

# Speaking Linear Algebra

A Verbal Phrasebook for Quantitative Geneticists

For teaching and rapid communication

December 2024

## 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.

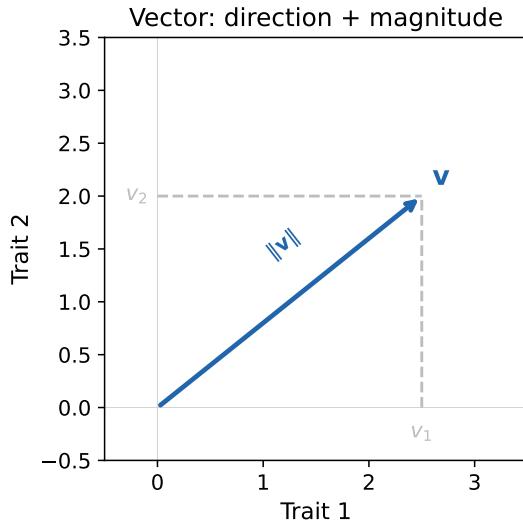


Figure 1: A vector as an arrow: direction plus magnitude. Components  $(v_1, v_2)$  give the coordinates.

### Say this:

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

### 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.

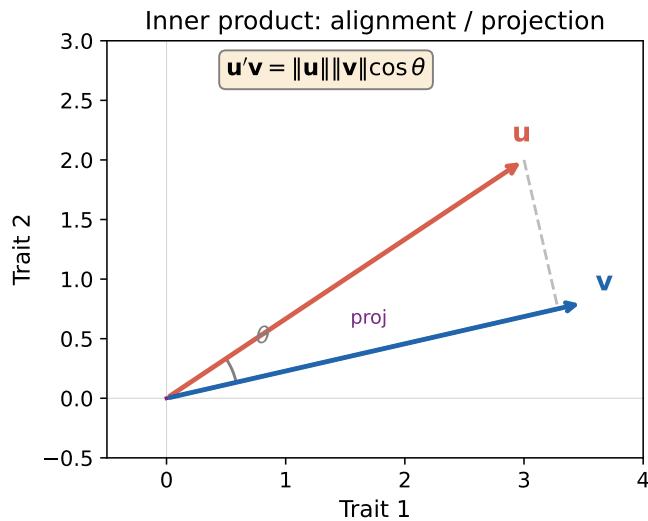


Figure 2: Inner product as projection.  $\mathbf{u}'\mathbf{v} = \|\mathbf{u}\| \|\mathbf{v}\| \cos \theta$  measures alignment.

**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  $u$ .

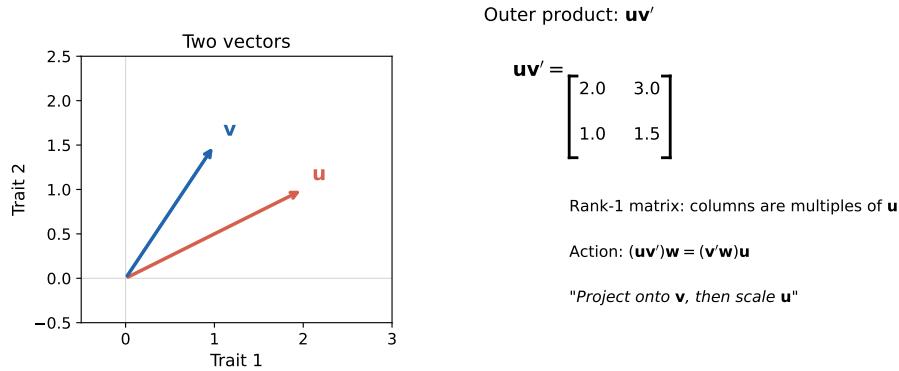


Figure 3: Outer product builds a matrix from two vectors. Its action: project onto  $v$ , then scale along  $u$ .

#### 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: $\mathbf{Mv}$

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

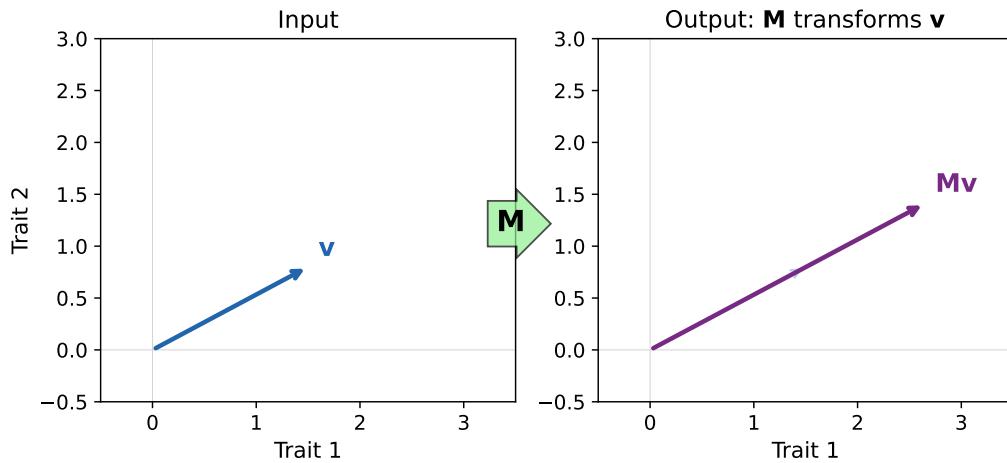


Figure 4:  $\mathbf{Mv}$ : the matrix  $\mathbf{M}$  transforms the arrow  $\mathbf{v}$  into a new arrow (generally different direction and length).

### 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”

### Mantra

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

### Biological translation

- |                             |  |
|-----------------------------|--|
| $\mathbf{G}\beta$           | “The response to selection: where does $\mathbf{G}$ send $\beta$ ? ” |
| $\mathbf{P}^{-1}\mathbf{z}$ | “The phenotype $\mathbf{z}$ in standardized (whitened) units”        |

## 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  $\mathbf{v}$

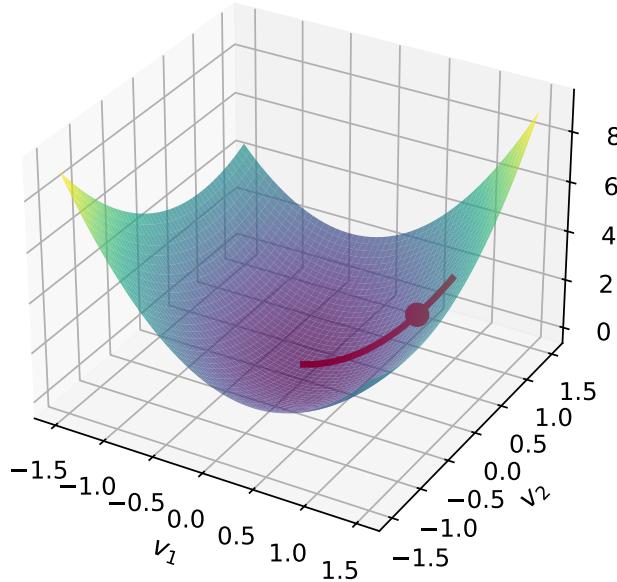


Figure 5: Quadratic form as height of a paraboloid. The surface shows  $\mathbf{v}'\mathbf{M}\mathbf{v}$  over all directions. The red curve traces one direction.

**Say this:**

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

**Mantra**

“ $\mathbf{v}'\mathbf{M}\mathbf{v}$  asks: *how much variance does  $\mathbf{M}$  have in direction  $\mathbf{v}$ ?*”

**Biological translation**

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

## 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”
- “Reverse the direction of the transformation”

Think this:

Key properties:

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

Mantra

“Symmetric matrices are their own transpose—what goes in equals what comes out.”

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

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

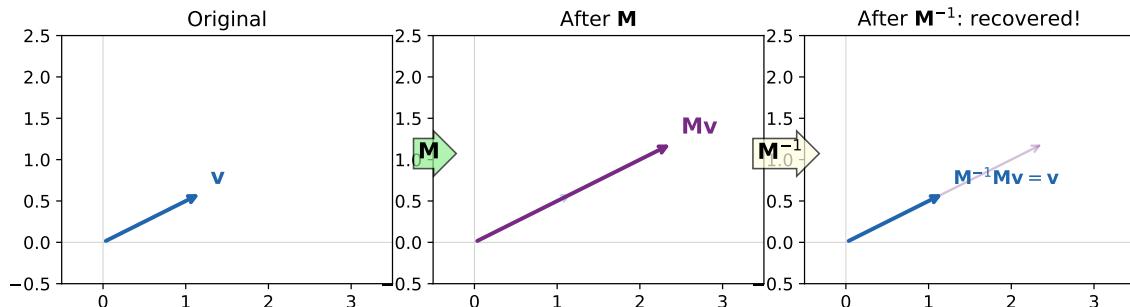


Figure 7: The inverse undoes the transformation. Apply  $\mathbf{M}$ , then  $\mathbf{M}^{-1}$ : you're back where you started.

### 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!

### 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.

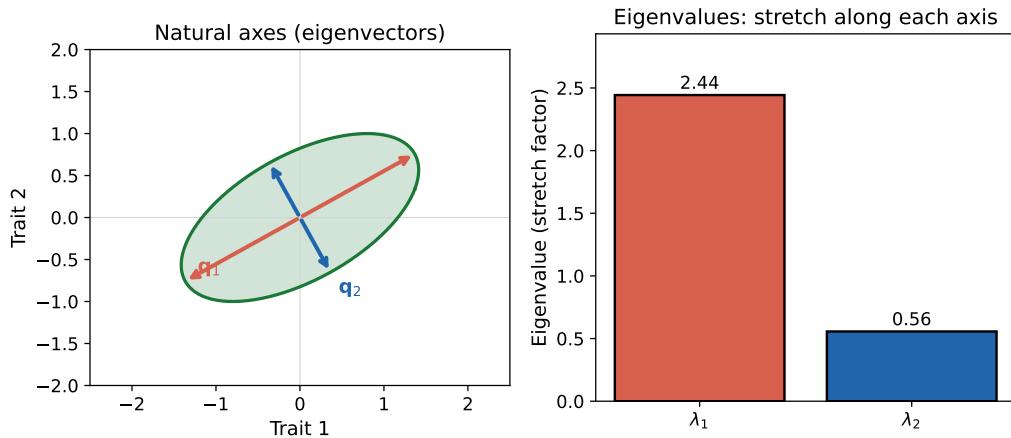


Figure 8: Left: Eigenvectors are the natural axes (directions of pure stretch). Right: Eigenvalues are the stretch factors.

### Say this:

- “Find the natural axes of  $\mathbf{M}$ ”
- “Directions where  $\mathbf{M}$  only stretches, no rotation”
- “Principal components”

### 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”:  $\mathbf{M}^{1/2}\mathbf{M}^{1/2} = \mathbf{M}$ .

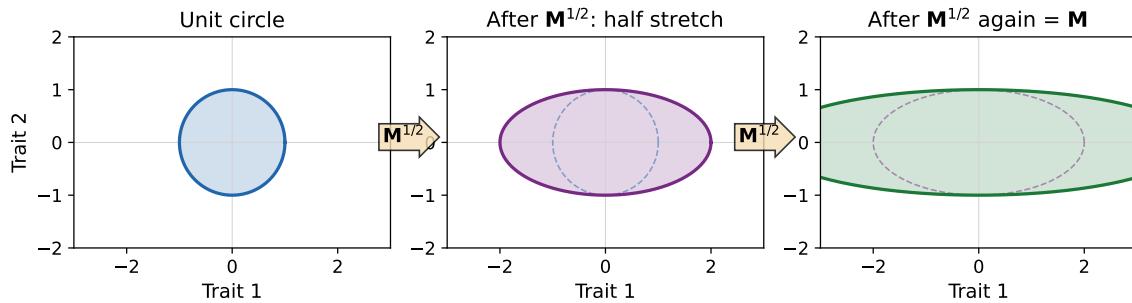


Figure 9: Matrix square root: applying  $\mathbf{M}^{1/2}$  twice gives  $\mathbf{M}$ . If  $\mathbf{M}$  stretches by 4,  $\mathbf{M}^{1/2}$  stretches by 2.

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

### 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).

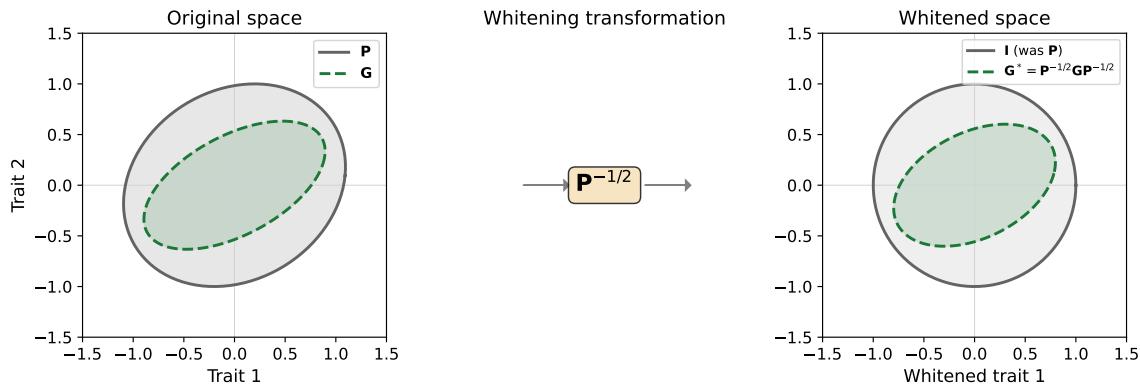


Figure 10: Whitening transformation. Left: Original space with  $\mathbf{P}$  (ellipse) and  $\mathbf{G}$  (dashed). Right: After whitening,  $\mathbf{P}$  becomes  $\mathbf{I}$  (circle), revealing  $\mathbf{G}^*$ .

### 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.

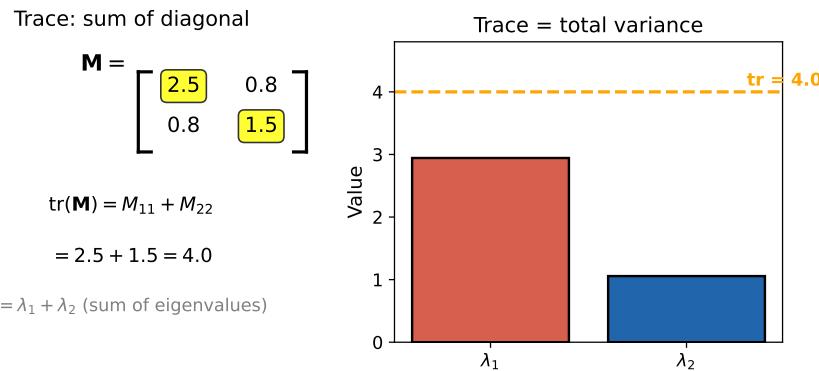


Figure 11: Trace: sum of diagonal elements = sum of eigenvalues = total variance.

### 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.

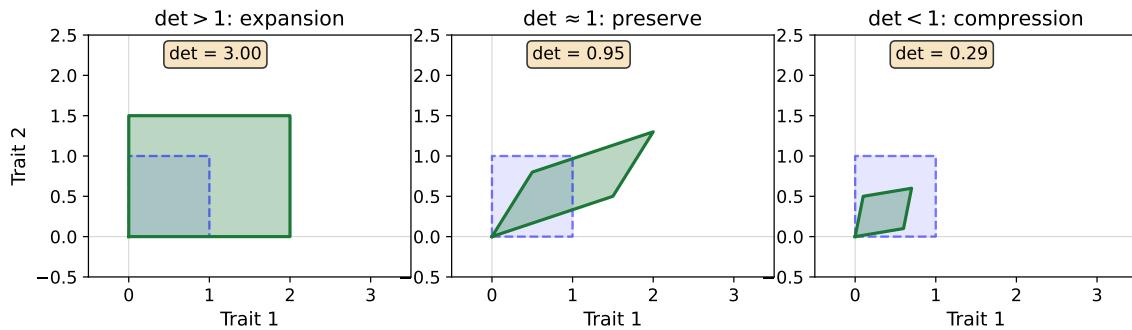


Figure 12: Determinant as volume scaling. Left: expansion ( $\det > 1$ ). Center: preservation ( $\det \approx 1$ ). Right: compression ( $\det < 1$ ).

### Say this:

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

### Think this:

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

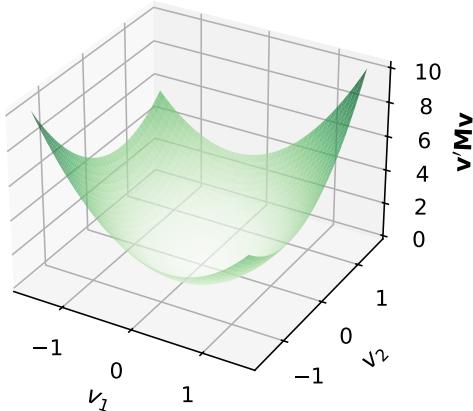
### Biological translation

- |                        |   |
|------------------------|---|
| $\det(\mathbf{G})$     | “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  $\mathbf{v} \neq \mathbf{0}$



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

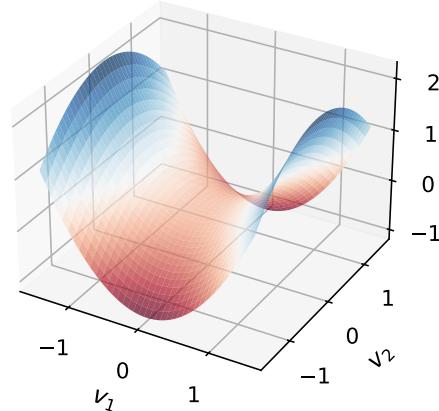


Figure 13: Left: Positive definite—bowl opens upward,  $\mathbf{v}'\mathbf{M}\mathbf{v} > 0$  for all  $\mathbf{v} \neq \mathbf{0}$ . Right: Indefinite—saddle shape, some directions give negative values.

**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*—the matrix is bowl-shaped with a unique minimum at the origin.”

**Biological translation**

All covariance matrices ( $\mathbf{G}, \mathbf{P}, \mathbf{E}$ ) must be positive semi-definite ( $\mathbf{M} \succeq 0$ ).

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.

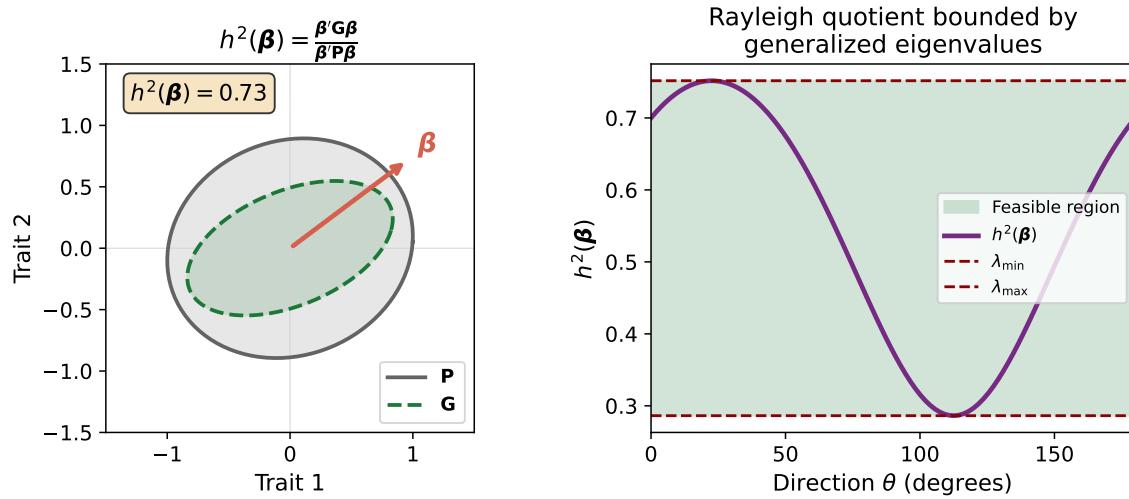


Figure 14: Left:  $\mathbf{G}$  and  $\mathbf{P}$  ellipses with direction  $\beta$ . Right:  $h^2(\beta)$  varies with direction but is bounded by  $\lambda_{\min}$  and  $\lambda_{\max}$ .

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

### 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  $\mathbf{g}_{\max}$ .

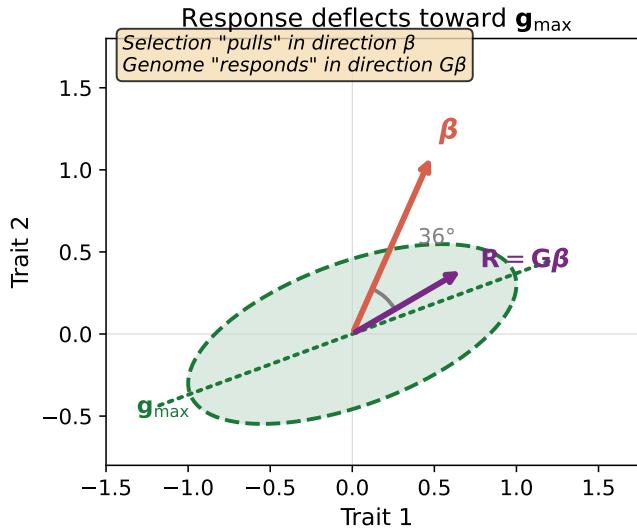


Figure 15: Response deflection. Selection pulls in direction  $\beta$ , but the response  $\mathbf{R} = \mathbf{G}\beta$  rotates toward the genetic line of least resistance  $\mathbf{g}_{\max}$ .

### 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”                         |
| $\beta \perp \mathbf{g}_{\max}$  | “Maximum deflection—selection against genetic variance” |

## 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 of $M$ in direction $v$ ” | Height of bowl             |
| $M'$           | “Flip across diagonal”              | Reverse transformation     |
| $M^{-1}$       | “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

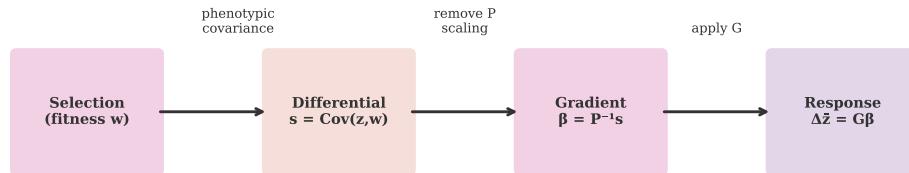


Figure 16: Overview of Lande's equation. Selection creates a phenotypic shift (the selection differential  $s$ ), which we decompose into a direction-independent gradient  $\beta$ , then filter through the genetic architecture  $\mathbf{G}$  to get the evolutionary response  $\Delta\bar{z}$ .

#### 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*

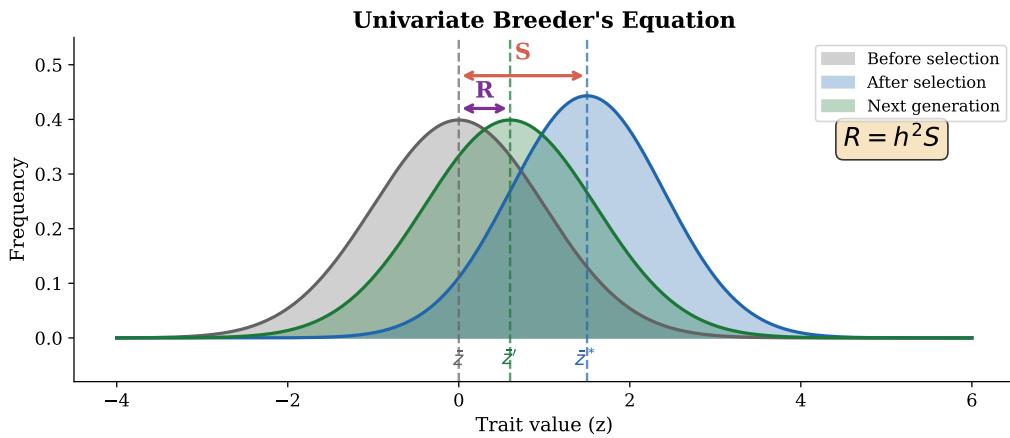


Figure 17: The univariate breeder's equation setup. Selection shifts the distribution (gray → blue), then inheritance filters that shift (blue → green). The response  $R$  is smaller than the selection differential  $S$  by a factor of  $h^2$ .

### 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:

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

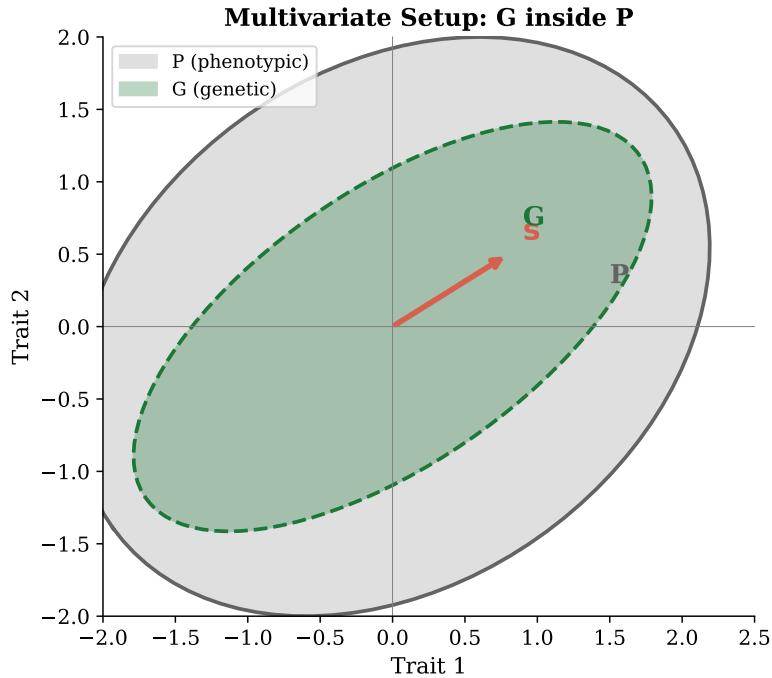


Figure 19: The multivariate setup.  $\mathbf{P}$  (gray ellipse) captures phenotypic variance and covariance.  $\mathbf{G}$  (green ellipse) captures genetic variance and covariance. The selection differential  $s$  (red arrow) shows how selection shifts the phenotypic mean.

### 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**.

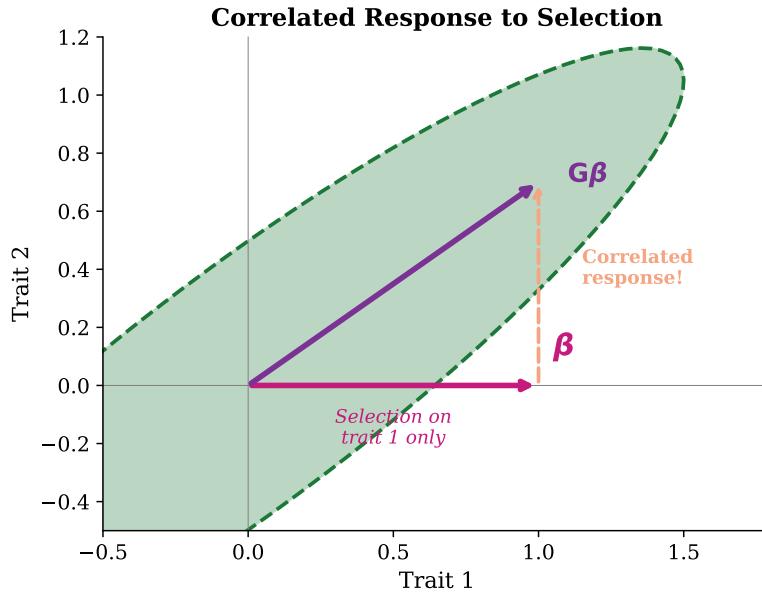


Figure 20: Correlated response. Even if selection acts only on trait 1 (horizontal arrow), the response (purple arrow) has a component in trait 2 because the traits are genetically correlated. The G-matrix encodes this coupling.

## 17.4 Step 3: The Robertson-Price Identity

The key to the multivariate derivation is a beautiful 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:  $\Delta \bar{z} = \text{Cov}(a, w) = \text{Cov}_G(z, w)$

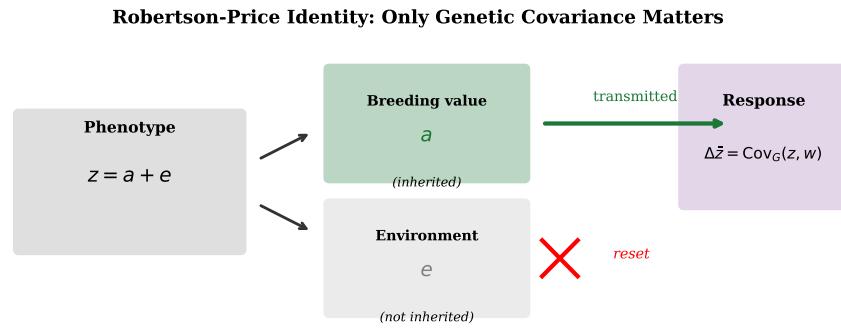


Figure 21: The Robertson-Price identity. Fitness selects on phenotypes, but only the genetic component (breeding value) is transmitted to offspring.

## 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.

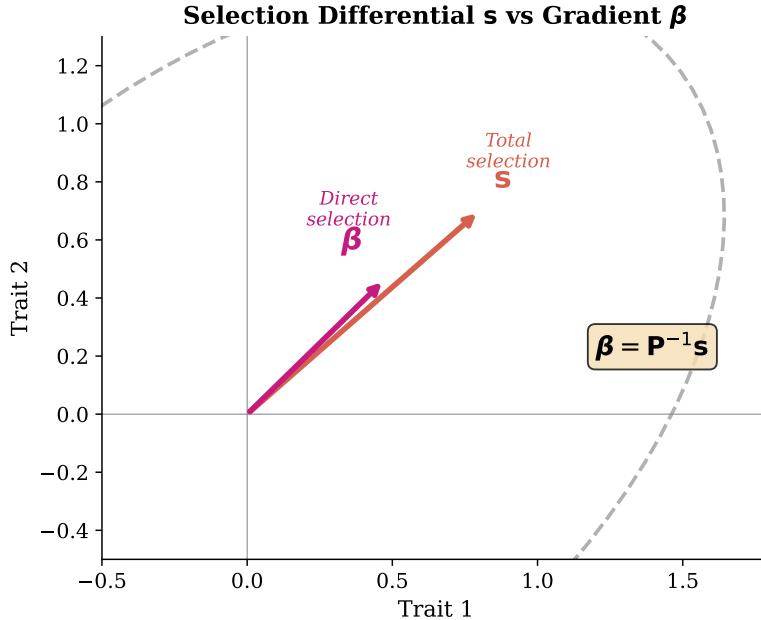


Figure 22: Selection differential vs gradient. The differential  $\mathbf{s}$  (red) includes correlated effects. The gradient  $\boldsymbol{\beta}$  (orange), obtained by applying  $\mathbf{P}^{-1}$ , isolates direct selection on each trait.

### 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

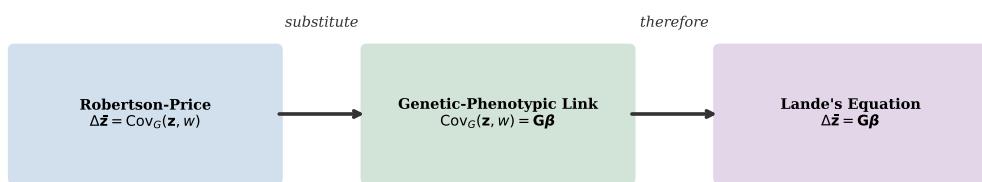


Figure 23: The logical flow of the derivation. Each arrow represents a key insight.

### 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  $\mathbf{g}_{\max}$ .”

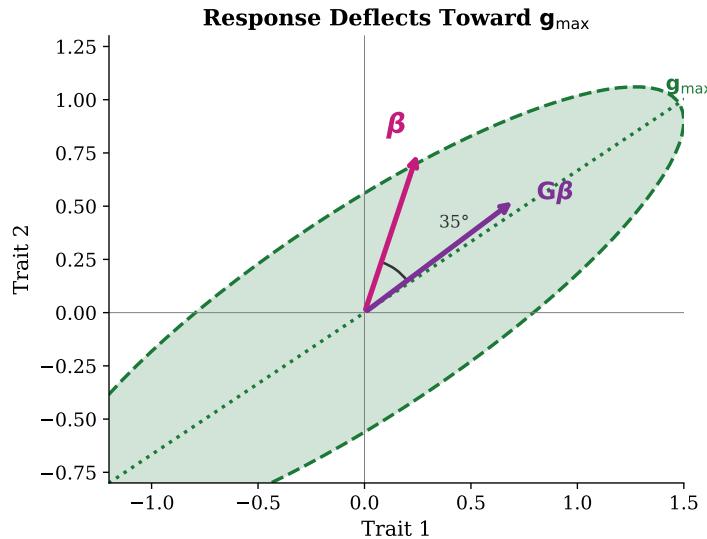


Figure 24: Deflection of evolutionary response. The selection gradient  $\beta$  (red) specifies the direction selection “wants” to go. The actual response  $\mathbf{G}\beta$  (purple) is rotated toward  $\mathbf{g}_{\max}$  (green dashed line), the genetic line of least resistance.

### 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

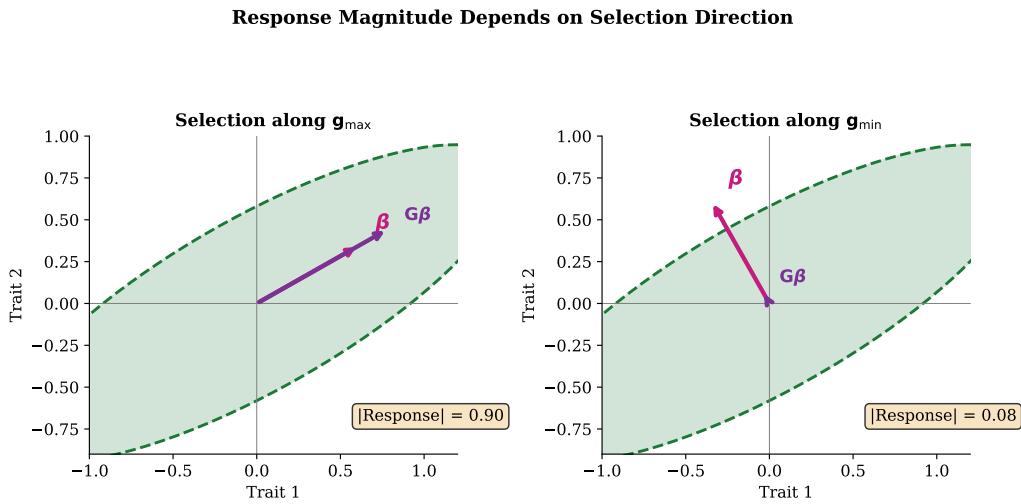


Figure 25: Response magnitude. Selection along  $\mathbf{g}_{\max}$  (left) produces a large response. Selection perpendicular to  $\mathbf{g}_{\max}$  (right) produces a small response. The G-matrix acts as a filter.

## 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  $\beta$ .

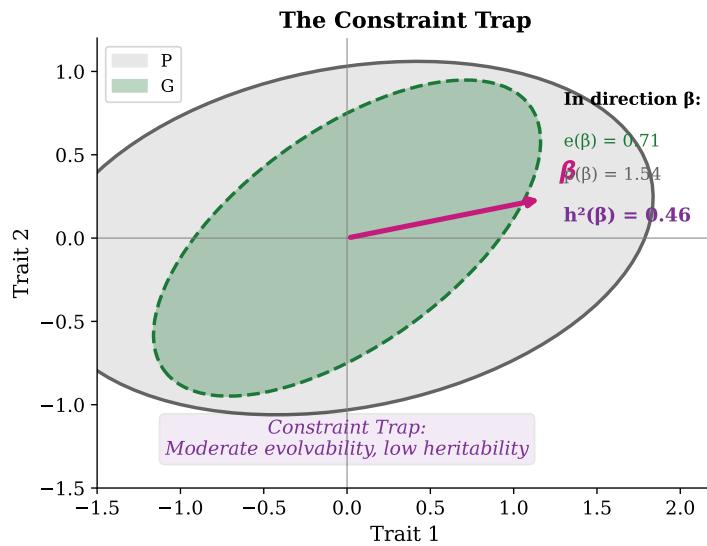


Figure 26: The constraint trap. In this direction, genetic variance (green) is reasonable, but phenotypic variance (gray) is much larger. The ratio  $h^2(\beta)$  is low, so the realized response is weak despite moderate evolvability.

## 17.9 Step 8: Summary and Key Takeaways

### 17.9.1 The Equation and Its Meaning

Lande's Multivariate Breeder's Equation

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

**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.”

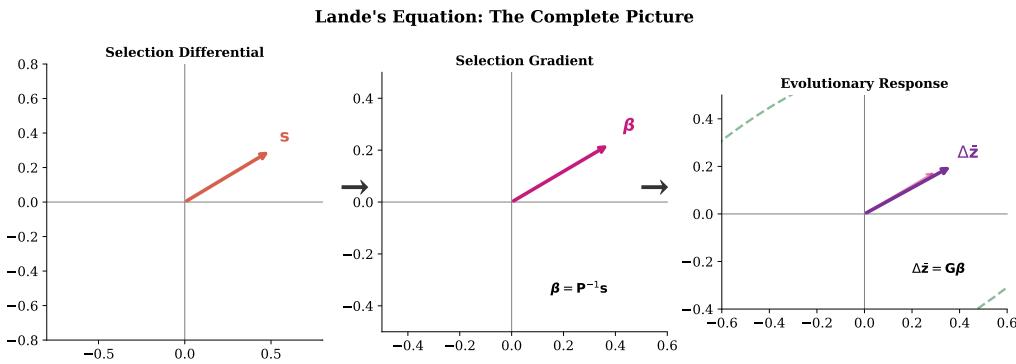


Figure 27: Visual summary of Lande's equation. Start with the selection differential (what phenotypic selection did), extract the gradient (what direct selection is), apply the G-matrix (where the genome sends it), arrive at the response.

### 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  $\mathbf{g}_{\max}$ ).

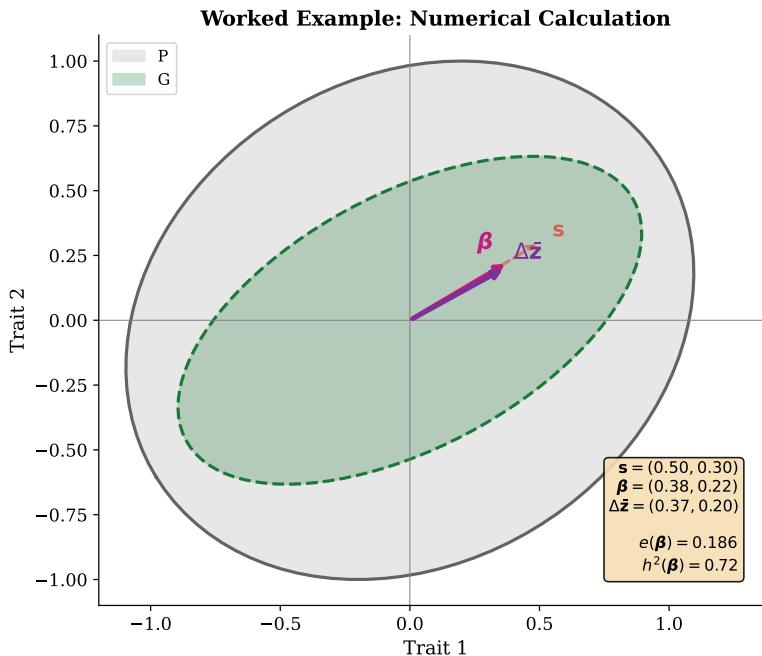


Figure 28: Worked example. The selection differential  $\mathbf{s}$  (gray dashed), selection gradient  $\boldsymbol{\beta}$  (red), and evolutionary response  $\Delta\bar{z}$  (purple) are shown with the G (green) and P (gray) ellipses.

### 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  $h^2(\beta)$ .

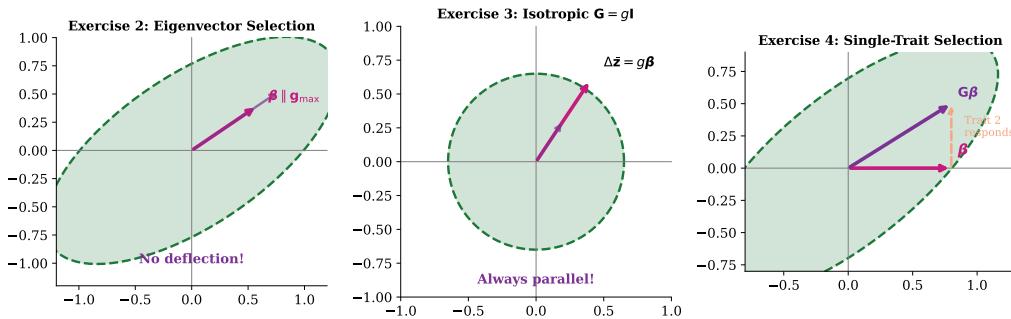


Figure 29: Visual aids for exercises.

# Appendices

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

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:

$$g(\mathbf{x}) = \sqrt{2\pi^{-n}|\mathbf{G}^{-1}|} \exp\left[-\frac{1}{2}(\mathbf{x} - \bar{\mathbf{x}})' \mathbf{G}^{-1} (\mathbf{x} - \bar{\mathbf{x}})\right]$$

$$\xi(\boldsymbol{\epsilon}) = \sqrt{2\pi^{-n}|\mathbf{E}^{-1}|} \exp\left[-\frac{1}{2}\boldsymbol{\epsilon}' \mathbf{E}^{-1} \boldsymbol{\epsilon}\right]$$

**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:

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

where  $\mathbf{P} = \mathbf{G} + \mathbf{E}$  is the phenotypic covariance matrix.

**Think this:**

**Geometric picture:** The phenotypic distribution is a multivariate normal “cloud” centered at  $\bar{\mathbf{z}}$ , 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.”

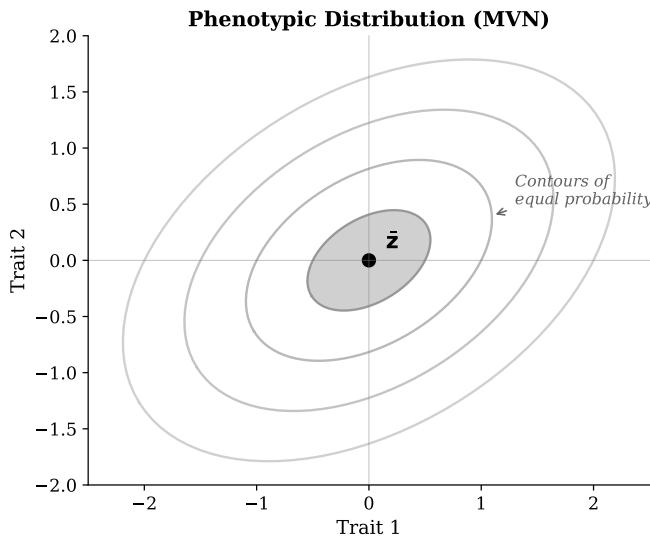


Figure 30: The phenotypic distribution as a multivariate normal cloud. Contours of equal probability are ellipses determined by  $\mathbf{P}$ . The center is the population mean  $\bar{z}$ .

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

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

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

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:

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

**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: $\beta = \nabla \ln \bar{W}$

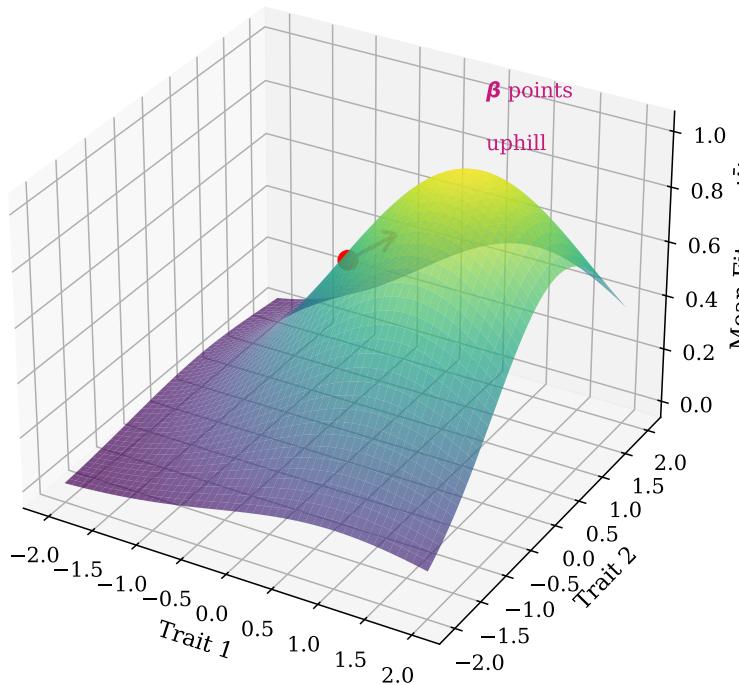


Figure 31: The adaptive landscape. Mean fitness  $\bar{W}$  is a surface over trait space. The selection gradient  $\beta = \nabla \ln \bar{W}$  points in the direction of steepest ascent.

#### 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**

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

**Verbal:** “The gradient of a MVN density points from each point 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.”

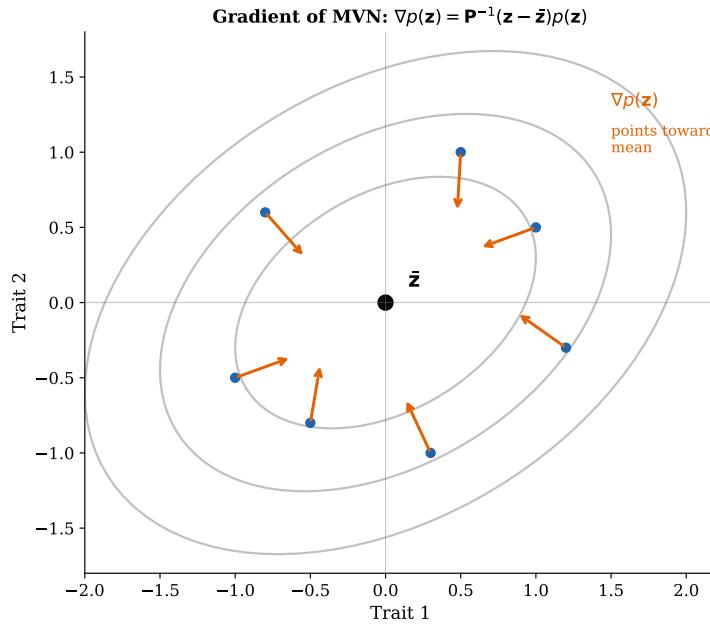


Figure 32: Gradient of the MVN density. At each point,  $\nabla p(\mathbf{z})$  points toward the mean, with magnitude proportional to  $p(\mathbf{z})$  and direction determined by  $\mathbf{P}^{-1}$ .

## 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:

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

### 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:

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

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

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

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

### The Selection Differential

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

**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

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

**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.”

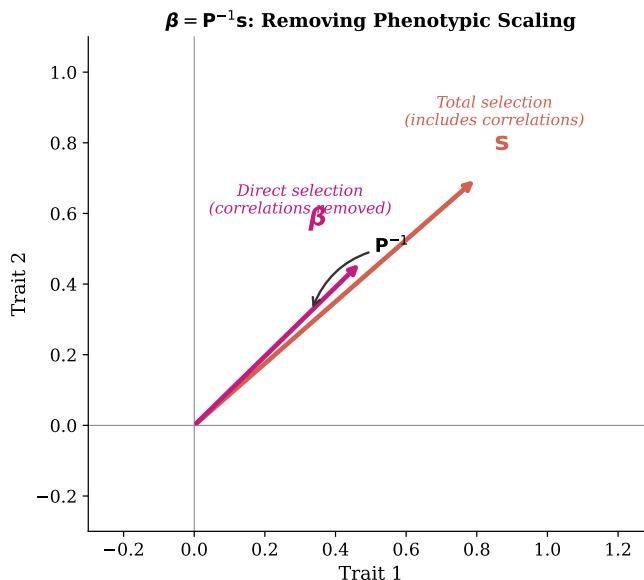


Figure 33: Selection differential  $\mathbf{s}$  versus selection gradient  $\boldsymbol{\beta}$ . The transformation  $\mathbf{P}^{-1}$  removes the effect of phenotypic correlations, isolating direct selection.

## 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  $\mathbf{x}$ :

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

**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:

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

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:

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

**Think this:**

**Compare the two expressions:**

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

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

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    | $\beta = \nabla \ln \bar{W}$                     | “Selection gradient points uphill on the fitness landscape”                          |
| 2    | $\nabla p(z) = \mathbf{P}^{-1}(z - \bar{z})p(z)$ | “Gradient of MVN points toward the mean, scaled by $\mathbf{P}^{-1}$ ”               |
| 3    | $\nabla \bar{W} = \mathbf{P}^{-1} \bar{W} s$     | “Gradient of mean fitness involves $\mathbf{P}^{-1}$ and the selection differential” |
| 4    | $\beta = \mathbf{P}^{-1} s$                      | “Selection gradient is standardized selection differential”                          |
| 5    | $\mathbf{G}^{-1} \Delta \bar{z} = \beta$         | “The same $\beta$ 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  $\beta$  bridges these two worlds—it appears in both

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

Combining these gives Lande's equation.

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

The derivative  $\frac{d[\mathbf{a}' \mathbf{M} \mathbf{a}]}{da} = 2\mathbf{M}\mathbf{a}$  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.

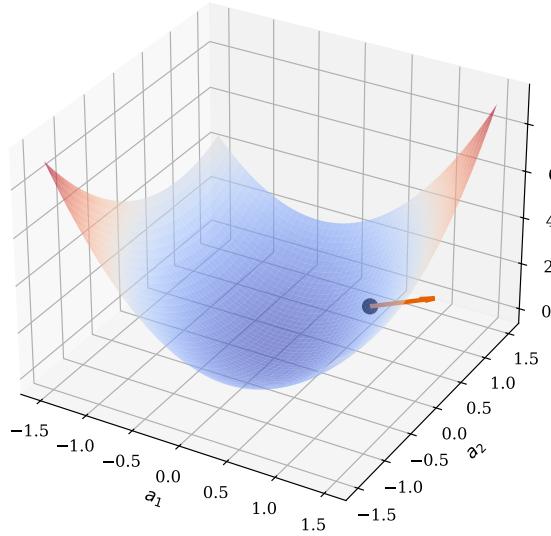
**Gradient of Quadratic Form:  $\nabla(a'Ma) = 2Ma$** 

Figure 34: The gradient of a quadratic form. At point  $a$ , the gradient  $2Ma$  points in the direction of steepest ascent on the  $M$ -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 key innovations 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  $\beta = P^{-1}s$
3. Running parallel derivations for phenotypes and breeding values to connect selection to response

The equation  $\Delta\bar{z} = G\beta$  has become one of the most important results in evolutionary quantitative genetics, forming the foundation for understanding multivariate evolution, genetic constraints, and the evolution of correlated characters.

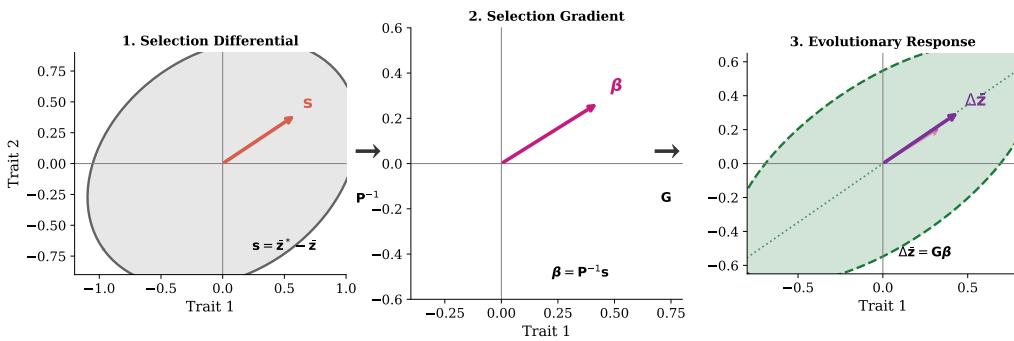
**Lande's Equation: The Complete Picture**

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