

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 \mathbf{v} represents a **direction with a magnitude**—an arrow from the origin in trait space.

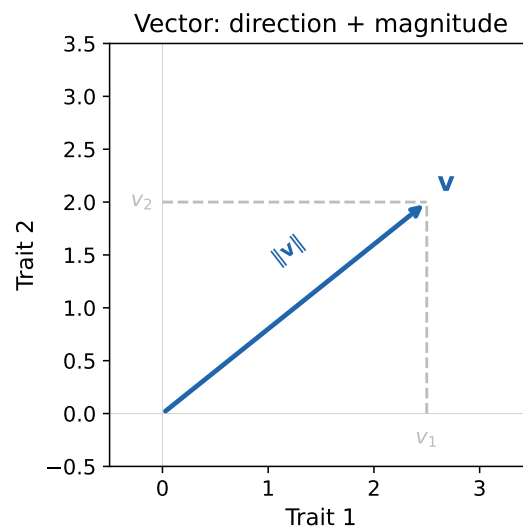


Figure 1: A vector as an arrow: direction plus magnitude. Components (v_1, v_2) give the coordinates.

Say this:

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

Biological translation

\mathbf{z}	phenotype vector (trait values for one individual)
$\boldsymbol{\beta}$	selection gradient (direction of steepest fitness increase)
\mathbf{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.

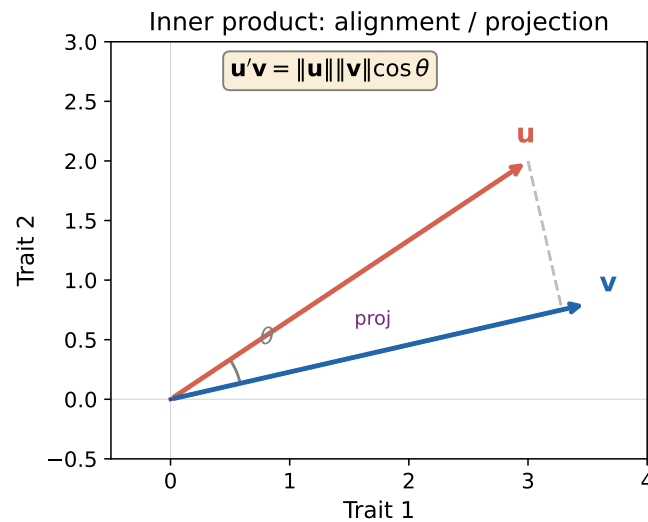


Figure 2: Inner product as projection. $\mathbf{u}'\mathbf{v} = \|\mathbf{u}\| \|\mathbf{v}\| \cos \theta$ measures alignment.

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 .

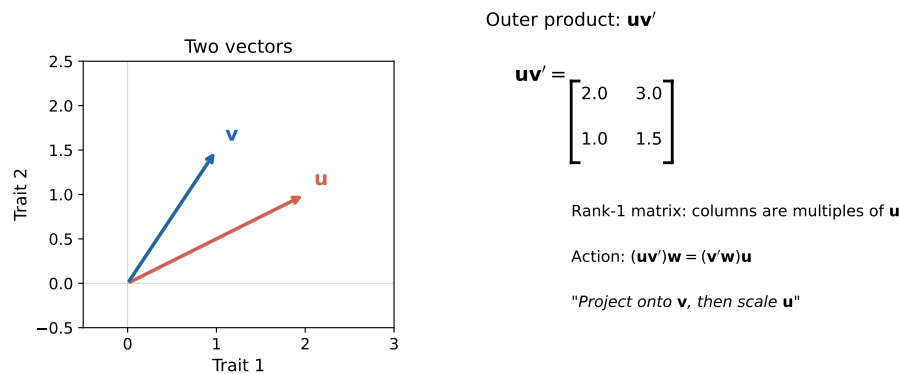


Figure 3: Outer product builds a matrix from two vectors. Its action: project onto v , then scale along u .

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: $M\mathbf{v}$

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

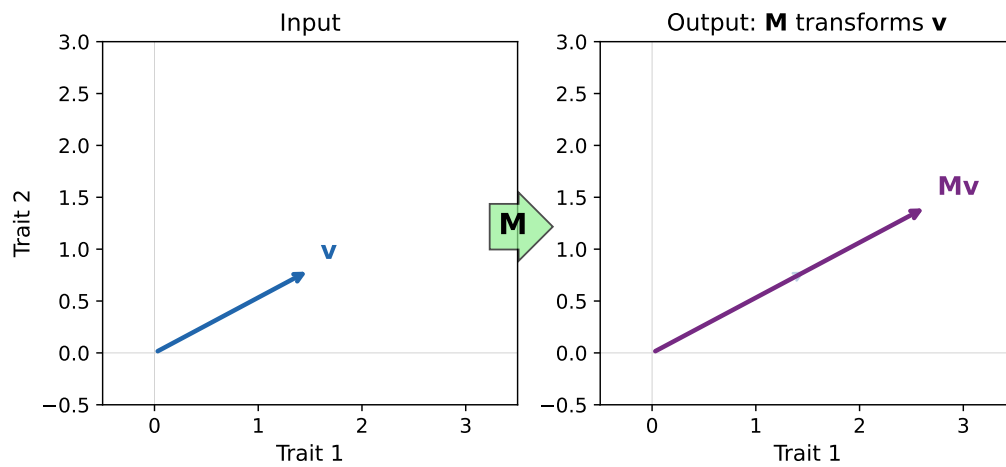


Figure 4: $M\mathbf{v}$: the matrix M transforms the arrow \mathbf{v} into a new arrow (generally different direction and length).

Say this:

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

Mantra

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

Biological translation

- | | |
|-----------------------|---|
| $G\boldsymbol{\beta}$ | “The response to selection: where does G send $\boldsymbol{\beta}$?” |
| $P^{-1}\mathbf{z}$ | “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}

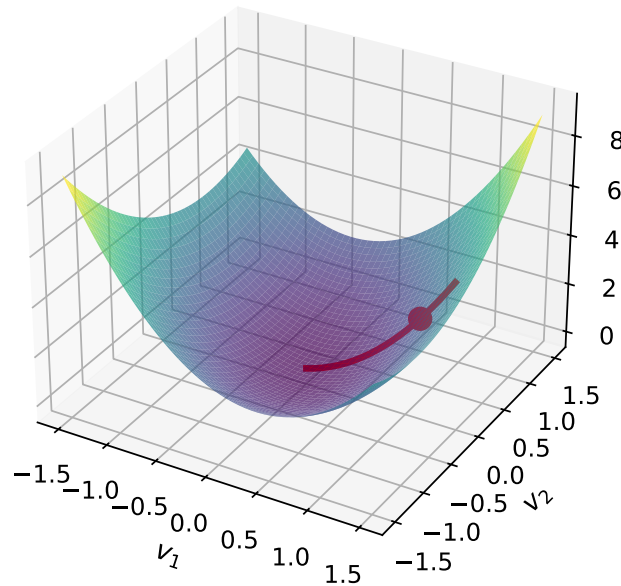


Figure 5: Quadratic form as height of a paraboloid. The surface shows $\mathbf{v}'\mathbf{M}\mathbf{v}$ over all directions. The red curve traces one direction.

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} ?*”

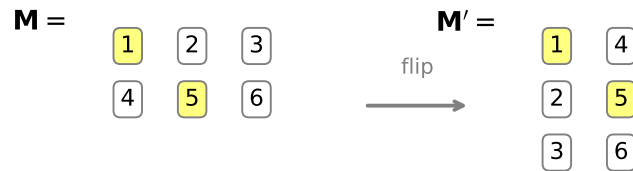
Biological translation

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

6 Transpose: \mathbf{M}'

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

Transpose: flip across diagonal



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: $\mathbf{M}^{-1}\mathbf{M} = \mathbf{I}$.

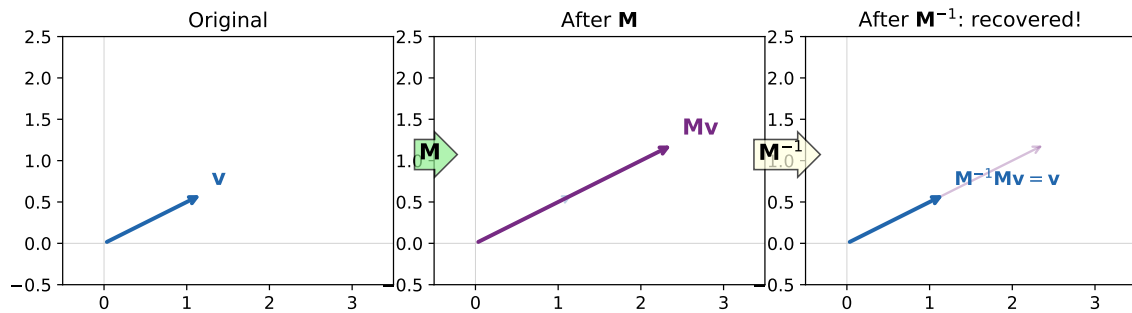


Figure 7: The inverse undoes the transformation. Apply \mathbf{M} , then \mathbf{M}^{-1} : you're back where you started.

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

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

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

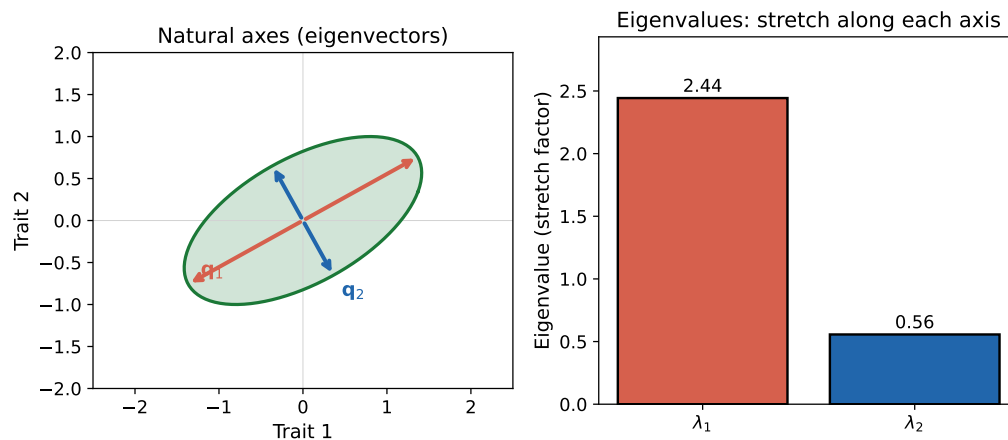


Figure 8: Left: Eigenvectors are the natural axes (directions of pure stretch). Right: Eigenvalues are the stretch factors.

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

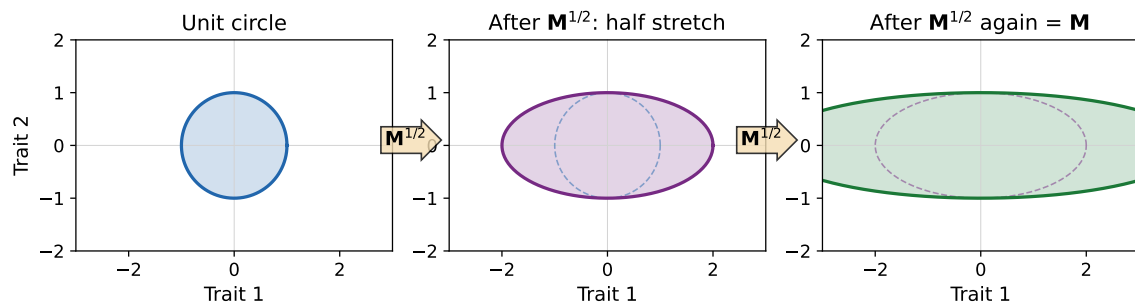


Figure 9: Matrix square root: applying $\mathbf{M}^{1/2}$ twice gives \mathbf{M} . If \mathbf{M} stretches by 4, $\mathbf{M}^{1/2}$ stretches by 2.

Say this:

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

Think this:

If $\mathbf{M} = \mathbf{Q}\mathbf{\Lambda}\mathbf{Q}'$, then $\mathbf{M}^{1/2} = \mathbf{Q}\mathbf{\Lambda}^{1/2}\mathbf{Q}'$
 where $\mathbf{\Lambda}^{1/2} = \text{diag}(\sqrt{\lambda_1}, \sqrt{\lambda_2}, \dots)$

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).

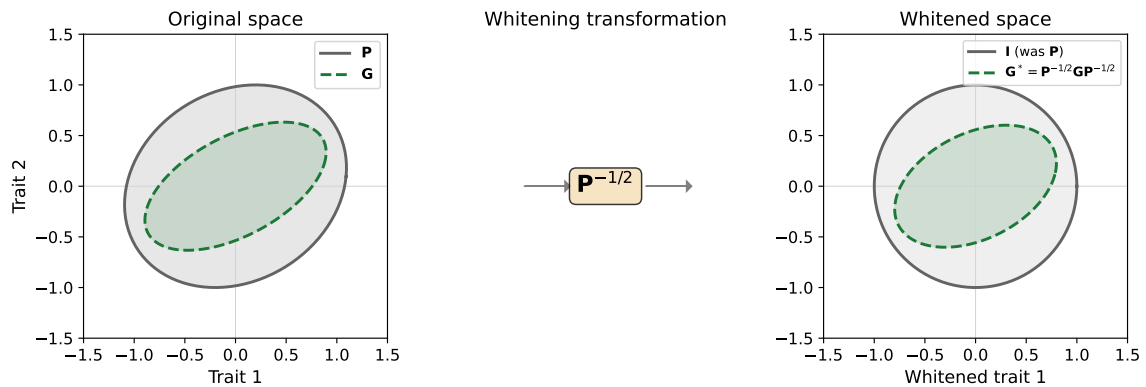


Figure 10: Whitening transformation. Left: Original space with \mathbf{P} (ellipse) and \mathbf{G} (dashed). Right: After whitening, \mathbf{P} becomes \mathbf{I} (circle), revealing \mathbf{G}^* .

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.

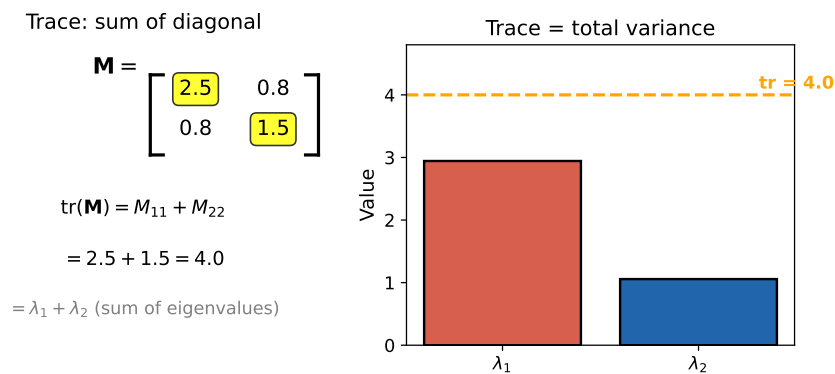


Figure 11: Trace: sum of diagonal elements = sum of eigenvalues = total variance.

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.

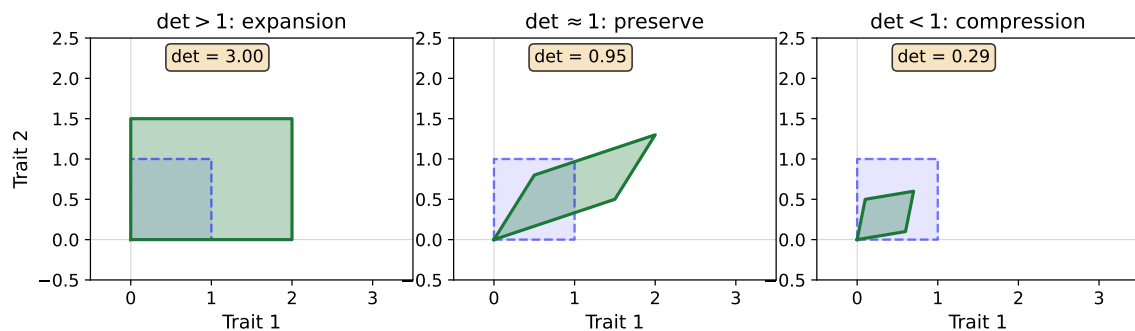


Figure 12: Determinant as volume scaling. Left: expansion ($\det > 1$). Center: preservation ($\det \approx 1$). Right: compression ($\det < 1$).

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.

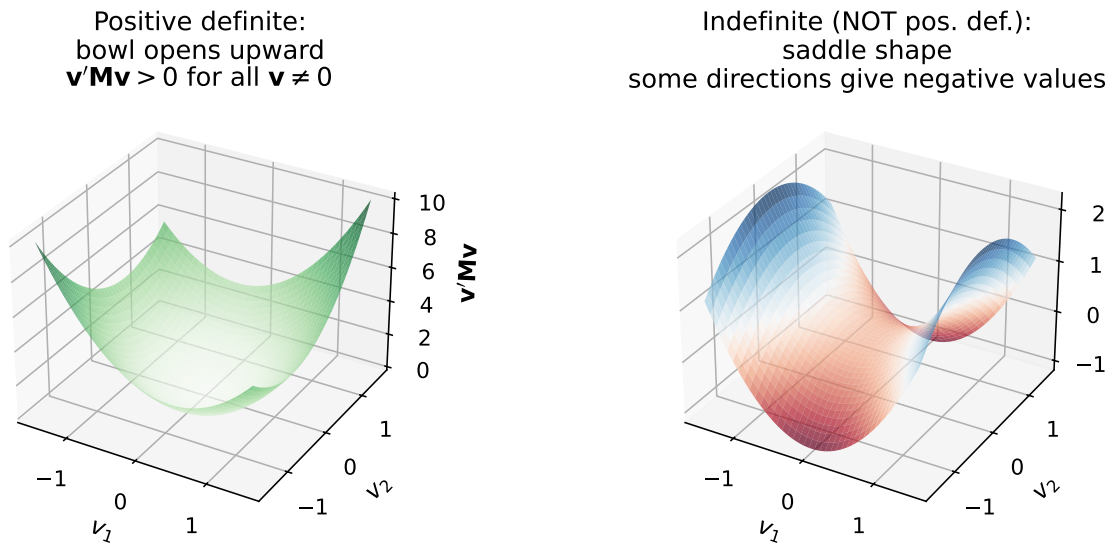


Figure 13: Left: Positive definite—bowl opens upward, $\mathbf{v}'\mathbf{M}\mathbf{v} > 0$ for all $\mathbf{v} \neq \mathbf{0}$. Right: Indefinite—saddle shape, some directions give negative values.

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.

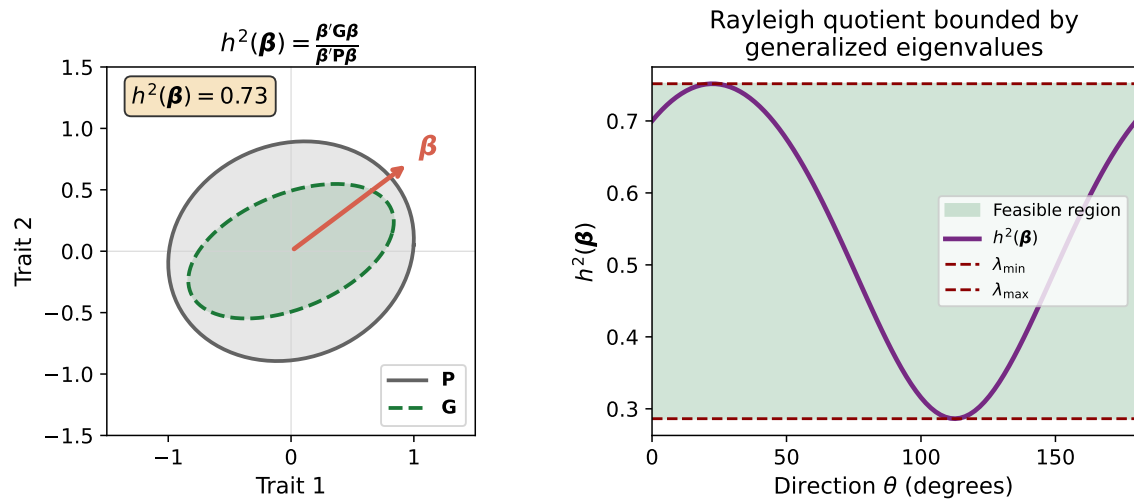


Figure 14: Left: \mathbf{G} and \mathbf{P} ellipses with direction β . Right: $h^2(\beta)$ varies with direction but is bounded by λ_{\min} and λ_{\max} .

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} .

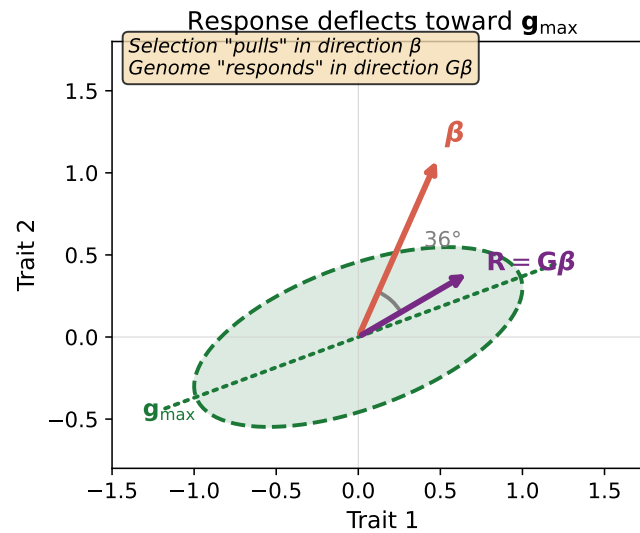


Figure 15: Response deflection. Selection pulls in direction β , but the response $\mathbf{R} = \mathbf{G}\beta$ rotates toward the genetic line of least resistance \mathbf{g}_{\max} .

Say this:

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

Mantra

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

16.2 Biological Translations

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

16.3 Three Key Mantras

1. $\mathbf{v}'\mathbf{M}\mathbf{v}$ asks: “How much variance does \mathbf{M} have in direction \mathbf{v} ?”
2. $\mathbf{G}\boldsymbol{\beta}$ asks: “Where does the genome send selection?” (If \mathbf{G} is anisotropic, response rotates toward \mathbf{g}_{\max} .)
3. Whitening asks: “What does \mathbf{G} look like when \mathbf{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 \mathbf{G} -matrix) and the **pattern of selection** (captured by the selection gradient β), can we predict the **evolutionary response** $\Delta\bar{z}$?

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

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

Think this:

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

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

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

Lande's Equation: From Selection to Response

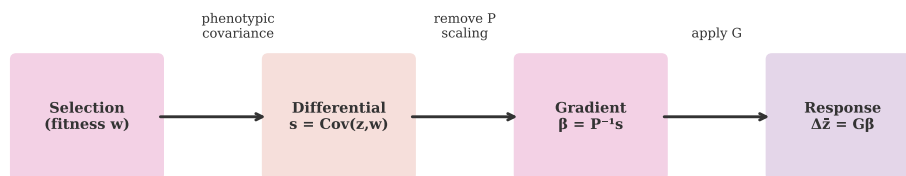


Figure 16: Overview of Lande's equation. Selection creates a phenotypic shift (the selection differential \mathbf{s}), which we decompose into a direction-independent gradient β , then filter through the genetic architecture \mathbf{G} to get the evolutionary response $\Delta\bar{z}$.

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*

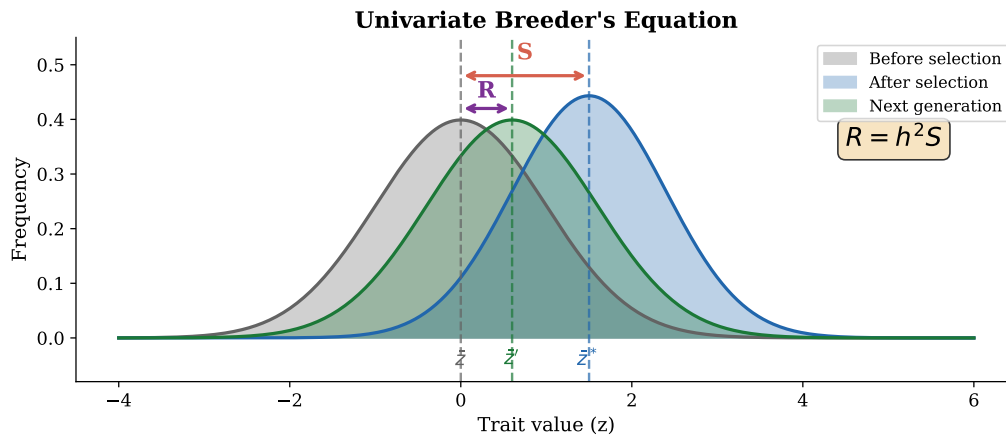


Figure 17: The univariate breeder's equation setup. Selection shifts the distribution (gray \rightarrow blue), then inheritance filters that shift (blue \rightarrow green). The response R is smaller than the selection differential S by a factor of h^2 .

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**:

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

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:

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

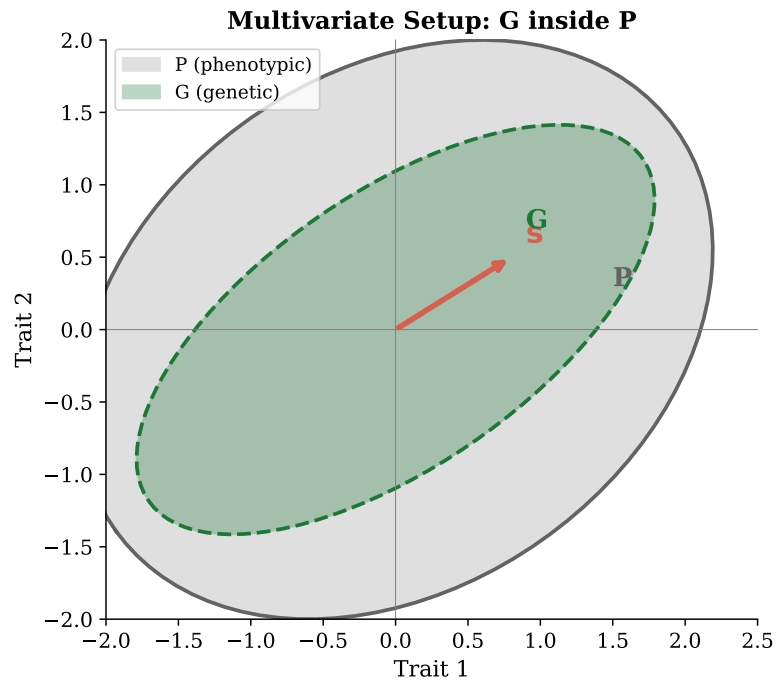


Figure 19: The multivariate setup. \mathbf{P} (gray ellipse) captures phenotypic variance and covariance. \mathbf{G} (green ellipse) captures genetic variance and covariance. The selection differential \mathbf{s} (red arrow) shows how selection shifts the phenotypic mean.

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**.

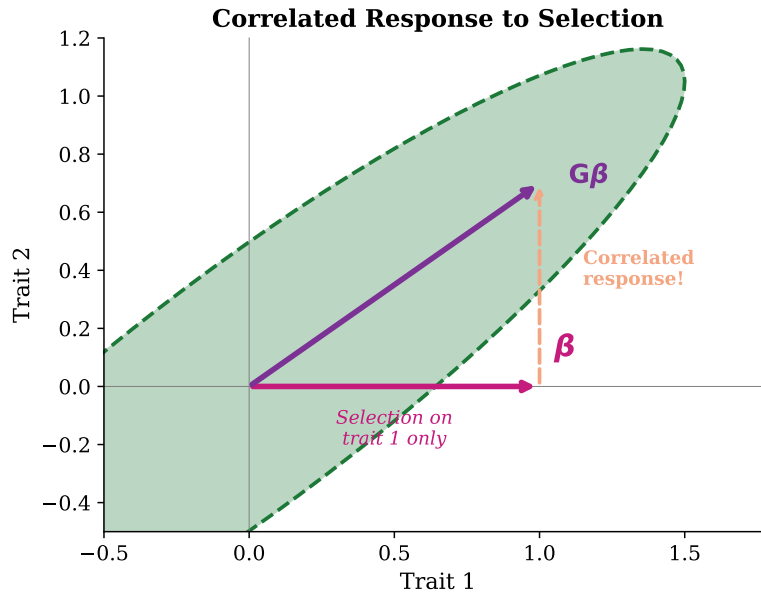


Figure 20: Correlated response. Even if selection acts only on trait 1 (horizontal arrow), the response (purple arrow) has a component in trait 2 because the traits are genetically correlated. The G-matrix encodes this coupling.

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

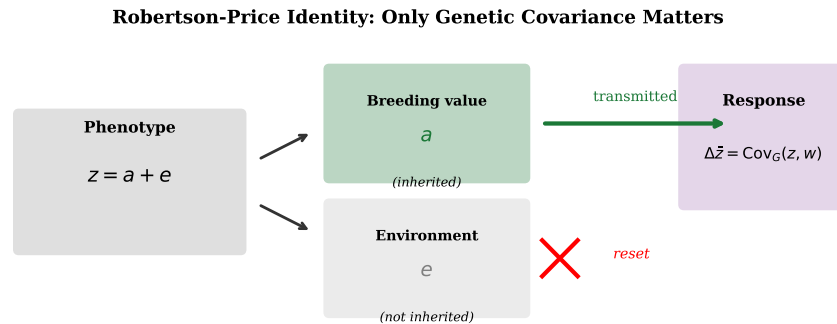


Figure 21: The Robertson-Price identity. Fitness selects on phenotypes, but only the genetic component (breeding value) is transmitted to offspring.

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.

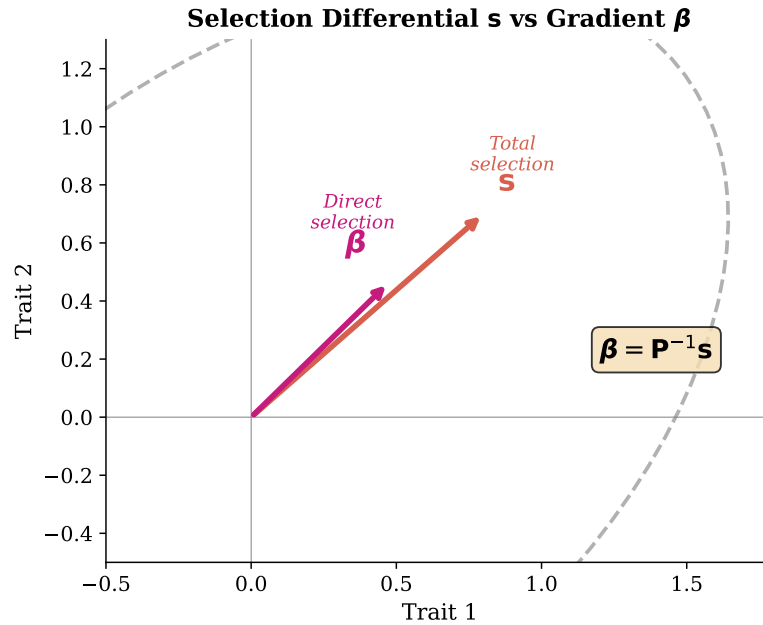


Figure 22: Selection differential vs gradient. The differential \mathbf{s} (red) includes correlated effects. The gradient $\boldsymbol{\beta}$ (orange), obtained by applying \mathbf{P}^{-1} , isolates direct selection on each trait.

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

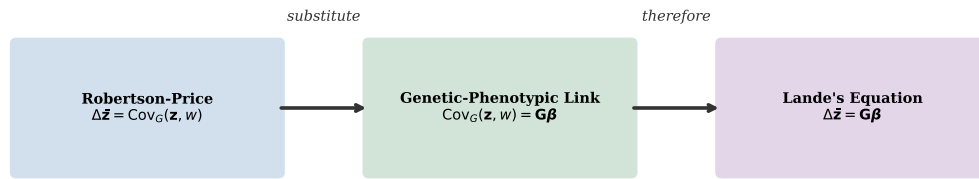


Figure 23: The logical flow of the derivation. Each arrow represents a key insight.

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} .”

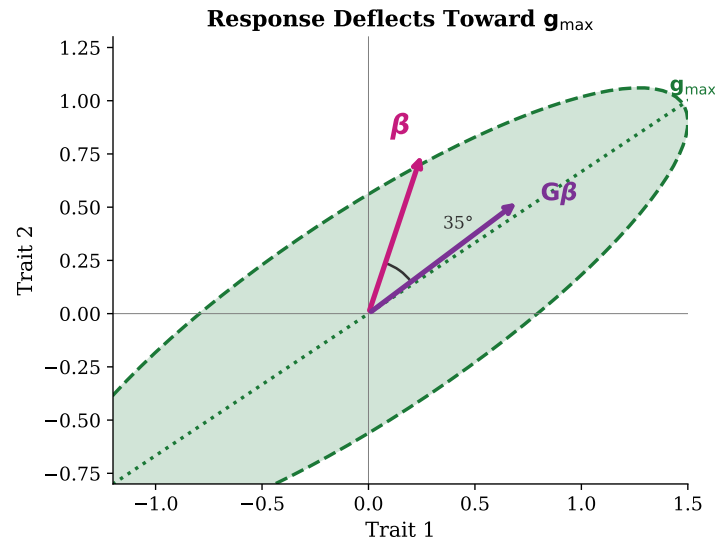


Figure 24: Deflection of evolutionary response. The selection gradient β (red) specifies the direction selection “wants” to go. The actual response $\mathbf{G}\beta$ (purple) is rotated toward \mathbf{g}_{\max} (green dashed line), the genetic line of least resistance.

17.7.2 When Does Deflection Occur?

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

- β 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 β : captured by $\beta'\mathbf{G}\beta$
- How the \mathbf{G} -matrix redistributes that variance across traits

Response Magnitude Depends on Selection Direction

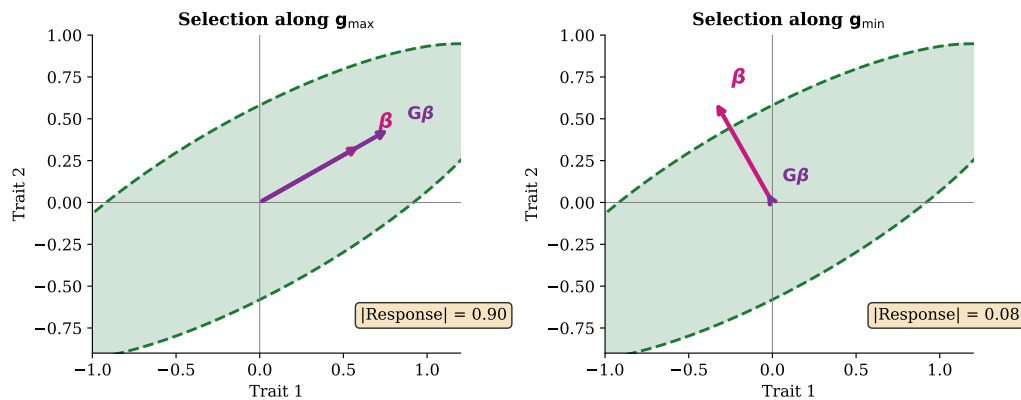


Figure 25: Response magnitude. Selection along \mathbf{g}_{\max} (left) produces a large response. Selection perpendicular to \mathbf{g}_{\max} (right) produces a small response. The \mathbf{G} -matrix acts as a filter.

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 β is:

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

Say this:

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

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 β 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 β .

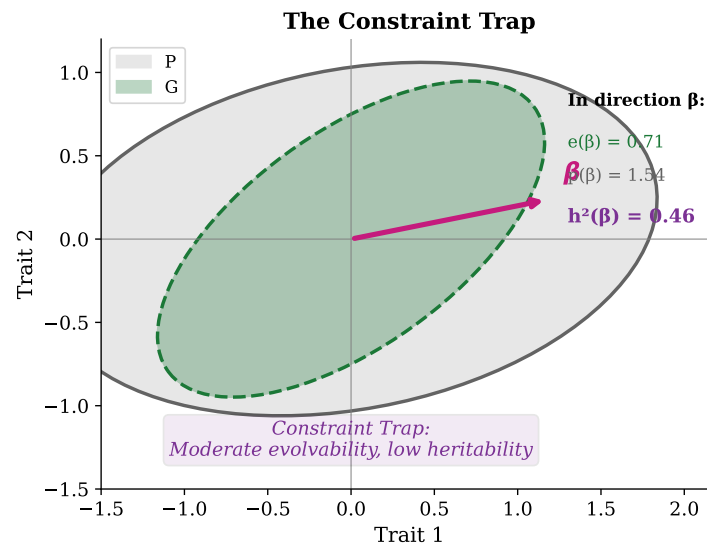


Figure 26: The constraint trap. In this direction, genetic variance (green) is reasonable, but phenotypic variance (gray) is much larger. The ratio $h^2(\beta)$ is low, so the realized response is weak despite moderate evolvability.

17.9 Step 8: Summary and Key Takeaways

17.9.1 The Equation and Its Meaning

Lande's Multivariate Breeder's Equation

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

In words:

- \mathbf{s} : How much did selection shift the phenotypic mean? (selection differential)
- $\mathbf{P}^{-1}\mathbf{s} = \beta$: 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 \mathbf{s} ."
2. "We extract the direct selection $\beta = \mathbf{P}^{-1}\mathbf{s}$ by running \mathbf{P} backwards—removing correlation effects."
3. "We ask: where does \mathbf{G} send β ? 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."

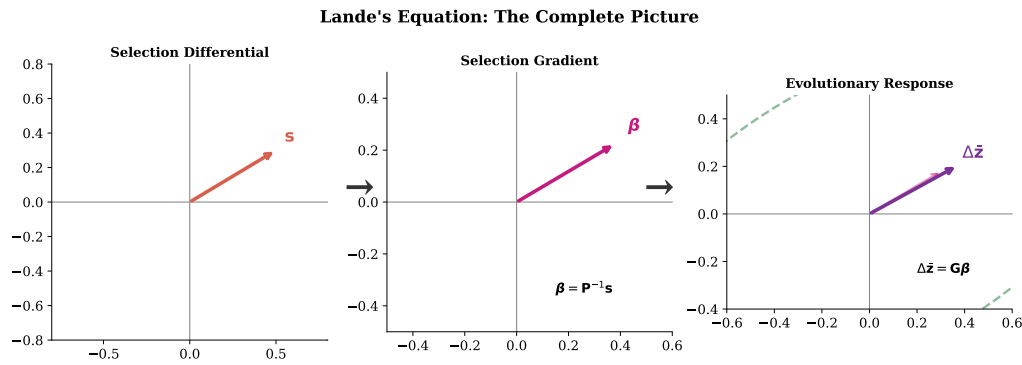


Figure 27: Visual summary of Lande's equation. Start with the selection differential (what phenotypic selection did), extract the gradient (what direct selection is), apply the G-matrix (where the genome sends it), arrive at the response.

17.9.3 The Communication Metaphor (Revisited)

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

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

Mantra

"Selection speaks in direction β . 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:

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

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

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

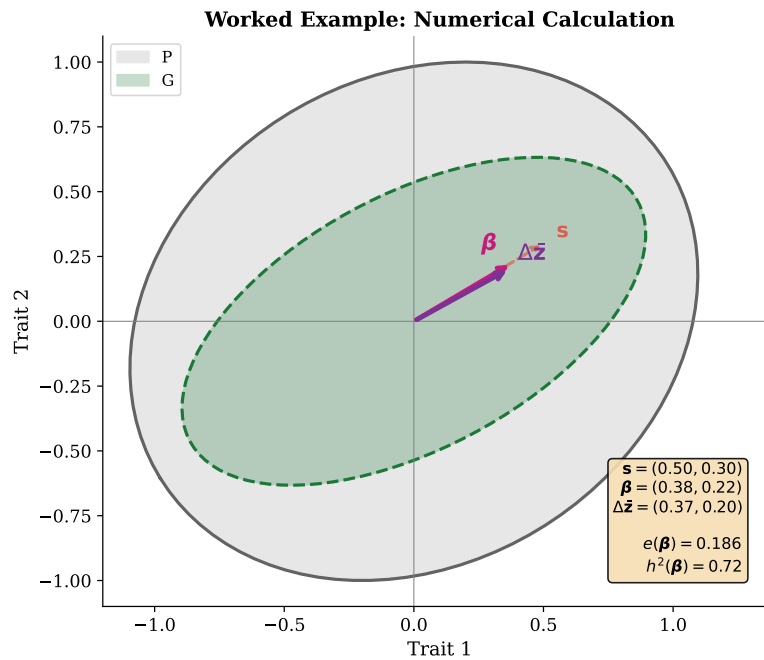


Figure 28: Worked example. The selection differential \mathbf{s} (gray dashed), selection gradient $\boldsymbol{\beta}$ (red), and evolutionary response $\Delta\bar{\mathbf{z}}$ (purple) are shown with the \mathbf{G} (green) and \mathbf{P} (gray) ellipses.

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 β 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 $\mathbf{s} = (s_1, 0)'$, compute β 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 $h^2(\beta)$.

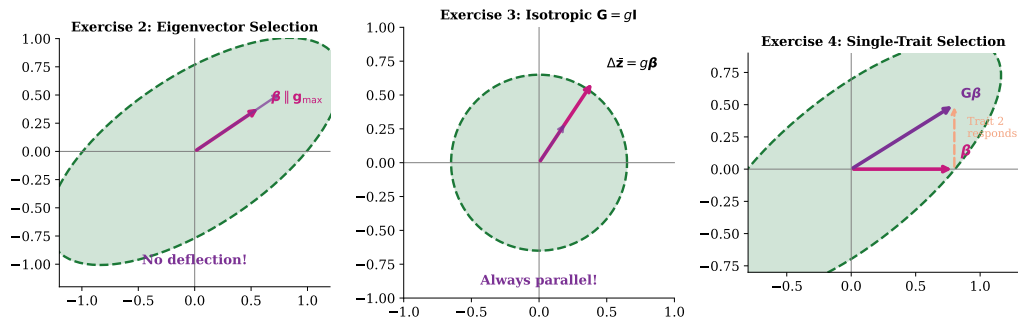


Figure 29: Visual aids for exercises.

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.”

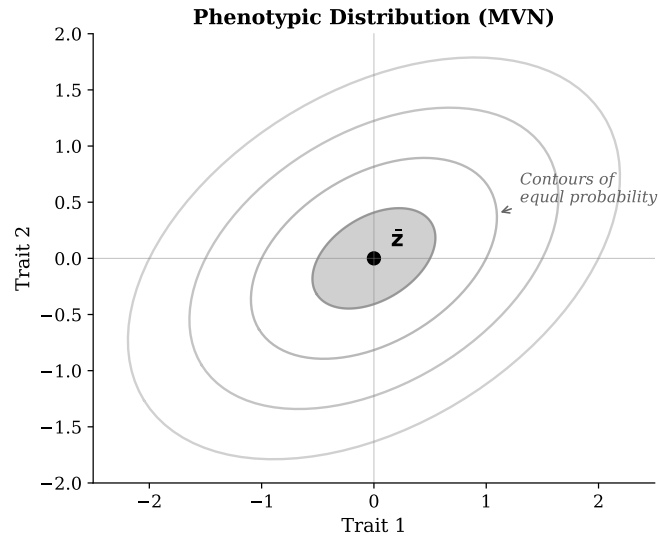


Figure 30: The phenotypic distribution as a multivariate normal cloud. Contours of equal probability are ellipses determined by \mathbf{P} . The center is the population mean $\bar{\mathbf{z}}$.

A.2 The Goal: Derive Lande's Equation

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

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

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 $\nabla \ln \bar{W} = \mathbf{G}^{-1} \Delta \bar{\mathbf{z}}$ 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** $\boldsymbol{\beta}$ is defined as:

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

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: “ ∇f points uphill on the f -surface.”

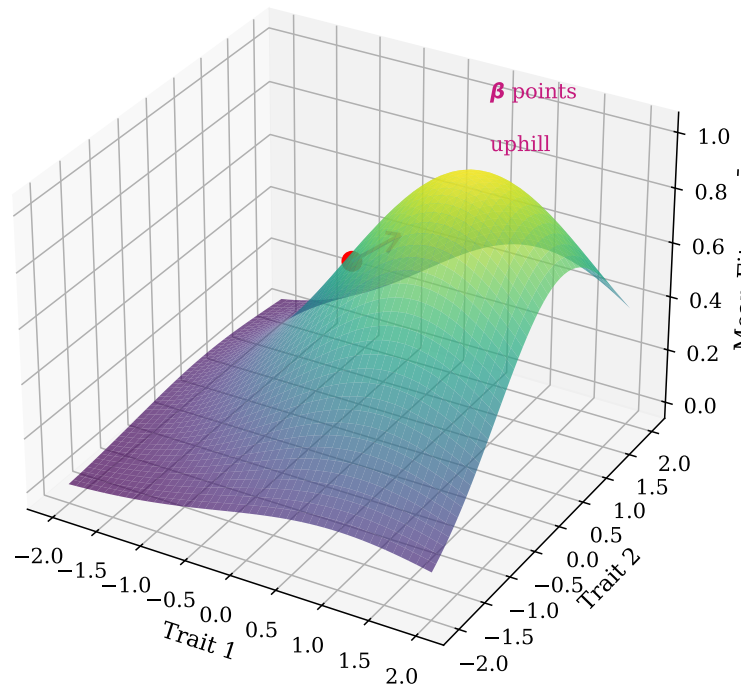
Adaptive Landscape: $\beta = \nabla \ln \bar{W}$ 

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 ∇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

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

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.”

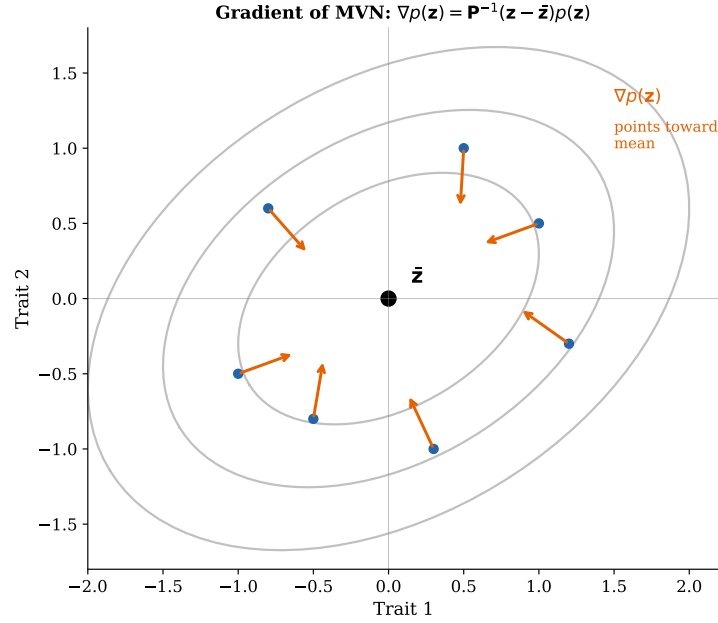


Figure 32: Gradient of the MVN density. At each point, $\nabla p(\mathbf{z})$ points toward the mean, with magnitude proportional to $p(\mathbf{z})$ and direction determined by \mathbf{P}^{-1} .

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 β :

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

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

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

Key Result: Selection Gradient

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

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.”

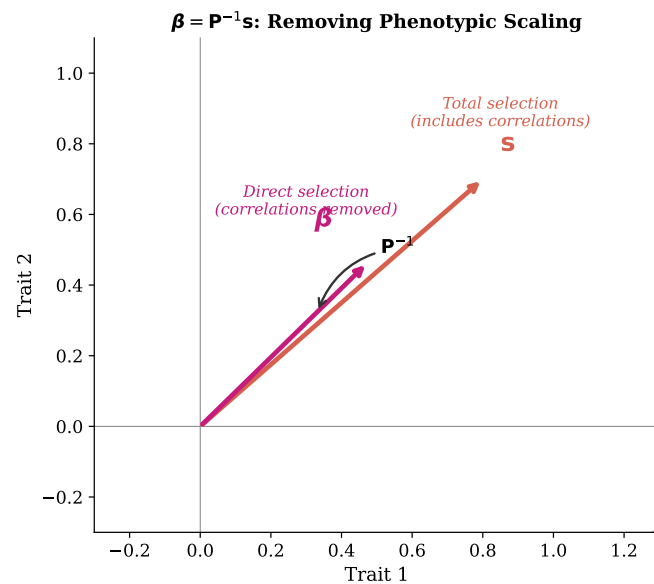


Figure 33: Selection differential \mathbf{s} versus selection gradient β . The transformation \mathbf{P}^{-1} removes the effect of phenotypic correlations, isolating direct selection.

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:

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

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

These must be equal!

A.7.3 Assembling Lande’s Equation

Equating the two expressions:

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

Multiplying both sides by \mathbf{G} :

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

Lande’s Equation: The Final Result

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

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	$\nabla p(\mathbf{z}) = \mathbf{P}^{-1}(\mathbf{z} - \bar{\mathbf{z}})p(\mathbf{z})$	“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	$\beta = \mathbf{P}^{-1} \mathbf{s}$	“Selection gradient is standardized selection differential”
5	$\mathbf{G}^{-1} \Delta \bar{\mathbf{z}} = \beta$	“The same β 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 β bridges these two worlds—it appears in both

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

Combining these gives Lande’s equation.

A.9 The Quadratic Form Derivative: A Closer Look

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

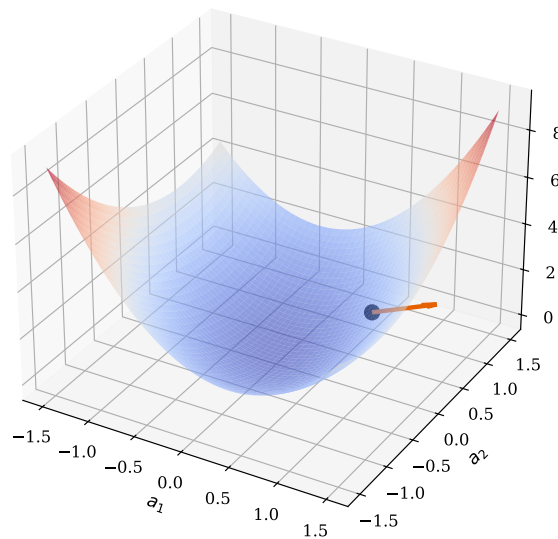
Gradient of Quadratic Form: $\nabla(\mathbf{a}'\mathbf{M}\mathbf{a}) = 2\mathbf{M}\mathbf{a}$ 

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 key innovations were:

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

The equation $\Delta\bar{\mathbf{z}} = \mathbf{G}\boldsymbol{\beta}$ 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

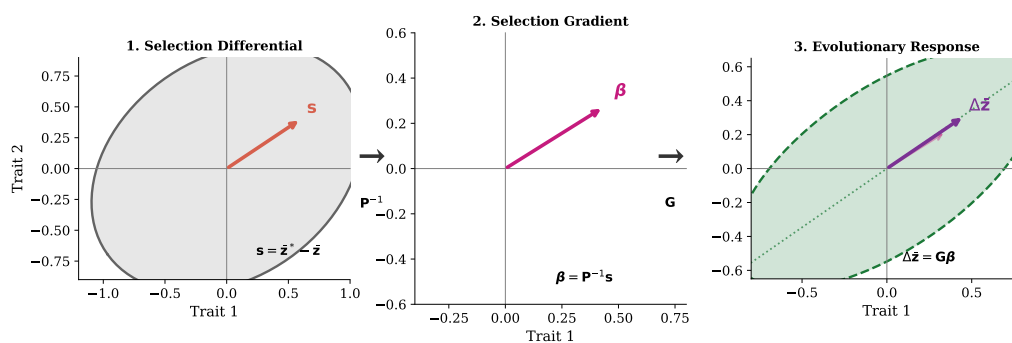


Figure 35: The complete picture. Selection creates \mathbf{s} , which becomes $\boldsymbol{\beta}$ after removing \mathbf{P} -scaling. The \mathbf{G} -matrix transforms $\boldsymbol{\beta}$ into the response $\Delta\bar{\mathbf{z}}$, generally deflecting it toward \mathbf{g}_{\max} .