Speaking Linear Algebra

A Verbal Phrasebook for Evolutionary Quantitative Geneticists

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Abstract

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

Contents

1 Vectors

A vector v represents a **direction with a magnitude**—an arrow from the origin in trait space.
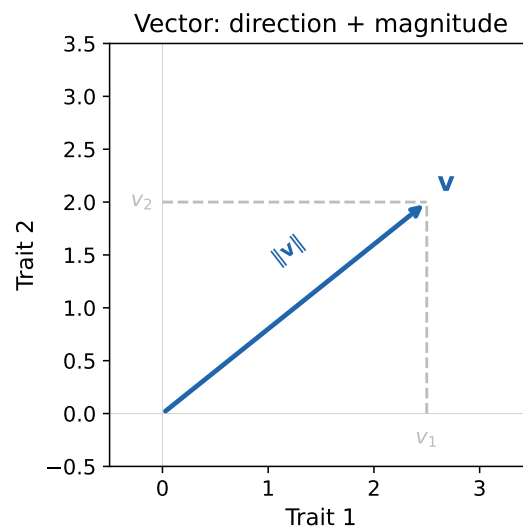
Figure 1: A vector as an arrow: direction plus magnitude. Components (v_1, v_2) give the coordinates.

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)
β	selection gradient (direction of steepest fitness increase)
$g_{\max}$	genetic line of least resistance (first eigenvector of $\mathbf{G}$)

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

The inner product $\boldsymbol{u}'\boldsymbol{v} = \sum_i u_i v_i$ measures **how aligned** two vectors are.
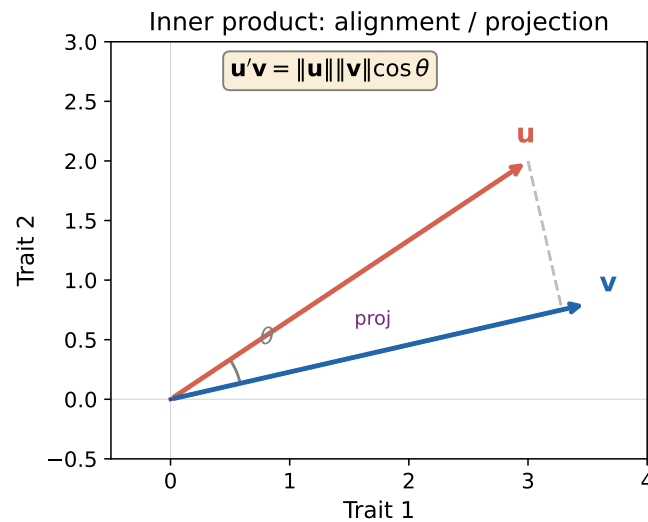
Figure 2: Inner product as projection. $\boldsymbol{u}'\boldsymbol{v} = \|\boldsymbol{u}\|\|\boldsymbol{v}\| \cos\theta$ measures alignment.

Say this:

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

Think this:

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

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

Biological translation

$\boldsymbol{\beta}'\boldsymbol{z} =$ "how far along the selection direction is this phenotype"

$\boldsymbol{u}'\boldsymbol{v} = 0$ means "$\boldsymbol{u}$ and $\boldsymbol{v}$ are orthogonal—no overlap"

3 Outer Product: uv'

The outer product creates a **rank-1 matrix** whose columns are scaled copies of $\boldsymbol{u}$.
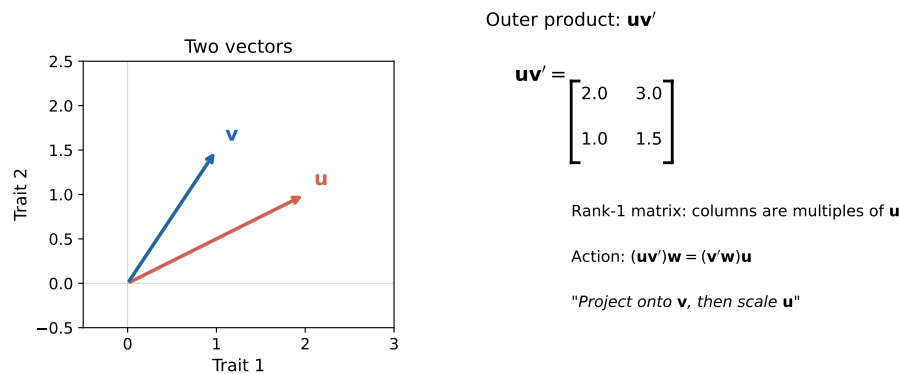
Figure 3: Outer product builds a matrix from two vectors. Its action: project onto $\boldsymbol{v}$, then scale along $\boldsymbol{u}$.

Say this:

- "Spread $\boldsymbol{u}$ along $\boldsymbol{v}$"
- "A rank-1 matrix that points from $\boldsymbol{v}$ toward $\boldsymbol{u}$"
- "Project onto $\boldsymbol{v}$, then stretch along $\boldsymbol{u}$"

Think this:

The action of $\boldsymbol{uv'}$ on any vector $\boldsymbol{w}$:

$$(\boldsymbol{uv'})\boldsymbol{w} = (\boldsymbol{v'w})\,\boldsymbol{u}$$

"How much $\boldsymbol{w}$ aligns with $\boldsymbol{v}$, times $\boldsymbol{u}$."

Biological translation

The covariance matrix is a sum of outer products:

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

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

Matrix-vector multiplication **transforms** the vector—rotating, stretching, or shearing it.
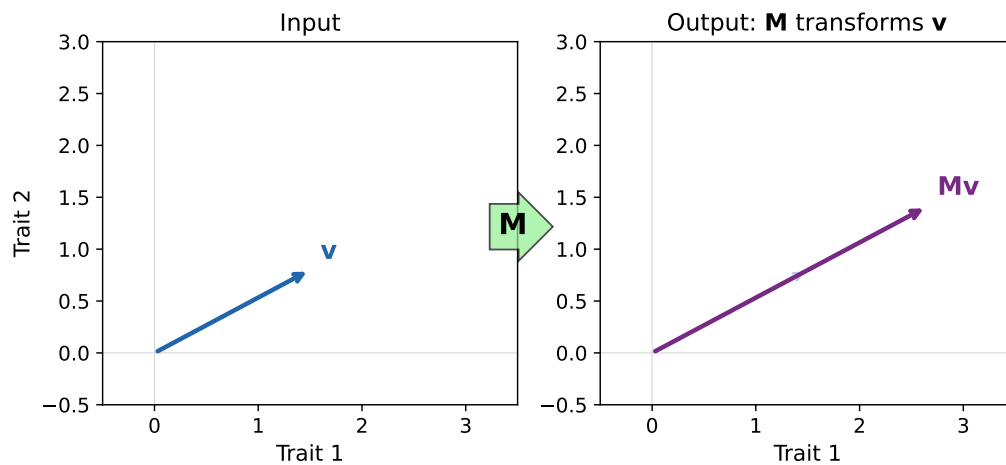
Figure 4: $\mathbf{M}\boldsymbol{v}$: the matrix $\mathbf{M}$ transforms the arrow $\boldsymbol{v}$ into a new arrow (generally different direction and length).

Say this:

- "$\mathbf{M}$ transforms $\boldsymbol{v}$"
- "Where does $\mathbf{M}$ send $\boldsymbol{v}$?"
- "$\mathbf{M}$ acts on $\boldsymbol{v}$"
- "Weighted combination of $\mathbf{M}$'s columns"

Mantra

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

Biological translation

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

$\mathbf{P}^{-1}\boldsymbol{z}$ "The phenotype $\boldsymbol{z}$ in standardized (whitened) units"

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

This is the **workhorse** of quantitative genetics. The quadratic form gives the "height" of the **M**-paraboloid at direction v.

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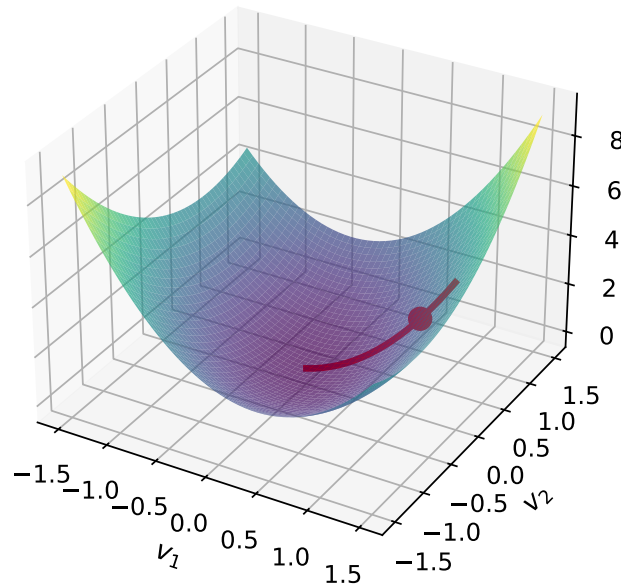
Figure 5: Quadratic form as height of a paraboloid. The surface shows $v'\mathbf{M}v$ over all directions. The red curve traces one direction.

Say this:

- "Variance of **M** in direction v"
- "Height of the **M**-bowl at v"
- "How much does **M** stretch space in direction v?"

Mantra

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

Biological translation

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

6   Transpose: $\mathbf{M}'$

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

Transpose: flip across diagonal

$\mathbf{M} =$ | 1 | 2 | 3 |
                 | 4 | 5 | 6 |

flip →

$\mathbf{M}' =$ | 1 | 4 |
                 | 2 | 5 |
                 | 3 | 6 |
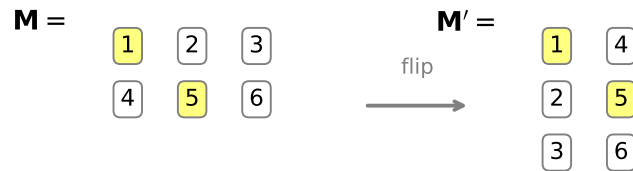
Rows ↔ Columns

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

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)
- $(\mathbf{M}v)'w = v'(\mathbf{M}'w)$ — "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: $\mathbf{M}^{-1}\mathbf{M} = \mathbf{I}$.
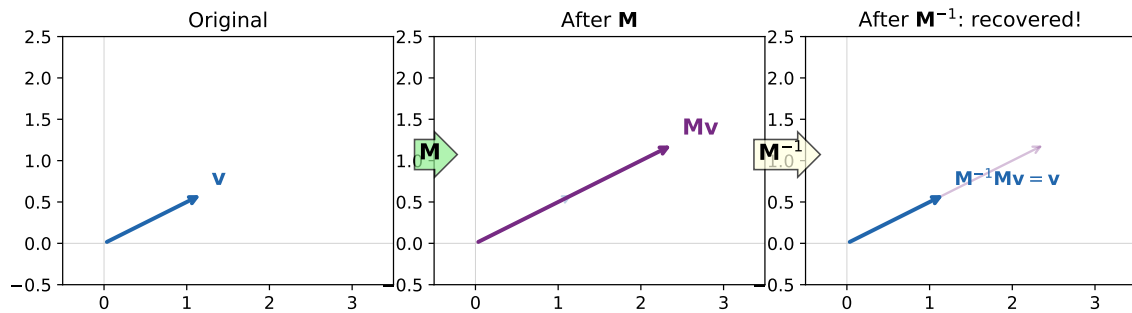
Figure 7: The inverse undoes the transformation. Apply $\mathbf{M}$, then $\mathbf{M}^{-1}$: you're back where you started.

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

$\boldsymbol{\beta}'\mathbf{G}^{-1}\boldsymbol{\beta}$	"How *constrained* is direction $\boldsymbol{\beta}$?"
$(\boldsymbol{\beta}'\mathbf{G}^{-1}\boldsymbol{\beta})^{-1}$	"Conditional evolvability $c(\boldsymbol{\beta})$"
$\mathbf{P}^{-1}\mathbf{G}$	"Genetic variance *relative to* phenotypic variance"

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

Eigendecomposition finds the **natural axes** of a matrix—directions where it acts by pure stretching.
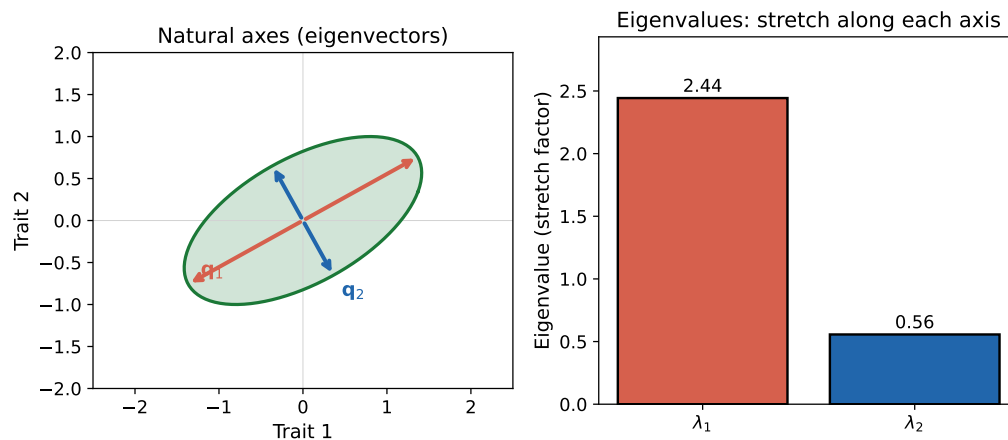
Figure 8: Left: Eigenvectors are the natural axes (directions of pure stretch). Right: Eigenvalues are the stretch factors.

> **Say this:**
> - "Find the natural axes of $\mathbf{M}$"
> - "Directions where $\mathbf{M}$ only stretches, no rotation"
> - "Principal components"

> **Think this:**
>
> $\mathbf{M}\boldsymbol{v} = \lambda\boldsymbol{v}$ means "$\mathbf{M}$ sends $\boldsymbol{v}$ to a scaled version of itself."
>
> Eigenvectors $\mathbf{Q}$: the skeleton of the matrix.
> Eigenvalues $\boldsymbol{\Lambda}$: the strength of each bone.

> **Biological translation**
>
> | | |
> |---|---|
> | $\boldsymbol{g}_{max}$ | "Genetic line of least resistance—maximum genetic variance" |
> | $\lambda_1/\sum_i \lambda_i$ | "Fraction of variance explained by $\boldsymbol{g}_{max}$" |
> | $\lambda_1 \gg \lambda_2$ | "$\mathbf{G}$ is cigar-shaped—highly constrained" |
> | $\lambda_1 \approx \lambda_2 \approx \cdots$ | "$\mathbf{G}$ is spherical—isotropic, no preferred direction" |

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

The square root is "half the transformation": $\mathbf{M}^{1/2}\mathbf{M}^{1/2} = \mathbf{M}$.
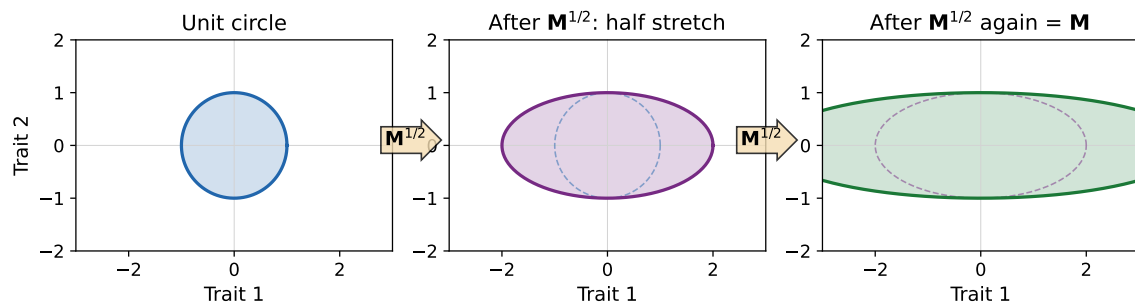
Figure 9: Matrix square root: applying $\mathbf{M}^{1/2}$ twice gives $\mathbf{M}$. If $\mathbf{M}$ stretches by 4, $\mathbf{M}^{1/2}$ stretches by 2.

Say this:

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

Think this:

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

where $\boldsymbol{\Lambda}^{1/2} = \mathrm{diag}(\sqrt{\lambda_1}, \sqrt{\lambda_2}, \ldots)$

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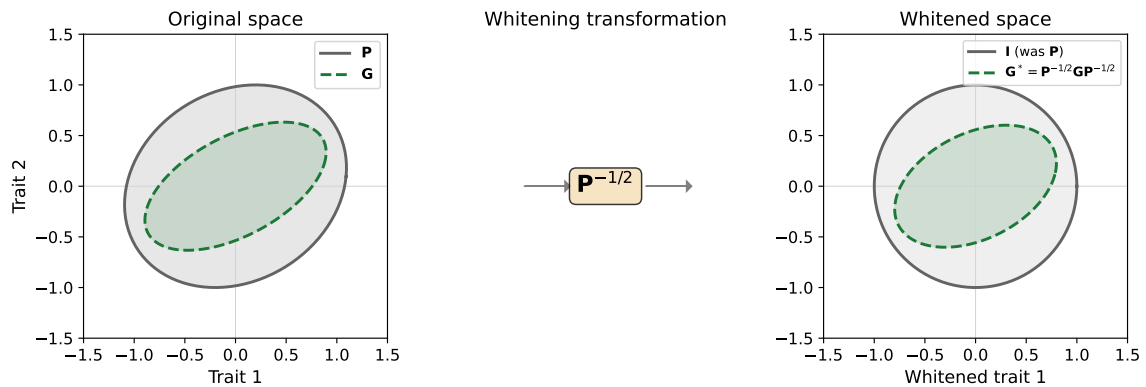
Figure 10: Whitening transformation. Left: Original space with $\mathbf{P}$ (ellipse) and $\mathbf{G}$ (dashed). Right: After whitening, $\mathbf{P}$ becomes $\mathbf{I}$ (circle), revealing $\mathbf{G}^*$.

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: $\lambda_{\min} \leq h^2(\boldsymbol{\beta}) \leq \lambda_{\max}$
- $V_{\mathrm{rel}}(\mathbf{G}^*)$ controls heterogeneity of $h^2(\boldsymbol{\beta})$

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

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

Trace: sum of diagonal

$$\mathbf{M} = \begin{bmatrix} 2.5 & 0.8 \\ 0.8 & 1.5 \end{bmatrix}$$

$$\mathrm{tr}(\mathbf{M}) = M_{11} + M_{22}$$

$$= 2.5 + 1.5 = 4.0$$

$$= \lambda_1 + \lambda_2 \text{ (sum of eigenvalues)}$$

Trace = total variance

tr = 4.0
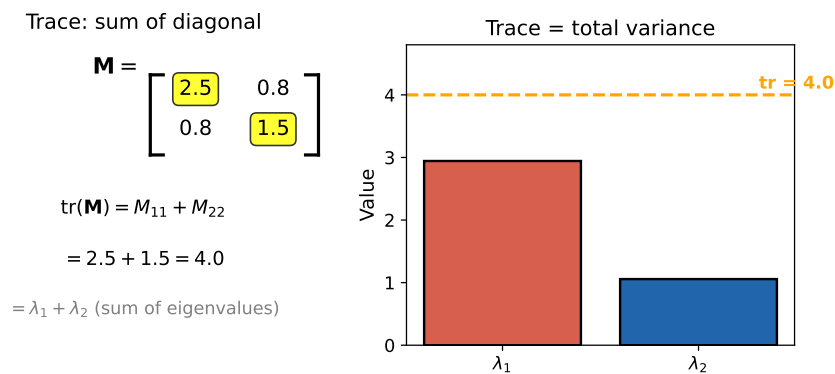
Figure 11: Trace: sum of diagonal elements = sum of eigenvalues = total variance.

Say this:

- "Sum of diagonal elements"
- "Total variance"
- "Sum of eigenvalues"

Think this:

Key properties:
- $\mathrm{tr}(\mathbf{AB}) = \mathrm{tr}(\mathbf{BA})$ — "Trace is cyclic"
- $\mathrm{tr}(\mathbf{M}) = \sum_i \lambda_i$ — "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

$\mathrm{tr}(\mathbf{G})/p = \bar{e}$ — "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.
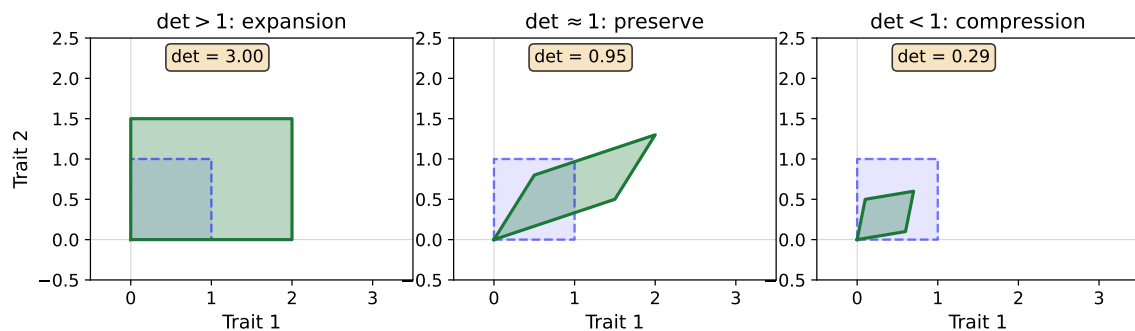
Figure 12: Determinant as volume scaling. Left: expansion (det > 1). Center: preservation (det ≈ 1). Right: compression (det < 1).

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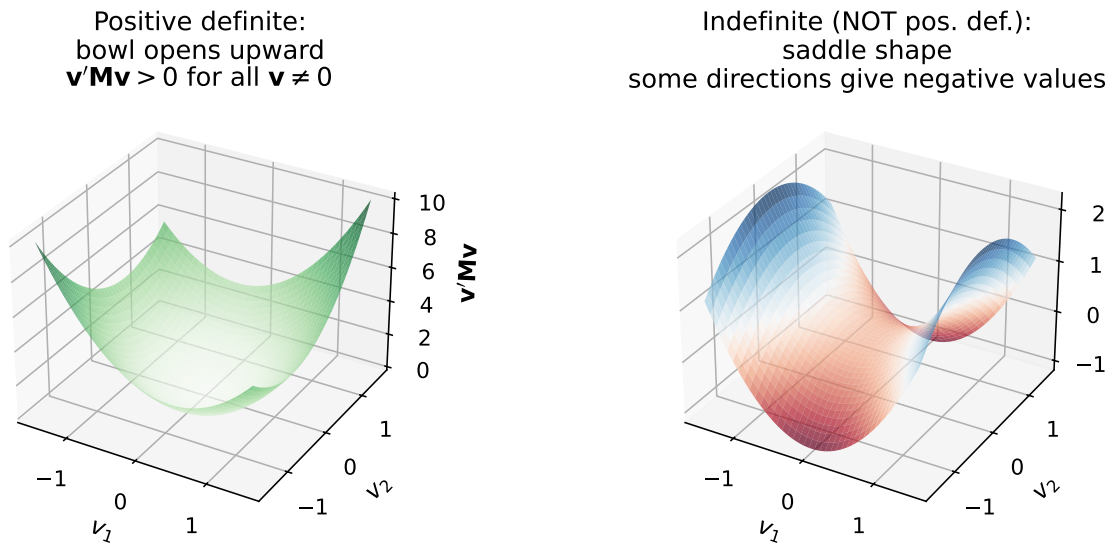
Figure 13: Left: Positive definite—bowl opens upward, $\boldsymbol{v}'\mathbf{M}\boldsymbol{v} > 0$ for all $\boldsymbol{v} \neq \mathbf{0}$. Right: Indefinite—saddle shape, some directions give negative values.

> **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 $R(\boldsymbol{v}) = \boldsymbol{v}'\mathbf{G}\boldsymbol{v}/\boldsymbol{v}'\mathbf{P}\boldsymbol{v}$ is bounded by generalized eigenvalues.
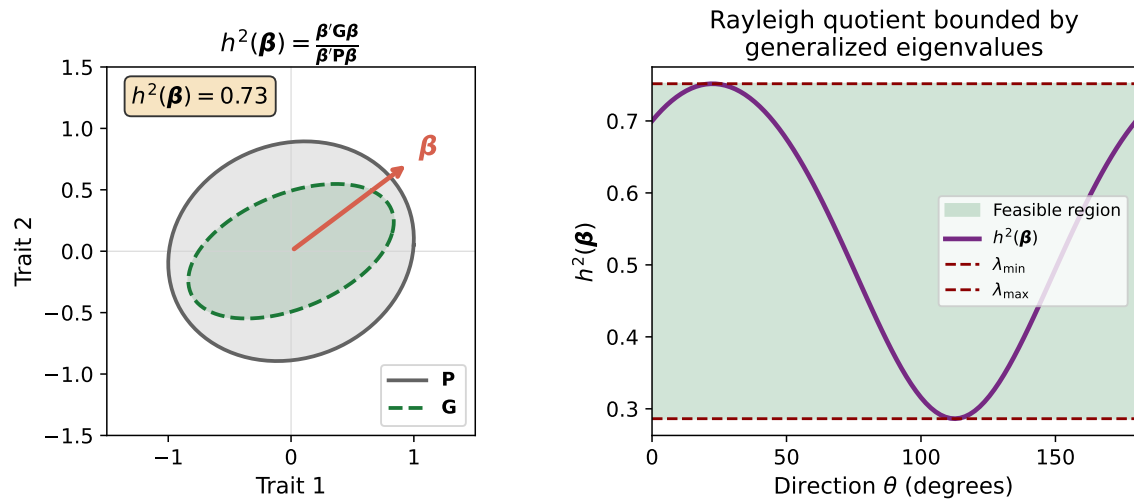
Figure 14: Left: $\mathbf{G}$ and $\mathbf{P}$ ellipses with direction $\boldsymbol{\beta}$. Right: $h^2(\boldsymbol{\beta})$ varies with direction but is bounded by $\lambda_{\min}$ and $\lambda_{\max}$.

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: $\mathbf{G}\boldsymbol{v} = \lambda\mathbf{P}\boldsymbol{v}$

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

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

Mantra

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

Biological translation

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

Generalized eigenvalues = extreme heritabilities

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

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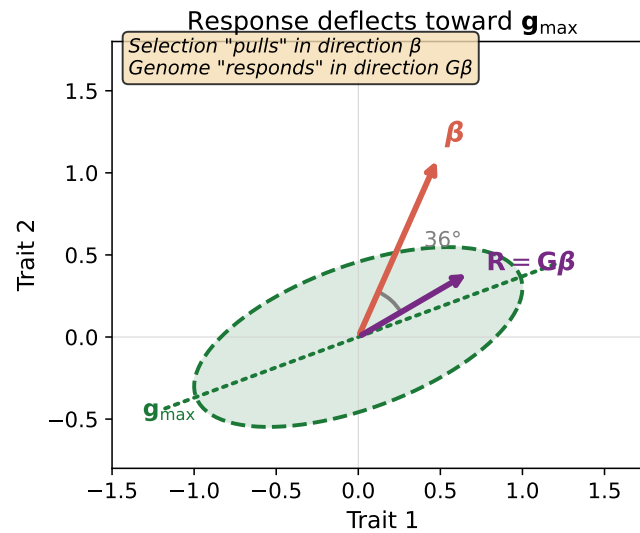
Figure 15: Response deflection. Selection pulls in direction $\boldsymbol{\beta}$, but the response $\boldsymbol{R} = \mathbf{G}\boldsymbol{\beta}$ rotates toward the genetic line of least resistance $\boldsymbol{g}_{\max}$.

Say this:

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

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 $\boldsymbol{g}_{\max}$."

Biological translation

$\angle(\boldsymbol{\beta}, \mathbf{G}\boldsymbol{\beta})$	"Deflection angle—message loss"
$\boldsymbol{\beta} \perp \boldsymbol{g}_{\max}$	"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
$\mathbf{M}v$	"Where does $\mathbf{M}$ send v?"	Transform the arrow
$v'\mathbf{M}v$	"Variance of $\mathbf{M}$ in direction 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
$\mathbf{Q\Lambda Q}'$	"$\mathbf{M}$ in its natural axes"	Eigenvectors + eigenvalues
$\mathrm{tr}(\mathbf{M})$	"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 $c(\boldsymbol{\beta})$
$g_{\max}$	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)
$V_{\mathrm{rel}}(\mathbf{G}^*)$	Eigenvalue dispersion $\to h^2$ heterogeneity

16.3 Three Key Mantras

1. $v'\mathbf{M}v$ asks: *"How much variance does $\mathbf{M}$ have in direction v?"*

2. $\mathbf{G}\boldsymbol{\beta}$ asks: *"Where does the genome send selection?"* (If $\mathbf{G}$ is anisotropic, response rotates toward $g_{\max}$.)

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

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

$$\boxed{\Delta \bar{z} = \mathbf{G}\boldsymbol{\beta}} \tag{1}$$

> **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 $\boldsymbol{\beta}$?"

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

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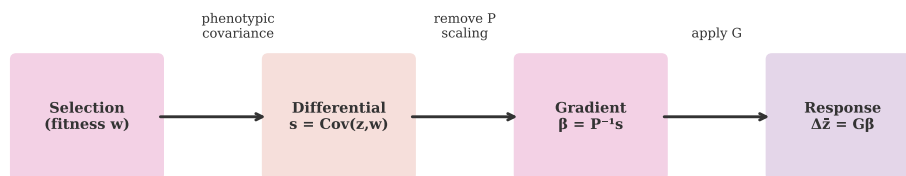
Figure 16: Overview of Lande's equation. Selection creates a phenotypic shift (the selection differential $\boldsymbol{s}$), which we decompose into a direction-independent gradient $\boldsymbol{\beta}$, then filter through the genetic architecture $\mathbf{G}$ to get the evolutionary response $\Delta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

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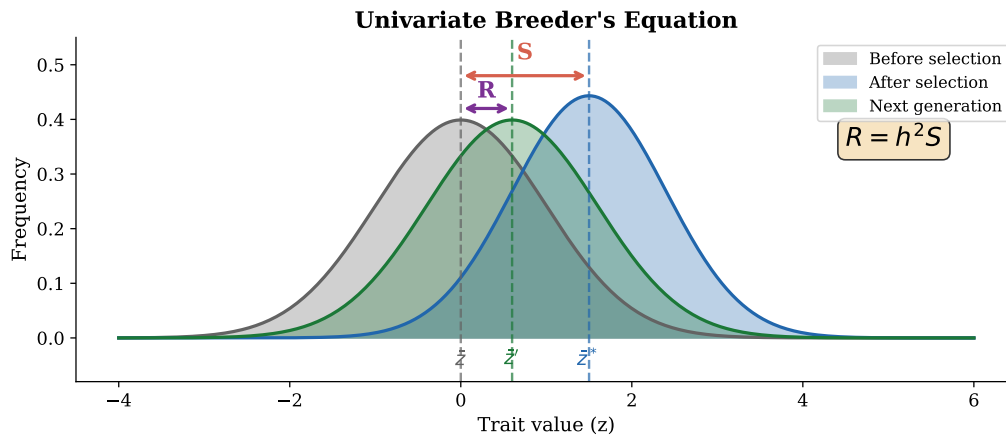
Figure 17: The univariate breeder's equation setup. Selection shifts the distribution (gray $\to$ blue), then inheritance filters that shift (blue $\to$ green). The response R is smaller than the selection differential S by a factor of h^2.

17.2.2   Two Key Quantities

> **Definition: Selection Differential**
>
> $$S = \bar{z}^* - \bar{z} = \mathrm{Cov}(z, w)$$
>
> **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

Selection Differential S

$$h^2 = \frac{V_G}{V_P}$$

Response R = h²S

Heritability
"filter"

*Lost to
environment*

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: $\boldsymbol{z} = (z_1, z_2, \ldots, z_p)'$.

17.3.1   What Changes?

1. **Variances become matrices:**

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

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

$$S \to \boldsymbol{s} = \mathrm{Cov}(\boldsymbol{z}, w) = \begin{pmatrix} \mathrm{Cov}(z_1, w) \\ \mathrm{Cov}(z_2, w) \\ \vdots \end{pmatrix}$$

3. **Response becomes a vector:**

$$R \to \Delta \bar{\boldsymbol{z}} = \bar{\boldsymbol{z}}' - \bar{\boldsymbol{z}}$$
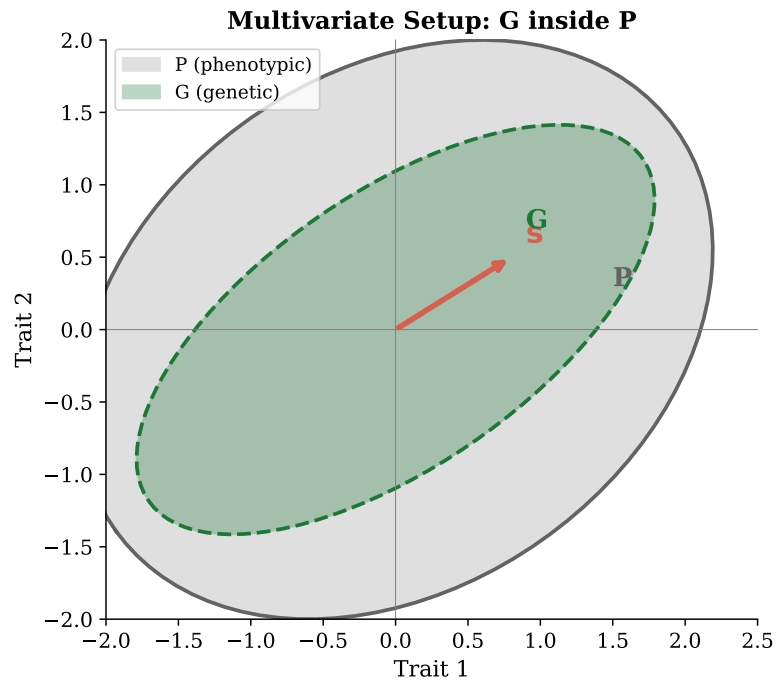
Figure 19: The multivariate setup. **P** (gray ellipse) captures phenotypic variance and covariance. **G** (green ellipse) captures genetic variance and covariance. The selection differential $\boldsymbol{s}$ (red arrow) shows how selection shifts the phenotypic mean.

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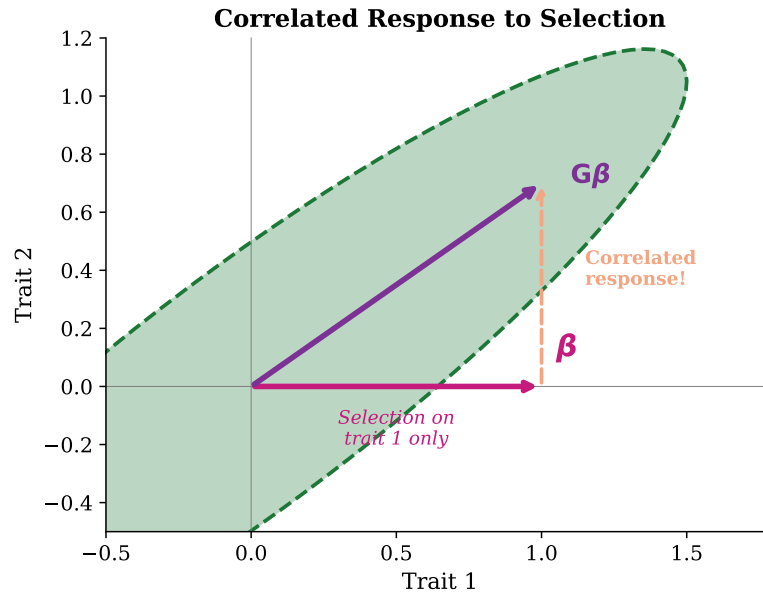
Figure 20: Correlated response. Even if selection acts only on trait 1 (horizontal arrow), the response (purple arrow) has a component in trait 2 because the traits are genetically correlated. The G-matrix encodes this coupling.

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:

$$\boxed{\Delta \bar{z} = \mathrm{Cov}_G(z, w)} \tag{3}$$

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: $\bar{a}^* - \bar{a} = \mathrm{Cov}(a, w)$

4. Therefore: $\Delta \bar{z} = \mathrm{Cov}(a, w) = \mathrm{Cov}_G(z, w)$

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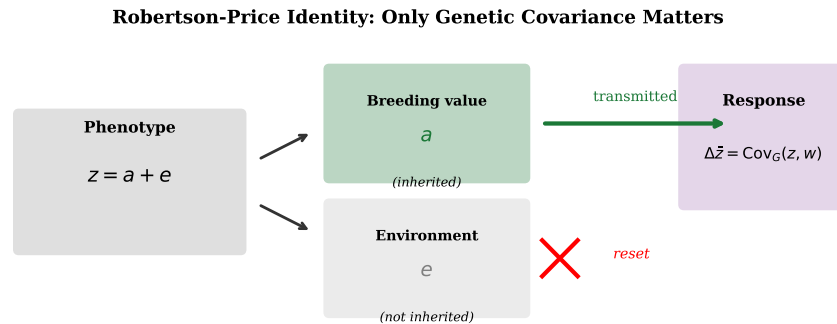
Figure 21: The Robertson-Price identity. Fitness selects on phenotypes, but only the genetic component (breeding value) is transmitted to offspring.

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:

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

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

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:

$$\boldsymbol{\beta} = \mathbf{P}^{-1}\boldsymbol{s} \tag{5}$$

Think this:

In words: "The selection gradient is the selection differential, standardized by phenotypic variance."
Using our verbal shortcuts: "$\mathbf{P}^{-1}\boldsymbol{s}$ runs $\mathbf{P}$ backwards on $\boldsymbol{s}$"—it removes the phenotypic scaling from the selection differential.

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

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

1. Direct selection on each trait

2. Indirect effects through correlated traits

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

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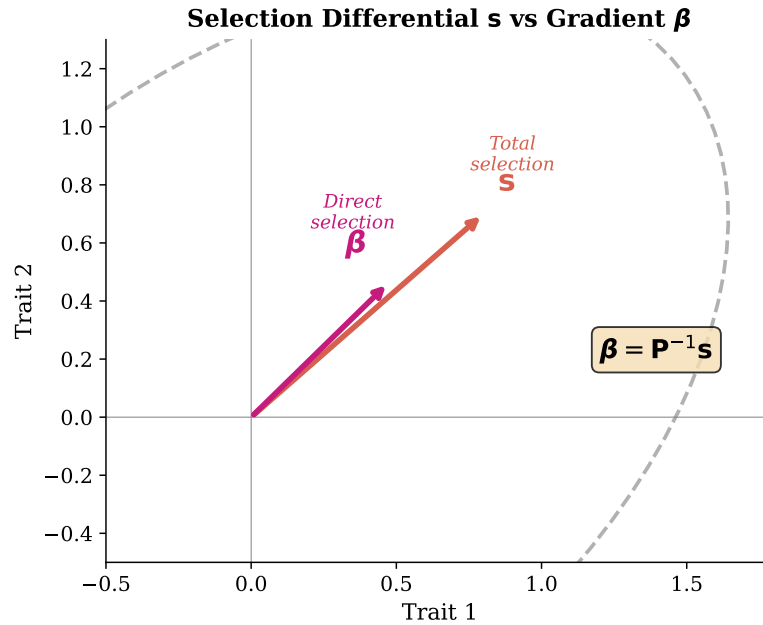
Figure 22: Selection differential vs gradient. The differential $\boldsymbol{s}$ (red) includes correlated effects. The gradient $\boldsymbol{\beta}$ (orange), obtained by applying $\mathbf{P}^{-1}$, isolates direct selection on each trait.

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:

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

$$= \sum_j G_{ij} \cdot \beta_j \tag{7}$$

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

> **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:** $\Delta \bar{z} = \mathrm{Cov}_G(\boldsymbol{z}, w)$

   "Response equals genetic covariance with fitness."

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

   "Genetic covariance with fitness equals G applied to the selection gradient."

3. **Therefore:**

$$\boxed{\Delta \bar{z} = \mathbf{G}\boldsymbol{\beta}} \tag{9}$$

Derivation Flow: Three Key Steps
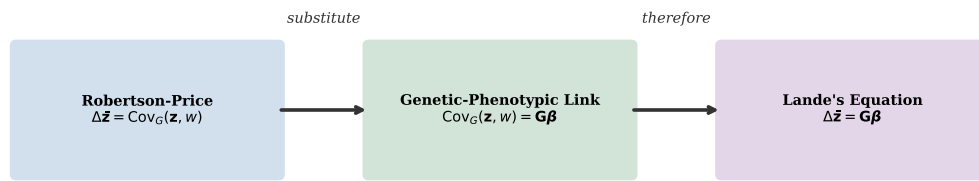
Figure 23: The logical flow of the derivation. Each arrow represents a key insight.

17.6.2 Alternative Form

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

$$\Delta \bar{z} = \mathbf{G}\mathbf{P}^{-1}\boldsymbol{s} \tag{10}$$

> **Think this:**
>
> **Reading this right-to-left:**
>
> 1. Start with the selection differential $\boldsymbol{s}$ (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 $\boldsymbol{g}_{\max}$."
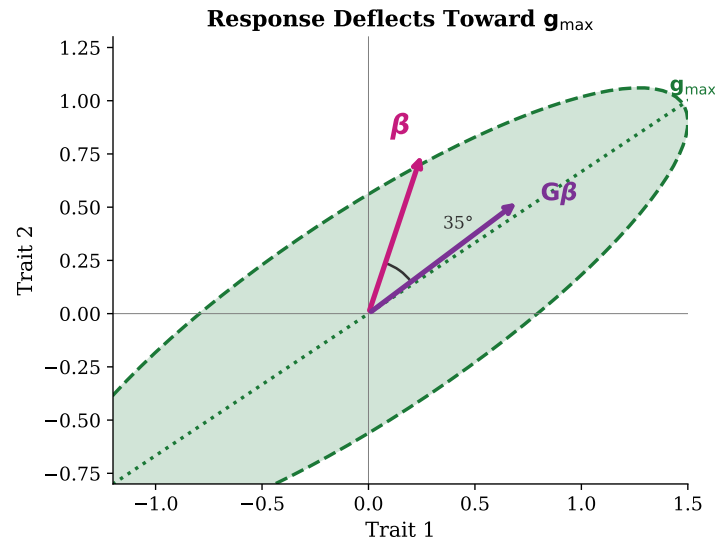
Figure 24: Deflection of evolutionary response. The selection gradient $\boldsymbol{\beta}$ (red) specifies the direction selection "wants" to go. The actual response $\mathbf{G}\boldsymbol{\beta}$ (purple) is rotated toward $\boldsymbol{g}_{\max}$ (green dashed line), the genetic line of least resistance.

17.7.2   When Does Deflection Occur?

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

- $\boldsymbol{\beta}$ 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:

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

This depends on:

- How much genetic variance exists in the direction of $\boldsymbol{\beta}$: captured by $\boldsymbol{\beta}'\mathbf{G}\boldsymbol{\beta}$

- How the G-matrix redistributes that variance across traits

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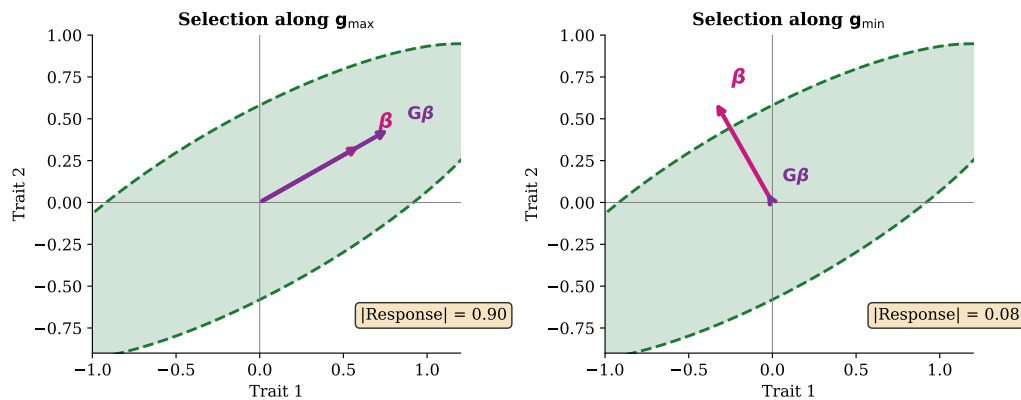
Figure 25: Response magnitude. Selection along $\boldsymbol{g}_{\max}$ (left) produces a large response. Selection perpendicular to $\boldsymbol{g}_{\max}$ (right) produces a small response. The G-matrix acts as a filter.

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 $\boldsymbol{\beta}$ is:

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

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

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:

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

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

17.8.3 The Constraint Trap

A **constraint trap** occurs when:

- Evolvability $e(\boldsymbol{\beta})$ is moderate to high

- But directional heritability $h^2(\boldsymbol{\beta})$ is low

This happens when environmental variance "swamps" the genetic signal in direction $\boldsymbol{\beta}$.
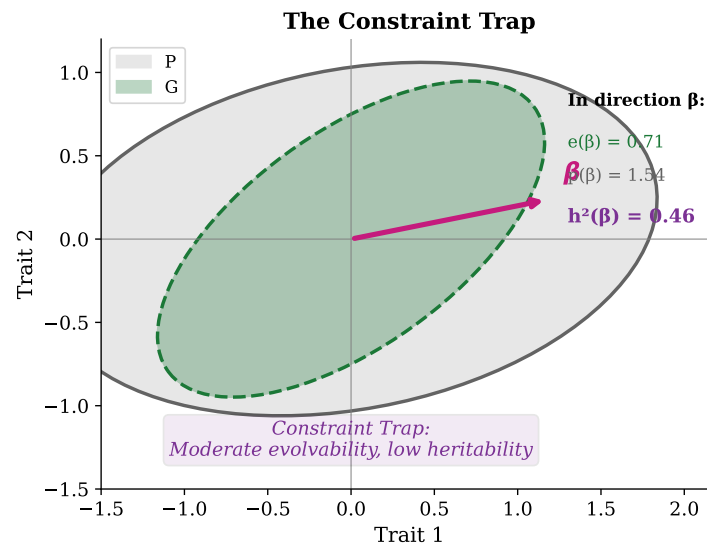
Figure 26: The constraint trap. In this direction, genetic variance (green) is reasonable, but phenotypic variance (gray) is much larger. The ratio $h^2(\boldsymbol{\beta})$ is low, so the realized response is weak despite moderate evolvability.

17.9 Step 8: Summary and Key Takeaways

17.9.1 The Equation and Its Meaning

Lande's Multivariate Breeder's Equation

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

In words:
- s: How much did selection shift the phenotypic mean? (selection differential)
- $\mathbf{P}^{-1}s = \boldsymbol{\beta}$: What was the *direct* selection on each trait? (selection gradient)
- $\mathbf{G}\boldsymbol{\beta}$: 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 $\boldsymbol{\beta} = \mathbf{P}^{-1}s$ by running $\mathbf{P}$ backwards—removing correlation effects."

3. "We ask: where does $\mathbf{G}$ send $\boldsymbol{\beta}$? That's the response $\Delta\bar{z}$."

4. "If $\mathbf{G}$ is anisotropic (cigar-shaped), the response rotates toward $\boldsymbol{g}_{\max}$—the genetic line of least resistance."

5. "The magnitude of response depends on evolvability $\boldsymbol{\beta}'\mathbf{G}\boldsymbol{\beta}$—how much genetic variance exists in the selection direction."
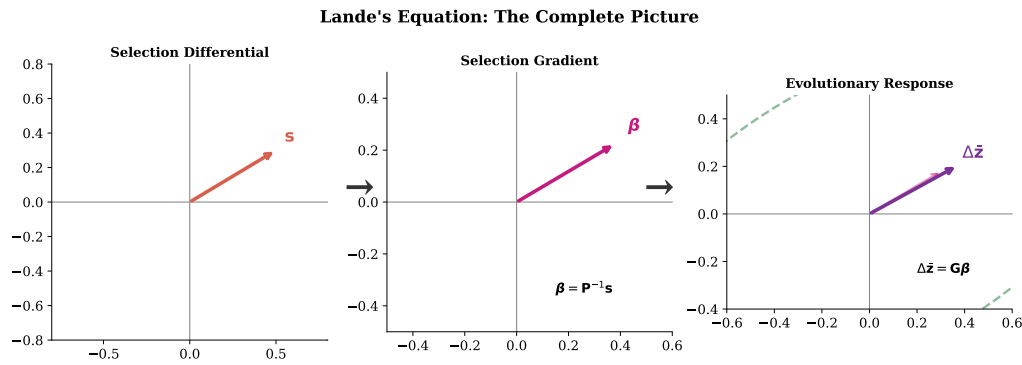
Figure 27: Visual summary of Lande's equation. Start with the selection differential (what phenotypic selection did), extract the gradient (what direct selection is), apply the G-matrix (where the genome sends it), arrive at the response.

17.9.3   The Communication Metaphor (Revisited)

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

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

> **Mantra**
>
> "Selection speaks in direction $\boldsymbol{\beta}$. The genome hears $\mathbf{G}\boldsymbol{\beta}$. 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:

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

17.10.2   Step-by-Step Calculation

1. Compute the selection gradient:

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

First, invert $\mathbf{P}$:

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

Then:

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

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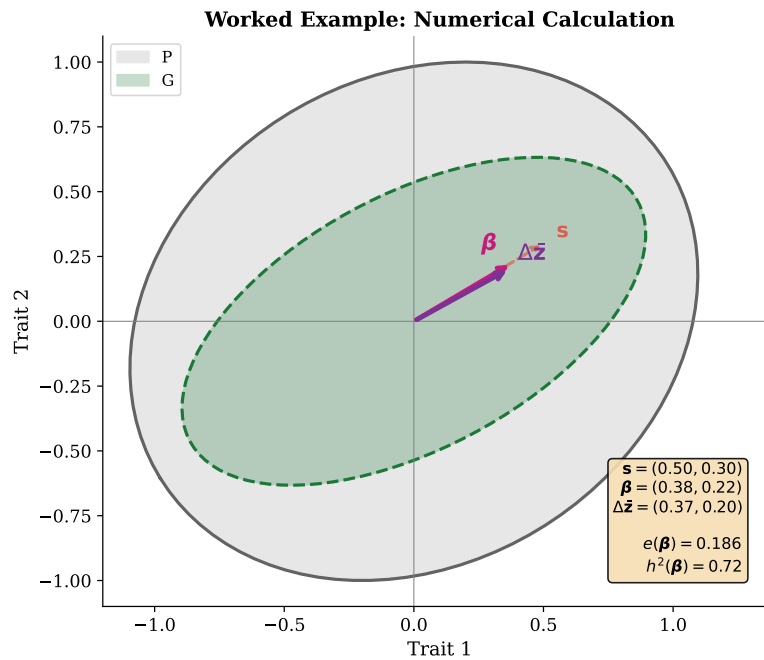
Figure 28: Worked example. The selection differential $\boldsymbol{s}$ (gray dashed), selection gradient $\boldsymbol{\beta}$ (red), and evolutionary response $\Delta\bar{z}$ (purple) are shown with the G (green) and P (gray) ellipses.

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 $\boldsymbol{\beta}$:

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

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

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 $\boldsymbol{\beta}$ is an eigenvector of $\mathbf{G}$, show that $\Delta \bar{\boldsymbol{z}} \parallel \boldsymbol{\beta}$ (no deflection).

3. **Isotropic G:** If $\mathbf{G} = g\mathbf{I}$, show that $\Delta \bar{\boldsymbol{z}} = g\boldsymbol{\beta}$ (response is always parallel to selection).

4. **Selection on a single trait:** If selection acts only on trait 1, so $\boldsymbol{s} = (s_1, 0)'$, compute $\boldsymbol{\beta}$ and $\Delta \bar{\boldsymbol{z}}$. When does trait 2 respond?

5. **Constraint trap:** Construct a $(\mathbf{G}, \mathbf{P})$ pair where some direction has high evolvability but low $h^2(\boldsymbol{\beta})$.
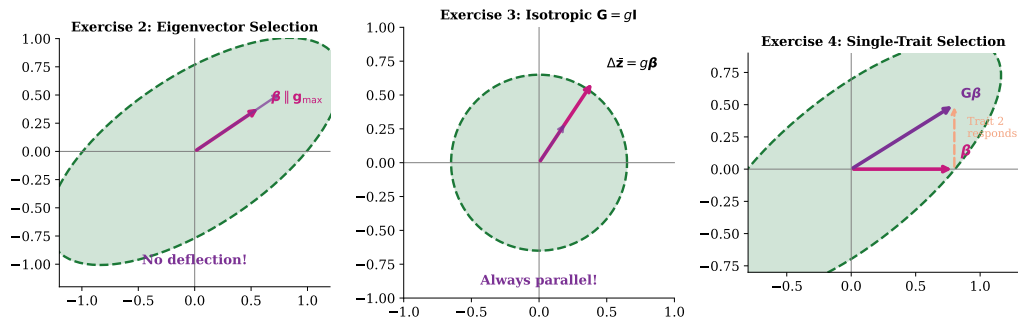

Figure 29: Visual aids for exercises.

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

$$\boldsymbol{z} = (z_1, z_2, \ldots, z_n)$$

Assumption 1: Additive Genetic Model

Each individual's phenotype decomposes as:

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

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

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

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

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

A.1.1   The Phenotypic Distribution

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

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

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 $\bar{\boldsymbol{z}}$, with shape determined by $\mathbf{P}$. The exponent $(\boldsymbol{z}-\bar{\boldsymbol{z}})'\mathbf{P}^{-1}(\boldsymbol{z}-\bar{\boldsymbol{z}})$ is the squared Mahalanobis distance from the mean.
Using our mantra: "$\mathbf{P}^{-1}$ in the exponent measures distance in $\mathbf{P}$-standardized units."
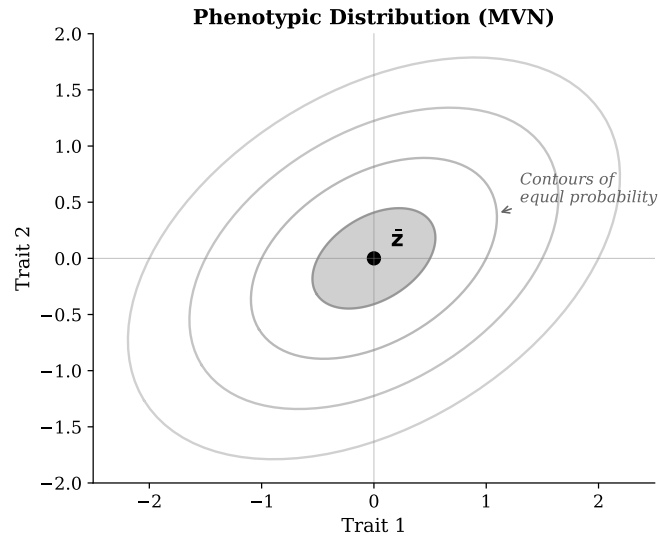
Figure 30: The phenotypic distribution as a multivariate normal cloud. Contours of equal probability are ellipses determined by $\mathbf{P}$. The center is the population mean $\bar{z}$.

A.2 The Goal: Derive Lande's Equation

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

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

The derivation proceeds in **five steps**:

1. Show that $\nabla\ln\bar{W} = \mathbf{P}^{-1}s$ (the selection gradient equals standardized selection differential)

2. Compute $\nabla p(z)$ for the multivariate normal

3. Plug into the expression for $\nabla\bar{W}$

4. Identify the selection differential 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 $W(z)$ be the fitness of an individual with phenotype z. The **mean fitness** of the population is:

$$\bar{W} = \int p(z)W(z)\,dz \tag{14}$$

> **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:

$$\boldsymbol{\beta} = \nabla\ln\bar{W} = \frac{1}{\bar{W}}\nabla\bar{W} \tag{15}$$

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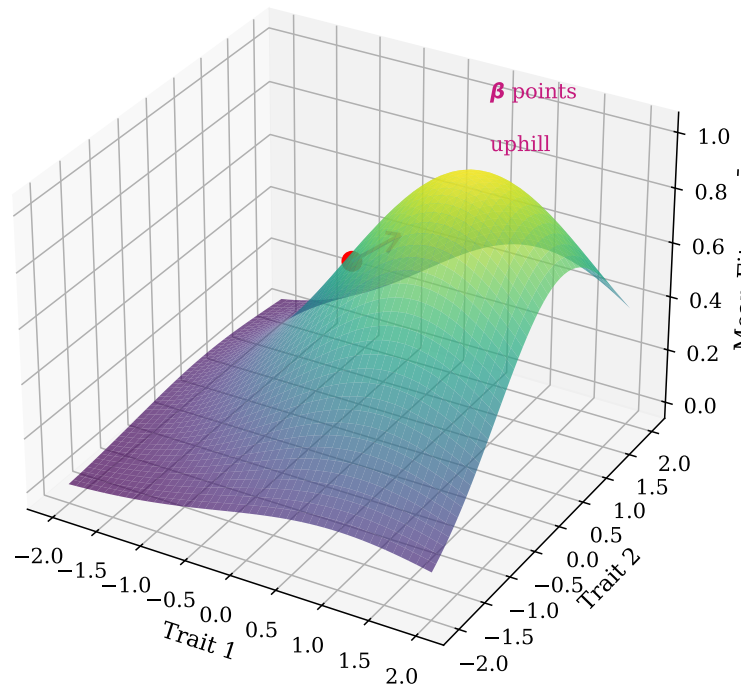
Figure 31: The adaptive landscape. Mean fitness $\bar{W}$ is a surface over trait space. The selection gradient $\boldsymbol{\beta} = \nabla \ln \bar{W}$ points in the direction of steepest ascent.

A.3.3 Key Calculus Identity

We use the chain rule for logarithms:

$$\nabla \ln \bar{W} = \frac{1}{\bar{W}} \nabla \bar{W} \tag{16}$$

> **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:

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

where:

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

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

A.4.2 Taking the Gradient

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

$$\nabla p(\boldsymbol{z}) = C\nabla \exp(u) = C\exp(u)\nabla u = p(\boldsymbol{z})\nabla u \tag{19}$$

> **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 $u = -\tfrac{1}{2}(\boldsymbol{z} - \bar{\boldsymbol{z}})'\mathbf{P}^{-1}(\boldsymbol{z} - \bar{\boldsymbol{z}})$.

> **Mantra**
>
> **Key result from linear algebra:** For any symmetric matrix $\mathbf{M}$ and vector $\boldsymbol{a}$:
>
> $$\frac{d[\boldsymbol{a}'\mathbf{M}\boldsymbol{a}]}{d\boldsymbol{a}} = 2\mathbf{M}\boldsymbol{a}$$
>
> **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 $\boldsymbol{a} = \boldsymbol{z} - \bar{\boldsymbol{z}}$ and $\mathbf{M} = \mathbf{P}^{-1}$:

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

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

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

> **Key Result: Gradient of MVN Density**
>
> $$\boxed{\nabla p(\boldsymbol{z}) = \mathbf{P}^{-1}(\boldsymbol{z} - \bar{\boldsymbol{z}}) \cdot p(\boldsymbol{z})}$$
>
> **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 $\boldsymbol{z}$, the gradient points in the direction $\mathbf{P}^{-1}(\boldsymbol{z} - \bar{\boldsymbol{z}})$—which is "toward the mean in $\mathbf{P}$-standardized coordinates."
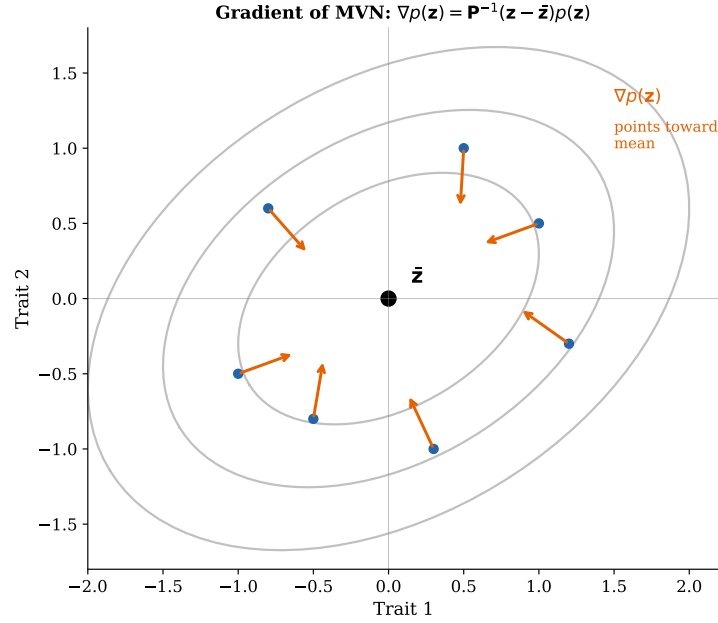
Figure 32: Gradient of the MVN density. At each point, $\nabla p(\boldsymbol{z})$ points toward the mean, with magnitude proportional to $p(\boldsymbol{z})$ and direction determined by $\mathbf{P}^{-1}$.

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

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

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

A.5.1   Pulling the Gradient Inside

The gradient operator can be pulled inside the integral:

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

Using the product rule:

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

> **Think this:**
>
> **Key assumption:** Fitness $W(\boldsymbol{z})$ depends on an individual's phenotype, not on the population mean $\bar{\boldsymbol{z}}$.
> Therefore: $\nabla W(\boldsymbol{z}) = \mathbf{0}$
> **Verbal:** "An individual's fitness doesn't change just because the population mean shifts."

This simplifies to:

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

A.5.2 Substituting the MVN Gradient

Plugging in equation (20):

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

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

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

Splitting the integral:

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

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

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

A.6 Step 4: Identifying the Selection Differential

A.6.1 The Mean Phenotype After Selection

The expression $\int \boldsymbol{z} \cdot p(\boldsymbol{z}) W(\boldsymbol{z}) \, d\boldsymbol{z}$ is related to the mean phenotype *after selection*.
   Define the **post-selection frequency** of phenotype $\boldsymbol{z}$:

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

> **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:

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

Therefore:

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

A.6.2 The Selection Differential Emerges

Substituting back:

$$\nabla \bar{W} = \mathbf{P}^{-1} \left[\bar{W} \cdot \bar{\boldsymbol{z}}^* - \bar{\boldsymbol{z}} \bar{W} \right] \tag{26}$$

$$= \mathbf{P}^{-1} \bar{W} \left[\bar{\boldsymbol{z}}^* - \bar{\boldsymbol{z}} \right] \tag{27}$$

$$= \mathbf{P}^{-1} \bar{W} \cdot \boldsymbol{s} \tag{28}$$

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

> **The Selection Differential**
>
> $$\boldsymbol{s} = \bar{z}^* - \bar{z} = \text{Cov}(\boldsymbol{z}, W)$$
>
> **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 $\boldsymbol{\beta}$:

$$\boldsymbol{\beta} = \nabla \ln \bar{W} = \frac{1}{\bar{W}} \nabla \bar{W} \tag{29}$$

$$= \frac{1}{\bar{W}} \cdot \mathbf{P}^{-1} \bar{W} \cdot \boldsymbol{s} \tag{30}$$

$$= \mathbf{P}^{-1} \boldsymbol{s} \tag{31}$$

> **Key Result: Selection Gradient**
>
> $$\boxed{\boldsymbol{\beta} = \nabla \ln \bar{W} = \mathbf{P}^{-1} \boldsymbol{s}}$$
>
> **Verbal:** "The selection gradient is the selection differential with phenotypic correlations removed—it measures *direct* selection on each trait."
> **Using our mantra:** "$\mathbf{P}^{-1} \boldsymbol{s}$ runs $\mathbf{P}$ backwards on $\boldsymbol{s}$—removing the phenotypic scaling."
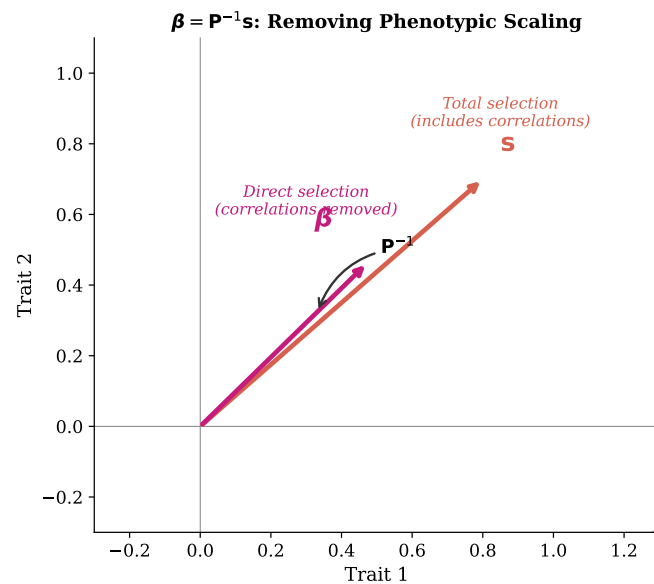
Figure 33: Selection differential $\boldsymbol{s}$ versus selection gradient $\boldsymbol{\beta}$. The transformation $\mathbf{P}^{-1}$ removes the effect of phenotypic correlations, isolating direct selection.

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 $\boldsymbol{x}$:

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

> **Say this:**
>
> **Verbal:** "The expected fitness of an individual with breeding value $\boldsymbol{x}$, averaging over all possible environmental effects."

Mean population fitness can also be written as:

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

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

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

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:

$$\nabla \ln \bar{W} = \mathbf{G}^{-1}\Delta\bar{\boldsymbol{z}} \tag{33}$$

> **Think this:**
>
> **Compare the two expressions:**
>
> $$\text{From phenotypes:} \quad \nabla \ln \bar{W} = \mathbf{P}^{-1}\boldsymbol{s} = \boldsymbol{\beta}$$
> $$\text{From breeding values:} \quad \nabla \ln \bar{W} = \mathbf{G}^{-1}\Delta\bar{\boldsymbol{z}}$$
>
> These must be equal!

A.7.3   Assembling Lande's Equation

Equating the two expressions:

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

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

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

> **Lande's Equation: The Final Result**
>
> $$\boxed{\Delta\bar{\boldsymbol{z}} = \mathbf{G}\boldsymbol{\beta} = \mathbf{G}\mathbf{P}^{-1}\boldsymbol{s}}$$
>
> **Verbal translation (reading right to left):**
>
> 1. Start with the selection differential $\boldsymbol{s}$ (how selection shifted phenotypes)
>
> 2. Apply $\mathbf{P}^{-1}$: "run $\mathbf{P}$ backwards" to get direct selection $\boldsymbol{\beta}$
>
> 3. Apply $\mathbf{G}$: "where does $\mathbf{G}$ send $\boldsymbol{\beta}$?" to get the response
>
> The derivation is complete.   ■

A.8 Summary: The Five Steps in Words

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

> **Mantra**
>
> **The core insight:** Selection acts on phenotypes ($\mathbf{P}$), but only genetics ($\mathbf{G}$) is inherited. The selection gradient $\boldsymbol{\beta}$ bridges these two worlds—it appears in both
>
> $$\boldsymbol{\beta} = \mathbf{P}^{-1}\boldsymbol{s} \quad \text{and} \quad \boldsymbol{\beta} = \mathbf{G}^{-1}\Delta\bar{z}$$
>
> Combining these gives Lande's equation.

A.9 The Quadratic Form Derivative: A Closer Look

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

A.9.1 Why This Works

Expand the quadratic form:

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

Taking the derivative with respect to a_k:

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

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

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

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

> **Say this:**
>
> **Verbal:** "The gradient of 'variance in direction $\boldsymbol{a}$' is $2\mathbf{M}\boldsymbol{a}$—it points in the direction $\mathbf{M}$ sends $\boldsymbol{a}$."

A.9.2 Connection to the Phrasebook

This is exactly Section 5 (Quadratic Form) in action! The quadratic form $\boldsymbol{a}'\mathbf{M}\boldsymbol{a}$ is the height of the $\mathbf{M}$-bowl at direction $\boldsymbol{a}$. Its gradient tells us which direction increases that height fastest.
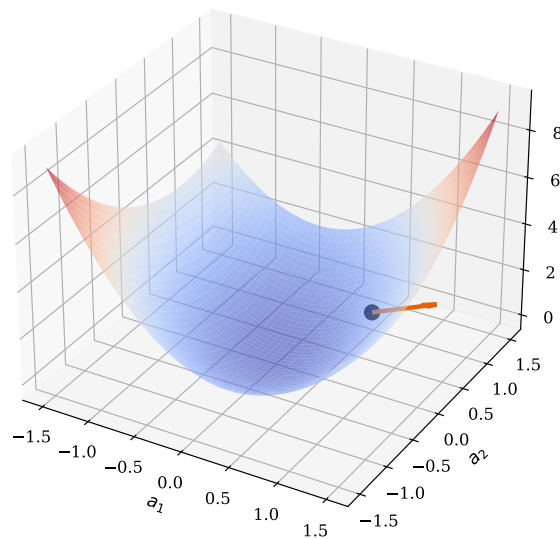
Figure 34: The gradient of a quadratic form. At point $\boldsymbol{a}$, the gradient $2\mathbf{M}\boldsymbol{a}$ points in the direction of steepest ascent on the $\mathbf{M}$-paraboloid.

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

3. Running parallel derivations for phenotypes and breeding values to connect selection to response

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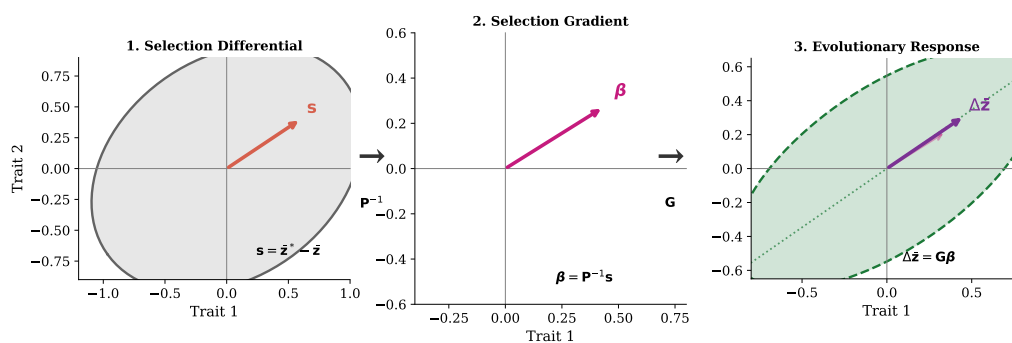

Figure 35: The complete picture. Selection creates $\boldsymbol{s}$, which becomes $\boldsymbol{\beta}$ after removing $\mathbf{P}$-scaling. The G-matrix transforms $\boldsymbol{\beta}$ into the response $\Delta \bar{\boldsymbol{z}}$, generally deflecting it toward $\boldsymbol{g}_{\max}$.