# Exercises for stability analysis

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**Exercise 1: Sexual selection revisited** Recall the model for sexual selection, where we studied the coevolution of a (mean) male trait $z$ and a (mean) female preference $p$. We assumed that natural selection favors $p = z = 0$, and that females with $p \gtrless 0$ favor males with large or small trait values, respectively.

Using the weak-selection approximation of Lande's equation from quantitative genetics, the linear version of this model was:

$$\frac{\mathrm{d}z}{\mathrm{d}t} = V_z(s_{\text{sex}}p - s_z z) - Cs_p p \tag{1a}$$

$$\frac{\mathrm{d}p}{\mathrm{d}t} = C(s_{\text{sex}}p - s_z z) - V_p s_p p, \tag{1b}$$

where

- $V_z$ and $V_p$ are the additive genetic variances for $z$ and $p$, respectively, and $C$ is the additive genetic covariance,
- $s_z$ and $s_p$ determine the strength of natural selection on the two traits, and $s_{\text{sex}}$ determines the strength of sexual selection.

The only equilibrium of this model is $z = p = 0$. A Fisherian run-away process occurs if this equilibrium is unstable. Following the standard protocol, the Jacobian of model (1) is given by

$$J = \begin{pmatrix} -V_z s_z & V_z s_{\text{sex}} - Cs_p \\ -Cs_z & -V_p s_p + Cs_{\text{sex}}. \end{pmatrix} \tag{2}$$

Note that, as (1) already is a linear model, $J$ is simply the matrix describing this linear model. Using the Routh-Hurwitz criterion, the model's equilibrium is stable (i.e. all eigenvalues have negative real part) if

$$\mathrm{tr}(\mathbf{J}) = -V_z s_z - V_p s_p + Cs_{\text{sex}} < 0 \tag{3a}$$

$$\det(\mathbf{J}) = s_p s_z(V_p V_z - C^2) > 0 \tag{3b}$$

It is a plausible assumption that $V_p V_z > C^2$ (i.e. genetic variances are stronger than covariances). Then, run-away sexual selection requires that sexual selection and the "sexy-sons" effect (represented by the term $Cs_{\text{sex}}$) is stronger than the combined action of natural selection on both traits ($V_z s_z + V_p s_p$).

Now let's look at a variant of this model. Assume that, instead of favoring females with zero preference, natural selection favors females preferring the most common type of males. (What mechanism could lead to such a fitness function?) The model then becomes

$$\frac{\mathsf{d}z}{\mathsf{d}t} = V_z(s_{\text{sex}}p - s_z z) - Cs_p(p - z) \tag{4a}$$

$$\frac{\mathsf{d}p}{\mathsf{d}t} = C(s_{\text{sex}}p - s_z z) - V_p s_p(p - z), \tag{4b}$$

Perform a stability analysis of this model, and compare the results to those of the original model.

**Answer:** The only equilibrium is still $p = z = 0$. The Jacobian becomes

$$J = \begin{pmatrix} Cs_p - V_z s_z & V_z s_{\text{sex}} - Cs_p \\ V_p s_p - Cs_z & -V_p s_p + Cs_{\text{sex}}. \end{pmatrix} \tag{5}$$

The new stability conditions are

$$\text{tr}(\mathbf{J}) = -V_z s_z - (V_p - C)s_p + Cs_{\text{sex}} < 0 \tag{6a}$$

$$\det(\mathbf{J}) = s_p(s_z - s_{\text{sex}})(V_p V_z - C^2) > 0 \tag{6b}$$

Comparing (3a) and (6a) shows that fulfilling the trace condition for stability becomes more difficult due to the term $Cs_p$. Thus, genetic correlation with the male trait reduces the effect of natural selection on the female preference. Furthermore, comparing (3b) and (6b) reveals that, even if we assume $V_p V_z > C^2$, the equilibrium will be unstable if $s_{\text{sex}} > s_z$, that is, if sexual selection on the male trait trait is stronger than natural selection. Both effects make coevolution more likely. This is to be expected, because natural selection no longer opposes the evolution of non-zero female preferences.

**Exercise 2.** Now let's look at another variant of the original model (1). Assume that natural selection favors a male trait $z = \theta \neq 0$. The model then becomes

$$\frac{\mathsf{d}z}{\mathsf{d}t} = V_z(s_{\text{sex}}p - s_z(z - \theta)) - Cs_p p \tag{7a}$$

$$\frac{\mathsf{d}p}{\mathsf{d}t} = C(s_{\text{sex}}p - s_z(z - \theta)) - V_p s_p p, \tag{7b}$$

What is the equilibrium of this model? What about its stability?

**Answer:** The new equilibrium is $z = \theta, p = 0$. The Jacobian of (7) is identical to (2), and thus, stability and the likelihood of coevolution are unaffected by the shift in the male optimum. This might seem surprising at first sight, but one has to remember how female preference is modeled. $p = 0$ means no preference, so it has no influence on $z$. Furthermore, female preference is "open-ended", and sexual selection on the male trait does not depend on the difference between $z$ and $p$, but only on $p$ alone.

**Exercise 3: Migration-selection balance in an island population** We will consider a mainland-island model of a haploid population with two alleles $A$ and $a$. $A$ is selectively favored in the mainland, whereas $a$ is favored on the island. More precisely, on the island, the fitnesses are $W_A = 1-s$ and $W_a = 1$. The island receives immigrants from the mainland such that, after selection, a fraction $m$ of individuals are migrants carrying the $A$ allele.

- Write down a recursion equation for the frequency $p$ of the $A$ allele on the island.
- Find the equilibria of this system and determine their stability.
- What do the results say about the maintenance of the locally adapted allele in the island population?

**Answer:** The dynamics of the $A$ allele are given by

$$p' = (1-m)\frac{p(1-s)}{p(1-s)+1-p} + m. \tag{8}$$

The equilibria are $p = 1$ (the locally adapted allele is lost) and $p = m/s$ (polymorphism de to migration-selection balance). The second equilibrium is biologically meaningful only if $m < s$, that is migration is weaker than selection. An equilibrium is stable if the derivative of the right-hand side of the recursion is between $-1$ and 1. For the $p = 1$ equilibrium, this derivative is $(1-m)/(1-s)$ and for the polymorphic equilibrium it is $(1-s)/(1-m)$. Thus, the polymorphic equilibrium is stable whenever it exists. Otherwise, the monomorphic equilibrium is stable.