Analyzing dynamical systems: Fisherian sexual selection

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Sexual selection

- Sexual selection is selection arising from differences in mating success.
- It is often invoked as an explanation for exaggerated male traits, such as the peacock's tail.

- There are a number of different types of sexual selection.
- Here, we will consider a model of "runaway sexual selection", first proposed verbally by R.A. Fisher.

Fisherian runaway sexual selection

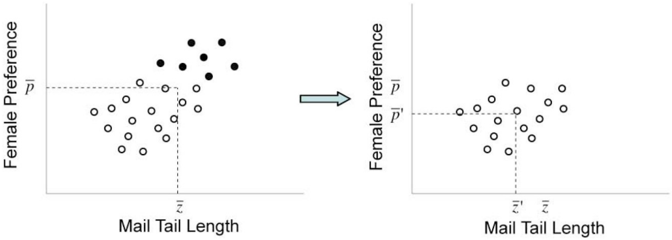
The runaway process assumes that a male trait and a female preference for the trait co-evolve to ever larger values due to a positive feedback:

- Males with large trait values have high fitness because they are attractive to females.
- Females with a strong preference have high fitness, because their sons will inherit their fathers attractive traits (**sexy sons**).

The model typically assumes that the process gets started by some other process (such as drift or natural selection) but later continuous independently.

The Fisher process and genetic correlations

Another way of looking at this problem is to note that, if the most choosy females mate with the most attractive males, this will lead to a **positive genetic correlation** between the male trait and the female preference. Then, selection on one trait will automatically also increase the other trait.



A linear model

There are different ways in which runaway sexual selection can be modeled. Here, we will look at a model where trait and preference are quantitative traits that can evolve in two directions.

- We consider two traits: a male display trait Z and the female preference P.
- Natural selection favors $Z = 0$ and $P = 0$.
- Females with $P > 0$ ($P < 0$) prefer males with large (small) trait values. Females with $P = 0$ have no preference.
- Let z and p denote the mean values of Z and P in the population.

Quantitative genetics

The above model is an example for a **quantitative genetic** model.

- It deals with quantitative (i.e. continuous) traits, that are most likely influenced by many loci.
- Instead of modeling the evolution of allele frequencies at different loci, we assume that the evolution of mean trait value is proportional to a (constant) genetic variance and a fitness gradient (the slope of a fitness landscape).
- Here, the fitness gradient is given by the selection parameters σ and s.

Case 1: No correlation

The mean phenotypes change according to

$$\frac{\mathrm{d}z}{\mathrm{d}t} = V_z(s_{\mathrm{sex}}p - s_z z)$$
$$\frac{\mathrm{d}p}{\mathrm{d}t} = -V_p s_p p$$

Here,

- s_{sex} determines the strength of sexual selection.
- s_z and s_p determine the strength of natural selection in Z and P.
- V_z and V_p are the genetic variances of Z and P.

Stability analysis

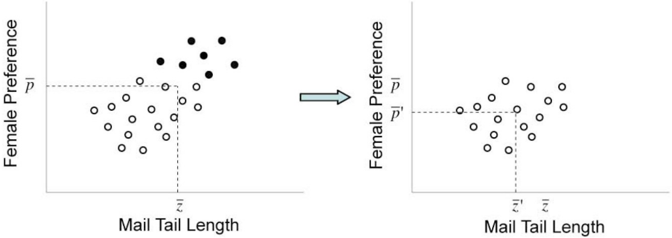
The above model can be written as

$$\begin{pmatrix} dz/dt \\ dp/dt \end{pmatrix} = \begin{pmatrix} -V_z s_z & V_z s_{\text{sex}} \\ 0 & -V_p s_p \end{pmatrix} \begin{pmatrix} z \\ p \end{pmatrix}$$

- It has a unique equilibrium at $z = p = 0$.
- The eigenvalues are $-V_z s_z$ and $-V_p s_p$ (triangular matrix).
- Therefore, the equilibrium is stable and no exaggerated male trait or female preference evolve.
- This is obvious, as p is independent of z and will always evolve towards 0, whereupon z will also evolve to 0.

Case 2: Genetic correlation between Z and P

- Now assume that Z and P are genetically correlated (e.g. because of linkage disequilibrium).
- Let C be the covariance between P and Z.
- If $C > 0$, selection on one trait will lead to a correlated response in the other trait (in the same direction).



The dynamics now become

$$\frac{\mathrm{d}z}{\mathrm{d}t} = V_z(s_{\mathrm{sex}}p - s_z z) - Cs_p p$$
$$\frac{\mathrm{d}p}{\mathrm{d}t} = C(s_{\mathrm{sex}}p - s_z z) - V_p s_p p,$$

which can be written as

$$\begin{pmatrix} \mathrm{d}z/\mathrm{d}t \\ \mathrm{d}p/\mathrm{d}t \end{pmatrix} = \begin{pmatrix} -V_z s_z & V_z s_{\mathrm{sex}} - Cs_p \\ -Cs_z & -V_p s_p + Cs_{\mathrm{sex}} \end{pmatrix} \begin{pmatrix} z \\ p \end{pmatrix}$$

The equilibrium is again at $z = p = 0$.

Stability

- According to the Routh-Hurwitz criteria, the equilibrium is stable if

$$\operatorname{tr}(\mathbf{M}) = -V_z s_z - V_p s_p + C s_{\text{sex}} < 0$$
$$\det(\mathbf{M}) = s_p s_z (V_p V_z - C^2) > 0$$

  where **M** is the matrix in the previous equation.
- The trace is negative if $C s_{\text{sex}} < V_z s_z + V_p s_p$, that is, if sexual selection and the sexy-sons effect are weaker than natural selection on the two traits.
- The determinant is positive if $V_p V_z > C$, that is, if the genetic variances of the two traits are stronger than the covariance, which is a plausible assumption.

Cycles

The system will perform cycles (with increasing or decreasing amplitude) if the eigenvalues are complex. The eigenvalues are given by

$$\lambda_{1,2} = \frac{1}{2}\left(\gamma \pm \sqrt{\gamma^2 - 4\det(\mathbf{M})}\right).$$

with $\gamma \equiv \mathrm{tr}(\mathbf{M})$. Assuming $\det(\mathbf{M}) > 0$, cycles occur if $\gamma^2 > 4\det(\mathbf{M})$. This condition implies strong sexual selection and correlation, but in a different way than for the stability condition $\gamma < 0$.

A nonlinear model

In the linear model, trait and preference evolve to infinite values if the equilibrium is unstable. This is clearly unrealistic. To enforce upper limits, we now assume that natural selection gets stronger as the magnitude of z or p grows larger. This can be done by multiplying quadratic terms $1 + p^2$ and $1 + z^2$ to the natural selection terms:

$$\frac{\mathrm{d}z}{\mathrm{d}t} = V_z(s_{\mathrm{sex}}p - s_z z(1 + z^2)) - C s_p p(1 + p^2)$$
$$\frac{\mathrm{d}p}{\mathrm{d}t} = C(s_{\mathrm{sex}}p - s_z z(1 + z^2)) - V_p s_p p(1 + p^2).$$

Stability analysis

The nonlinear model still has only one equilibrium at $z = p = 0$. To derive the Jacobian, define $\frac{\mathrm{d}z}{\mathrm{d}t} = f(p, z)$, $\frac{\mathrm{d}p}{\mathrm{d}t} = g(p, z)$. Then

$$\mathbf{J} = \begin{pmatrix} \frac{\partial f}{\partial z} & \frac{\partial f}{\partial p} \\ \frac{\partial g}{\partial z} & \frac{\partial g}{\partial p} \end{pmatrix}\Bigg|_{z=p=0}$$

$$= \begin{pmatrix} -V_z s_z(1+3z^2) & V_z s_{\mathrm{sex}} - C c_p(1+3p^2) \\ -C s_z(1+3z^3) & C s_{\mathrm{sex}} - V_p s_p(1+3p^3) \end{pmatrix}\Bigg|_{z=p=0}$$

$$= \begin{pmatrix} -V_z s_z & V_z s_{\mathrm{sex}} - C c_p \\ -C s_z & C s_{\mathrm{sex}} - V_p s_p \end{pmatrix}$$

J is identical to the matrix **M** describing the linear model (with correlation). This is to be expected, as **J** describes the linearization of the nonlinear system close to the equilibrium. In consequence, our previous conclusions about stability still hold true:

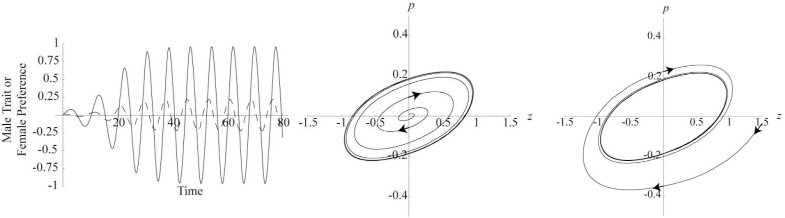
- The equilibrium is stable (i.e., no exaggerated traits and preferences evolve) if $\gamma < 0$ (i.e., $Cs_{\text{sex}} < V_z s_z + V_p s_p$) and $V_z V_p > C^2$.
- The system will perform oscillations close to the equilibrium if $\gamma^2 > \det(\mathbf{J})$.

However, the linear stability analysis does not tell us what happens at a greater distance from the equilibrium.

Non-equilibrium dynamics

Simulations suggest two types of non-equilibrium dynamics:

- If the eigenvalues are real, the runaway process leads to the evolution of ever larger (or smaller) traits and preferences (despite our nonlinear terms).
- If the eigenvalues are complex, the system performs **stable limit cycles** (a locally stable cyclic **attractor**).



Why cycles?

- Trait z and preference p increase.
- At some point, the large p becomes too costly for the females.
- Natural selection for decreased p leads to a correlated decrease in z.
- As $p \to 0$, z decreases further due to natural selection.
- As a correlated response, p decreases further and becomes negative.
- This selects for males with negative z and induces correlated further decrease in p.
- At some point, the strongly negative p becomes too costly for the females . . .

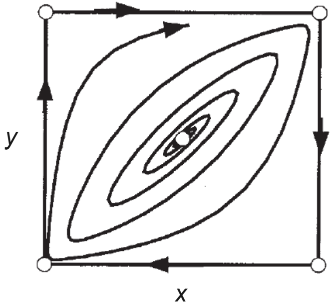
Two-dimensional non-linear systems

In general, analyzing the non-equilibrium behavior of non-linear systems is difficult. However, two-dimensional continuous-time systems have a somewhat limited repertoire. According to the **Poincaré-Bendixon theorem**, such a system will do one of the following:

- Approach an equilibrium,
- Increase without bounds,
- Perform a stable limit cycle,
- Approach a heteroclinic cycle (or cycle graph) of connected saddle points (see below).

In particular, chaos is not possible, as it requires at least 3 interacting variables.

Heteroclinic cycles



- A heteroclinic cycle connects saddle points.
- An example is a system where both variables oscillate between a maximal and a minimal value.
- While approaching such a cycle, the system gets slower and slower and stays longer and longer near the saddles.

Just for the sake of exactness . . .

- The Poincaré-Bendixon theorem only applies to homogeneous systems of the form $dx/dt = f(x, y), dy/dt = g(x, y)$.
- It does not apply to inhomogeneous systems, in which the right-hand side of the differential equations depend themselves on time, nor to systems with a time delay.
- There is no comparable result for discrete-time systems, and even a single difference equation can produce chaos.

Bifurcations

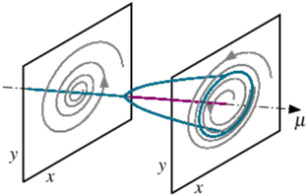
A bifurcation point is a point in parameter space where the behavior of a dynamical system changes qualitatively, e.g.

- An equilibrium changes stability
- An equilibrium appears or disappears
- A non-equilibrium attractor appears or disappears

There are many different types of bifurcations. In our model, the stable limit cycle arises via a **Hopf bifurcation** at $\gamma = 0$.

The Hopf bifurcation

At a Hopf bifurcation, a stable limit cycle is born while an equilibrium loses stability.



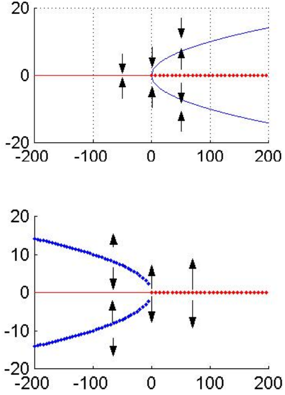
This is the case if

- The dominant eigenvalue is complex.
- The real part of the dominant eigenvalue changes from negative to positive (with a non-zero slope).

An additional complication

There are two kinds of Hopf bifurcation:

- In a **supercritical** Hopf bifurcation, a stable equilibirum is replaced by a stable limit cycle (around an unstable equilibrium).
- In a **subcritical** hopf bifurcation, an unstable equilibrium is replaced by an unstable limite cycle (around a stable equilibrium.)



Sub- or supercritical?

- A Hopf bifurcation is supercritical if the equilibrium is stable at the bifurcation point, and subcritical if the equilibrium is unstable.
- Unfortunately, this cannot be determined by linear stability analysis, because at the bifurcation point, the real part of the dominant eigenvalue is zero and stability is determined by higher-order terms.
- Otto and Day provide a *Mathematica* package on their website to do this calculation.
- If you don't care about a mathematical proof, you can just look at simulations.