

6 “Price equation” and “Selection in quantitative characters”

There are several levels of population description. At the most fundamental level, we describe all genotypes represented in the population. With two alleles at each of L loci, one needs 2^{2L} dynamic variables to describe the population. In some situations (for example if the population is at Hardy-Weinberg proportions), one can use a simpler description based on 2^L gamete frequencies instead of genotype frequencies. Invoking further assumptions (e.g. linkage equilibrium assumption justified by assuming that selection is weak) one can simplify the approach even more by using allele frequencies. This gives only L dynamic variables. Next, we consider the simplest approach for describing populations based on using a single dynamic variable representing the average value of a quantitative character.

6.1 Standard model for a quantitative character

Quantitative traits are phenotypic traits that exhibit continuous variation and are subject to microenvironmental effects. Examples: size, weight etc. Quantitative traits are thought to be controlled by *many* loci with *small* effects.

The standard model for a quantitative character is described by equation

$$z = g + e,$$

where z is the trait value, g is the contribution of genotype (“genotypic value”; the average trait value for a group of organisms with the same genotype), and e is the contribution of microenvironment. First, we will assume that g and e are independent (that is there is no genotype-environment interaction). *Genotypic value* g can be thought of as a sum of contributions from many loci:

$$g = \sum(\alpha_i + \alpha'_i),$$

where α_i and α'_i are the contributions of the i -th locus from paternal and maternal gamete, respectively. The above model implies that the trait is additive. *Microenvironmental deviation* e is usually modeled as a random variable with zero mean and a constant variance:

$$\begin{aligned}\bar{e} &= 0, \\ \text{var}\{e\} &= E.\end{aligned}$$

Population state is described by the *genotypic distribution*, $p(g)$, of g in the population. One can also define the moments: the mean value, \bar{g} , variance, G , etc.:

$$\begin{aligned}\bar{g} &= \int gp(g)dg, \\ G &= \int (g - \bar{g})^2 p(g)dg.\end{aligned}$$

Phenotypic distribution, $p(z)$, has the mean, \bar{z} , and the phenotypic variance, P :

$$\begin{aligned}\bar{z} &= \bar{g}, \\ P &\equiv \text{var}\{z\} = G + E.\end{aligned}$$

6.2 Types of viability selection

In major locus models that we studied before fitness was usually assigned to genotype, e.g. w_{AA} is fitness of genotype **AA** (genotype \Rightarrow fitness). With quantitative traits fitness depends on phenotype which in turn is controlled by genotype and environment (genotype + environment \Rightarrow phenotype \Rightarrow fitness).

Examples of phenotypic fitness function, $w = w(z)$.

Directional selection:

$$w = a + bz \text{ or } w = e^{az}.$$

Here, fitness function monotonically increases (or decreases) with z .

Stabilizing selection:

$$w = 1 - sx^2 \text{ or } w = e^{-az^2}.$$

Here, fitness reaches a maximum at an intermediate value of z .

Disruptive selection:

$$w = e^{-a(z-1)^2} + e^{-a(z+1)^2}.$$

Here, fitness increases with deviation from an intermediate value of z .

The mean fitness of the population is defined as

$$\bar{w} = \int w(z)p(z)dz = \int w(g)p(g)dg,$$

where the (induced) genotypic fitness is

$$w(g) = \int w(g+e)p(e)de.$$

6.3 Robertson-Price formula

If $p(z)$ is the phenotypic distribution before selection, then the phenotypic distribution after selection is

$$p_s(z) = \frac{w(z)}{\bar{w}}p(z).$$

Let $\psi = \psi(z)$ be a function of z . The mean value of ψ before selection is

$$\bar{\psi} = \int \psi(z)p(z)dz.$$

After selection

$$\bar{\psi}_s = \int \psi(z)p_s(z)dz = \int \psi(z)\frac{p(z)w(z)}{\bar{w}}dz.$$

The change in $\bar{\psi}$ as a result of selection is

$$\Delta\bar{\psi} \equiv \bar{\psi}_s - \bar{\psi} = \int \psi(z)\frac{p(z)w(z)}{\bar{w}}dz - \bar{\psi} = \frac{\int [\psi(z)w(z)]p(z)dz - \bar{\psi}\bar{w}}{\bar{w}} = \frac{\bar{\psi}w - \bar{\psi}\bar{w}}{\bar{w}}.$$

Thus,

$$\Delta\bar{\psi} = \frac{cov(\psi, w)}{\bar{w}}, \tag{51}$$

where $cov(a, b)$ is the covariance of a and b . This is the Robertson-Price formula. Note that no specific assumptions about the distributions and selection regimes have been made so far.

For example, if $\psi = z$, then

$$\Delta\bar{z} = \frac{cov(z, w)}{\bar{w}}. \tag{52}$$

If $\psi = z^2$, then

$$\Delta\bar{z}^2 = \frac{cov(z^2, w)}{\bar{w}}. \tag{53}$$

The Robertson-Price formula predicts the change in a specific population characteristic as a result of within-generation selection. Under some additional assumptions it can be used to describe the changes between generations. For example, if the trait z is additive, then recombination and segregation will not change its mean value. Thus, equation (52) describes the change in the mean trait value between two subsequent generations.

Homework: Assume that the distribution of z before selection has mean \bar{z} , variance P and third moment μ_3 ($\mu_3 \equiv \int (z - \bar{z})^3 p(z) dz$). Find $\Delta \bar{z}$ for linear and quadratic fitness functions ($w_{lin} = a + bz, w_{quad} = 1 - sz^2$).

6.4 Lande formula: normal approximation

Let us assume that both the distribution of g and the distribution of e are Gaussian:

$$p(g) = \frac{1}{\sqrt{2\pi G}} \exp\left(-\frac{(g - \bar{g})^2}{2G}\right),$$

$$p(e) = \frac{1}{\sqrt{2\pi E}} \exp\left(-\frac{e^2}{2E}\right).$$

The distribution of z will be normal as well:

$$p(z) = \frac{1}{\sqrt{2\pi P}} \exp\left(-\frac{(z - \bar{z})^2}{2P}\right),$$

where $P = G + E, \bar{z} = \bar{g}$. Differentiating \bar{w} with respect to \bar{g}

$$\begin{aligned} \frac{\partial \bar{w}}{\partial \bar{g}} &= \int w(g) \frac{\partial p(g)}{\partial \bar{g}} dg = \int w(g) \frac{g - \bar{g}}{G} p(g) dg \\ &= \frac{1}{G} \left[\int w(g) g p(g) dg - \bar{g} \int w(g) p(g) dg \right]. \end{aligned}$$

Thus,

$$\frac{1}{\bar{w}} \frac{\partial \bar{w}}{\partial \bar{g}} = \frac{1}{G} \left[\int g \frac{w(g) p(g)}{\bar{w}} dg - \bar{g} \right] = \frac{1}{G} (\bar{g}_s - \bar{g}) = \frac{1}{G} R, \quad (54)$$

where $R \equiv \bar{g}_s - \bar{g}$ is *selection response*.

In a similar way, differentiating \bar{w} with respect to \bar{z}

$$\begin{aligned} \frac{\partial \bar{w}}{\partial \bar{z}} &= \int w(z) \frac{\partial p(z)}{\partial \bar{z}} dz = \int w(z) \frac{z - \bar{z}}{P} p(z) dz \\ &= \frac{1}{P} \left[\int w(z) z p(z) dz - \bar{z} \int w(z) p(z) dz \right]. \end{aligned}$$

Thus,

$$\frac{1}{\bar{w}} \frac{\partial \bar{w}}{\partial \bar{z}} = \frac{1}{P} \left[\int z \frac{w(z) p(z)}{\bar{w}} dz - \bar{z} \right] = \frac{1}{P} (\bar{z}_s - \bar{z}) = \frac{1}{P} S, \quad (55)$$

where $S \equiv \bar{z}_s - \bar{z}$ is *selection differential*.

Combining (54) and (55),

$$R = \frac{G}{P} S = h^2 S, \quad (56)$$

where

$$h^2 = \frac{G}{G + E}$$

is *heritability* (in the broad sense). Heritability characterizes the proportion of heritable genetic variation in the overall phenotypic variation. Equation (56) is known as the breeders' equation. It shows that selection response equals heritability times selection differential.

From (54),

$$R = G \frac{\partial \ln \bar{w}}{\partial \bar{g}} \quad (57)$$

For an additive trait, segregation and recombination do not change the mean trait value ($\bar{g}' = \bar{g}_s$, $R = \Delta \bar{g} \equiv \bar{g}' - \bar{g}$). Thus, the change in \bar{g} between generations

$$\Delta \bar{g} = G \frac{\partial \ln \bar{w}}{\partial \bar{g}} \quad (58)$$

(Lande, 1976). If genotypic variance G does not change, one can use (58) for predicting the long-term dynamics. Because $\bar{z} = \bar{g}$ and $\partial \ln \bar{w} / \partial \bar{g} = \partial \ln \bar{w} / \partial \bar{z}$, one can also write

$$\Delta \bar{z} = G \frac{\partial \ln \bar{w}}{\partial \bar{z}}. \quad (59)$$

Implications: gradient-type dynamics (evolution towards an equilibrium, no cycles, no chaos, average fitness is maximized).

6.5 Lande formula: multivariate case

Let there be n phenotypic traits:

$$z_i = g_i + e_i, \quad i = 1, \dots, n.$$

Assume that the distribution of the genotypic values g_i is multivariate normal with the mean $\bar{g} = (\bar{g}_1, \dots, \bar{g}_n)^T$ and a $n \times n$ covariance vector G . Then the change in \bar{g} in one generation is

$$\Delta \bar{g} = G \frac{\partial \ln \bar{w}}{\partial \bar{g}},$$

where the vector of selection gradients $\frac{\partial \ln \bar{w}}{\partial \bar{g}} = (\frac{\partial \ln \bar{w}}{\partial \bar{g}_1}, \dots, \frac{\partial \ln \bar{w}}{\partial \bar{g}_n})^T$ (Lande, 1979).

For example in the case of two traits x and y

$$\begin{pmatrix} \Delta \bar{x} \\ \Delta \bar{y} \end{pmatrix} = \begin{pmatrix} G_x & C \\ C & G_y \end{pmatrix} \begin{pmatrix} \frac{\partial \ln \bar{w}}{\partial \bar{x}} \\ \frac{\partial \ln \bar{w}}{\partial \bar{y}} \end{pmatrix}, \quad (60)$$

where G_x and G_y are genotypic variances, and C is covariance of x and y . Note that even if a trait, say y , does not affect fitness ($\partial \ln \bar{w} / \partial \bar{y} = 0$), it will change if $C \neq 0$ (correlated response to selection).

6.6 Lande formula: weak selection approximation

The assumption that all relevant distributions stay normal is not easy to justify. Also, the mean fitness of the population can be found easily only in some special cases. Here, we consider an alternative method of the derivation of equations analogous to (58) based on less restrictive assumptions.

We start with the Robertson-Price formula

$$\Delta \bar{g} = \frac{\text{cov}(g, w)}{\bar{w}}. \quad (61)$$

Expanding $w = w(g)$ in a Taylor series at $g = \bar{g}$, one gets

$$w(g) = w(\bar{g}) + \frac{dw}{dg}(g - \bar{g}) + \frac{1}{2} \frac{d^2w}{dg^2}(g - \bar{g})^2 + \dots \quad (62)$$

Using the covariance properties, we find that

$$\begin{aligned} \text{cov}(g, w(g)) &= \text{cov}(g - \bar{g}, w(g)) \\ &= \text{cov}(g - \bar{g}, w(\bar{g}) + \frac{dw}{dg}(g - \bar{g}) + \frac{1}{2} \frac{d^2w}{dg^2}(g - \bar{g})^2 + \dots) \\ &= 0 + \frac{dw}{dg} \text{cov}(g - \bar{g}, g - \bar{g}) + \frac{1}{2} \frac{d^2w}{dg^2} \text{cov}(g - \bar{g}, (g - \bar{g})^2) + \dots \\ &= G \frac{dw}{dg} + \frac{1}{2} \frac{d^2w}{dg^2} \mu_3 + \dots, \end{aligned}$$

where $\mu_3 = \int (g - \bar{g})^3 p(g) dg$ is the third moment of the distribution of g (which measures asymmetry of $p(g)$) and all derivatives are evaluated at $g = \bar{g}$.

Computing the expectation of both sides of (62), one can see that

$$\begin{aligned} \bar{w} &= w(\bar{g}) + \frac{dw}{dg} \overline{(g - \bar{g})} + \frac{1}{2} \frac{d^2w}{dg^2} \overline{(g - \bar{g})^2} + \dots \\ &= w(\bar{g}) + \frac{1}{2} G \frac{d^2w}{dg^2} + \dots \end{aligned}$$

Thus,

$$\Delta \bar{g} = \frac{G \frac{dw}{dg} + \frac{1}{2} \frac{d^2w}{dg^2} \mu_3 + \dots}{w(\bar{g}) + \frac{1}{2} G \frac{d^2w}{dg^2} + \dots}$$

which can be approximated by

$$\Delta \bar{g} = G \frac{d \ln w}{dg}, \quad (63)$$

where the derivative is evaluated at $g = \bar{g}$. Note that to apply (63) one needs to know the derivative of the individual fitness rather than the mean fitness of the population. The approximation is good is

$$G \frac{d^2w}{dg^2} \ll w(\bar{g}), \quad \mu_3 \frac{d^2w}{dg^2} \ll G \frac{dw}{dg}.$$

The former condition is satisfied if differences between fitnesses are small (weak selection). The latter condition is satisfied if differences between selection gradients, dw/dg , are small (weak non-linearity in selection; if $w(g)$ is linear, all derivatives higher than first will be zero). Note that equation (63) can be used even if individual fitness depends on the state of the population (that is with frequency dependent fitness, e.g. $w = w(z, \bar{z})$).

6.7 Coevolution in an exploiter-victim system

Consider a system of two coevolving species, X and Y . Species X , the “victim”, suffers from (possibly indirect) interactions with species Y , while species Y , the “exploiter”, benefits from these interactions. Assume that, within each species, individuals differ from one another with respect to an additive polygenic character, x in species X and y in species Y . Characters x and y are under direct (stabilizing) natural selection and also determine the strength of within and between species interactions. These interactions will be incorporated in the model by assuming that fitnesses of individuals with phenotype x in species X , $W_x(x, p_y)$, and phenotype y in species Y , $W_y(y, p_x)$, depend on the phenotypic distributions p_x and p_y , *i.e.*, fitnesses are frequency-dependent.

The changes in the mean values between generations can be approximated by equations

$$\Delta \bar{x} = G_x \frac{\partial \ln W_x(x, p_y)}{\partial x}, \quad (64a)$$

$$\Delta \bar{y} = G_y \frac{\partial \ln W_y(y, p_x)}{\partial y}, \quad (64b)$$

where G_x and G_y are the corresponding additive genetic variances and the partial derivatives are evaluated at $x = \bar{x}$, $y = \bar{y}$.

Assume that two types of selection (stabilizing natural selection and selection arising from interactions between species) operate independently throughout the life span of individuals. This allows one to express the overall fitness as a product of two fitness components:

$$W_x(x, p_y) = W_{x,stab}(x) \cdot W_{xy,int}(x, p_y), \quad (65a)$$

$$W_y(y, p_x) = W_{y,stab}(y) \cdot W_{yx,int}(y, p_x), \quad (65b)$$

where, for example, $W_{x,stab}$ and $W_{xy,int}$ describe direct stabilizing selection and selection on x arising from between species interactions. Fitness consequences of direct interactions between individuals can be described in the following way. First, one introduces a function $\alpha_{ij}(u, v)$ measuring a fitness component for an individual of species i with phenotype u interacting with an individual of species j with phenotype v . To find the fitness component of phenotype u , one then integrates $\alpha_{ij}(u, v)$ over the phenotypic distribution of species j . For example, the fitness component of phenotype x in species X resulting from interactions with species Y is

$$W_{xy,int}(x, p_y) = \int \alpha_{xy}(x, y) p_y(y) dy$$

for an appropriate function α_{xy} . If selection is weak, the integral is approximately $\alpha_{xy}(x, \bar{y})$ (because $\alpha_{xy}(x, y) \approx \alpha_{xy}(x, \bar{y}) + \alpha'_{xy}(x, y)(y - \bar{y}) \approx \alpha_{xy}(x, \bar{y})$). We will use a Gaussian form for α 's leading to

$$W_{xy,int}(x, p_y) = \alpha_{xy}(x, \bar{y}) = \exp[\beta_x(x - \bar{y})^2], \quad (66a)$$

$$W_{yx,int}(y, p_x) = \alpha_{yx}(y, \bar{x}) = \exp[-\beta_y(y - \bar{x})^2]. \quad (66b)$$

Here $\beta_x > 0$ and $\beta_y > 0$ characterize the victim's loss and the exploiter's gain resulting from between species interactions. If species X and Y are a prey and its predator, or a host and its parasite, then x and y can be considered as describing individual size or some other quantitative character. Equation (66) implies that for each predator (or parasite) there is an optimum prey (or host) size (or some other quantitative character). If species X and Y represent a Batesian model-mimic pair, then x and y can be considered as describing coloration patterns. Equation (66) implies that a model loses the least when it is “different” from the modal phenotype of the mimic species, while a mimic gains the most when it is “similar” to the modal phenotype of the model species.

In analyzing the model dynamics we will make the standard assumption that additive genetic variances G_x and G_y are constant (for example, maintained by a balance between mutation and selection). This is also implied by the weak selection approximation. It is useful to start with a model where stabilizing selection is absent.

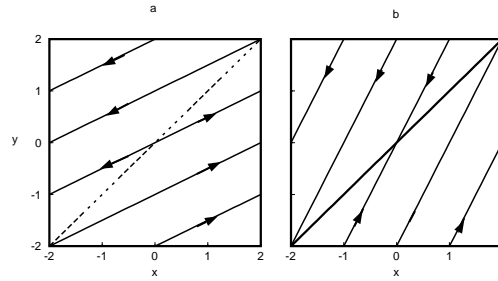


Figure 5: **The phase-plane dynamics with no stabilizing selection. (a) $R < 1$ (the line of equilibria $\bar{y} = \bar{x}$ is unstable). (b) $R > 1$ (the line of equilibria $\bar{y} = \bar{x}$ is stable).**

6.7.1 No stabilizing selection

Let us first assume that stabilizing selection is absent ($W_{x,stab} = W_{y,stab} = const$). To derive the dynamic equations below, we approximate the difference equations (64) by the corresponding differential equations and re-scale time to $\tau = 2\beta_x G_x t$. The dynamics of coevolution are described by

$$\dot{\bar{x}} = \bar{x} - \bar{y}, \tag{67a}$$

$$\dot{\bar{y}} = R(\bar{x} - \bar{y}), \tag{67b}$$

where $R = (\beta_y/\beta_x)(G_y/G_x)$.

The straight line $\bar{x} = \bar{y}$ represents a line of equilibria. This line is stable if $R > 1$ and is unstable if $R < 1$ (see Fig. 5). Species X wins (*i.e.*, escapes and increases its “distance” from Y as time goes on) if its loss from interactions is bigger than species Y ’s gain ($\beta_x > \beta_y$) and/or its genetic variance is larger than that of Y ($G_x > G_y$). Otherwise, species Y wins and the mean values for both species coincide after some transient time. One can say that in this model a species with a stronger incentive and/or ability to win wins.

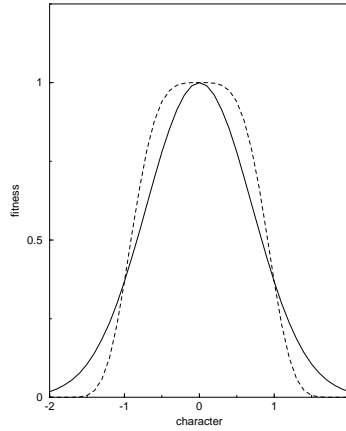


Figure 6: **Comparison of Gaussian fitness function (solid line) and quartic exponential fitness function (dashed line) for $s = 1, x_0 = 0$.**

6.7.2 Gaussian stabilizing selection

A standard choice of a fitness function describing stabilizing selection is Gaussian:

$$W_{x,stab} = \exp[-s_x(x - x_0)^2],$$

$$W_{y,stab} = \exp[-s_y(y - y_0)^2],$$

where x_0 and y_0 are “optimum” trait values, and s_x and s_y are parameters characterizing the strength of stabilizing selection. Introducing new variables $u = \bar{x} - x_0, v = \bar{y} - y_0$, the dynamics are described by

$$\dot{u} = -e_x u + u - v + d, \tag{68a}$$

$$\dot{v} = R(-e_y v + u - v + d), \tag{68b}$$

where dimensionless parameters $e_x = s_x/\beta_x, e_y = s_y/\beta_y$ characterize the strength of stabilizing selection relative to selection arising from between-species interactions, and $d = x_0 - y_0$ is the difference of the optimum values.

Because this is a linear system, its dynamics are clear.

Homework: interpret the dynamical regimes of (68) in biological terms.

6.7.3 “Quartic exponential” stabilizing selection

Stabilizing selection refers to situations when fitness decreases with deviation from some “optimum” value. There are different ways to choose a specific functional form of a fitness function describing stabilizing selection. Although a Gaussian function is a popular choice, it is used primary because of its mathematical convenience. Here, we will use an exponential function of fourth order polynomials

$$W_{x,stab} = \exp[-s_x(x - x_0)^4], \tag{69a}$$

$$W_{y,stab} = \exp[-s_y(y - y_0)^4]. \tag{69b}$$

Stabilizing selection described by (69) is weaker than Gaussian selection near the optimum phenotype but becomes stronger beyond a certain value (see Fig.6). With stabilizing selection as specified in equation (69), the dynamic

equations for the deviations of the mean values from x_0 and y_0 are

$$\dot{u} = -2e_x u^3 + u - v + d, \tag{70a}$$

$$\dot{v} = R(-2e_y v^3 + u - v + d), \tag{70b}$$

where parameters e_x , e_y , R and d are defined by the same formulae as above.

Homework: Find the conditions for existence and stability of equilibria of system (70) assuming that $d = 0$. Represent these conditions using a two-dimensional parameter space (k, R) with $k = (e_x/e_y)^{1/3}$. (*Hint:* see Fig.7.) Use *Maple* (or your favorite software) to draw trajectories of (70) corresponding to different dynamical patterns. Interpret the conditions for cycling in biological terms.

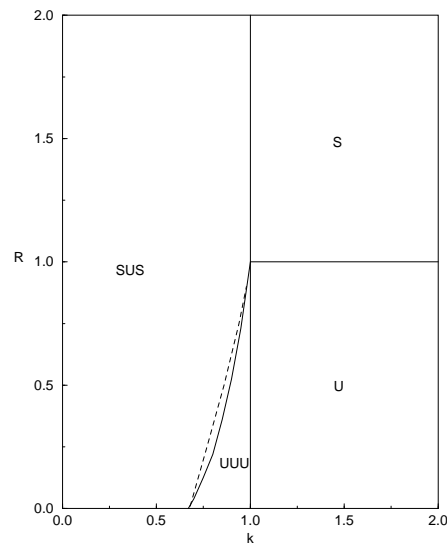


Figure 7: Areas in parameter space (k, R) corresponding to different patterns of existence and stability of equilibria in (70).

6.8 Sexual selection

In many species, females prefer mates with extreme characters that are apparently useless or deleterious for survival, such as bright colors, elaborate ornaments and conspicuous songs. Sexual selection was proposed by Darwin to explain the evolution of such traits. The distinction between natural and sexual selection is that the former arises from differences in individual *survival* and/or *fecundity* whereas the latter arises from differences in *mating success*. Two types of sexual selection are emphasized: intra-sexual selection (competition among individuals of the same sex for access to the other sex) and inter-sexual selection (choice of individuals of one sex by the other).

6.8.1 Lande's model (1981, Proc. Natl. Acad. Sci. USA 78: 3721-3725)

We consider two trait: a trait, y , expressed in males only (e.g., plumage in birds) and a trait, x , expressed in females only (preference for y). We assume that there are two components of male fitness:

$$w = w_{stab} w_{sex},$$

coming from stabilizing selection that acts directly on the trait, $w_{stab} = \exp[-s(y - \theta)^2]$ and from sexual selection, w_{sex} , which is defined below. We assume that there is no direct selection in females. However, females will evolve as a result of correlated selection.

We define a preference function $\psi(y|x)$ as the probability that male y is chosen by female x . There are several possibilities for choosing a specific function $\psi(y|x)$:

$$\begin{aligned} \text{"open - ended preference"} : \psi(y|x) &= \exp(\alpha xy) \\ \text{"absolute preference"} : \psi(y|x) &= \exp[-\alpha(y - x)^2] \\ \text{"relative preference"} : \psi(y|x) &= \exp[-\alpha(y - (\bar{y} + x))^2] \end{aligned}$$

The fitness component w_{sex} is defined as as the probability to be chosen:

$$w_{sex} = \int \psi(y|x)p(x)dx = \begin{cases} \exp[\alpha y \bar{x}] \\ \exp[-\alpha(y - \bar{x})^2] \\ \exp[-\alpha(y - \bar{y} - \bar{x})^2] \end{cases},$$

where $p(x)$ is the distribution of x in females.

The corresponding *selection gradients* are

$$\frac{\partial \ln w_{sex}}{\partial y} \Big|_{y=\bar{y}} = \begin{cases} \alpha \bar{x} \\ -2\alpha(\bar{y} - \bar{x}) \\ 2\alpha \bar{x} \end{cases}$$

and can be represented as $\alpha'(\bar{x} - \epsilon\bar{y})$, where $\epsilon = 0$ or 1 and $\alpha' = \alpha$ or $2\alpha'$. Thus, the overall selection gradient is

$$\frac{\partial \ln w_{sex}}{\partial y} \Big|_{y=\bar{y}} = -s(\bar{y} - \theta) + \alpha'(\bar{x} - \epsilon\bar{y}),$$

where the first term is coming from stabilizing natural selection. The change in \bar{y} in one generation is $\Delta\bar{y} = G_y \partial \ln w_{sex} / \partial y \Big|_{y=\bar{y}}$, where G_y is the variance of y in males. The correlated change in \bar{y} in one generation is $\Delta\bar{x} = C \partial \ln w_{sex} / \partial y \Big|_{y=\bar{y}}$, where C is covariance of x and y (coming from pleiotropy and/or linkage disequilibrium; see equation 60). Using the differential approximation, the dynamic equations become

$$\begin{aligned} \dot{\bar{x}} &= C[-s(\bar{y} - \theta) + \alpha'(\bar{x} - \epsilon\bar{y})], \\ \dot{\bar{y}} &= G_y[-s(\bar{y} - \theta) + \alpha'(\bar{x} - \epsilon\bar{y})]. \end{aligned}$$

Re-scaling time to $\tau = tG_y\alpha'$, these equations can be rewritten as

$$\dot{\bar{x}} = r[\bar{x} - (\epsilon + \frac{s}{\alpha'})\bar{y} + \frac{s}{\alpha'}\theta], \quad (71a)$$

$$\dot{\bar{y}} = \bar{x} - (\epsilon + \frac{s}{\alpha'})\bar{y} + \frac{s}{\alpha'}\theta. \quad (71b)$$

where $r = C/G_y$.

The analysis of (71) is simple (this is a linear system). There is a line of equilibria

$$\bar{x} = (\epsilon + \frac{s}{\alpha'})\bar{y} - \frac{s}{\alpha'}\theta,$$

which is unstable if $r > \epsilon + \frac{s}{\alpha'}$ and is stable if $r < \epsilon + \frac{s}{\alpha'}$. Thus, there are two different dynamical regimes: runaway evolution towards infinite trait values or evolution towards the line of equilibria. In the first regime, sexual selection drives the evolution of exaggerated male characters. This regime is promoted if stabilizing selection is weaker than sexual selection ($s \ll \alpha'$) or if genetic covariance of male and female traits is large ($r \gg 1$). In the second regime, sexual selection leads to a line of equilibria. This regime is promoted if stabilizing selection is stronger than sexual selection ($s \gg \alpha'$) or if genetic covariance of male and female traits is small ($r \ll 1$). Note that finite populations will diverge along the line of equilibria by random genetic drift.

6.8.2 Sexual conflict

(see the Nature paper)