Selection on multiple characters[1]

Let z_1, z_2, $\ldots$, z_n be the phenotype of each character that we are studying. We'll use $\boldsymbol{z}$ to denote the vector of these characters before selection and $\boldsymbol{z}^*$ to denote the vector after selection. The selection differential, $\boldsymbol{s}$, is also a vector given by

$$\boldsymbol{s} = \boldsymbol{z}^* - \boldsymbol{z} \quad .$$

Suppose $p(\boldsymbol{z})$ is the probability that any individual has phenotype $\boldsymbol{z}$, and let $W(\boldsymbol{z})$ be the fitness (absolute viability) of an individual with phenotype $\boldsymbol{z}$. Then the mean absolute fitness is

$$\bar{W} = \int W(\boldsymbol{z})p(\boldsymbol{z})d\boldsymbol{z} \quad .$$

The relative fitness of phenotype $\boldsymbol{z}$ can be written as

$$w(\boldsymbol{z}) = \frac{W(\boldsymbol{z})}{\bar{W}} \quad .$$

Using relative fitnesses the mean relative fitness, $\bar{w}$, is 1. Now

$$\boldsymbol{z}^* = \int \boldsymbol{z}w(\boldsymbol{z})p(\boldsymbol{z})d\boldsymbol{z} \quad .$$

Recall that $Cov(X, Y) = E(X - \mu_x)(Y - \mu_y) = E(XY) - \mu_x\mu_y$. Consider

$$\begin{aligned} \boldsymbol{s} &= \boldsymbol{z}^* - \boldsymbol{z} \\ &= \int \boldsymbol{z}w(\boldsymbol{z})p(\boldsymbol{z})d\boldsymbol{z} - \bar{\boldsymbol{z}} \\ &= E(w, z) - \bar{w}\bar{\boldsymbol{z}} \quad , \end{aligned}$$

since $\bar{w} = 1$. In short,

$$\boldsymbol{s} = Cov(w, z) \quad .$$

If we assume that all genetic effects are additive, then the phenotype of an individual can be written as

$$\boldsymbol{z} = \boldsymbol{x} + \boldsymbol{e} \quad ,$$

where $\boldsymbol{x}$ is the additive genotype and $\boldsymbol{e}$ is the environmental effect. We'll denote by $\boldsymbol{G}$ the matrix of genetic variances and covariances and by $\boldsymbol{E}$ the matrix of environmental variances and covariances. The matrix of phenotype variances and covariances, $\boldsymbol{P}$, is then given by

$$\boldsymbol{P} = \boldsymbol{G} + \boldsymbol{E} \quad .$$

[1] Based on Lande and Arnold, *Evolution* 27:1210-1226; 1983

Now, if we're willing to assume that the regression of additive genetic effects on phenotype is linear and that the environmental variance is the same for every genotype, then we can predict how phenotypes will change from one generation to the next

$$\boldsymbol{x}^* - \boldsymbol{x} = \boldsymbol{G}\boldsymbol{P}^{-1}(\boldsymbol{z}^* - \boldsymbol{z})$$
$$\bar{\boldsymbol{z}'} - \bar{\boldsymbol{z}} = \boldsymbol{G}\boldsymbol{P}^{-1}(\boldsymbol{z}^* - \boldsymbol{z})$$
$$\Delta\bar{\boldsymbol{z}} = \boldsymbol{G}\boldsymbol{P}^{-1}\boldsymbol{s}$$

But we have already seen that $\boldsymbol{s} = Cov(w, z)$. Thus,

$$\beta = \boldsymbol{P}^{-1}\boldsymbol{s}$$

is a set of partial regression coefficients of relative fitness on the characters, i.e., the dependence of relative fitness on that character alone holding all others constant.
Note:

$$\begin{aligned} s_i &= \sum_{j=1}^{n} \beta_j P_{ij} \\ &= \beta_1 P_{i1} + \cdots + \beta_i P_{ii} + \cdots + \beta_n P_{in} \end{aligned}$$

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

An example: selection in a pentastomid bug

94 individuals collected along shoreline of Lake Michigan in Parker County, Indiana after storm. 39 were alive, 55 dead.

Means

Character	mean before selection	standard deviation
head	0.880	0.034
thorax	2.038	0.049
scutellum	1.526	0.057
wing	2.337	0.043

Correlations

	head	thorax	scutellum	wing
head	1.00	0.72	0.50	0.60
thorax		1.00	0.59	0.71
scutellum			1.00	0.62
wing				1.00

Selection analysis

Character	s	s'	β	β'
head	-0.004	-0.11	-0.7 ± 4.9	-0.03 ± 0.17
thorax	-0.003	-0.06	11.6 ± 3.9**	0.58 ± 0.19**
scutellum	-0.16*	-0.28*	-2.8 ± 2.7	-0.17 ± 0.15
wing	-0.019**	-0.43**	-16.6 ± 4.0**	-0.74 ± 0.18**