

# Speaking Linear Algebra

A Verbal Phrasebook for Evolutionary Biologists

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## Abstract

This guide provides **verbal shortcuts** and **geometric intuitions** for common linear algebra operations. The goal: fluency in “speaking” matrix operations with students and colleagues without resorting to indices and summations. Each operation includes a figure, verbal phrases, geometric interpretation, and biological translation for quantitative genetics.

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## 1 Vectors

A vector  $v$  represents a **direction with a magnitude**—an arrow from the origin in trait space.

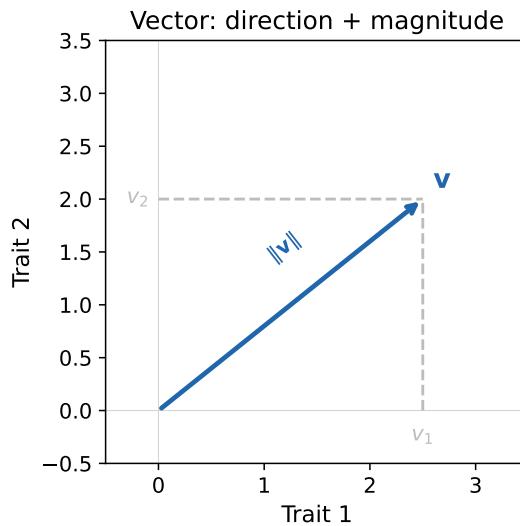


Figure 1: A vector as an arrow: direction plus magnitude. Components  $(v_1, v_2)$  give the coordinates.

### Say this:

- “A direction with a magnitude”
- “A point in trait space”
- “A list of trait values”

We picture vectors as *arrows* from the origin, but we can also label them by the *point* they reach, or by the *list* of their coordinates. These are three views of the same object.

### Biological translation

- |            |   |
|------------|---|
| $z$        | phenotype vector (trait values for one individual)                    |
| $\beta$    | selection gradient (direction of steepest fitness increase)           |
| $g_{\max}$ | genetic line of least resistance (first eigenvector of $\mathbf{G}$ ) |

## 2 Inner Product (Dot Product): $\mathbf{u}'\mathbf{v}$

The inner product  $\mathbf{u}'\mathbf{v} = \sum_i u_i v_i$  measures **how aligned** two vectors are.

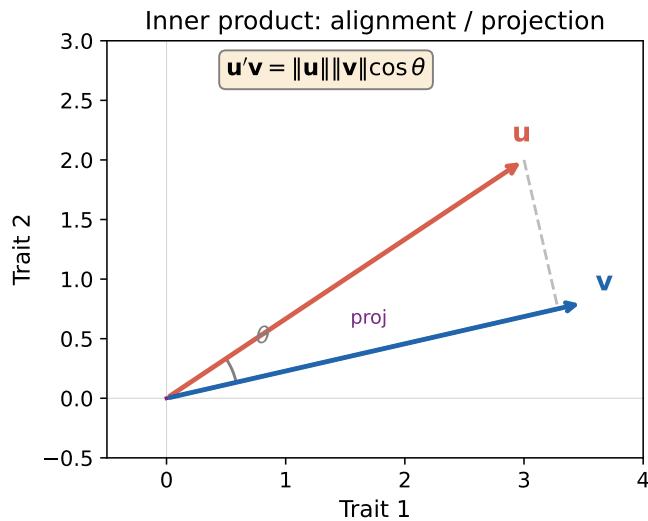


Figure 2: Inner product as projection.  $\mathbf{u}'\mathbf{v} = \|\mathbf{u}\| \|\mathbf{v}\| \cos \theta$  measures alignment.

**Say this:**

- “How much does  $\mathbf{u}$  point in the direction of  $\mathbf{v}$ ? ”
- “ $\mathbf{u}$  projected onto  $\mathbf{v}$ , times the length of  $\mathbf{v}$ ”
- “Overlap between  $\mathbf{u}$  and  $\mathbf{v}$ ”

**Think this:**

$$\mathbf{u}'\mathbf{v} = \|\mathbf{u}\| \|\mathbf{v}\| \cos \theta$$

- Same direction: **large positive**
- Perpendicular: **zero**
- Opposite: **large negative**

**Biological translation**

$\beta'z$  = “how far along the selection direction is this phenotype”

$\mathbf{u}'\mathbf{v} = 0$  means “ $\mathbf{u}$  and  $\mathbf{v}$  are orthogonal—no overlap”

### 3 Outer Product: $uv'$

The outer product creates a **rank-1 matrix** whose columns are scaled copies of  $u$ .

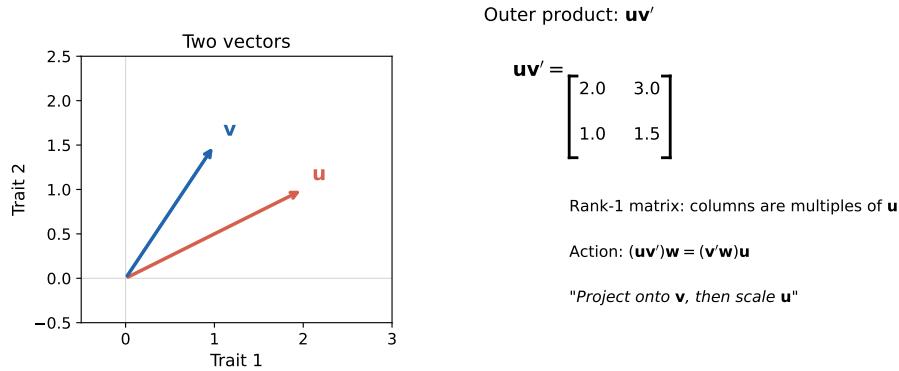


Figure 3: Outer product builds a matrix from two vectors. Its action: project onto  $v$ , then scale along  $u$ .

#### Say this:

- “Spread  $u$  along  $v$ ”
- “A rank-1 matrix that points from  $v$  toward  $u$ ”
- “Project onto  $v$ , then stretch along  $u$ ”

#### Think this:

The action of  $uv'$  on any vector  $w$ :

$$(uv')w = (v'w)u$$

“How much  $w$  aligns with  $v$ , times  $u$ . ”

#### Biological translation

The covariance matrix is a sum of outer products:

$$\Sigma = \frac{1}{n} \sum_{i=1}^n (z_i - \bar{z})(z_i - \bar{z})'$$

## 4 Matrix-Vector Multiplication: $\mathbf{M}\mathbf{v}$

Matrix-vector multiplication **transforms** the vector—rotating, stretching, or shearing it.

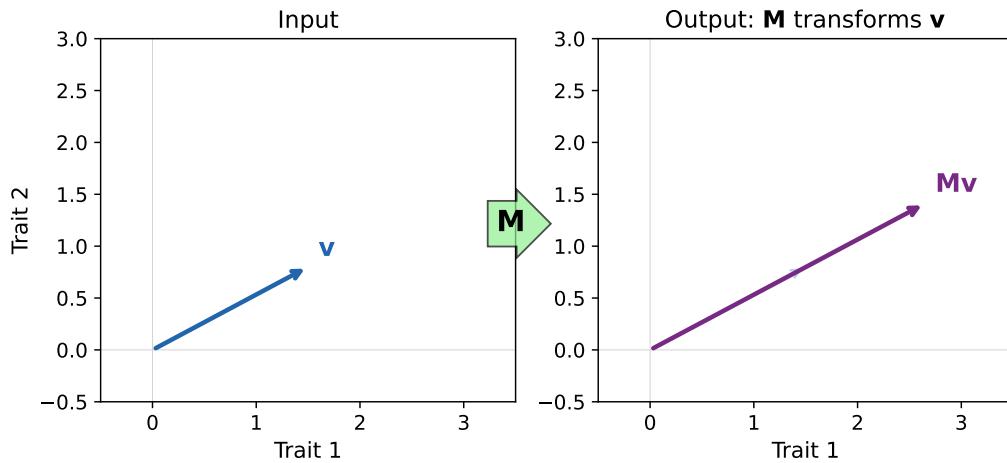


Figure 4:  $\mathbf{M}\mathbf{v}$ : the matrix  $\mathbf{M}$  transforms the arrow  $\mathbf{v}$  into a new arrow (generally different direction and length).

**Say this:**

- “ $\mathbf{M}$  transforms  $\mathbf{v}$ ”
- “Where does  $\mathbf{M}$  send  $\mathbf{v}$ ? ”
- “ $\mathbf{M}$  acts on  $\mathbf{v}$ ”
- “Weighted combination of  $\mathbf{M}$ ’s columns”

**Think this:**

The “columns” view:  $\mathbf{M}\mathbf{v} = v_1 \cdot (\text{1st column}) + v_2 \cdot (\text{2nd column}) + \dots$

The coefficients in  $\mathbf{v}$  tell you how to mix the columns of  $\mathbf{M}$ .

**Mantra**

“When we write  $\mathbf{G}\boldsymbol{\beta}$ , we’re asking: *where does the G-matrix send the selection direction  $\boldsymbol{\beta}$ ?*”

**Biological translation**

$\mathbf{G}\boldsymbol{\beta}$  “The response to selection: where does  $\mathbf{G}$  send  $\boldsymbol{\beta}$ ? ”

$\mathbf{P}^{-1}\mathbf{z}$  “The phenotype  $\mathbf{z}$  in precision-weighted units”

**Note:**  $\mathbf{P}^{-1}\mathbf{z}$  is *not* whitened—that requires  $\mathbf{P}^{-1/2}\mathbf{z}$  (see Section 10).

## 5 Quadratic Form: $\mathbf{v}'\mathbf{M}\mathbf{v}$

This is the **workhorse** of quantitative genetics. The quadratic form gives the “height” of the  $\mathbf{M}$ -paraboloid at direction  $\mathbf{v}$ .

Quadratic form: height of  $\mathbf{M}$ -bowl at  $\mathbf{v}$

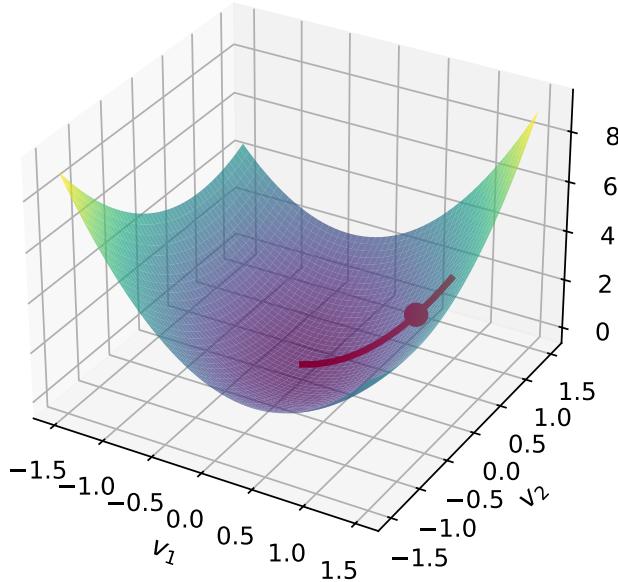


Figure 5: Quadratic form as height of a paraboloid. The surface shows  $\mathbf{v}'\mathbf{M}\mathbf{v}$  over all directions. The red curve traces one direction.

### Say this:

- “Variance *encoded by*  $\mathbf{M}$  in direction  $\mathbf{v}$ ”
- “Height of the  $\mathbf{M}$ -bowl at  $\mathbf{v}$ ”
- “How much does  $\mathbf{M}$  stretch space in direction  $\mathbf{v}$ ? ”

**Scaling:** If you scale  $\mathbf{v}$  by a constant  $c$ , the value  $\mathbf{v}'\mathbf{M}\mathbf{v}$  scales by  $c^2$ . For thinking about “variance per unit step,” it is natural to imagine  $\mathbf{v}$  as a unit vector.

### Mantra

“ $\mathbf{v}'\mathbf{M}\mathbf{v}$  asks: *how much variance encoded by  $\mathbf{M}$  lies in direction  $\mathbf{v}$ ?*”  
(Strictly, this is “variance” only when  $\mathbf{M}$  is a covariance matrix.)

### Biological translation

$\boldsymbol{\beta}'\mathbf{G}\boldsymbol{\beta}$	“Genetic variance in direction $\boldsymbol{\beta}$ ” = evolvability $e(\boldsymbol{\beta})$
$\boldsymbol{\beta}'\mathbf{P}\boldsymbol{\beta}$	“Phenotypic variance in direction $\boldsymbol{\beta}$ ”
$\frac{\boldsymbol{\beta}'\mathbf{G}\boldsymbol{\beta}}{\boldsymbol{\beta}'\mathbf{P}\boldsymbol{\beta}}$	“Heritability in direction $\boldsymbol{\beta}$ ” = $h^2(\boldsymbol{\beta})$
$(\mathbf{z} - \bar{\mathbf{z}})' \mathbf{P}^{-1} (\mathbf{z} - \bar{\mathbf{z}})$	“Mahalanobis distance squared” (deviation from mean)

## 6 Transpose: $\mathbf{M}'$

The transpose flips a matrix across its diagonal—rows become columns.

Transpose: flip across diagonal

$$\mathbf{M} = \begin{array}{ccc} 1 & 2 & 3 \\ 4 & 5 & 6 \end{array} \quad \xrightarrow{\text{flip}} \quad \mathbf{M}' = \begin{array}{cc} 1 & 4 \\ 2 & 5 \\ 3 & 6 \end{array}$$

Rows  $\leftrightarrow$  Columns

$(2 \times 3) \rightarrow (3 \times 2)$

For symmetric  $\mathbf{M}$ :  $\mathbf{M}' = \mathbf{M}$

Figure 6: Transpose: flip rows and columns. Diagonal elements (yellow) stay in place.

Say this:

- “Flip rows and columns”
- “Mirror across the diagonal”
- “Move a matrix from one side of a dot product to the other”

Think this:

Key properties:

- $(\mathbf{AB})' = \mathbf{B}'\mathbf{A}'$  — “Transpose reverses order”
- $\mathbf{M} = \mathbf{M}'$  for symmetric matrices (all covariance matrices)
- $(\mathbf{M}\mathbf{v})' = \mathbf{v}'(\mathbf{M}')$  — “Move  $\mathbf{M}$  across the dot product by transposing”

Mantra

“Symmetric matrices equal their own transpose—left- and right-multiplication behave the same in dot products.”

## 7 Inverse: $\mathbf{M}^{-1}$

The inverse **undoes** the transformation:  $\mathbf{M}^{-1}\mathbf{M} = \mathbf{I}$ .

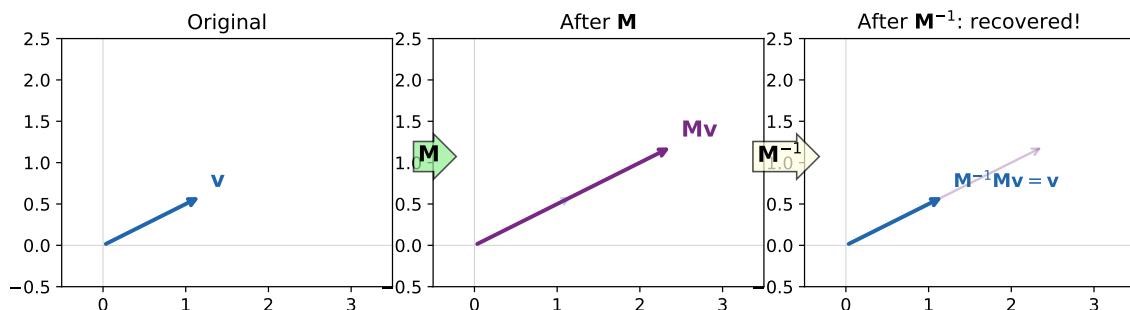


Figure 7: The inverse undoes the transformation. Apply  $\mathbf{M}$ , then  $\mathbf{M}^{-1}$ : you're back where you started.

### Say this:

- “Undo the transformation”
- “Run  $\mathbf{M}$  backwards”
- “The matrix that satisfies  $\mathbf{M}^{-1}\mathbf{M} = \mathbf{I}$ ”

### Think this:

- If  $\mathbf{M}$  stretches by factor  $\lambda$ , then  $\mathbf{M}^{-1}$  shrinks by  $1/\lambda$
- Eigenvalues of  $\mathbf{M}^{-1}$  are  $1/\lambda_i$  (reciprocals)
- **Warning:**  $\mathbf{M}^{-1}$  amplifies directions where  $\mathbf{M}$  was small!
- If  $\mathbf{M}$  is nearly singular (some tiny eigenvalues),  $\mathbf{M}^{-1}$  blows up noise in those directions

### Biological translation

$\beta' \mathbf{G}^{-1} \beta$	“How <i>constrained</i> is direction $\beta$ ? ”
$(\beta' \mathbf{G}^{-1} \beta)^{-1}$	“Conditional evolvability $c(\beta)$ ”
$\mathbf{P}^{-1} \mathbf{G}$	“Genetic variance <i>relative to</i> phenotypic variance”

## 8 Eigendecomposition: $\mathbf{M} = \mathbf{Q}\Lambda\mathbf{Q}'$

Eigendecomposition finds the **natural axes** of a matrix—directions where it acts by pure stretching.

For the symmetric matrices we care about ( $\mathbf{G}$ ,  $\mathbf{P}$ ,  $\mathbf{E}$ ), we can write  $\mathbf{M} = \mathbf{Q}\Lambda\mathbf{Q}'$  with orthogonal  $\mathbf{Q}$  and real eigenvalues.

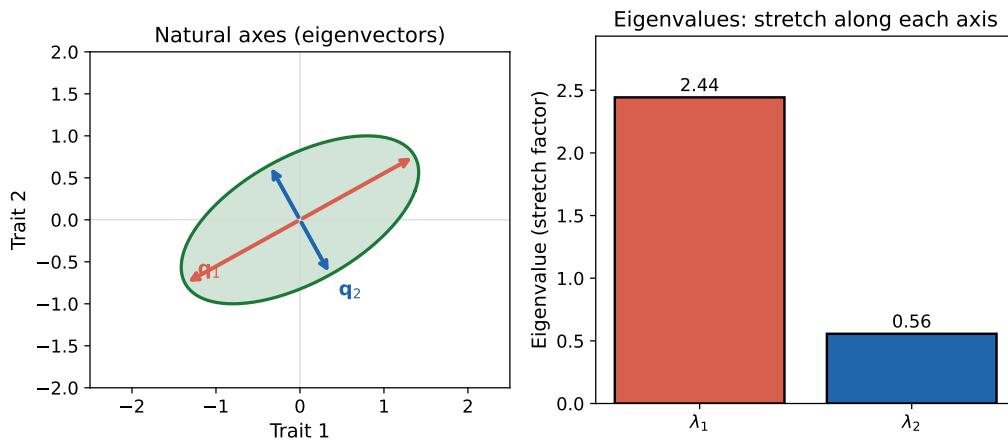


Figure 8: Left: Eigenvectors are the natural axes (directions of pure stretch). Right: Eigenvalues are the stretch factors.

### Say this:

- “Find the natural axes of  $\mathbf{M}$ ”
- “Directions where  $\mathbf{M}$  only stretches, no rotation”
- “For covariance matrices, these are the principal component directions”

### Think this:

$\mathbf{M}\mathbf{v} = \lambda\mathbf{v}$  means “ $\mathbf{M}$  sends  $\mathbf{v}$  to a scaled version of itself.”

Eigenvectors  $\mathbf{Q}$ : the skeleton of the matrix.

Eigenvalues  $\Lambda$ : the strength of each bone.

### Biological translation

$\mathbf{g}_{\max}$	“Genetic line of least resistance—maximum genetic variance”
$\lambda_1 / \sum_i \lambda_i$	“Fraction of variance explained by $\mathbf{g}_{\max}$ ”
$\lambda_1 \gg \lambda_2$	“ $\mathbf{G}$ is cigar-shaped—highly constrained”
$\lambda_1 \approx \lambda_2 \approx \dots$	“ $\mathbf{G}$ is spherical—isotropic, no preferred direction”

## 9 Matrix Square Root: $\mathbf{M}^{1/2}$

The square root is “half the transformation”:  $\mathbf{M}^{1/2}\mathbf{M}^{1/2} = \mathbf{M}$ .

For symmetric positive definite matrices (like  $\mathbf{P}$ ,  $\mathbf{G}$ ), there is a unique symmetric square root  $\mathbf{M}^{1/2}$ .

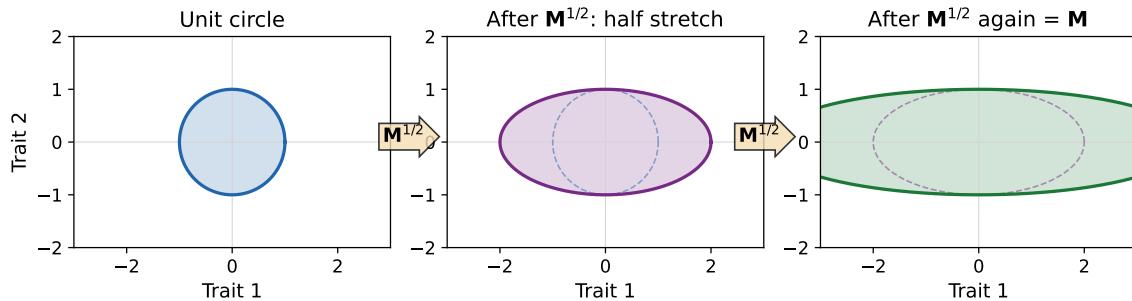


Figure 9: Matrix square root: applying  $\mathbf{M}^{1/2}$  twice gives  $\mathbf{M}$ . If  $\mathbf{M}$  stretches by 4,  $\mathbf{M}^{1/2}$  stretches by 2.

### Say this:

- “Half the transformation”
- “The matrix that, applied twice, gives  $\mathbf{M}$ ”
- “Square root the eigenvalues, keep the eigenvectors”

### Think this:

If  $\mathbf{M} = \mathbf{Q}\Lambda\mathbf{Q}'$ , then  $\mathbf{M}^{1/2} = \mathbf{Q}\Lambda^{1/2}\mathbf{Q}'$

where  $\Lambda^{1/2} = \text{diag}(\sqrt{\lambda_1}, \sqrt{\lambda_2}, \dots)$

This requires all eigenvalues to be non-negative (positive semidefinite).

### Biological translation

$\mathbf{P}^{1/2}$  “Half the phenotypic scaling”

$\mathbf{P}^{-1/2}$  “Whiten: remove phenotypic scaling”

## 10 Whitening: $\mathbf{P}^{-1/2}\mathbf{M}\mathbf{P}^{-1/2}$

Whitening expresses  $\mathbf{M}$  in coordinates where  $\mathbf{P} = \mathbf{I}$  (phenotypic variance is isotropic).

Assuming  $\mathbf{P}$  is positive definite (invertible), we can define  $\mathbf{P}^{-1/2}$  and whiten.

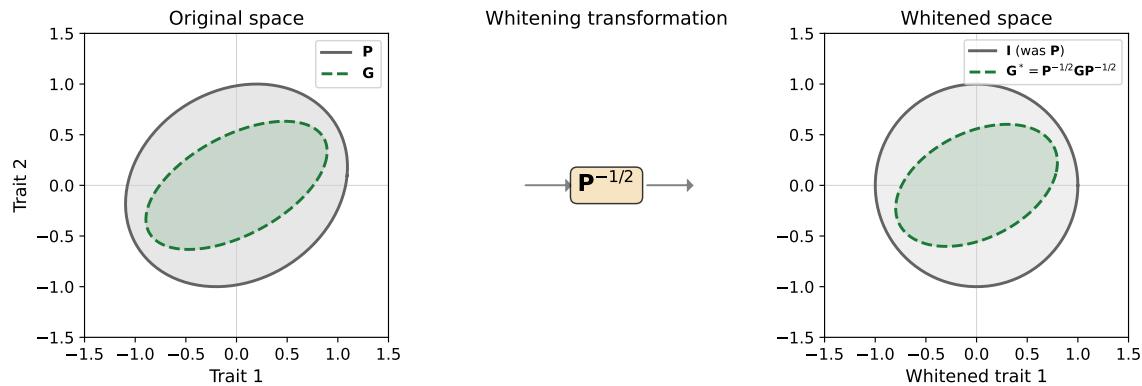


Figure 10: Whitening transformation. Left: Original space with  $\mathbf{P}$  (ellipse) and  $\mathbf{G}$  (dashed). Right: After whitening,  $\mathbf{P}$  becomes  $\mathbf{I}$  (circle), revealing  $\mathbf{G}^*$ .

### Say this:

- “Express  $\mathbf{M}$  in units where  $\mathbf{P} = \mathbf{I}$ ”
- “Remove phenotypic scaling from  $\mathbf{M}$ ”
- “The *shape* of  $\mathbf{G}$  relative to  $\mathbf{P}$ ”

### Mantra

“Whitening asks: *if phenotypic variance were isotropic, what would genetic variance look like?*”

### Biological translation

$$\mathbf{G}^* = \mathbf{P}^{-1/2}\mathbf{G}\mathbf{P}^{-1/2}$$

- Eigenvalues of  $\mathbf{G}^*$  are the generalized eigenvalues of  $(\mathbf{G}, \mathbf{P})$
- They bound directional heritability:  $\lambda_{\min} \leq h^2(\boldsymbol{\beta}) \leq \lambda_{\max}$
- $V_{\text{rel}}(\mathbf{G}^*)$  controls heterogeneity of  $h^2(\boldsymbol{\beta})$

## 11 Trace: $\text{tr}(\mathbf{M})$

The trace is the sum of diagonal elements—the **total variance** for covariance matrices.

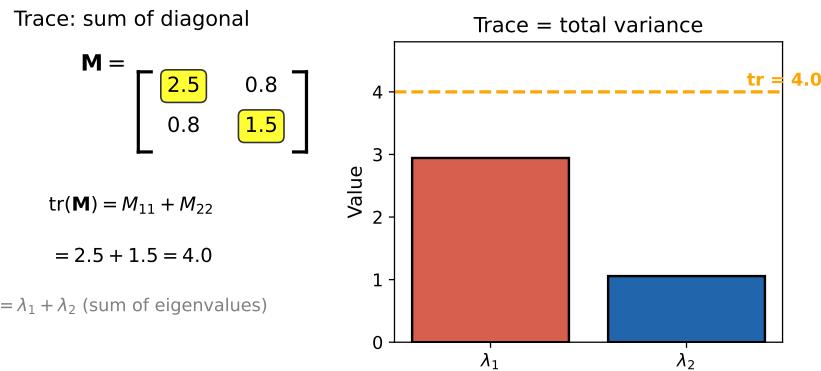


Figure 11: Trace: sum of diagonal elements = sum of eigenvalues = total variance.

### Say this:

- “Sum of diagonal elements”
- “Total variance”
- “Sum of eigenvalues”

### Think this:

Key properties:

- $\text{tr}(\mathbf{AB}) = \text{tr}(\mathbf{BA})$  — “Trace is cyclic”
- $\text{tr}(\mathbf{M}) = \sum_i \lambda_i$  — “Trace equals sum of eigenvalues”

### Mantra

“Trace is the *total size* of a matrix; eigenvalues are how that total is *distributed* across directions.”

### Biological translation

$\text{tr}(\mathbf{G})/p = \bar{e}$  — “Average evolvability” (Hansen & Houle 2008)

## 12 Determinant: $\det(\mathbf{M})$

The determinant is the **volume scaling factor**—how much  $\mathbf{M}$  expands or compresses space.

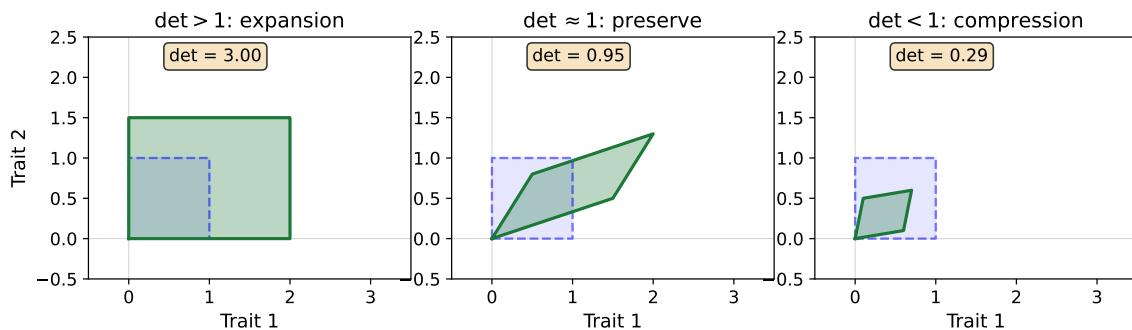


Figure 12: Determinant as volume scaling. Left: expansion ( $\det > 1$ ). Center: preservation ( $\det \approx 1$ ). Right: compression ( $\det < 1$ ).

### Say this:

- “Volume scaling factor”
- “Product of eigenvalues”
- “How much does  $\mathbf{M}$  expand or compress space?”

### Think this:

For covariance matrices (which have non-negative determinants):

- $\det(\mathbf{M}) > 1$ : expansion
- $\det(\mathbf{M}) = 1$ : volume-preserving
- $0 < \det(\mathbf{M}) < 1$ : compression
- $\det(\mathbf{M}) = 0$ : singular (collapses a dimension)

(More generally,  $|\det(\mathbf{M})|$  is the volume scaling; negative determinant flips orientation.)

### Biological translation

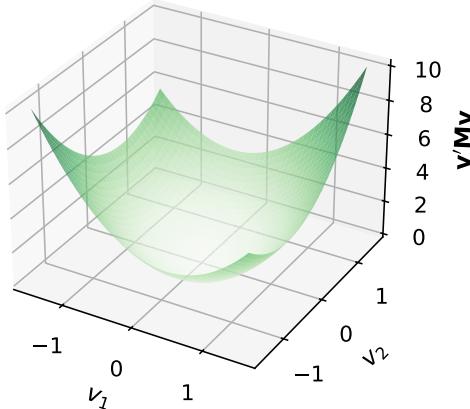
$\det(\mathbf{G})$       “Generalized genetic variance—product along principal axes”

$\det(\mathbf{G}) = 0$     “ $\mathbf{G}$  is singular: no variance in some direction”

## 13 Positive Definite: $\mathbf{M} \succ 0$

A positive definite matrix has all positive eigenvalues—its paraboloid opens upward everywhere.

Positive definite:  
bowl opens upward  
 $\mathbf{v}'\mathbf{M}\mathbf{v} > 0$  for all  $\mathbf{v} \neq 0$



Indefinite (NOT pos. def.):  
saddle shape  
some directions give negative values

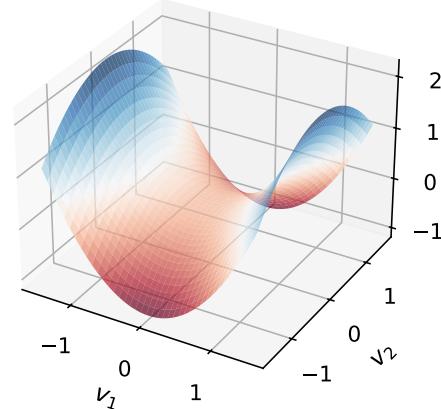


Figure 13: Left: Positive definite—bowl opens upward,  $\mathbf{v}'\mathbf{M}\mathbf{v} > 0$  for all  $\mathbf{v} \neq 0$ . Right: Indefinite—saddle shape, some directions give negative values.

**Say this:**

- “All eigenvalues positive”
- “The bowl opens upward everywhere”
- “Variance is positive in every direction”

**Mantra**

“Positive *definite* means no flat or negative directions—every direction has positive variance.”

“Positive *semidefinite* allows flat directions (zero eigenvalues) but no negative ones.”

**Biological translation**

All covariance matrices ( $\mathbf{G}$ ,  $\mathbf{P}$ ,  $\mathbf{E}$ ) must be positive semi-definite ( $\mathbf{M} \succeq 0$ ): in some directions the quadratic form may be zero if there is no variance.

Biological constraint:  $\mathbf{E} = \mathbf{P} - \mathbf{G} \succeq 0$  (environmental variance cannot be negative).

## 14 Generalized Eigenvalues & Rayleigh Quotient

The Rayleigh quotient  $R(\mathbf{v}) = \mathbf{v}'\mathbf{G}\mathbf{v}/\mathbf{v}'\mathbf{P}\mathbf{v}$  is bounded by generalized eigenvalues.

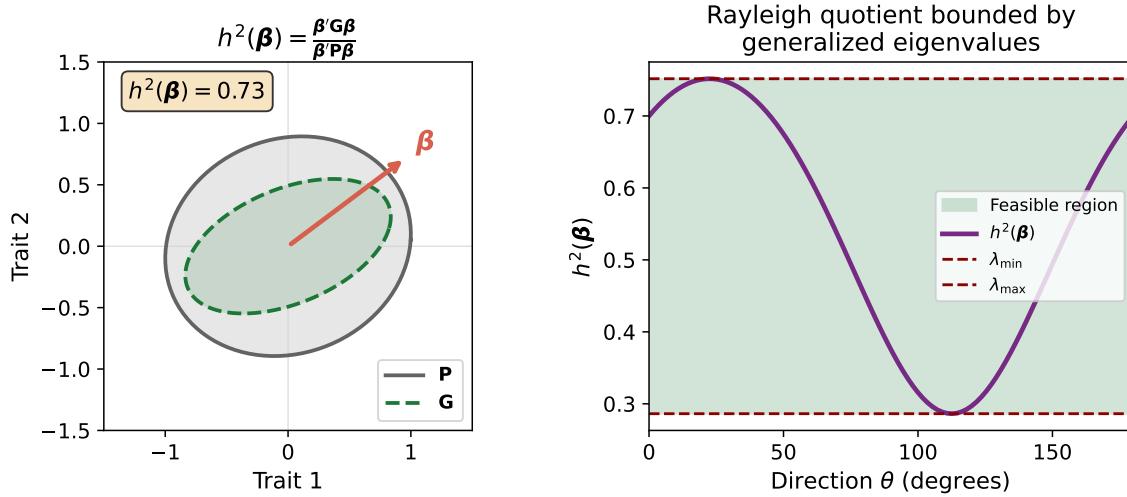


Figure 14: Left:  $\mathbf{G}$  and  $\mathbf{P}$  ellipses with direction  $\beta$ . Right:  $h^2(\beta)$  varies with direction but is bounded by  $\lambda_{\min}$  and  $\lambda_{\max}$ .

### Say this:

- “Ratio of two quadratic forms”
- “ $\mathbf{G}$ -variance per unit of  $\mathbf{P}$ -variance”
- “Height of the  $\mathbf{G}$ -bowl relative to the  $\mathbf{P}$ -bowl”

### Think this:

Generalized eigenvalue problem:  $\mathbf{G}\mathbf{v} = \lambda\mathbf{P}\mathbf{v}$

“Find directions where  $\mathbf{G}$  and  $\mathbf{P}$  act by the same relative scaling.”

Bounds:  $\lambda_{\min} \leq R(\mathbf{v}) \leq \lambda_{\max}$

These bounds are the eigenvalues of the whitened matrix  $\mathbf{G}^* = \mathbf{P}^{-1/2}\mathbf{G}\mathbf{P}^{-1/2}$  (Section 10).

### Mantra

“The Rayleigh quotient asks: *what fraction of  $\mathbf{P}$ -variance is  $\mathbf{G}$ -variance, in direction  $\mathbf{v}$ ?*”

### Biological translation

$$h^2(\beta) = \frac{\beta' \mathbf{G} \beta}{\beta' \mathbf{P} \beta} \quad \text{bounded by} \quad \lambda_{\min} \leq h^2(\beta) \leq \lambda_{\max}$$

Generalized eigenvalues = extreme heritabilities

## 15 Response to Selection: $\mathbf{G}\beta$

The response  $\mathbf{R} = \mathbf{G}\beta$  is generally **deflected** from the selection direction toward  $\mathbf{g}_{\max}$ .

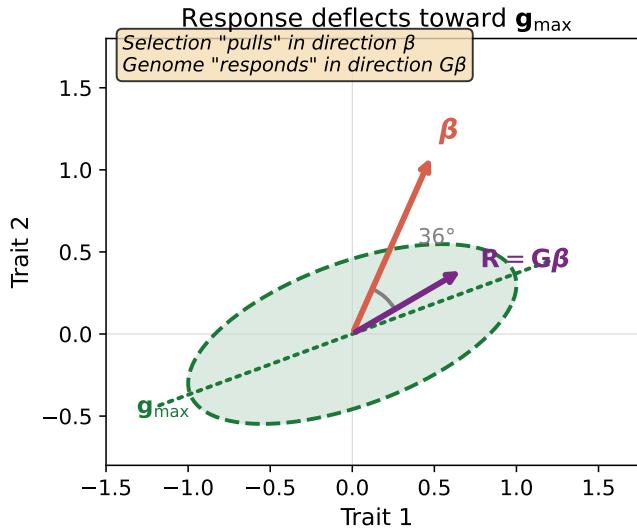


Figure 15: Response deflection. Selection pulls in direction  $\beta$ , but the response  $\mathbf{R} = \mathbf{G}\beta$  rotates toward the genetic line of least resistance  $\mathbf{g}_{\max}$ .

### Say this:

- “Where does the genome send selection?”
- “The response to selection in direction  $\beta$ ”
- “Genetic variance in direction  $\beta$ , projected back into trait space”

### Mantra

“Selection pulls in direction  $\beta$ , but the genome responds in direction  $\mathbf{G}\beta$ .  
If  $\mathbf{G}$  is anisotropic, the response *rotates* toward  $\mathbf{g}_{\max}$ .”

### Biological translation

- |                                  |   |
|----------------------------------|---|
| $\angle(\beta, \mathbf{G}\beta)$ | “Deflection angle—message loss”                                   |
| $\beta \perp \mathbf{g}_{\max}$  | “Strong deflection—selection pulls where genetic variance is low” |

## 16 Quick Reference Card

### 16.1 Core Operations

Symbol	Say this	Think this
$u'v$	“How aligned are $u$ and $v$ ? ”	Projection / overlap
$uv'$	“Spread $u$ along $v$ ”	Rank-1 matrix
$Mv$	“Where does $M$ send $v$ ? ”	Transform the arrow
$v'Mv$	“Variance encoded by $M$ in direction $v$ ”	Height of bowl
$M'$	“Flip across diagonal”	Move across dot product
$M^{-1}$	“Run $M$ backwards”	Undo transformation
$M^{1/2}$	“Half the transformation”	Square root eigenvalues
$Q\Lambda Q'$	“ $M$ in its natural axes”	Eigenvectors + eigenvalues
$\text{tr}(M)$	“Total variance”	Sum of eigenvalues
$\det(M)$	“Volume scaling factor”	Product of eigenvalues

### 16.2 Biological Translations

Expression	Biological meaning
$G\beta$	Response to selection
$\beta'G\beta$	Evolvability in direction $\beta$
$\beta'G\beta/\beta'P\beta$	Directional heritability $h^2(\beta)$
$(\beta'G^{-1}\beta)^{-1}$	Conditional evolvability $c(\beta)$
$g_{\max}$	Genetic line of least resistance
$\lambda_1/\sum_i \lambda_i$	Genetic constraint (variance concentration)
$G^* = P^{-1/2}GP^{-1/2}$	Whitened $G$ (P-standardized)
$V_{\text{rel}}(G^*)$	Eigenvalue dispersion $\rightarrow h^2$ heterogeneity

### 16.3 Three Key Mantras

1.  $v'Mv$  asks: “How much variance does  $M$  have in direction  $v$ ? ”
2.  $G\beta$  asks: “Where does the genome send selection? ” (If  $G$  is anisotropic, response rotates toward  $g_{\max}$ .)
3. Whitening asks: “What does  $G$  look like when  $P$  is a sphere? ”

# Part I

## Derivations from First Principles

### 17 Lande's Multivariate Breeder's Equation

#### 17.1 The Question We Want to Answer

Imagine a population of organisms with multiple correlated traits—say, body size and beak depth in birds. Natural selection favors certain combinations. **How will the population evolve?**

Specifically: if we know the **genetic architecture** (the G-matrix) and the **pattern of selection** (captured by the selection gradient  $\beta$ ), can we predict the **evolutionary response**  $\Delta\bar{z}$ ?

The answer is **Lande's equation**:

$$\boxed{\Delta\bar{z} = \mathbf{G}\beta} \quad (1)$$

**Think this:**

**In words:** “The change in mean phenotype equals the G-matrix applied to the selection gradient.”

Using our verbal shortcuts: “Where does  $\mathbf{G}$  send  $\beta$ ? ”

Let's derive this from first principles, explaining each step in plain language.

#### Lande's Equation: From Selection to Response

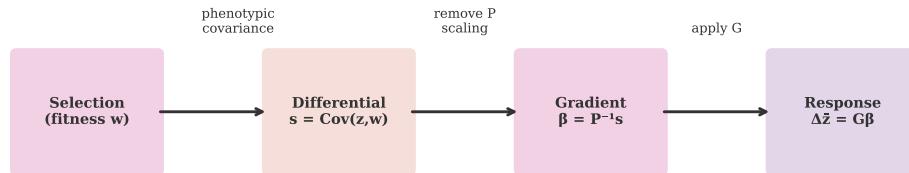


Figure 16: Overview of Lande's equation. Selection creates a phenotypic shift (the selection differential  $s$ ), which we decompose into a direction-independent gradient  $\beta$ , then filter through the genetic architecture  $\mathbf{G}$  to get the evolutionary response  $\Delta\bar{z}$ .

#### 17.2 Step 1: The Univariate Breeder's Equation (Warm-up)

Before tackling multiple traits, let's recall the single-trait case. This grounds us in familiar territory.

##### 17.2.1 The Setup

Consider a single trait  $z$  (e.g., body size). In a population:

- $\bar{z}$  = mean phenotype before selection
- $\bar{z}^*$  = mean phenotype *after* selection (among survivors/reproducers)
- $\bar{z}'$  = mean phenotype in the *next generation*

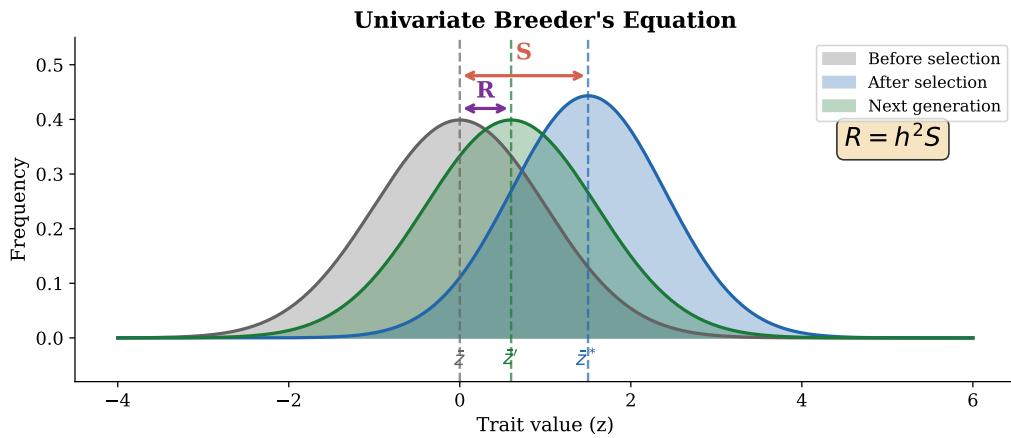


Figure 17: The univariate breeder's equation setup. Selection shifts the distribution (gray → blue), then inheritance filters that shift (blue → green). The response  $R$  is smaller than the selection differential  $S$  by a factor of  $h^2$ .

### 17.2.2 Two Key Quantities

Definition: Selection Differential

$$S = \bar{z}^* - \bar{z} = \text{Cov}(z, w)$$

**In words:** “How much did selection shift the mean?” Equivalently, “How much does the trait covary with fitness  $w$ ?“

Definition: Response to Selection

$$R = \bar{z}' - \bar{z}$$

**In words:** “How much does the mean actually change across generations?”

### 17.2.3 The Key Insight: Not All of $S$ Gets Through

Selection shifts the phenotypic mean by  $S$ . But only the **genetic component** of that shift is inherited. The environmental component is “reset” each generation.

#### Mantra

The fraction of phenotypic variance that is genetic is  $h^2 = V_G/V_P$ . So the fraction of the selection differential that “gets through” to the next generation is also  $h^2$ .

This gives us the **univariate breeder's equation**:

$$R = h^2 S \tag{2}$$

**Verbal translation:** “Response equals heritability times selection differential.”

### The Breeder's Equation: Only Genetic Variance is Inherited



Figure 18: The breeder's equation as a filter. Selection creates shift  $S$ ; heritability  $h^2$  determines what fraction persists to the next generation.

### 17.3 Step 2: The Multivariate Challenge

Now consider  $p$  traits simultaneously:  $\mathbf{z} = (z_1, z_2, \dots, z_p)'$ .

#### 17.3.1 What Changes?

##### 1. Variances become matrices:

- $V_P \rightarrow \mathbf{P}$  (phenotypic variance-covariance matrix)
- $V_G \rightarrow \mathbf{G}$  (genetic variance-covariance matrix)

##### 2. Selection differential becomes a vector:

$$S \rightarrow \mathbf{s} = \text{Cov}(\mathbf{z}, w) = \begin{pmatrix} \text{Cov}(z_1, w) \\ \text{Cov}(z_2, w) \\ \vdots \end{pmatrix}$$

##### 3. Response becomes a vector:

$$R \rightarrow \Delta \bar{\mathbf{z}} = \bar{\mathbf{z}}' - \bar{\mathbf{z}}$$

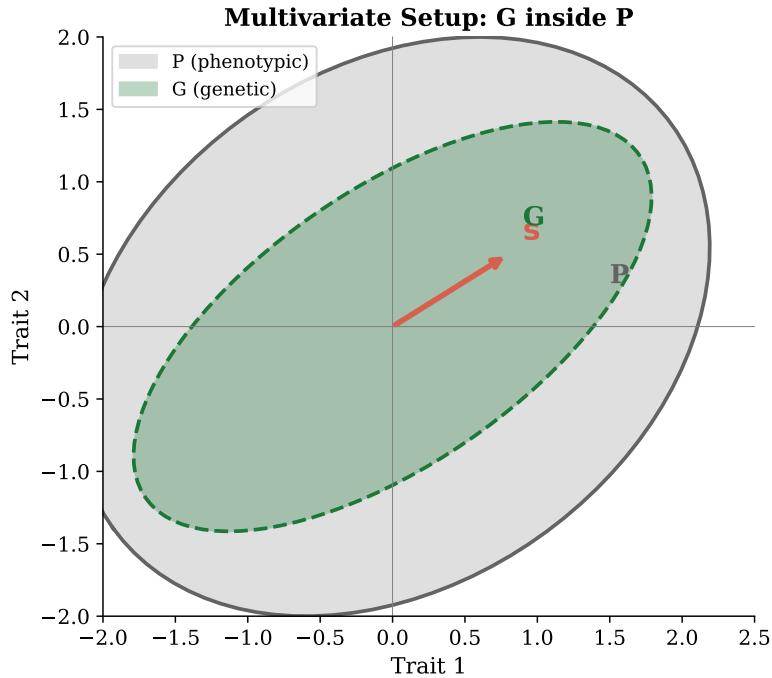


Figure 19: The multivariate setup.  $\mathbf{P}$  (gray ellipse) captures phenotypic variance and covariance.  $\mathbf{G}$  (green ellipse) captures genetic variance and covariance. The selection differential  $s$  (red arrow) shows how selection shifts the phenotypic mean.

### 17.3.2 The Naive Guess (Wrong!)

You might guess: “Just apply  $h^2$  to each trait separately.”

$$\Delta \bar{z}_i \stackrel{?}{=} h_i^2 \cdot s_i \quad (\text{WRONG})$$

**Why this fails:** Traits are *correlated*. Selection on trait 1 can cause a response in trait 2, even if trait 2 wasn’t directly selected! This is **correlated response to selection**.

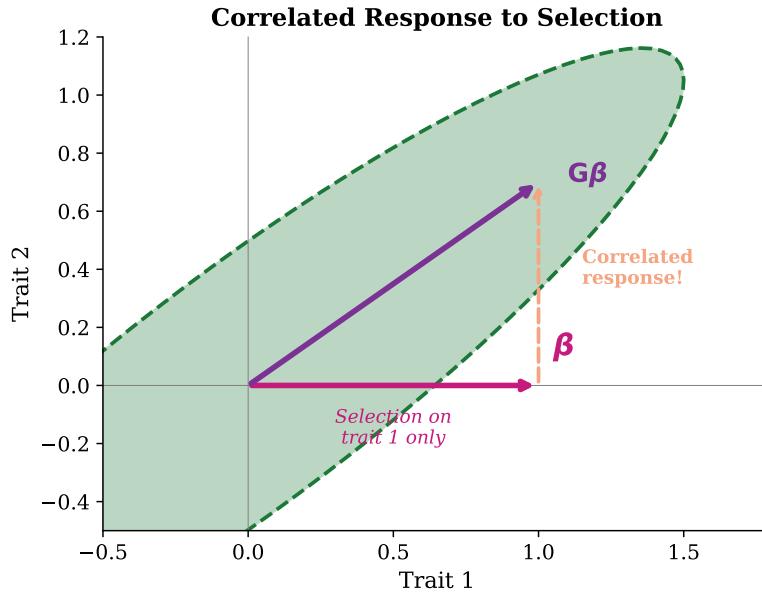


Figure 20: Correlated response. Even if selection acts only on trait 1 (horizontal arrow), the response (purple arrow) has a component in trait 2 because the traits are genetically correlated. The G-matrix encodes this coupling.

## 17.4 Step 3: The Robertson-Price Identity

The key to the multivariate derivation is an important result known as the **Robertson-Price identity** (or secondary theorem of natural selection).

### 17.4.1 Statement

For any trait  $z$  and fitness  $w$ :

$$\Delta \bar{z} = \text{Cov}_G(z, w) \quad (3)$$

where  $\text{Cov}_G$  denotes the *genetic* (additive) covariance.

**Think this:**

**In words:** “The evolutionary change in a trait equals the genetic covariance between that trait and fitness.”

**Intuition:** Only the *genetic* component of the phenotype-fitness association gets transmitted to offspring.

### 17.4.2 Sketch of Proof

1. Decompose each individual's phenotype:  $z_i = a_i + e_i$  (breeding value + environment)
2. The mean phenotype in offspring depends on mean breeding value:  $\bar{z}' \approx \bar{a}^*$
3. The change in mean breeding value under selection:  $\bar{a}^* - \bar{a} = \text{Cov}(a, w)$
4. Therefore:  $\Delta \bar{z} = \text{Cov}(a, w) = \text{Cov}_G(z, w)$

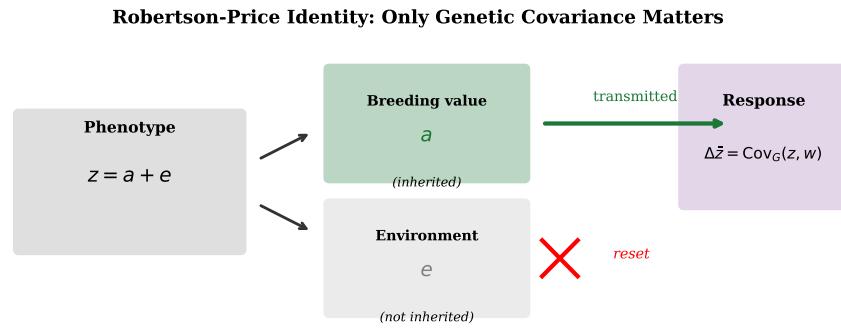


Figure 21: The Robertson-Price identity. Fitness selects on phenotypes, but only the genetic component (breeding value) is transmitted to offspring.

## 17.5 Step 4: Connecting Genetic and Phenotypic Covariances

We have:  $\Delta\bar{z} = \text{Cov}_G(z, w)$ .

But we observe *phenotypes*, not breeding values. We need to express  $\text{Cov}_G(z, w)$  in terms of quantities we can measure.

### 17.5.1 The Key Relationship

Here's where linear algebra earns its keep. For the additive genetic model:

$$\text{Cov}_G(z_i, w) = \sum_j G_{ij} \cdot \beta_j \quad (4)$$

where  $\beta_j = \frac{\partial \ln \bar{w}}{\partial z_j}$  is the **selection gradient**—the partial regression of (log) fitness on trait  $j$ , holding other traits constant.

**Say this:**

**In matrix notation:**

$$\text{Cov}_G(\mathbf{z}, w) = \mathbf{G}\boldsymbol{\beta}$$

**Verbal translation:** “The genetic covariance with fitness equals  $\mathbf{G}$  applied to the selection gradient.”

Using our mantra: “ $\mathbf{G}\boldsymbol{\beta}$  asks: where does  $\mathbf{G}$  send  $\boldsymbol{\beta}$ ?“

### 17.5.2 Why This Works

Let's unpack this step by step.

**Step 4a: What is the selection gradient  $\boldsymbol{\beta}$ ?**

The selection gradient  $\boldsymbol{\beta}$  is defined as:

$$\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{s} \quad (5)$$

**Think this:**

**In words:** “The selection gradient is the selection differential, standardized by phenotypic variance.”

**Using our verbal shortcuts:** “ $\mathbf{P}^{-1}\mathbf{s}$  runs  $\mathbf{P}$  backwards on  $\mathbf{s}$ ”—it removes the phenotypic scaling from the selection differential.

### Why do we need $\mathbf{P}^{-1}$ ?

The selection differential  $\mathbf{s} = \text{Cov}(\mathbf{z}, w)$  conflates two things:

1. Direct selection on each trait
2. Indirect effects through correlated traits

The selection gradient  $\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{s}$  isolates the *direct* selection on each trait, controlling for correlations.

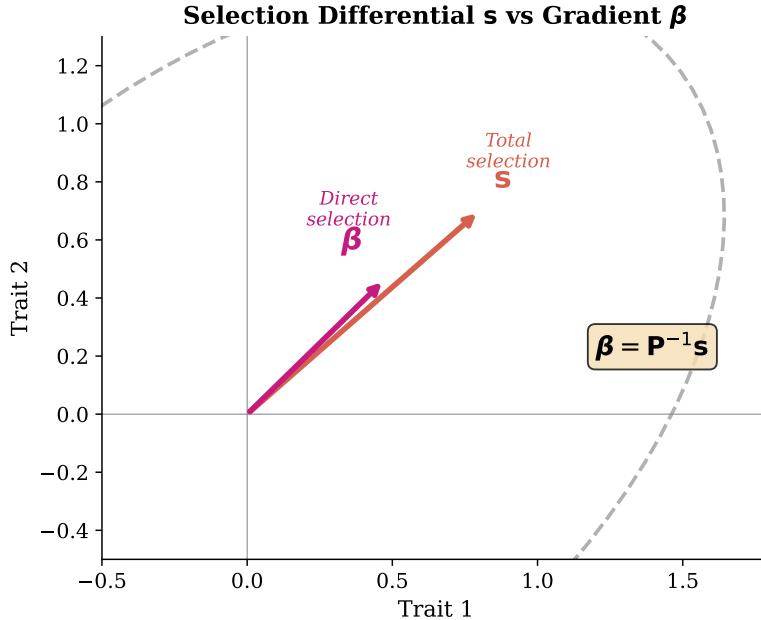


Figure 22: Selection differential vs gradient. The differential  $\mathbf{s}$  (red) includes correlated effects. The gradient  $\boldsymbol{\beta}$  (orange), obtained by applying  $\mathbf{P}^{-1}$ , isolates direct selection on each trait.

### Step 4b: Connecting genetic covariance to selection gradient

The breeding value  $a_i$  for trait  $i$  can be written as:

$$a_i = \sum_j G_{ij} \cdot (P^{-1})_{jk} \cdot z_k + \text{terms uncorrelated with } z$$

The covariance of  $a_i$  with fitness  $w$  is:

$$\text{Cov}(a_i, w) = \sum_j G_{ij} \cdot \underbrace{(P^{-1})_{jk} \cdot \text{Cov}(z_k, w)}_{=\beta_j} \quad (6)$$

$$= \sum_j G_{ij} \cdot \beta_j \quad (7)$$

$$= (\mathbf{G}\boldsymbol{\beta})_i \quad (8)$$

#### Mantra

Each element of  $\mathbf{G}\boldsymbol{\beta}$  is a dot product: row  $i$  of  $\mathbf{G}$  dotted with  $\boldsymbol{\beta}$ .

**Verbal:** “How aligned is the genetic variance of trait  $i$  (with all traits) with the selection gradient?”

## 17.6 Step 5: Assembling Lande’s Equation

Now we combine our results.

### 17.6.1 The Chain of Reasoning

1. **Robertson-Price:**  $\Delta\bar{z} = \text{Cov}_G(\mathbf{z}, w)$

“Response equals genetic covariance with fitness.”

2. **Genetic-phenotypic link:**  $\text{Cov}_G(\mathbf{z}, w) = \mathbf{G}\boldsymbol{\beta}$

“Genetic covariance with fitness equals  $\mathbf{G}$  applied to the selection gradient.”

3. **Therefore:**

$$\boxed{\Delta\bar{z} = \mathbf{G}\boldsymbol{\beta}} \quad (9)$$

#### Derivation Flow: Three Key Steps

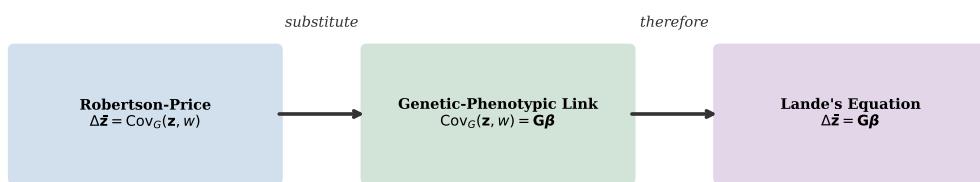


Figure 23: The logical flow of the derivation. Each arrow represents a key insight.

### 17.6.2 Alternative Form

Since  $\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{s}$ , we can also write:

$$\Delta\bar{z} = \mathbf{G}\mathbf{P}^{-1}\mathbf{s} \quad (10)$$

**Think this:**

**Reading this right-to-left:**

1. Start with the selection differential  $\mathbf{s}$  (how selection shifted phenotypes)
2. Apply  $\mathbf{P}^{-1}$ : “run  $\mathbf{P}$  backwards” to get direct selection  $\boldsymbol{\beta}$
3. Apply  $\mathbf{G}$ : “where does  $\mathbf{G}$  send  $\boldsymbol{\beta}$ ?” to get the response

## 17.7 Step 6: Geometric Interpretation

Now let’s visualize what Lande’s equation tells us.

### 17.7.1 The Response is Deflected

In general,  $\Delta\bar{z} = \mathbf{G}\boldsymbol{\beta}$  does **not** point in the same direction as  $\boldsymbol{\beta}$ .

**Mantra**

“Selection pulls in direction  $\boldsymbol{\beta}$ , but the genome responds in direction  $\mathbf{G}\boldsymbol{\beta}$ . If  $\mathbf{G}$  is anisotropic, the response *rotates* toward  $\mathbf{g}_{\max}$ .”

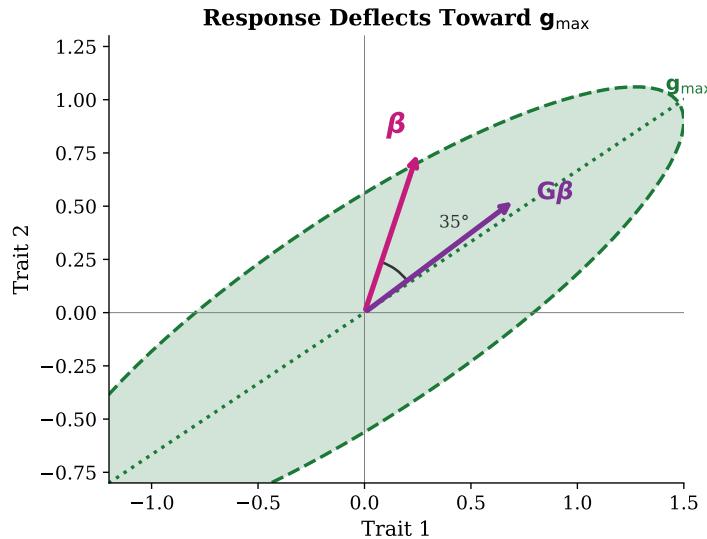


Figure 24: Deflection of evolutionary response. The selection gradient  $\beta$  (red) specifies the direction selection “wants” to go. The actual response  $\mathbf{G}\beta$  (purple) is rotated toward  $\mathbf{g}_{\max}$  (green dashed line), the genetic line of least resistance.

### 17.7.2 When Does Deflection Occur?

The response aligns with selection  $(\mathbf{G}\beta \parallel \beta)$  only when:

- $\beta$  is an eigenvector of  $\mathbf{G}$ , OR
- $\mathbf{G}$  is isotropic ( $\mathbf{G} = g\mathbf{I}$  for some scalar  $g$ )

Otherwise, the response is **deflected** toward directions of high genetic variance.

### 17.7.3 The Magnitude of Response

The length of the response vector is:

$$\|\Delta \bar{z}\| = \|\mathbf{G}\beta\|$$

This depends on:

- How much genetic variance exists in the direction of  $\beta$ : captured by  $\beta' \mathbf{G} \beta$
- How the G-matrix redistributes that variance across traits

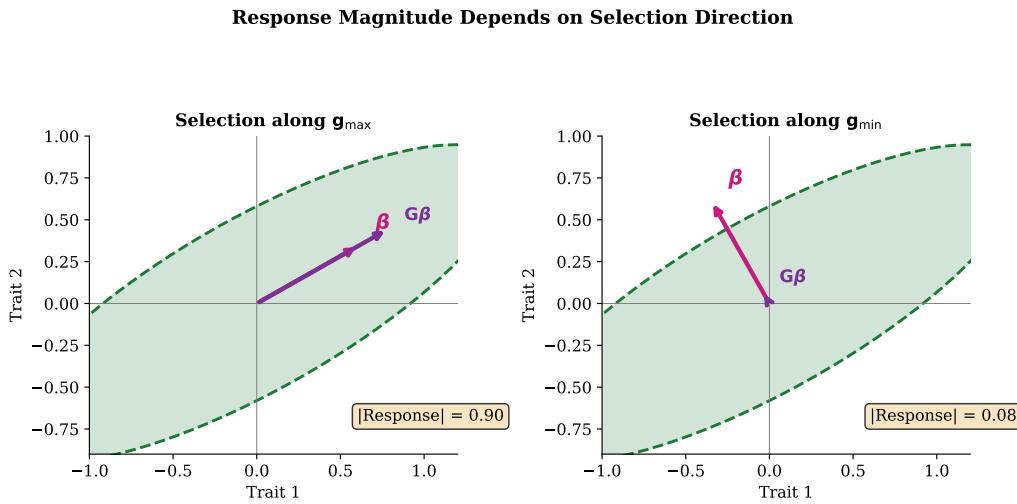


Figure 25: Response magnitude. Selection along  $\mathbf{g}_{\max}$  (left) produces a large response. Selection perpendicular to  $\mathbf{g}_{\max}$  (right) produces a small response. The G-matrix acts as a filter.

## 17.8 Step 7: Connection to Directional Heritability

Here's where our earlier work pays off.

### 17.8.1 Evolvability as Response Magnitude

The **evolvability** in direction  $\beta$  is:

$$e(\beta) = \beta' \mathbf{G} \beta \quad (11)$$

**Say this:**

**Verbal:** “How much genetic variance does  $\mathbf{G}$  have in direction  $\beta$ ? ”  
This is the quadratic form—the height of the G-bowl at direction  $\beta$ .

### 17.8.2 But Evolvability Isn't the Whole Story

High evolvability doesn't guarantee a large *realized* response. Why? Because selection may be weak in high-variance directions.

The **directional heritability** tells us what fraction of *phenotypic* variance is genetic:

$$h^2(\beta) = \frac{\beta' \mathbf{G} \beta}{\beta' \mathbf{P} \beta} \quad (12)$$

**Think this:**

**Verbal:** “What fraction of phenotypic variance in direction  $\beta$  is genetic? ”  
This is the Rayleigh quotient of  $(\mathbf{G}, \mathbf{P})$ .

### 17.8.3 The Constraint Trap

A **constraint trap** occurs when:

- Evolvability  $e(\beta)$  is moderate to high
- But directional heritability  $h^2(\beta)$  is low

This happens when environmental variance “swamps” the genetic signal in direction  $\beta$ .

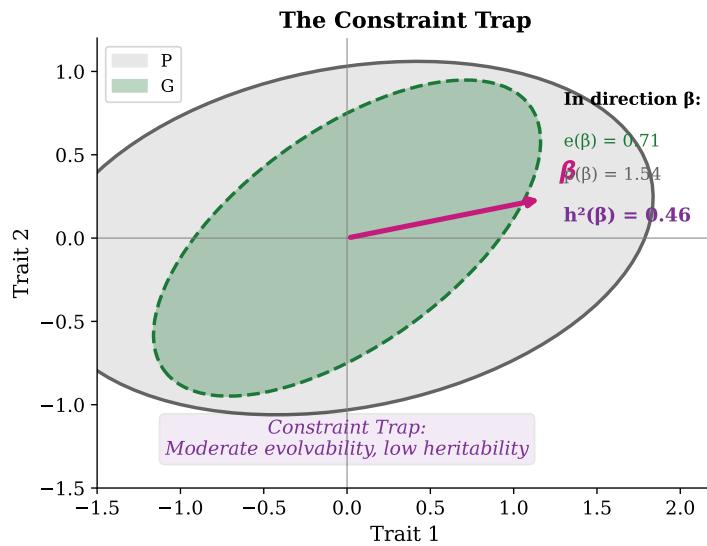


Figure 26: The constraint trap. In this direction, genetic variance (green) is reasonable, but phenotypic variance (gray) is much larger. The ratio  $h^2(\beta)$  is low, so the realized response is weak despite moderate evolvability.

## 17.9 Step 8: Summary and Key Takeaways

### 17.9.1 The Equation and Its Meaning

Lande's Multivariate Breeder's Equation

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

**In words:**

- $s$ : How much did selection shift the phenotypic mean? (selection differential)
- $\mathbf{P}^{-1}s = \beta$ : What was the *direct* selection on each trait? (selection gradient)
- $\mathbf{G}\beta$ : Where does the G-matrix send that selection? (evolutionary response)

### 17.9.2 The Verbal Playbook

When explaining Lande's equation, use this sequence:

1. “Selection creates a phenotypic shift  $s$ .”
2. “We extract the direct selection  $\beta = \mathbf{P}^{-1}s$  by running  $\mathbf{P}$  backwards—removing correlation effects.”
3. “We ask: where does  $\mathbf{G}$  send  $\beta$ ? That’s the response  $\Delta \bar{z}$ .”
4. “If  $\mathbf{G}$  is anisotropic (cigar-shaped), the response rotates toward  $\mathbf{g}_{\max}$ —the genetic line of least resistance.”
5. “The magnitude of response depends on evolvability  $\beta' \mathbf{G} \beta$ —how much genetic variance exists in the selection direction.”

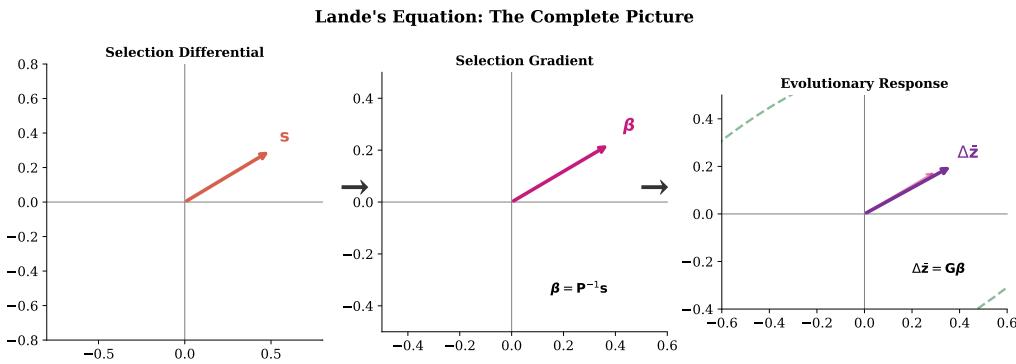


Figure 27: Visual summary of Lande's equation. Start with the selection differential (what phenotypic selection did), extract the gradient (what direct selection is), apply the G-matrix (where the genome sends it), arrive at the response.

### 17.9.3 The Communication Metaphor (Revisited)

Remember our communication channel metaphor? Lande's equation fits perfectly:

Communication	Symbol	Genetics
Message (sentence)	$\beta$	Selection gradient
Channel vocabulary	$G$	Genetic variance
Channel filter	$P$	Phenotypic variance
What gets through	$G\beta$	Evolutionary response

#### Mantra

“Selection speaks in direction  $\beta$ . The genome hears  $G\beta$ . The difference is constraint.”

## 17.10 Worked Example

Let's apply everything to a concrete 2-trait example.

### 17.10.1 Setup

Suppose we have:

$$G = \begin{pmatrix} 0.8 & 0.3 \\ 0.3 & 0.4 \end{pmatrix}, \quad P = \begin{pmatrix} 1.2 & 0.2 \\ 0.2 & 1.0 \end{pmatrix}, \quad s = \begin{pmatrix} 0.5 \\ 0.3 \end{pmatrix}$$

### 17.10.2 Step-by-Step Calculation

#### 1. Compute the selection gradient:

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

First, invert  $P$ :

$$P^{-1} = \frac{1}{1.2 \times 1.0 - 0.2 \times 0.2} \begin{pmatrix} 1.0 & -0.2 \\ -0.2 & 1.2 \end{pmatrix} = \frac{1}{1.16} \begin{pmatrix} 1.0 & -0.2 \\ -0.2 & 1.2 \end{pmatrix} \approx \begin{pmatrix} 0.862 & -0.172 \\ -0.172 & 1.034 \end{pmatrix}$$

Then:

$$\beta = \begin{pmatrix} 0.862 & -0.172 \\ -0.172 & 1.034 \end{pmatrix} \begin{pmatrix} 0.5 \\ 0.3 \end{pmatrix} = \begin{pmatrix} 0.862(0.5) - 0.172(0.3) \\ -0.172(0.5) + 1.034(0.3) \end{pmatrix} = \begin{pmatrix} 0.379 \\ 0.224 \end{pmatrix}$$

**Verbal:** “Running  $\mathbf{P}$  backwards on  $\mathbf{s}$  gives the direct selection  $\boldsymbol{\beta}$ .”

**2. Compute the response:**

$$\Delta\bar{z} = \mathbf{G}\boldsymbol{\beta} = \begin{pmatrix} 0.8 & 0.3 \\ 0.3 & 0.4 \end{pmatrix} \begin{pmatrix} 0.379 \\ 0.224 \end{pmatrix} = \begin{pmatrix} 0.8(0.379) + 0.3(0.224) \\ 0.3(0.379) + 0.4(0.224) \end{pmatrix} = \begin{pmatrix} 0.370 \\ 0.203 \end{pmatrix}$$

**Verbal:** “Where does  $\mathbf{G}$  send  $\boldsymbol{\beta}$ ? To  $(0.370, 0.203)$ .”

**3. Check the deflection:**

Angle of  $\boldsymbol{\beta}$ :  $\arctan(0.224/0.379) \approx 30.6$

Angle of  $\Delta\bar{z}$ :  $\arctan(0.203/0.370) \approx 28.8$

Deflection:  $30.6 - 28.8 = 1.8$  toward trait 1 (toward  $\mathbf{g}_{\max}$ ).

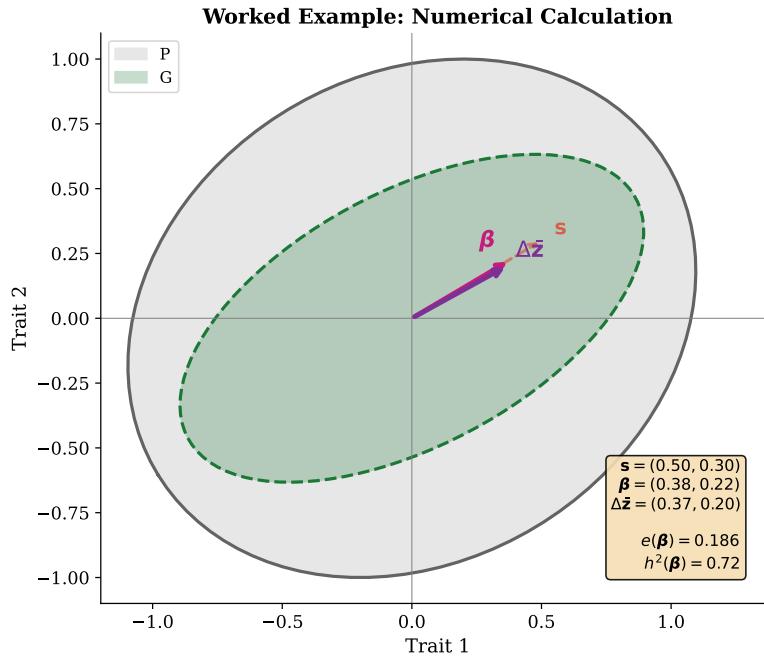


Figure 28: Worked example. The selection differential  $\mathbf{s}$  (gray dashed), selection gradient  $\boldsymbol{\beta}$  (red), and evolutionary response  $\Delta\bar{z}$  (purple) are shown with the G (green) and P (gray) ellipses.

### 17.10.3 Computing Evolvability and Directional Heritability

**Evolvability:**

$$e(\boldsymbol{\beta}) = \boldsymbol{\beta}'\mathbf{G}\boldsymbol{\beta} = (0.379, 0.224) \begin{pmatrix} 0.370 \\ 0.203 \end{pmatrix} = 0.379(0.370) + 0.224(0.203) = 0.186$$

**Phenotypic variance in direction  $\boldsymbol{\beta}$ :**

$$\boldsymbol{\beta}'\mathbf{P}\boldsymbol{\beta} = \boldsymbol{\beta}'\mathbf{s} = 0.379(0.5) + 0.224(0.3) = 0.257$$

(Note:  $\boldsymbol{\beta}'\mathbf{P}\boldsymbol{\beta} = \boldsymbol{\beta}'\mathbf{s}$  since  $\mathbf{s} = \mathbf{P}\boldsymbol{\beta}$ .)

**Directional heritability:**

$$h^2(\boldsymbol{\beta}) = \frac{e(\boldsymbol{\beta})}{\boldsymbol{\beta}'\mathbf{P}\boldsymbol{\beta}} = \frac{0.186}{0.257} = 0.72$$

**Verbal:** “In the selection direction, 72% of phenotypic variance is genetic.”

### 17.11 Exercises for the Reader

1. **Verify the univariate limit:** Show that when  $p = 1$ , Lande's equation reduces to  $R = h^2 S$ .
2. **Eigenvector selection:** If  $\beta$  is an eigenvector of  $\mathbf{G}$ , show that  $\Delta \bar{z} \parallel \beta$  (no deflection).
3. **Isotropic  $\mathbf{G}$ :** If  $\mathbf{G} = g\mathbf{I}$ , show that  $\Delta \bar{z} = g\beta$  (response is always parallel to selection).
4. **Selection on a single trait:** If selection acts only on trait 1, so  $s = (s_1, 0)'$ , compute  $\beta$  and  $\Delta \bar{z}$ . When does trait 2 respond?
5. **Constraint trap:** Construct a  $(\mathbf{G}, \mathbf{P})$  pair where some direction has high evolvability but low  $h^2(\beta)$ .

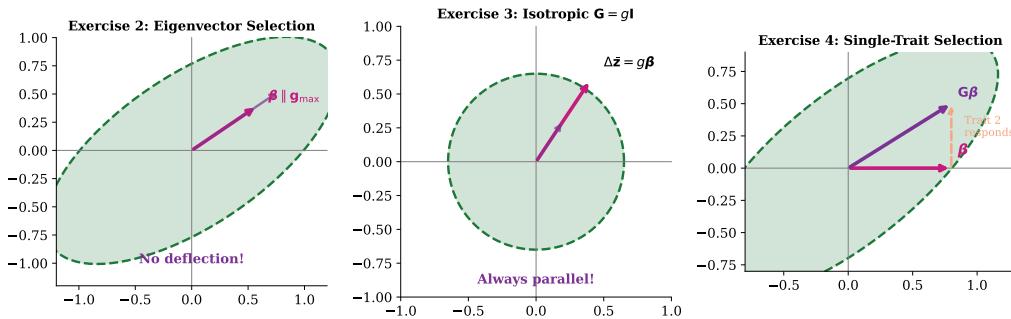


Figure 29: Visual aids for exercises.

# Appendices

## A Rausher's Rigorous Derivation of Lande's Equation

**You do not need this appendix to use Lande's equation.** The main text gives you the meaning and the working recipe. This appendix is for readers who want to see how the calculus and linear algebra combine under the hood.

In the main text, we derived Lande's equation using the Robertson-Price identity and presented  $\beta = \mathbf{P}^{-1}\mathbf{s}$  as a definition. Here we present the rigorous derivation following Rausher's approach, which *derives* this relationship from first principles using multivariate calculus.

This appendix serves two purposes:

1. To show the full mathematical machinery underlying Lande's equation
2. To practice “speaking linear algebra” on a real derivation

### A.1 Setup and Assumptions

We begin with a population of individuals, each characterized by a vector of  $n$  traits:

$$\mathbf{z} = (z_1, z_2, \dots, z_n)$$

#### Assumption 1: Additive Genetic Model

Each individual's phenotype decomposes as:

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

where  $\mathbf{x}$  is the **breeding value** (additive genetic component) and  $\boldsymbol{\epsilon}$  is the **environmental deviation**.

**Verbal:** “Phenotype equals genes plus environment.”

#### Assumption 2: Multivariate Normality

Both  $\mathbf{x}$  and  $\boldsymbol{\epsilon}$  follow multivariate normal distributions:

$$g(\mathbf{x}) \propto \exp\left[-\frac{1}{2}(\mathbf{x} - \bar{\mathbf{x}})' \mathbf{G}^{-1} (\mathbf{x} - \bar{\mathbf{x}})\right]$$

$$\xi(\boldsymbol{\epsilon}) \propto \exp\left[-\frac{1}{2}\boldsymbol{\epsilon}' \mathbf{E}^{-1} \boldsymbol{\epsilon}\right]$$

(We write  $\propto$  for “proportional to,” suppressing the normalizing constants  $(2\pi)^{-n/2}|\mathbf{G}|^{-1/2}$  etc., which won't affect the derivation.)

**Verbal:** “Breeding values are MVN with covariance  $\mathbf{G}$ ; environmental deviations are MVN with covariance  $\mathbf{E}$ .”

#### A.1.1 The Phenotypic Distribution

Since  $\mathbf{z} = \mathbf{x} + \boldsymbol{\epsilon}$  and both are normal, phenotypes are also multivariate normal:

$$p(\mathbf{z}) = C \exp\left[-\frac{1}{2}(\mathbf{z} - \bar{\mathbf{z}})' \mathbf{P}^{-1} (\mathbf{z} - \bar{\mathbf{z}})\right] \quad (13)$$

where  $C = (2\pi)^{-n/2}|\mathbf{P}|^{-1/2}$  is the normalizing constant and  $\mathbf{P} = \mathbf{G} + \mathbf{E}$  is the phenotypic covariance matrix.

**Think this:**

**Geometric picture:** The phenotypic distribution is a multivariate normal “cloud” centered at  $\bar{z}$ , with shape determined by  $\mathbf{P}$ . The exponent  $(\mathbf{z} - \bar{\mathbf{z}})' \mathbf{P}^{-1} (\mathbf{z} - \bar{\mathbf{z}})$  is the squared Mahalanobis distance from the mean.

**Using our mantra:** “ $\mathbf{P}^{-1}$  in the exponent measures distance in  $\mathbf{P}$ -standardized units.”

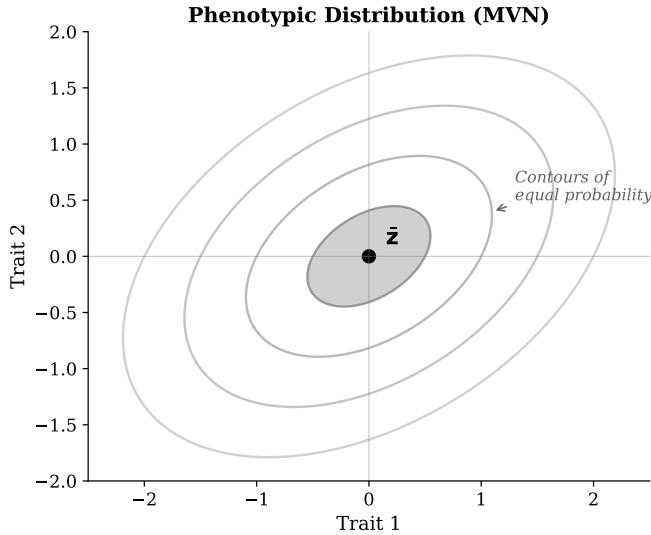


Figure 30: The phenotypic distribution as a multivariate normal cloud. Contours of equal probability are ellipses determined by  $\mathbf{P}$ . The center is the population mean  $\bar{z}$ .

## A.2 The Goal: Derive Lande’s Equation

Lande’s equation relates the change in mean phenotype to selection:

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

The derivation proceeds in **five steps**:

1. Show that  $\nabla \ln \bar{W} = \mathbf{P}^{-1} \mathbf{s}$  (the selection gradient equals standardized selection differential)
2. Compute  $\nabla p(\mathbf{z})$  for the multivariate normal
3. Plug into the expression for  $\nabla \bar{W}$
4. Identify the selection differential  $\mathbf{s}$
5. Derive  $\nabla \ln \bar{W} = \mathbf{G}^{-1} \Delta \bar{z}$  and combine

## A.3 Step 1: The Selection Gradient

### A.3.1 Mean Fitness

Let  $W(\mathbf{z})$  be the fitness of an individual with phenotype  $\mathbf{z}$ . The **mean fitness** of the population is:

$$\bar{W} = \int p(\mathbf{z}) W(\mathbf{z}) d\mathbf{z} \quad (14)$$

### Say this:

**Verbal:** “Mean fitness is the average of individual fitnesses, weighted by how common each phenotype is.”

### A.3.2 The Selection Gradient

The **selection gradient**  $\beta$  is defined as:

$$\beta = \nabla \ln \bar{W} = \frac{1}{\bar{W}} \nabla \bar{W} \quad (15)$$

Here  $\nabla$  (“nabla”) is the vector of partial derivatives with respect to each trait mean:  $\nabla = (\partial/\partial \bar{z}_1, \partial/\partial \bar{z}_2, \dots)$ . You can think of it as “the arrow that points uphill on the surface.”

### Think this:

#### What does this mean?

The gradient  $\nabla \ln \bar{W}$  points in the direction of steepest increase in log mean fitness. It’s the **tangent to the adaptive landscape**—the direction that maximizes the rate of fitness increase.

**Using our mantra:** “ $\nabla f$  points uphill on the  $f$ -surface.”

### Adaptive Landscape: $\beta = \nabla \ln \bar{W}$

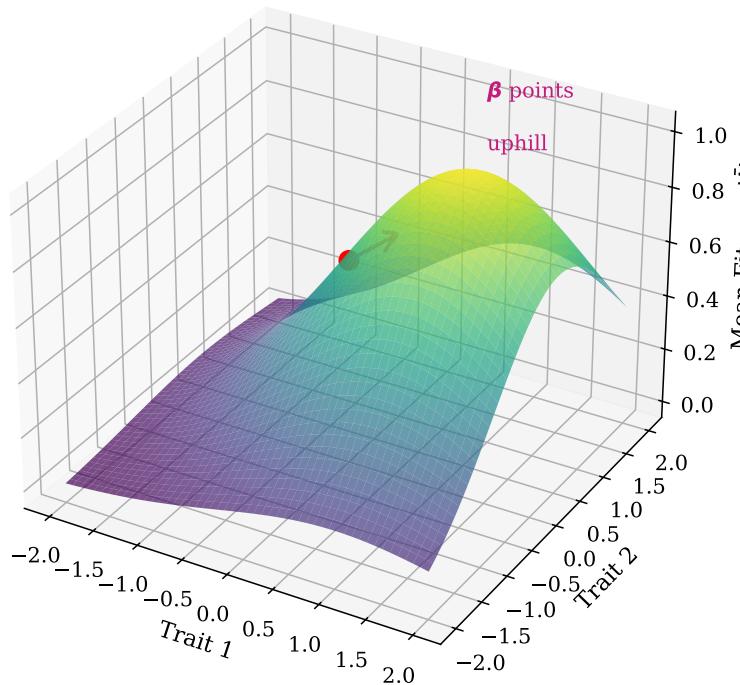


Figure 31: The adaptive landscape. Mean fitness  $\bar{W}$  is a surface over trait space. The selection gradient  $\beta = \nabla \ln \bar{W}$  points in the direction of steepest ascent.

### A.3.3 Key Calculus Identity

We use the chain rule for logarithms:

$$\nabla \ln \bar{W} = \frac{1}{\bar{W}} \nabla \bar{W} \quad (16)$$

**Say this:**

**Verbal:** “The gradient of log-fitness equals the gradient of fitness, divided by fitness.”  
This is just the multivariate version of  $\frac{d \ln x}{dt} = \frac{1}{x} \frac{dx}{dt}$ .

## A.4 Step 2: Computing the Gradient of the MVN Density

This is the technical heart of the derivation. We need to differentiate the MVN density.

### A.4.1 Rewriting the Density

Write equation (13) as:

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

where:

$$C = \sqrt{2\pi^{-n} |\mathbf{P}^{-1}|} \quad (\text{normalizing constant}) \quad (17)$$

$$u = -\frac{1}{2}(\mathbf{z} - \bar{\mathbf{z}})' \mathbf{P}^{-1} (\mathbf{z} - \bar{\mathbf{z}}) \quad (\text{the exponent}) \quad (18)$$

### A.4.2 Taking the Gradient

Since  $C$  doesn't depend on  $\mathbf{z}$ :

$$\nabla p(\mathbf{z}) = C \nabla \exp(u) = C \exp(u) \nabla u = p(\mathbf{z}) \nabla u \quad (19)$$

**Say this:**

**Verbal:** “The gradient of a Gaussian is the Gaussian times the gradient of its exponent.”  
This uses  $\frac{d}{dx} e^u = e^u \frac{du}{dx}$ .

### A.4.3 The Quadratic Form Derivative

Now we need  $\nabla u$  where  $u = -\frac{1}{2}(\mathbf{z} - \bar{\mathbf{z}})' \mathbf{P}^{-1} (\mathbf{z} - \bar{\mathbf{z}})$ .

**Mantra**

**Key result from linear algebra:** For any symmetric matrix  $\mathbf{M}$  and vector  $\mathbf{a}$ :

$$\frac{d[\mathbf{a}' \mathbf{M} \mathbf{a}]}{d\mathbf{a}} = 2\mathbf{M}\mathbf{a}$$

**Verbal:** “The derivative of a quadratic form is twice the matrix times the vector.”  
This is the multivariate version of  $\frac{d}{dx}(ax^2) = 2ax$ .

Applying this to our exponent with  $\mathbf{a} = \mathbf{z} - \bar{\mathbf{z}}$  and  $\mathbf{M} = \mathbf{P}^{-1}$ :

$$\nabla[(\mathbf{z} - \bar{\mathbf{z}})' \mathbf{P}^{-1} (\mathbf{z} - \bar{\mathbf{z}})] = 2\mathbf{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}})$$

Taking the gradient with respect to  $\bar{\mathbf{z}}$  (noting  $\nabla_{\bar{\mathbf{z}}}(\mathbf{z} - \bar{\mathbf{z}}) = -\mathbf{I}$ ):

$$\nabla p(\mathbf{z}) = p(\mathbf{z}) \cdot \mathbf{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}}) \quad (20)$$

Key Result: Gradient of MVN Density (w.r.t. Mean)

$$\boxed{\nabla_{\bar{\mathbf{z}}} p(\mathbf{z}) = \mathbf{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}}) \cdot p(\mathbf{z})}$$

**Verbal:** “The gradient *with respect to the population mean* points from each phenotype back toward the mean, scaled by  $\mathbf{P}^{-1}$  and weighted by the density itself.”

**Geometric:** At each point  $\mathbf{z}$ , the gradient points in the direction  $\mathbf{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}})$ —which is “toward the mean in  $\mathbf{P}$ -standardized coordinates.”

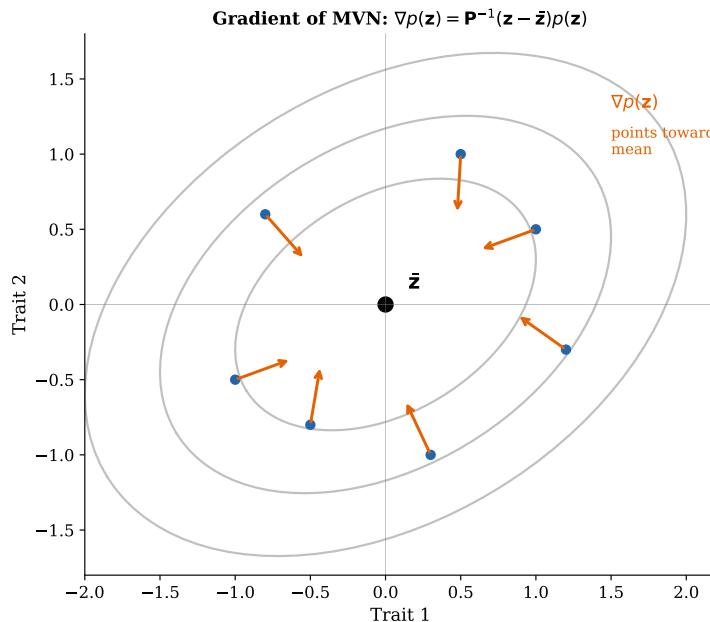


Figure 32: Gradient of the MVN density. At each point,  $\nabla p(\mathbf{z})$  points toward the mean, with magnitude proportional to  $p(\mathbf{z})$  and direction determined by  $\mathbf{P}^{-1}$ .

## A.5 Step 3: Computing the Gradient of Mean Fitness

Now we compute the gradient of mean fitness. From equation (14):

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

### A.5.1 Pulling the Gradient Inside

The gradient operator can be pulled inside the integral:

$$\nabla \bar{W} = \int \nabla [p(\mathbf{z}) W(\mathbf{z})] d\mathbf{z}$$

Using the product rule:

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

**Think this:**

**Key assumption:** Fitness  $W(\mathbf{z})$  depends on an individual's phenotype, not on the population mean  $\bar{\mathbf{z}}$ .

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

**Verbal:** "An individual's fitness doesn't change just because the population mean shifts."

This simplifies to:

$$\nabla \bar{W} = \int [\nabla p(\mathbf{z})] W(\mathbf{z}) d\mathbf{z} \quad (21)$$

**A.5.2 Substituting the MVN Gradient**

Plugging in equation (20):

$$\nabla \bar{W} = \int \mathbf{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}}) \cdot p(\mathbf{z}) \cdot W(\mathbf{z}) d\mathbf{z} \quad (22)$$

$$= \mathbf{P}^{-1} \int (\mathbf{z} - \bar{\mathbf{z}}) \cdot p(\mathbf{z}) \cdot W(\mathbf{z}) d\mathbf{z} \quad (23)$$

**Say this:**

**Verbal:** "We pulled  $\mathbf{P}^{-1}$  outside the integral because it doesn't depend on  $\mathbf{z}$ ."

Splitting the integral:

$$\nabla \bar{W} = \mathbf{P}^{-1} \left[ \int \mathbf{z} \cdot p(\mathbf{z}) W(\mathbf{z}) d\mathbf{z} - \bar{\mathbf{z}} \int p(\mathbf{z}) W(\mathbf{z}) d\mathbf{z} \right] \quad (24)$$

The second integral is just  $\bar{W}$  (mean fitness). So:

$$\nabla \bar{W} = \mathbf{P}^{-1} \left[ \int \mathbf{z} \cdot p(\mathbf{z}) W(\mathbf{z}) d\mathbf{z} - \bar{\mathbf{z}} \bar{W} \right] \quad (25)$$

**A.6 Step 4: Identifying the Selection Differential****A.6.1 The Mean Phenotype After Selection**

The expression  $\int \mathbf{z} \cdot p(\mathbf{z}) W(\mathbf{z}) d\mathbf{z}$  is related to the mean phenotype *after selection*.

Define the **post-selection frequency** of phenotype  $\mathbf{z}$ :

$$p'(\mathbf{z}) = \frac{W(\mathbf{z}) \cdot p(\mathbf{z}) \cdot N}{\int W(\mathbf{z}) p(\mathbf{z}) N d\mathbf{z}} = \frac{W(\mathbf{z}) \cdot p(\mathbf{z})}{\bar{W}}$$

**Say this:**

**Verbal:** "After selection, phenotypes with higher fitness are more common. The new frequency is the old frequency times fitness, normalized."

The mean phenotype after selection is:

$$\bar{\mathbf{z}}^* = \int \mathbf{z} \cdot p'(\mathbf{z}) d\mathbf{z} = \frac{1}{\bar{W}} \int \mathbf{z} \cdot W(\mathbf{z}) \cdot p(\mathbf{z}) d\mathbf{z}$$

Therefore:

$$\int \mathbf{z} \cdot p(\mathbf{z}) W(\mathbf{z}) d\mathbf{z} = \bar{W} \cdot \bar{\mathbf{z}}^*$$

### A.6.2 The Selection Differential Emerges

Substituting back:

$$\nabla \bar{W} = \mathbf{P}^{-1} [\bar{W} \cdot \bar{z}^* - \bar{z} \bar{W}] \quad (26)$$

$$= \mathbf{P}^{-1} \bar{W} [\bar{z}^* - \bar{z}] \quad (27)$$

$$= \mathbf{P}^{-1} \bar{W} \cdot \mathbf{s} \quad (28)$$

where  $\mathbf{s} = \bar{z}^* - \bar{z}$  is the **selection differential**.

#### The Selection Differential

$$\mathbf{s} = \bar{z}^* - \bar{z} = \text{Cov}(\mathbf{z}, W)$$

**Verbal:** “The selection differential is how much selection shifted the phenotypic mean—equivalently, the covariance between phenotype and fitness.”

### A.6.3 The Selection Gradient

Now we can compute  $\boldsymbol{\beta}$ :

$$\boldsymbol{\beta} = \nabla \ln \bar{W} = \frac{1}{\bar{W}} \nabla \bar{W} \quad (29)$$

$$= \frac{1}{\bar{W}} \cdot \mathbf{P}^{-1} \bar{W} \cdot \mathbf{s} \quad (30)$$

$$= \mathbf{P}^{-1} \mathbf{s} \quad (31)$$

#### Key Result: Selection Gradient

$$\boxed{\boldsymbol{\beta} = \nabla \ln \bar{W} = \mathbf{P}^{-1} \mathbf{s}}$$

**Verbal:** “The selection gradient is the selection differential with phenotypic correlations removed—it measures *direct* selection on each trait.”

**Using our mantra:** “ $\mathbf{P}^{-1} \mathbf{s}$  runs  $\mathbf{P}$  backwards on  $\mathbf{s}$ —removing the phenotypic scaling.”

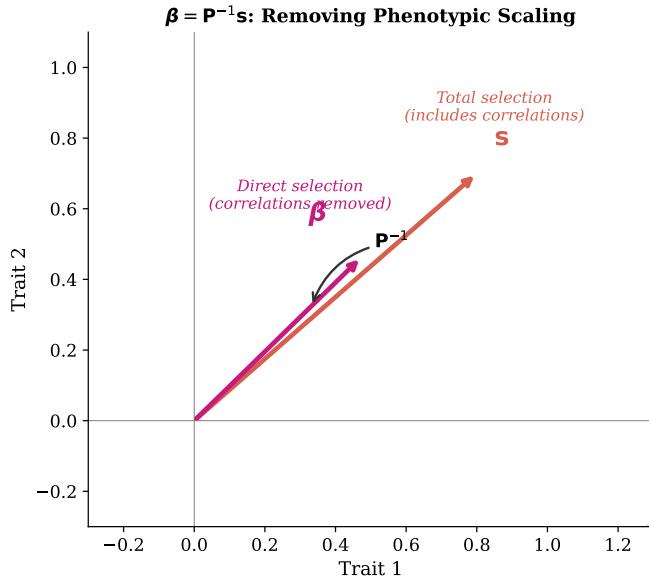


Figure 33: Selection differential  $s$  versus selection gradient  $\beta$ . The transformation  $\mathbf{P}^{-1}$  removes the effect of phenotypic correlations, isolating direct selection.

## A.7 Step 5: Connecting to the Evolutionary Response

The final step relates the selection gradient to the change in mean phenotype across generations.

### A.7.1 The Parallel Derivation

Rausher's insight: run the *same* derivation, but for breeding values instead of phenotypes.

Define the mean fitness of individuals with breeding value  $\mathbf{x}$ :

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

**Say this:**

**Verbal:** “The expected fitness of an individual with breeding value  $\mathbf{x}$ , averaging over all possible environmental effects.”

Mean population fitness can also be written as:

$$\bar{W} = \int g(\mathbf{x}) \tilde{W}(\mathbf{x}) d\mathbf{x}$$

Running the same Steps 1-4 on this expression gives:

$$\frac{1}{\bar{W}} \int \tilde{W}(\mathbf{x}) \mathbf{x} g(\mathbf{x}) d\mathbf{x} - \bar{\mathbf{x}} = \Delta \bar{\mathbf{x}} = \Delta \bar{\mathbf{z}} \quad (32)$$

The last equality holds because mean breeding value equals mean phenotype (environmental effects average to zero).

### A.7.2 The Analog Expression

Following the same logic as before, we get:

$$\nabla \ln \bar{W} = \mathbf{G}^{-1} \Delta \bar{\mathbf{z}} \quad (33)$$

Think this:

Compare the two expressions:

From phenotypes:  $\nabla \ln \bar{W} = \mathbf{P}^{-1} \mathbf{s} = \boldsymbol{\beta}$

From breeding values:  $\nabla \ln \bar{W} = \mathbf{G}^{-1} \Delta \bar{z}$

These must be equal!

### A.7.3 Assembling Lande's Equation

Equating the two expressions:

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

Multiplying both sides by  $\mathbf{G}$ :

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

Lande's Equation: The Final Result

$$\boxed{\Delta \bar{z} = \mathbf{G} \boldsymbol{\beta} = \mathbf{G} \mathbf{P}^{-1} \mathbf{s}}$$

**Verbal translation (reading right to left):**

1. Start with the selection differential  $\mathbf{s}$  (how selection shifted phenotypes)
2. Apply  $\mathbf{P}^{-1}$ : “run  $\mathbf{P}$  backwards” to get direct selection  $\boldsymbol{\beta}$
3. Apply  $\mathbf{G}$ : “where does  $\mathbf{G}$  send  $\boldsymbol{\beta}$ ?” to get the response

The derivation is complete. ■

## A.8 Summary: The Five Steps in Words

Step	Math	Verbal Translation
1	$\boldsymbol{\beta} = \nabla \ln \bar{W}$	“Selection gradient points uphill on the fitness landscape”
2	$\nabla p(\mathbf{z}) = \mathbf{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}})p(\mathbf{z})$	“Gradient of MVN points toward the mean, scaled by $\mathbf{P}^{-1}$ ”
3	$\nabla \bar{W} = \mathbf{P}^{-1} \bar{W} \mathbf{s}$	“Gradient of mean fitness involves $\mathbf{P}^{-1}$ and the selection differential”
4	$\boldsymbol{\beta} = \mathbf{P}^{-1} \mathbf{s}$	“Selection gradient is standardized selection differential”
5	$\mathbf{G}^{-1} \Delta \bar{z} = \boldsymbol{\beta}$	“The same $\boldsymbol{\beta}$ controls both phenotypic selection and genetic response”

### Mantra

**The core insight:** Selection acts on phenotypes ( $\mathbf{P}$ ), but only genetics ( $\mathbf{G}$ ) is inherited. The selection gradient  $\boldsymbol{\beta}$  bridges these two worlds—it appears in both

$$\boldsymbol{\beta} = \mathbf{P}^{-1} \mathbf{s} \quad \text{and} \quad \boldsymbol{\beta} = \mathbf{G}^{-1} \Delta \bar{z}$$

Combining these gives Lande's equation.

## A.9 The Quadratic Form Derivative: A Closer Look

The derivative  $\frac{d[a'Ma]}{da} = 2Ma$  is central to this derivation. Let's unpack it.

### A.9.1 Why This Works

Expand the quadratic form:

$$\mathbf{a}'\mathbf{M}\mathbf{a} = \sum_i \sum_j a_i M_{ij} a_j$$

Taking the derivative with respect to  $a_k$ :

$$\frac{\partial}{\partial a_k} [\mathbf{a}'\mathbf{M}\mathbf{a}] = \sum_j M_{kj} a_j + \sum_i a_i M_{ik} = (\mathbf{M}\mathbf{a})_k + (\mathbf{M}'\mathbf{a})_k$$

For symmetric  $\mathbf{M}$  (where  $\mathbf{M} = \mathbf{M}'$ ):

$$\frac{\partial}{\partial a_k} [\mathbf{a}'\mathbf{M}\mathbf{a}] = 2(\mathbf{M}\mathbf{a})_k$$

Assembling all components:  $\nabla_{\mathbf{a}}[\mathbf{a}'\mathbf{M}\mathbf{a}] = 2\mathbf{M}\mathbf{a}$ .

**Say this:**

**Verbal:** “The gradient of ‘variance in direction  $\mathbf{a}$ ’ is  $2\mathbf{M}\mathbf{a}$ —it points in the direction  $\mathbf{M}$  sends  $\mathbf{a}$ . ”

### A.9.2 Connection to the Phrasebook

This is exactly Section 5 (Quadratic Form) in action! The quadratic form  $\mathbf{a}'\mathbf{M}\mathbf{a}$  is the height of the  $\mathbf{M}$ -bowl at direction  $\mathbf{a}$ . Its gradient tells us which direction increases that height fastest.

**Gradient of Quadratic Form:  $\nabla(\mathbf{a}'\mathbf{M}\mathbf{a}) = 2\mathbf{M}\mathbf{a}$**

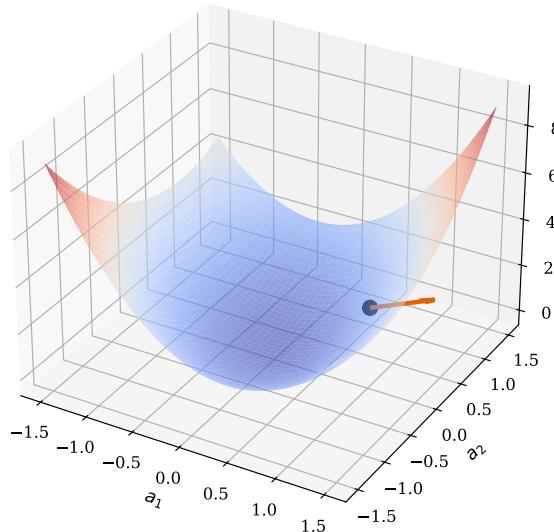


Figure 34: The gradient of a quadratic form. At point  $\mathbf{a}$ , the gradient  $2\mathbf{M}\mathbf{a}$  points in the direction of steepest ascent on the  $\mathbf{M}$ -paraboloid.

## A.10 Historical Note

This derivation follows Lande's original 1979 paper (Evolution 33: 402-416), as presented in teaching notes by Mark Rausher. The main insights were:

1. Recognizing that the selection gradient  $\beta = \nabla \ln \bar{W}$  is the natural measure of directional selection
2. Using multivariate normal theory to derive  $\beta = \mathbf{P}^{-1} s$
3. Running parallel derivations for phenotypes and breeding values to connect selection to response

The equation  $\Delta \bar{z} = \mathbf{G}\beta$  has become a foundational result in evolutionary quantitative genetics, forming the basis for understanding multivariate evolution, genetic constraints, and the evolution of correlated characters.

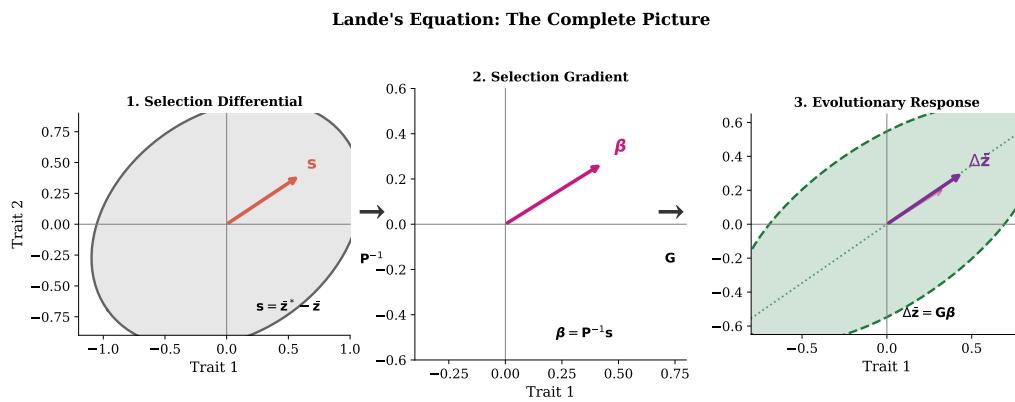


Figure 35: The complete picture. Selection creates  $s$ , which becomes  $\beta$  after removing  $\mathbf{P}$ -scaling. The  $G$ -matrix transforms  $\beta$  into the response  $\Delta \bar{z}$ , generally deflecting it toward  $\mathbf{g}_{\max}$ .