Parents determine the traits of their offspring via both genetic inheritance and through their own traits. A simple model of this (Kirkpatrick & Lande 1989) assumes an individual's trait value is $z = a + e + mz'$, where a is the influence of genetics, e is the influence of environment, and mz' is the influence of their parent's trait (assuming only one parent's trait influences the offspring – this is typically referred to as 'maternal effects' but equally applies to fathers). Here z' is their parent's trait value and $0 \leq m \leq 1$ is the proportion of the parent's trait that is passed down. To give a concrete example, the trait value could be size, and larger parents produce larger offspring regardless of genetics.

Assuming stabilizing selection around an optimal trait value of 0, this model produces the following recursions for the mean genetic value, $\bar{a}$, and mean trait value, $\bar{z}$, in generation $t + 1$,

$$\bar{a}(t+1) = \bar{a}(t) - k_g \bar{z}(t)$$
$$\bar{z}(t+1) = \bar{a}(t) + (m(1-k_p) - k_g)\bar{z}(t)$$

where $0 \leq k_g < 1$ is the evolutionary potential of the genetic value and $0 \leq k_p < 1$ is the evolutionary potential of the trait value.

1. [4/20 points] We can write this system of equations in matrix form, $\vec{x}(t+1) = \mathbf{M}\vec{x}(t)$, where $\vec{x}(t) = \begin{pmatrix} \bar{a}(t) \\ \bar{z}(t) \end{pmatrix}$ and $\mathbf{M}$ is a matrix of parameters (m, k_g, k_p). Write out the entries of $\mathbf{M}$.

$$\mathbf{M} = \begin{pmatrix} 1 & -k_g \\ 1 & m(1-k_p) - k_g \end{pmatrix}$$

2. [4/20 points] Find the equilibrium of this model, $\hat{\vec{x}}$.

Equilibrium is achieved when $\vec{x}(t+1) = \vec{x}(t) = \hat{\vec{x}}$. So

$$\hat{\vec{x}} = \mathbf{M}\hat{\vec{x}}$$

implying $\hat{\vec{x}} = \vec{0}$.

3. [4/20 points] To determine the stability of $\hat{\vec{x}}$, calculate the eigenvalues of $\mathbf{M}$.

To find the eigenvalues we find the λ that solve $|\mathbf{M}-\lambda\mathbf{I}| = 0$, i.e., the roots of the characteristic polynomial. In this 2x2 case, we know the polynomial can be written in terms of the trace and determinant of $\mathbf{M}$, and has roots

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

The trace is $\text{Tr}(\mathbf{M}) = 1 + m(1-k_p) - k_g$ and the determinant is $\text{Det}(\mathbf{M}) = m(1-k_p) - k_g + k_g = m(1-k_p)$.

4. [4/20 points] Determine the conditions under which the dynamics will be oscillatory.

The dynamics will be oscillatory when the eigenvalues are complex. This occurs when the term inside the square root is negative, i.e., $\text{Tr}(\mathbf{M})^2 < 4\text{Det}(\mathbf{M})$. This doesn't simplify very nicely in this example, but one can notice that this can only be true if $m > 0$, i.e., if there is some maternal effect.

5. [4/20 points] Given the dynamics are oscillatory, show that the equilibrium is stable if $m(1-k_p) < 1$.

Stability requires the absolute value of the eigenvalues to be less than one. The absolute value of a complex number, $A + Bi$, is $\sqrt{A^2 + B^2}$. We can write A and B in terms of the trace and determinant by rearranging,

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

So we have $A = \text{Tr}(\mathbf{M})/2$ and $B = \pm\sqrt{4\text{Det}(\mathbf{M}) - \text{Tr}(\mathbf{M})^2}/2$. This implies that the absolute value of both eigenvalues is

$$\begin{aligned}
A^2 + B^2 &= \frac{\text{Tr}(\mathbf{M})^2}{4} + \frac{4\text{Det}(\mathbf{M}) - \text{Tr}(\mathbf{M})^2}{4} \\
&= \text{Det}(\mathbf{M}).
\end{aligned}$$

So, when there are oscillations, we have stability when

$$\begin{aligned}\sqrt{\text{Det}(\mathbf{M})} &< 1\\ \text{Det}(\mathbf{M}) &< 1\\ m(1-k_p) &< 1.\end{aligned}$$

Since $m < 1$ and $0 < k_p$, this is always true.