_m(t))$$

$$\overline{M}(t) = m_{AA}p_f(t)p_m(t) + m_{Aa}[p_f(t)(1-p_m(t)) + (1-p_f(t))p_m(t)] + m_{aa}(1-p_f(t))(1-p_m(t)).$$

(a) (2/30) Verify that both $\hat{p}_f = \hat{p}_m = 0$ and $\hat{p}_f = \hat{p}_m = 1$ are equilibria. We call these boundary equilibria, which represent the loss and fixation of the A allele, respectively.

> **Solution**
>
> Setting $p_f(t) = p_m(t) = 0$ in the recursions gives $p_f(t+1) = 0/\overline{F}(t) = 0$ and $p_m(t+1) = 0/\overline{M}(t) = 0$, verifying that $\hat{p}_f = \hat{p}_m = 0$ is an equilibrium.
>
> Similarly, setting $p_f(t) = p_m(t) = 1$ in the recursions gives $p_f(t+1) = f_{AA}/\overline{F}(t) = f_{AA}/f_{AA} = 1$ and $p_m(t+1) = m_{AA}/\overline{M}(t) = m_{AA}/m_{AA} = 1$, verifying that $\hat{p}_f = \hat{p}_m = 1$ is also an equilibrium.

(b) (3/30) There is a third equilibrium where both alleles may be present (i.e., polymorphic). We can determine the stability of this equilibrium by determining when both of the boundary equilibria are unstable. Deriving and factoring the Jacobian takes a little work, but in the end the Jacobian evaluated at each of the boundary equilibria reduces to

$$\mathbf{J}\big|_{p_m=p_f=0} = \begin{bmatrix} \frac{m_{Aa}}{2m_{aa}} & \frac{m_{Aa}}{2m_{aa}} \\ \frac{f_{Aa}}{2f_{aa}} & \frac{f_{Aa}}{2f_{aa}} \end{bmatrix}$$

$$\mathbf{J}\big|_{p_m=p_f=1} = \begin{bmatrix} \frac{m_{Aa}}{2m_{AA}} & \frac{m_{Aa}}{2m_{AA}} \\ \frac{f_{Aa}}{2f_{AA}} & \frac{f_{Aa}}{2f_{AA}} \end{bmatrix}.$$

Show that the leading eigenvalue of $\mathbf{J}\big|_{p_m=p_f=0}$ is $\lambda_A = \frac{f_{Aa}/f_{aa} + m_{Aa}/m_{aa}}{2}$. By symmetry the leading eigenvalue of $\mathbf{J}\big|_{p_m=p_f=1}$ is $\lambda_a = \frac{f_{Aa}/f_{AA} + m_{Aa}/m_{AA}}{2}$.

(c) (2/30) Describe in a sentence or two what λ_A represents, biologically.

(d) (2/30) To model a conflict between the sexes we assume the a allele is favoured in females ($f_{AA} = 1 - s_f$, $f_{Aa} = 1 - h_f s_f$, $f_{aa} = 1$, with $0 < s_f < 1$ and $0 < h_f < 1$) but the A allele is favoured in males ($m_{AA} = 1$, $m_{Aa} = 1 - h_m s_m$, $m_{aa} = 1 - s_m$, with $0 < s_m < 1$ and $0 < h_m < 1$). The expressions for λ_A and λ_a get a little more complicated with this parameterization, but under the special case of $h_f + h_m = 1$ we have both $\lambda_A > 1$ and $\lambda_a > 1$ when
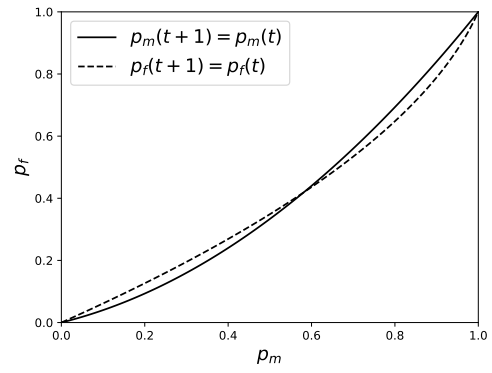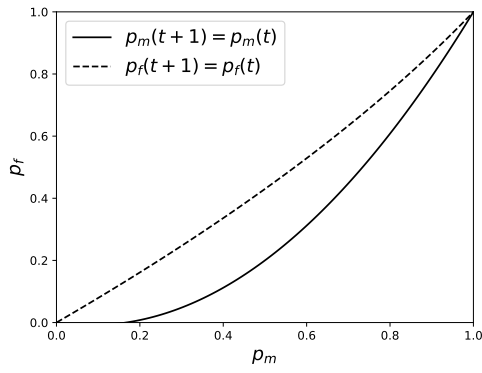
$$\frac{s_f}{1 + s_f} < s_m < \frac{s_f}{1 - s_f}.$$

Describe in a sentence or two why, biologically, stability of the polymorphic equilibrium restricts s_m (or, equivalently, s_f) to an intermediate value.

(e) (1/30) Below we plot the nullclines for two sets of parameter values. In one sentence, state which plot (left or right) has a biologically valid polymorphic equilibrium and why.

Question 3 (10/30) Competition for resources is often asymmetric in the sense that individuals with larger traits (eg, body size) have a competitive advantage. Here we'll look at the evolutionary consequences of this asymmetry following a model of Matsuda & Abrams (1994).

(a) (2/30) We start by considering a resident population, where all individuals have trait value x. Let the dynamics of the number of residents, n, be described by logistic growth,

$$\frac{\mathrm{d}n}{\mathrm{d}t} = rn\left(1 - \frac{n}{K(x)}\right),$$

where $r > 0$ is the intrinsic growth rate and $K(x) > 0$ is the carrying capacity of a population composed entirely of individuals with trait value x. Show that the only non-zero equilibrium is $\hat{n} = K(x)$.

> **Solution**
>
> We set the differential equation to zero and solve for $\hat{n}$,
>
> $$0 = r\hat{n}\left(1 - \frac{\hat{n}}{K(x)}\right),$$
>
> so that $\hat{n} = 0$ or, dividing both sides by $\hat{n}$,
>
> $$0 = r\left(1 - \frac{\hat{n}}{K(x)}\right)$$
> $$0 = 1 - \frac{\hat{n}}{K(x)}$$
> $$\frac{\hat{n}}{K(x)} = 1$$
> $$\hat{n} = K(x).$$

(b) (2/30) Now consider a mutant population with trait value x_m. Let the number of mutants change according to
$$\frac{\mathrm{d}n_m}{\mathrm{d}t} = rn_m\left(1 - \frac{n_m + \alpha(x_m, x)n}{K(x_m)}\right),$$
where $\alpha(x_m, x)$ describes the strength of competition that individuals with trait value x exert on individuals with trait value x_m. Use this equation to show that invasion fitness (the growth rate of a rare mutant into a population of residents at equilibrium) is $\lambda(x_m, x) = r(1 - \alpha(x_m, x)K(x)/K(x_m))$.

> **Solution**
>
> Dividing $\frac{\mathrm{d}n_m}{\mathrm{d}t}$ by n_m gives the growth rate of a mutant,
>
> $$\frac{\mathrm{d}n_m}{n_m\mathrm{d}t} = r\left(1 - \frac{n_m + \alpha(x_m, x)n}{K(x_m)}\right).$$

7

When mutants are rare, $n_m = 0$, and the resident is at equilibrium, $n = K(x)$, we have

$$\frac{\mathrm{d}n_m}{n_m \mathrm{d}t} = r\left(1 - \frac{\alpha(x_m, x)K(x)}{K(x_m)}\right),$$

which we define as our invasion fitness, $\lambda(x_m, x)$. The same result could be found from the bottom right entry of the Jacobian of $\frac{\mathrm{d}n}{\mathrm{d}t}$ and $\frac{\mathrm{d}n_m}{\mathrm{d}t}$ evaluated at $n_m = 0$ and $n = K(x)$,

$$\frac{\partial}{\partial n_m}\left.\frac{\mathrm{d}n_m}{\mathrm{d}t}\right|_{n_m=0, n=K(x)} = r\left(1 - \frac{\alpha(x_m, x)K(x)}{K(x_m)}\right).$$

(c) (4/30) To be more concrete, let's choose some specific functions for carrying capacity and competition,

$$K(x) = K_0 \exp\left(-\frac{\log(x/x_0)^2}{2w^2}\right)$$

$$\alpha(x_m, x) = \exp\left(-(x_m - x)\beta - \frac{(x_m - x)^2}{4\sigma^2}\right).$$

We now restrict to positive trait values, $x > 0$, e.g., body size. In the first equation, $K_0 > 0$ is the maximum carrying capacity, achieved when a population has trait $x_0 > 0$, and w describes how quickly carrying capacity declines as x departs from x_0. In the second equation, $\beta > 0$ describes the strength of competitive asymmetry in favour of larger x and σ describes how quickly the symmetric aspect of competition declines with differences in trait value, $x_m - x$.

Given that $\left.\frac{\partial \alpha(x_m, x)}{\partial x_m}\right|_{x_m=x} = -\beta$ and $\left.\frac{\mathrm{d}K(x_m)}{\mathrm{d}x_m}\right|_{x_m=x} = \frac{-\log(x/x_0)}{w^2 x}K(x)$, use the invasion fitness to show that the selection gradient is $D(x) = r\left(\beta - \frac{\log(x/x_0)}{w^2 x}\right)$.

Solution

The selection gradient is the slope of invasion fitness with respect to mutant trait value

evaluated at the resident trait value,

$$D(x) = \left.\frac{\partial \lambda(x_m, x)}{\partial x_m}\right|_{x_m=x}$$

$$= \left.\frac{\partial}{\partial x_m}\left(r\left(1 - \frac{\alpha(x_m, x)K(x)}{K(x_m)}\right)\right)\right|_{x_m=x}$$

$$= -rK(x)\left.\frac{\partial}{\partial x_m}\left(\frac{\alpha(x_m, x)}{K(x_m)}\right)\right|_{x_m=x}$$

$$= -rK(x)\left.\frac{\frac{\partial \alpha(x_m,x)}{\partial x_m}K(x_m) - \alpha(x_m, x)\frac{\mathrm{d}K(x_m)}{\mathrm{d}x_m}}{K(x_m)^2}\right|_{x_m=x}$$

$$= -rK(x)\frac{-\beta K(x) - \alpha(x, x)\frac{-\log(x/x_0)}{w^2 x}K(x)}{K(x)^2}$$

$$= r\left(\beta - \frac{\log(x/x_0)}{w^2 x}\right).$$

(d) (2/30) Because $\frac{\log(x/x_0)}{w^2 x}$ has a maximum value of $1/(w^2 x_0 e)$, where e is the base of the natural logarithms, if the strength of asymmetric competition is large enough, $\beta > 1/(w^2 x_0 e)$, the selection gradient is always positive, $D(x) > 0$. In a sentence, describe what this means for the evolution of x in the long run. In another sentence, describe what this means for equilibrium population size, $K(x)$, in the long run.

Solution

Since the sign of the selection gradient determines the direction of evolution, if the selection gradient is always positive the trait will always increase, approaching infinity. As the trait, x, approaches infinity the equilibrium population size, $K(x)$, approaches zero, meaning that evolution drives the population extinct.

9