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Multivariate Generalization of R = h²s : Lande's equation

In class, we have seen that the expected response of a single quantitative trait to selection is given by the standard equation

$$\mathrm{R} = h^2\mathbf{s} \quad ,$$

where R, the response to selection, is the change in the mean phenotype of the trait from one generation to the next, h^2 is the heritability of the trait, and **s**, the selection differential, is the difference in mean phenotype between the selected individuals and the population before selection.

In this handout I show how to derive the multivariate generalization of this equation--an equation that can be used to predict the change in mean phenotype of a suite of correlated characters. This equation was originally derived by Lande (Evolution 33: 402-416; 1979).

Preliminary definitions and assumptions

We start by defining a vector,

$$\mathbf{z} = (\mathrm{z}_1, \mathrm{z}_2, \mathrm{z}_3, \ldots, \mathrm{z}_n),$$

in which each measurement is the phenotypic value of a different character for a particular individual. The mean value of this vector in the population is then

$$\overline{\mathrm{z}} = (\overline{\mathrm{z}}_1, \overline{\mathrm{z}}_2, \overline{\mathrm{z}}_3, \ldots, \overline{\mathrm{z}}_n) \quad .$$

We will assume that each of these characters is genetically variable, **and that the genetic variation for each character is entirely additive genetic variation.** Then in this situation, one can write, for character i in any individual,

$$\mathrm{z}_i = \mathrm{x}_i + \epsilon_i \quad ,$$

where x_i is the breeding value of character i, and ϵ_i is that character's environmental deviation in that individual. In vector notation,

$$\mathbf{z} = \mathbf{x} + \boldsymbol{\epsilon} \quad .$$

An additional assumption that is made is that the frequency distributions of **x** and ϵ are **multivariate normal.** A single trait, say y, that has a normal distribution has a frequency distribution f that is given by the formula

$$f(\mathrm{y}) = \frac{1}{\sigma\sqrt{2\pi}} \exp^{-\frac{1}{2}\left[\frac{\mathrm{y}-\mu}{\sigma}\right]^2} \quad (1),$$

where μ is the population mean of the trait and σ is its standard deviation. With a complex phenotype, however, we are not dealing with a single trait but with a vector of traits. The analagous frequency distribution for such a vector--say the vector of breeding values--is given by the formula

$$g(\mathbf{x}) = \sqrt{2\pi^{-m}|\mathbf{G}^{-1}|} \quad \exp^{\left[-\frac{1}{2}(\mathbf{x}-\bar{\mathbf{x}})^{\mathrm{T}}\mathbf{G}^{-1}(\mathbf{x}-\bar{\mathbf{x}})\right]} \ ,$$

where **G** is the **additive genetic variance-covariance** matrix. A diagonal element, G_{ii}, of this matrix, is the genetic variance of character *i*, whereas an off-diagonal element, G_{ij}, is the additive genetic covariance between character *i* and character *j*. A slice through this frequency distribution parallel to one of the character axes would give a normal curve described by equation (1) above.

It is also assumed that for each trait, the environmental deviations are normally distributed, and that jointly, the vector of environmental deviations,

$$\boldsymbol{\epsilon} = \mathbf{z} - \mathbf{x} \ ,$$

has a multivariate normal frequency distribution, ξ, given by

$$\xi(\mathbf{z}-\mathbf{x}) = \sqrt{2\pi^{-m}|\mathbf{E}^{-1}|} \quad \exp^{\left[-\frac{1}{2}(\mathbf{z}-\mathbf{x})^{\mathrm{T}}\mathbf{E}^{-1}(\mathbf{z}-\mathbf{x})\right]} \ ,$$

where, **E** is the **variance-covariance matrix of environmental deviations.** A diagonal element, E_{ii}, of this matrix is the variance of the environmental deviations of character *i*, whereas an off-diagonal element, E_{ij}, is the covariance of environmental deviations for characters *i* and *j*. As was true for the distribution of breeding values, a slice through this distribution parallel to one of the character axes would yield a distribution for that trait that is described by Eq. (1).

The frequency distribution of phenotypes is derived as follows. Let $p(\mathbf{z})$ be the frequency with which phenotype **z** occurs in the population. Now, this phenotype can arise in a number of ways. In particular, an individual whose breeding value is **x** and whose environmental deviation is $(\mathbf{z}-\mathbf{x})$ has a phenotype of $\mathbf{x} + (\mathbf{z}-\mathbf{x}) = \mathbf{z}$. The probability of having breeding value **x** is $g(\mathbf{x})$ (defined above), and the probability of having an environmental deviation of $(\mathbf{z}-\mathbf{x})$ is $\xi(\mathbf{x})$ (defined above). The probability of having both together is simply the product of the individual probabilities, is

$$p(\mathbf{z}|\mathbf{x}) = g(\mathbf{x})\, \xi(\mathbf{z} - \mathbf{x}) \ .$$

This is the probability of obtaining phenotype **z** by having a particular breeding value **x**. To get the total probability of an individual having phenotype **z**, one simply sums the above probabilities for all possible breeding values, *i.e*

$$p(\mathbf{z}) = \int g(\mathbf{x})\, \xi(\mathbf{z} - \mathbf{x})\, d\mathbf{x} \ .$$

If one substitutes in the expression for g and ξ above and performs the integration, one gets

$$p(\mathbf{z}) = \sqrt{2\pi^{-m}|\mathbf{P}^{-1}|}\ \exp^{\left[-\frac{1}{2}(\mathbf{z}-\bar{\mathbf{z}})^{T}\mathbf{P}^{-1}(\mathbf{z}-\bar{\mathbf{z}})\right]} \quad ,$$

where $\mathbf{P} = \mathbf{G} + \mathbf{E}$ is the phenotypic variance-covariance matrix, *i.e.* a diagonal element, P_{ii}, of this matrix is the phenotypic variance of character i, and an off-diagonal element, P_{ij}, is the phenotypic covariance of characters i and j.

Derivation of Multivariate Response to Selection

The goal of this section is to derive the following relationship (the Lande equation) between the magnitude of selection and the expected response of a multivariate phenotype to that selection:

$$\Delta\bar{\mathbf{z}} = \mathbf{G}\ \nabla\, ln\ \bar{\mathbf{W}} = \mathbf{G}\,\mathbf{P}^{-1}\mathbf{s} = \mathbf{G}\boldsymbol{\beta} \ .$$

In this equation, $\Delta\bar{\mathbf{z}}$ is the change in the vector of mean phenotypic values from one generation to the next. **G** and **P** are the additive genetic and phenotypic variance-covariance matrices, as defined above, **s** is the vector of selection differentials (*i.e.* s_i is the difference in mean phenotype between selected and unselected individuals for the i^{th} character), and $\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{s}$ is the **selection gradient**. The symbol ∇ is known as the **gradient operator**. For any function f of variables x_1, x_2, ... x_n, the gradient operator is defined as the vector of partial derivatives,

$$\nabla f = \left[\frac{\partial f}{\partial x_1}\ ,\ \frac{\partial f}{\partial x_2}\ , \ldots ,\ \frac{\partial f}{\partial x_n} \right] \ .$$

Note a couple features of the Lande equation:

(1) For a single trait, $\mathbf{G} = V_A$ and $\mathbf{P} = V_P$, so, from the Lande equation

$$\Delta\bar{z} = \frac{V_A}{V_P}\, s \ ,$$

which is the standard formula for the change in the mean of a single character subject to selection. The standard equation $R = h^2 s$ is thus just a special case of the Lande equation.

(2) From the equation, it is evident that

$$\beta = \nabla \, ln \, \bar{\mathbf{W}} = \frac{1}{\bar{\mathbf{W}}} \nabla \bar{\mathbf{W}} \quad .$$

As discussed in class, this means that the selection gradient is proportional to the tangent to the adaptive landscape ($\bar{\mathbf{W}}$), and thus points in the direction of change in $\bar{\mathbf{z}}$ that produces the maximal increase in mean fitness.

The derivation of the Lande equation will be broken down into five steps.

Step 1

To start, note that mean fitness in the population is

$$\bar{\mathbf{W}} = \int p(\mathbf{z}) \, \mathbf{W}(\mathbf{z}) \, dz \qquad (2) .$$

This relationship follows from the definition of a mean.

Our first task is to find an expression for $\nabla \, ln \, \bar{\mathbf{W}}$, in particular to show that

$$\nabla \, ln \, \bar{\mathbf{W}} = \mathbf{P}^{-1}\mathbf{s}.$$

First, we recognize that

$$\nabla \, ln \, \bar{\mathbf{W}} = \frac{1}{\bar{\mathbf{W}}} \nabla \bar{\mathbf{W}} \qquad (2a).$$

This follows from applying the standard result from calculus,

$$\frac{d \, ln \, \mathrm{x}}{dt} = \frac{1}{\mathrm{x}} \frac{d \mathrm{x}}{dt} \quad ,$$

to each element of $\nabla \, ln \, \bar{\mathbf{W}}$.

The next problem is to find an expression for $\nabla \bar{\mathbf{W}}$. From equation (2), we have

$$\nabla \bar{\mathbf{W}} = \nabla \left[\int p(\mathbf{z}) \, \mathbf{W}(\mathbf{z}) \, d\mathbf{z} \right] \quad .$$

Just like in one-variable calculus, the gradient operator, which is essentially a derivative, can be pulled inside the integral sign to give

$$\nabla \bar{\mathbf{W}} = \int \nabla \left[p(\mathbf{z}) \, \mathbf{W}(\mathbf{z}) \, d\mathbf{z} \right] \quad .$$

Now, the gradient operator acts just like a simple derivative. Therefore, one can use the chain rule

(Remember the chain rule-- $\frac{d f(x)g(x)}{dx} = g(x)\frac{d f(x)}{dx} + f(x)\frac{d g(x)}{dx}$

i.e, the derivative of a product of two functions is equal to the product of one function times the derivative of the other, plus the product of the second function times the derivative of the first.) to obtain

$$\nabla \bar{\mathbf{W}} = \int [\nabla p(\mathbf{z})]\, \mathbf{W}(\mathbf{z})\, d\mathbf{z} + \int p(\mathbf{z})[\nabla \mathbf{W}(\mathbf{z})]d\mathbf{z} \qquad (3) .$$

Next note that **W** is not a function of $\bar{\mathbf{z}}$. Fitness is a function of an individual's phenotype, but the fitness of an individual with a particular phenotype does not depend on what the **mean** phenotype is in the population. In other words, we assume here that fitness is not frequency dependent, *i.e.* it does not depend on the relative proportions of different phenotypes in the population. This means that

$$\nabla \mathbf{W}(\mathbf{z}) = 0 \ ,$$

since the gradient operator takes derivatives with respect to the **means** of the characters, *i.e.*

$$\nabla \mathbf{W}(\mathbf{z}) = \left[\frac{\partial}{\partial \bar{z}_1}, \frac{\partial}{\partial \bar{z}_2}, \ldots, \frac{\partial}{\partial \bar{z}_n}\right] \mathbf{W}(\mathbf{z}) = 0 \ .$$

Consequently, equation (3) reduces to

$$\nabla \bar{\mathbf{W}} = \int [\nabla p(\mathbf{z})]\, \mathbf{W}(\mathbf{z})\, d\mathbf{z} \qquad \textbf{(3a).}$$

Step 2

The next step of the derivation is to find an expression for $\nabla\, p(\mathbf{z})$. To do so we use the probability density function for phenotype **z** that we derived before:

$$p(\mathbf{z}) = \sqrt{2\pi^{-m}|\mathbf{P}^{-1}|}\ \exp^{[-\frac{1}{2}(\mathbf{z}-\bar{\mathbf{z}})^{T}\mathbf{P}^{-1}(\mathbf{z}-\bar{\mathbf{z}})]} \qquad (4).$$

We will evaluate $\nabla\, p(\mathbf{z})$ using this expression. First note that equation (4) can be rewritten as

$$p(\mathbf{z}) = C \exp(u) \ ,$$

where

$$C = \sqrt{2\pi^{-m}|\mathbf{P}^{-1}|} \ ,$$

and

$$u = -\tfrac{1}{2}(\mathbf{z}-\bar{\mathbf{z}})^{\mathrm{T}}\mathbf{P}^{-1}(\mathbf{z}-\bar{\mathbf{z}}) \qquad (4).$$

Therefore,

$$\begin{aligned}\nabla p(\mathbf{z}) &= \nabla C \exp(u) \\ &= C \nabla \exp(u)\end{aligned} \qquad (5).$$

(Gradients work just like derivatives--you can pull out a constant from inside the gradient operator.)

Next, we want to evaluate $\nabla \exp(u)$. Applying the standard calculus rule

$$\frac{d\exp(y)}{dx} = \exp(y)\frac{dy}{dx}$$

to each element of the gradient operator, we have

$$\nabla \exp(u) = \exp(u)\,\nabla u = \exp(u)\left[-\tfrac{1}{2}\nabla[(\mathbf{z}-\bar{\mathbf{z}})^{\mathrm{T}}\mathbf{P}^{-1}(\mathbf{z}-(\bar{\mathbf{z}}))]\right]$$

The expression $(\mathbf{z}-\bar{\mathbf{z}})^{\mathrm{T}}\mathbf{P}^{-1}(\mathbf{z}-\bar{\mathbf{z}})$ is a **quadratic form**. In general, a quadratic form is any expression of the type

$$\mathbf{a}^{\mathrm{T}}\mathbf{M}\,\mathbf{a} \ ,$$

where **a** is a vector and **M** is a symmetric matrix. In general, the derivative of a quadratic form is

$$\frac{d[\mathbf{a}^{\mathrm{T}}\mathbf{M}\,\mathbf{a}]}{dx} = 2\,\mathbf{M}\,\mathbf{a}\frac{d\mathbf{a}}{dx}$$

(for proof, see, *e.g.*, N. H. Timm, Multivariate Analysis, Brooks/Cole Publishers, 1975, pp. 96-103). Applying this rule to our quadratic form, we get

$$\nabla[(\mathbf{z}-\bar{\mathbf{z}})^{\mathrm{T}}\mathbf{P}^{-1}(\mathbf{z}-\bar{\mathbf{z}})] = 2\,\mathbf{P}^{-1}(\mathbf{z}-\bar{\mathbf{z}})\ \nabla(\mathbf{z}-\bar{\mathbf{z}}) \qquad (7).$$

Recognizing that $\nabla(\mathbf{z}-\bar{\mathbf{z}}) = \nabla\mathbf{z} - \nabla\bar{\mathbf{z}}$, that $\nabla\bar{\mathbf{z}} = \mathbf{I}$, the identity matrix, and that $\nabla\mathbf{z} = \mathbf{0}$ because **z** is not a function of $\bar{\mathbf{z}}$, the denominator of the gradient operator, (7) simplifies to

$$\nabla[(\mathbf{z}-\bar{\mathbf{z}})^{\mathrm{T}}\mathbf{P}^{-1}(\mathbf{z}-\bar{\mathbf{z}})] = -2\,\mathbf{P}^{-1}(\mathbf{z}-\bar{\mathbf{z}}) \ .$$

Plugging this back into equation (6) then gives

$$\nabla \exp(u) = \exp(u)\, \nabla u = \mathbf{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}})\exp(u) \ .$$

Next, we plug this expression into equation (5), which yields

$$\nabla p(\mathbf{z}) = C[\nabla \exp(u)] = \mathbf{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}})\, C \exp(u)$$

$$= \mathbf{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}})\, p(\mathbf{z}) \qquad (8).$$

Step 3

The next step of the proof is to plug equation (8) into equation (3) and simplify. Replacement gives

$$\nabla \bar{\mathbf{W}} = \int \mathbf{W}(\mathbf{z})\, [\mathrm{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}})]\, p(\mathbf{z})\, d\mathbf{z}$$

$$= \int \mathbf{W}(\mathbf{z})\, [\mathrm{P}^{-1}\mathbf{z}]\, p(\mathbf{z})\, d\mathbf{z} \quad - \quad \int \mathbf{W}(\mathbf{z})\, [\mathbf{P}^{-1}\bar{\mathbf{z}}\,]\, p(\mathbf{z})\, d\mathbf{z} \ .$$

First, simplifying the right-hand term by pulling out the constant $\mathbf{P}^{-1}\bar{\mathbf{z}}$ yields

$$\nabla \bar{\mathbf{W}} = \int \mathbf{W}(\mathbf{z})\, [\mathrm{P}^{-1}\mathbf{z}]\, p(\mathbf{z})\, d\mathbf{z} \quad - \quad \mathbf{P}^{-1}\bar{\mathbf{z}} \int \mathbf{W}(\mathbf{z})\, p(\mathbf{z})\, d\mathbf{z} \ .$$

But the expression involving the second integral is just the mean value of fitness in the population, so

$$\nabla \bar{\mathbf{W}} = \int \mathbf{W}(\mathbf{z})\, [\mathrm{P}^{-1}\mathbf{z}]\, p(\mathbf{z})\, d\mathbf{z} \quad - \quad \mathbf{P}^{-1}\bar{\mathbf{z}}\ \bar{\mathbf{W}} \ .$$

By pulling the constant $\mathbf{P}^{-1}$ out of the remaining integral, one obtains

$$\nabla \bar{\mathbf{W}} = \mathbf{P}^{-1}[\int \mathbf{W}(\mathbf{z})\, \mathbf{z}\, p(\mathbf{z})\, d\mathbf{z} \quad - \quad \bar{\mathbf{z}}\ \bar{\mathbf{W}}\,] \ .$$

Substututing this expression in to equation (2a) then yields

$$\nabla\, ln\, \bar{\mathbf{W}} = \tfrac{1}{\bar{\mathbf{W}}}\, \nabla \bar{\mathbf{W}} = \tfrac{1}{\bar{\mathbf{W}}}\, \mathbf{P}^{-1}[\int \mathbf{W}(\mathbf{z})\, \mathbf{z}\, p(\mathbf{z})\, d\mathbf{z} \quad - \quad \bar{\mathbf{z}}\ \bar{\mathbf{W}}\,]$$

$$= \mathbf{P}^{-1}[\ \tfrac{1}{\bar{\mathbf{W}}} \int \mathbf{W}(\mathbf{z})\, \mathbf{z}\, p(\mathbf{z})\, d\mathbf{z} \quad - \quad \bar{\mathbf{z}}\ ] \quad (8a).$$

Step 4

Next, the relationship (1a) is obtained by showing that the expression in brackets above is equal to **s**, the vector of selection differentials. To do this, we rewrite the expression in brackets as

$$\frac{1}{\bar{\mathbf{W}}}\int \mathbf{W}(\mathbf{z})\,\mathbf{z}\,p(\mathbf{z})\,d\mathbf{z} \quad - \quad \bar{\mathbf{z}} \quad = \quad \int \frac{\mathbf{W}(\mathbf{z})\,p(\mathbf{z})\,\mathbf{z}}{\bar{\mathbf{W}}}\,d\mathbf{z} \quad - \quad \bar{\mathbf{z}} \;(9).$$

But, by definition of a mean,

$$\bar{\mathbf{W}} = \int p(\mathbf{z})\,\mathbf{W}(\mathbf{z})\,d\mathbf{z} \;,$$

so equation (9) can be rewritten as

$$\frac{1}{\bar{\mathbf{W}}}\int \mathbf{W}(\mathbf{z})\,\mathbf{z}\,p(\mathbf{z})\,d\mathbf{z} \quad - \quad \bar{\mathbf{z}} \quad = \quad \int \frac{\mathbf{W}(\mathbf{z})\,p(\mathbf{z})}{\int p(\mathbf{z})\,\mathbf{W}(\mathbf{z})\,d\mathbf{z}}\,\mathbf{z}\,d\mathbf{z} \quad - \quad \bar{\mathbf{z}} \;.$$

Moreover, we can multiply the numerator and denominator of a ratio by *N*, the number of individuals in the population before selection, without changing that ratio:

$$\frac{1}{\bar{\mathbf{W}}}\int \mathbf{W}(\mathbf{z})\,\mathbf{z}\,p(\mathbf{z})\,d\mathbf{z} \quad - \quad \bar{\mathbf{z}} \quad = \quad \int \frac{\mathbf{W}(\mathbf{z})\,p(\mathbf{z})\,N}{\int p(\mathbf{z})\,\mathbf{W}(\mathbf{z})\,N\,d\mathbf{z}}\,\mathbf{z}\,d\mathbf{z} \quad - \quad \bar{\mathbf{z}} \;\; (10).$$

But the ratio associated with the left-hand integral,

$$\frac{\mathbf{W}(\mathbf{z})\,p(\mathbf{z})\,N}{\int p(\mathbf{z})\,\mathbf{W}(\mathbf{z})\,N\,d\mathbf{z}} \;,$$

is just the number of individuals of phenotype **z** surviving selective mortality divided by the total number of surviving individuals in the population. In other words, it is the frequency of phenotype **z** among the selected individuals, which we will designate by $p\prime(\mathbf{z})$. Consequently, equation (10) is

$$\frac{1}{\bar{\mathbf{W}}}\int \mathbf{W}(\mathbf{z})\,\mathbf{z}\,p(\mathbf{z})\,d\mathbf{z} \quad - \quad \bar{\mathbf{z}} \quad = \quad \int p\prime(\mathbf{z})\,\mathbf{z}\,d\mathbf{z} \quad - \quad \bar{\mathbf{z}} \;\; (11).$$

But the expression involving the right-hand integral is just the mean phenotype among the selected individuals; therefore, the entire right-hand side of the equation is just the difference between the mean phenotype vector of the population before and after selection, which is the selection differential, *i.e.*

$$\frac{1}{\bar{\mathbf{W}}}\int \mathbf{W}(\mathbf{z})\,\mathbf{z}\,p(\mathbf{z})\,d\mathbf{z} \quad - \quad \bar{\mathbf{z}} \quad = \quad \mathbf{s} \;.$$

Substituting this into equation (8a) then yields

$$\nabla \, ln \, \bar{\mathbf{W}} \;=\; \mathbf{P}^{-1}\mathbf{s} \;=\; \boldsymbol{\beta} \qquad (11a).$$

This is part of the Lande equation. In particular, this shows that the selection gradient, $\boldsymbol{\beta}$, is equal to the gradient of the logarithm of mean fitness. And it is a standard calculus result that the gradient of a function indicates the direction of change in the independent variables that produce the greatest change in the dependent variable. In other words, the gradient of log mean fitness points in the diretion of change in $\bar{\mathbf{z}}$ that produces the maximal change in mean fitness. As discussed in class, the components of $\boldsymbol{\beta}$ represent directional selection acting directly on the individual characters.

Step 5

The final step in the derivation is to relate the above equation to change in the mean phenotype. Because this involves a derivation completely parallel to the one just undertaken, only the main points will be sketched.

First, recognize that the mean fitness of an individual with breeding value $\mathbf{x}$, $\tilde{\mathbf{W}}(\mathbf{x})$, is given by the equation

$$\tilde{\mathbf{W}}(\mathbf{x}) \;=\; \int \xi(\mathbf{z}-\mathbf{x})\, \mathbf{W}(\mathbf{z})\, d\mathbf{z} \quad .$$

The mean fitness of the population is just the sum of the frequencies of particular values of $\mathbf{x}$ times the mean fitness of individuals with breeding value equal to $\mathbf{x}$:

$$\bar{\mathbf{W}} \;=\; \int g(\mathbf{x})\, \tilde{\mathbf{W}}(\mathbf{x})\, d\mathbf{x} \quad .$$

We then manipulate this equation just like equation (2) was manipulated. When this is done, one obtains the analogue of equation (11):

$$\frac{1}{\bar{\mathbf{W}}} \int \tilde{\mathbf{W}}(\mathbf{x})\, \mathbf{x}\, g(\mathbf{x})\, d\mathbf{x} \;-\; \bar{\mathbf{x}} \;=\; \int g'(\mathbf{x})\, \mathbf{x}\, d\mathbf{x} \;-\; \bar{\mathbf{x}} \quad (12),$$

where $g'(\mathbf{x})$ is the frequency of breeding value $\mathbf{x}$ among the selected individuals. Consequently, the right-hand side of the equation is simply the difference in mean breeding value between the selected and unselected individuals.

From here, one must realize that if all genetic variation is additive, then the mean breeding value of the offspring of the selected individuals will be equal to the mean breeding value of the selected individuals. Consequently, the expression

$$\int g'(\mathbf{x})\, \mathbf{x}\, d\mathbf{x}$$

is equal to the mean breeding value in the next generation. Equation (12) thus becomes

$$\frac{1}{\overline{\mathrm{W}}}\int \tilde{\mathbf{W}}(\mathbf{x})\,\mathbf{x}\,g(\mathbf{x})\,d\mathbf{x} \quad - \quad \overline{\mathbf{x}} \quad = \quad \Delta\overline{\mathbf{x}} \quad = \quad \Delta\overline{\mathbf{z}} \qquad (13).$$

(Remember that mean breeding value equals mean phenotpyic value.)

The analogue of equation (8a) in this step is

$$\nabla\, ln\, \overline{\mathbf{W}} \;=\; \mathbf{G}^{-1}\Big[\, \frac{1}{\overline{\mathrm{W}}}\int \tilde{\mathbf{W}}(\mathbf{x})\,\mathbf{x}\,g(\mathbf{x})\,d\mathbf{x} \quad - \quad \overline{\mathbf{x}}\ \Big] \;.$$

Subsistuting equation (13) into this then yields

$$\nabla\, ln\, \overline{\mathbf{W}} \;=\; \mathbf{G}^{-1}\,\Delta\overline{\mathbf{z}} \quad ,$$

which is the other part of the Lande equation. Equating this equation and equation (11a) gives

$$\mathbf{G}^{-1}\,\Delta\overline{\mathbf{z}} \;=\; \mathbf{P}^{-1}\mathbf{s} \;=\; \boldsymbol{\beta}$$

Multiplying each side of the equation by **G** then gives

$$\Delta\overline{\mathbf{z}} \;=\; \mathbf{G}\,\mathbf{P}^{-1}\mathbf{s} \;=\; \mathbf{G}\,\boldsymbol{\beta} \quad .$$

This is Lande's equation for evolutionary change in a multivariate phenotype. The derivation is thus completed.