Selection on Quantitative Traits

A. Fitness and Fisher's fundamental theorem of natural selection

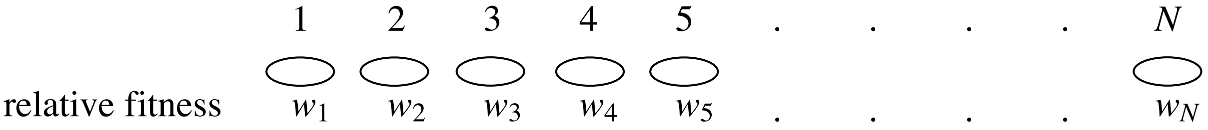
Fitness is a property of an individual, a measure of how well this individual will be represented in the next generation; if we have non-overlapping generations, a measure of fitness is how many zygotes replace the original zygote

- can subdivide any fitness measure into more fitness components, for example, survival and fecundity, or survival between certain life stages and fecundity, etc.

- if survival is our measure of fitness (because we can measure this fitness component) we can let $w = 1$ if an individual survives and $w = 0$ if they do not survive (where w = relative fitness)

Fitness itself is a quantitative character and is polygenic, but it is not generally normally distributed.

Consider N individuals at the zygote stage:



(where relative fitness is the representation of this individual in the next generation)

- mean fitness $$\overline{w} = \frac{1}{N}\sum_i w_i$$

- variance in fitness $$\sigma_w^2 = \frac{1}{N-1}\sum_i \left(w_i - \overline{w}\right)^2$$

- since fitness is a quantitative trait, we can, in principle, calculate the components of the variance

$$\sigma_w^2 = \sigma_{Aw}^2 + \sigma_{Dw}^2 + \sigma_{Iw}^2 + \sigma_{Ew}^2 + \text{covariance terms}$$

Fisher's fundamental theorem of natural selection

The change in mean fitness in one generation can be written:

$$\Delta\overline{w} = \frac{\sigma_{Aw}^2}{\overline{w}}$$

- note that differences in fitness imply selection, since some organisms do "better" than others, and thus leave more offspring

Response to selection

We would like to rewrite the equation for the response to selection ($R = h^2S$) so that it applies to natural populations.

Consider a population with a large number (N) of individuals. Let the fitness of an individual, w_i, equal 1 if the individual survives and 0 if it dies.

N_s = number of survivors
$N - N_s$ = number of individuals that die

$$\overline{w} = \frac{1}{N}\sum_i w_i = \frac{1}{N}\left(N_s(1) + (N - N_s)(0)\right)$$
$$= \frac{N_s}{N}$$

- the mean fitness is the proportion of survivors

- we have some phenotypic trait, x, which we can measure in these organisms

$$\bar{x} = \frac{1}{N}\sum_i x_i \qquad \sigma_x^2 = \frac{1}{N-1}\sum_i \left(x_i - \bar{x}\right)^2$$

and $S = \bar{x}_s - \bar{x}$, where $\bar{x}_s$ is the mean of the phenotypic trait in the individuals that survive. Then,

$$\bar{x}_s = \frac{1}{N_s}\sum_{j=1}^{N_s} x_j$$ where the x_j are the survivors, and there are N_s of them.

- we can re-write the equation for the mean of the trait in the survivors by weighting all of the x_i by 1 if they survive and 0 if they do not

$$\bar{x}_s = \frac{1}{N_s}\sum_{i=1}^{N} x_i w_i = \frac{1}{\bar{w}\,N}\sum_{i=1}^{N} x_i w_i \qquad \text{since } \bar{w} = \frac{N_s}{N},\ N_s = \bar{w}N$$

- this lets us write S as:

$$\bar{x}_s - \bar{x} = \frac{1}{\bar{w}\,N}\sum_i x_i w_i - \bar{x} = \frac{1}{\bar{w}\,N}\sum_i x_i w_i - \frac{1}{\bar{w}}\bar{x}\bar{w}$$

$$= \frac{\frac{1}{N}\sum_i x_i w_i - \bar{x}\bar{w}}{\bar{w}}$$

- for N large, the numerator is Cov(x,w)

$$Cov(x,w) = \frac{1}{N-1}\sum_i (x_i - \bar{x})(w_i - \bar{w})$$

$$\left(\text{if N is large, } \frac{1}{N-1} \approx \frac{1}{N}\right)$$

$$\approx \frac{1}{N}\sum_i (x_i - \bar{x})(w_i - \bar{w}) = \frac{1}{N}\sum_i \left[x_i w_i - x_i\bar{w} - \bar{x}w_i + \bar{x}\bar{w}\right]$$

$$= \frac{1}{N}\sum_i x_i w_i - \frac{1}{N}\sum_i x_i\bar{w} - \frac{1}{N}\sum_i \bar{x}w_i + \frac{1}{N}\sum_i \bar{x}\bar{w}$$

$$= \frac{1}{N}\sum_i x_i w_i - \bar{w}\frac{1}{N}\sum_i x_i - \bar{x}\frac{1}{N}\sum_i w_i + \frac{N\bar{x}\bar{w}}{N} = \frac{1}{N}\sum_i x_i w_i - \bar{w}\bar{x} - \bar{x}\bar{w} + \bar{x}\bar{w}$$

$$= \frac{1}{N}\sum_i x_i w_i - \bar{x}\bar{w}$$

$$S = \bar{x}_s - \bar{x} = \frac{Cov(x,w)}{\bar{w}} \quad \left(\text{or } S = Cov\left(x, \frac{w}{\bar{w}}\right)\right)$$

- we can then write the equation for the response to selection as:

$$R = h^2 S = \frac{\sigma_{Ax}^2}{\sigma_x^2} \frac{Cov(x,w)}{\overline{w}}$$

- the right part of this equation can be separated as follows:

$$\sigma_{Ax}^2 \quad \text{and} \quad \frac{Cov\left(x, \frac{w}{\overline{w}}\right)}{\sigma_x^2} = \beta_x$$

where β_x is the regression coefficient of fitness on the phenotypic character (when fitness is scaled by mean fitness)

and σ_{Ax}^2 is the additive component of genetic variance for the phenotypic trait, x

$$\boxed{R = \sigma_{Ax}^2 \beta_x}$$

if the trait is fitness itself:

$$R = \Delta\overline{w} = \sigma_{Aw}^2 \beta_w = \sigma_{Aw}^2 \frac{Cov\left(w, \frac{w}{\overline{w}}\right)}{\sigma_w^2}$$

$$= \sigma_{Aw}^2 \frac{\frac{1}{\overline{w}} Cov(w,w)}{\sigma_w^2} = \sigma_{Aw}^2 \frac{1}{\overline{w}} \frac{\sigma_w^2}{\sigma_w^2}$$

$$\Delta\overline{w} = \frac{\sigma_{Aw}^2}{\overline{w}}$$

(which is Fisher's theorem)

In-class Activities: Lecture #4 - Part A

Exercise 1

A big windstorm occurred and blew some sparrows against your building. Some of the sparrows were killed and some were just stunned. You realized that this is an excellent opportunity to study an episode of natural selection. You collected a sample of birds and measured their wings. Measurements are in centimeters.

survived	died
10.2	9.1
11.3	10.5
9.8	9.2
10.4	10.5
11.1	9.6
10.8	10.0
11.2	
10.9	

(a) Calculate the mean and variance in fitness in this episode of selection.
(b) Calculate β, the regression of fitness on the phenotypic trait.

C. Correlated Response to Selection

It is important to distinguish between phenotypic covariance and additive genetic covariance when trying to understand the evolution of correlated characters. It is the additive genetic covariance that determines how the characters evolve.

Phenotypic covariance

We have 2 quantitative traits, x and y, measured in the same group of organisms:

ind. #	x	y
1	x_1	y_1
2	x_2	y_2
$\vdots$	$\vdots$	$\vdots$
n	x_n	y_n

- we can calculate the means and variances of these two traits separately

$$\bar{x} = \frac{1}{n}\sum_i x_i; \qquad \sigma_x^2 = \frac{1}{n-1}\sum_i (x_i - \bar{x})^2$$

$$\bar{y} = \frac{1}{n}\sum_i y_i; \qquad \sigma_y^2 = \frac{1}{n-1}\sum_i (y_i - \bar{y})^2$$

- we can also measure the phenotypic covariance between these two characters

$$\sigma_{Pxy} = Cov_P(x, y) = \frac{1}{n}\sum_i (x_i - \bar{x})(y_i - \bar{y})$$

- this would summarize the relationship between the characters in this sample (or population); can also calculate the phenotypic correlation coefficient

$$r_P = \frac{Cov_P(x, y)}{\sigma_x \sigma_y}$$

$$-1 \leq r_P \leq 1$$

Note: if *x* is height in meters (*m*) and *y* is weight in kilograms (*kg*), then $Cov_P(x,y)$ has units of *m·kg* and r_P is unitless; you can change the covariance by changing the units you measure the characters in, but you wouldn't change the correlation coefficient.

- if r_P differs from 0, the two characters are phenotypically correlated

Additive genetic covariance

If you apply directional selection to one of the characters, the *additive genetic covariance* between them will determine how the other character will respond.

- if you select on character *x*, get the following direct response to selection:

$$R_x = h_x^2 S_x = \frac{\sigma_{Ax}^2}{\sigma_x^2} S_x$$

- the correlated response in *y* will be:

$$CR_y = \frac{Cov_A(x, y)}{\sigma_{Ax}^2} R_x$$

$$= \frac{Cov_A(x, y)}{\sigma_{Ax}^2} \frac{\sigma_{Ax}^2}{\sigma_x^2} S_x$$

$$= \frac{Cov_A(x, y)}{\sigma_x^2} S_x$$

this is the correlated response to selection or the indirect response

- similarly, with direct selection on *y*, the direct response in *y*:

$$R_y = h_y^2 S_y = \frac{\sigma_{Ay}^2}{\sigma_y^2} S_y$$

and the correlated response in *x* will be:

$$CR_x = \frac{Cov_A(x,y)}{\sigma_{Ay}^2} R_y$$

$$= \frac{Cov_A(x,y)}{\sigma_{Ay}^2} \frac{\sigma_{Ay}^2}{\sigma_y^2} S_y$$

$$= \frac{Cov_A(x,y)}{\sigma_y^2} S_y$$

We can also define an additive genetic correlation coefficient:

$$r_A = \frac{Cov_A(x,y)}{\sigma_{Ax}\sigma_{Ay}}$$

$$-1 \le r_A \le 1$$

In-class Activities: Lecture #4 - Part B

Exercise 1

A herd of diary cattle yields milk with a fat content of 3.4% ± 0.65% (mean ± standard deviation) and protein content of 3.3% ± 0.45%. The heritabilities of these two traits are 0.60 and 0.70, respectively, and the additive genetic correlation is 0.55.

If a selection differential of 0.675 for percent protein is applied for one generation of selection, what percent protein and percent fat is expected to result?

C. Multivariate Selection

Models of quantitative genetics can be straightforwardly extended to more than two characters (Lande 1979, Arnold and Wade 1984).

What happens if we select on several phenotypic character at the same time?

Imagine a group of phenotypic characters $z_1, z_2, z_3, \ldots$ and let $\bar{\mathbf{z}}$ indicate a vector of the means of these phenotypic characters.

In the same way that we can define the phenotypic and additive genetic variances and covariances for 2 traits (x and y), we can define phenotypic and additive genetic variances and covariances for any number of traits. These can be given as matrices.

Example: three phenotypic characters z_1, z_2, z_3.

matrix of phenotypic variances and covariances:

$$\boldsymbol{P} = \begin{pmatrix} \sigma^{\mathbf{2}}_{z_1} & Cov(z_1,z_2) & Cov(z_1,z_3) \\ Cov(z_1,z_2) & \sigma^{\mathbf{2}}_{z_2} & Cov(z_2,z_3) \\ Cov(z_1,z_3) & Cov(z_2,z_3) & \sigma^{\mathbf{2}}_{z_3} \end{pmatrix}$$

matrix of additive genetic variances and covariances:

$$\mathbf{G} = \begin{pmatrix} \sigma^{\mathbf{2}}_{Az_1} & Cov_A(z_1,z_2) & Cov_A(z_1,z_3) \\ Cov_A(z_1,z_2) & \sigma^{\mathbf{2}}_{Az_2} & Cov_A(z_2,z_3) \\ Cov_A(z_1,z_3) & Cov_A(z_2,z_3) & \sigma^{\mathbf{2}}_{Az_3} \end{pmatrix}$$

The correlated response in trait y (from selection on trait x) is:

$$CR_y = \frac{Cov_A(x,y)}{\sigma_x^2} S_x$$

The equivalent equation for the change in mean phenotype of the group of characters $\mathbf{z}$ is:

$$\Delta\bar{\mathbf{z}} = \mathbf{GP^{-1}S} = \mathbf{G}\beta$$

where **G** and **P** are as above, **S** is a vector of the selection differentials for all of the traits, $\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{S}$ is a vector of selection gradients.

For a single character, earlier we found: $\beta_x = \dfrac{Cov\left(x, \dfrac{w}{\overline{w}}\right)}{\sigma_{Px}^2} = \dfrac{S_x}{\sigma_{Px}^2}$

Note that each entry of the vector **S**,

$$s_i = \sum_j \beta_j P_{ij} = \beta_1 P_{i1} + \beta_2 P_{i2} + \cdots + \beta_n P_{in}$$

gives the total selective differential on character i, including the indirect effects of selection on other characters.

- additive genetic covariance keeps the response to selection from being independent
- if **G** were the identity matrix, mean phenotype would follow the path of steepest ascent up the mean fitness surface
- instead, genetic covariance results from a trajectory that departs from the steepest ascent