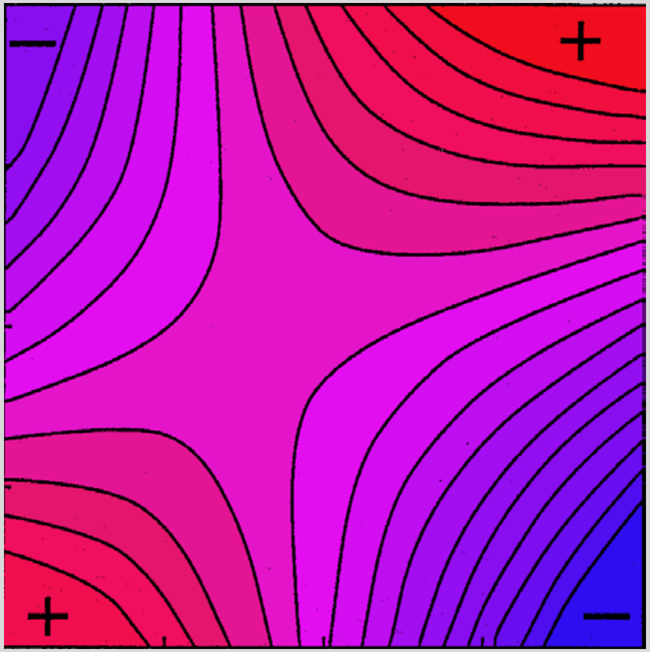
2.2 Selection as a Surface



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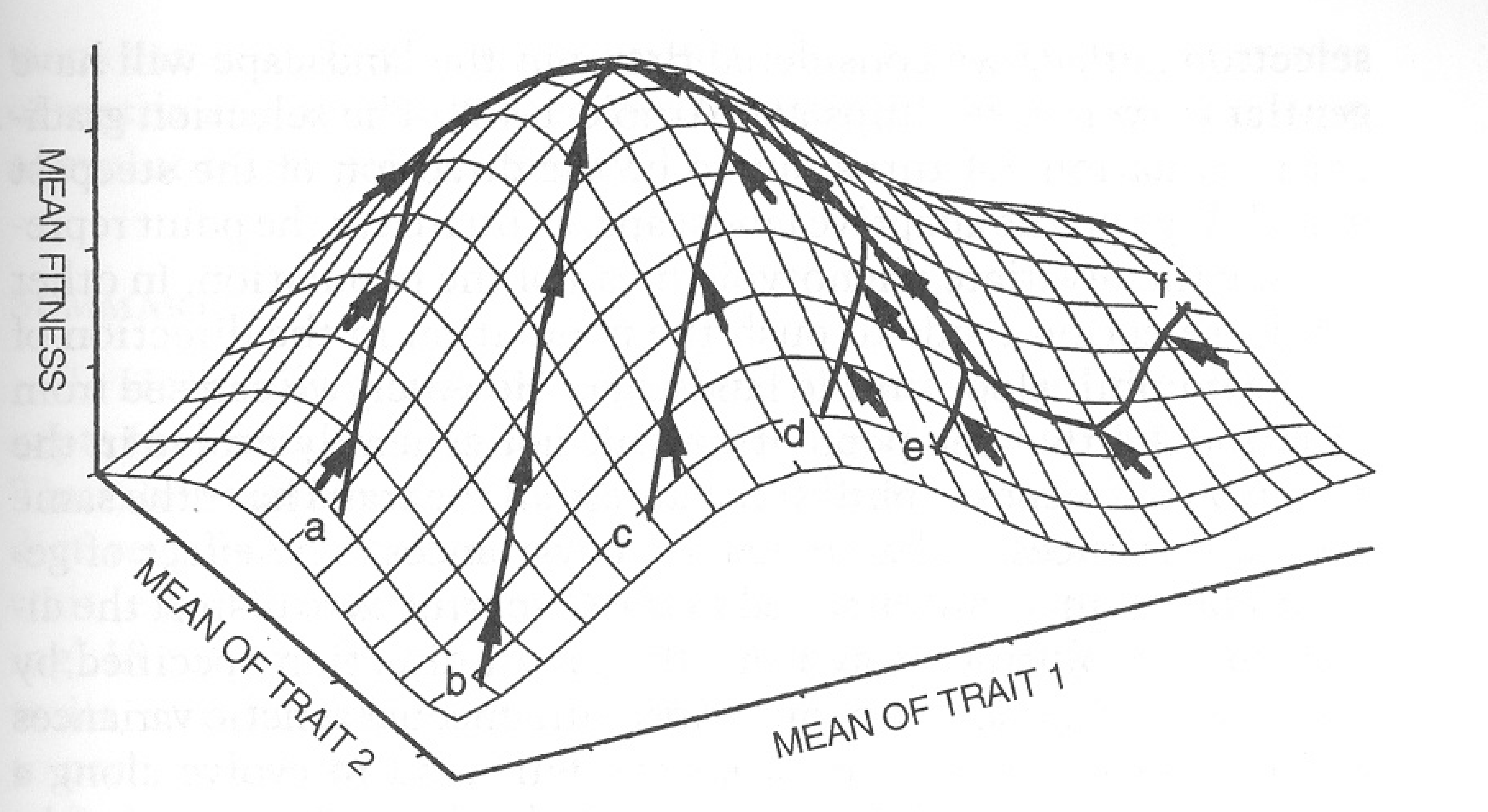
Evolution of the trait mean on an adaptive landscape: more than a metaphor



Two Parts

1. Selection as a set of coefficients

2. Selection as a surface

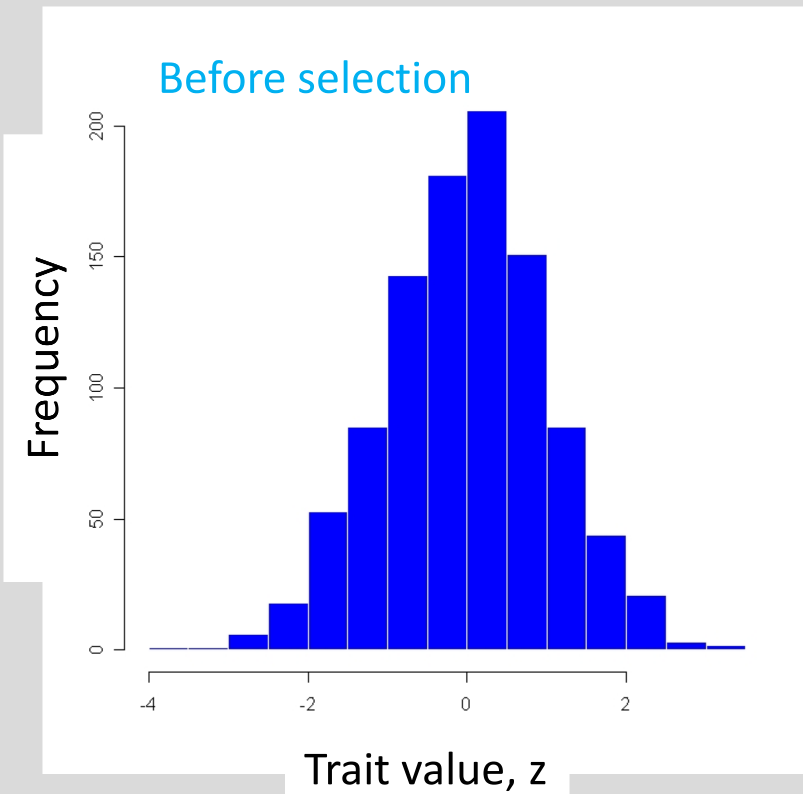
Part 1. Selection as a Set of Coefficients

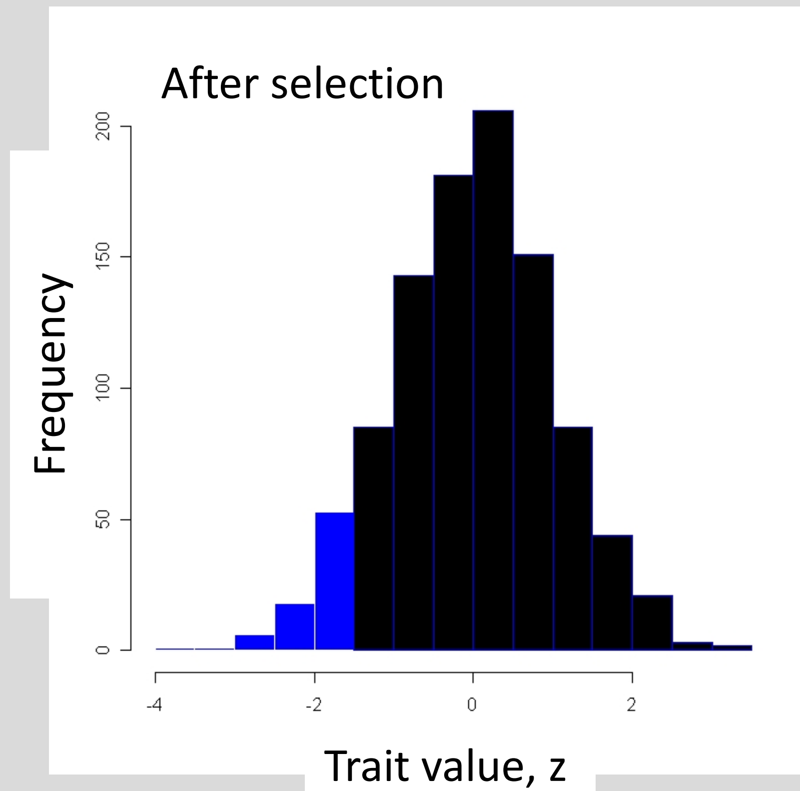
Thesis

- Selection changes trait distributions.
- The contrast between distributions before and after selection provides a powerful description of the force of selection.
- Multivariate measures of selection can correct for the effects of correlations between traits.

1. Selection changes the univariate trait distribution

a. The contrast between distributions before and after selection is particularly revealing





2. Shift in the trait mean, the linear selection differential, s

a. A particular example

$$s = \bar{z}^* - \bar{z} = 0.16 - (-0.01) = 0.17$$

b. The general case

$$\bar{z} = \int p(z) z dz$$

where p(z) is trait frequency before selection

$$\bar{z}^* = \int p(z)^* z dz$$

where p(z)* is trait frequency after selection

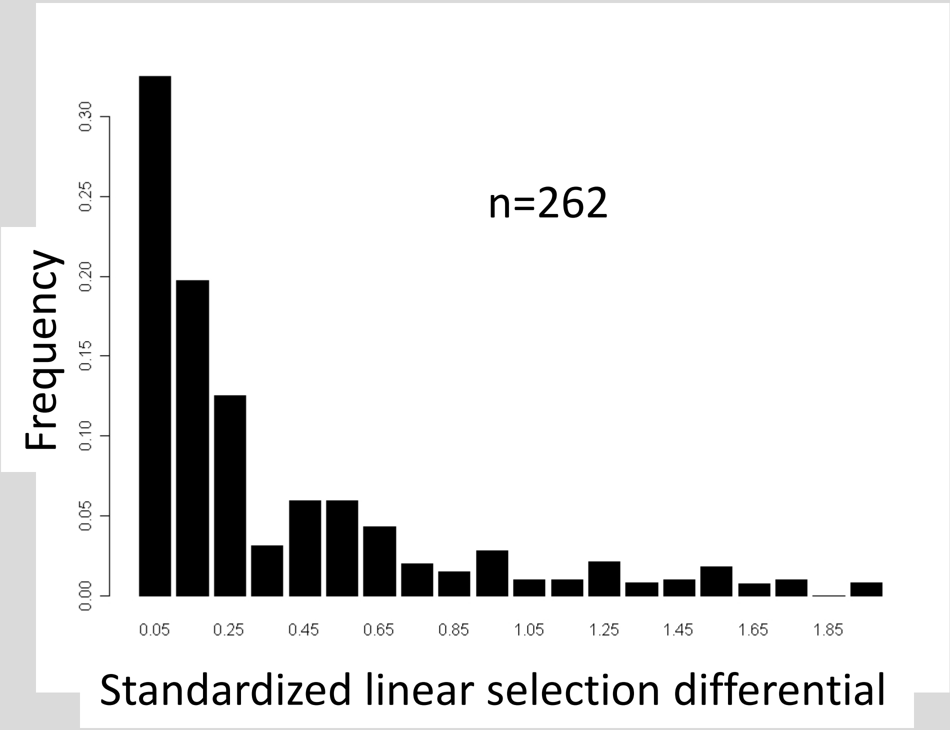
$$p(z)^* = w(z)p(z)$$

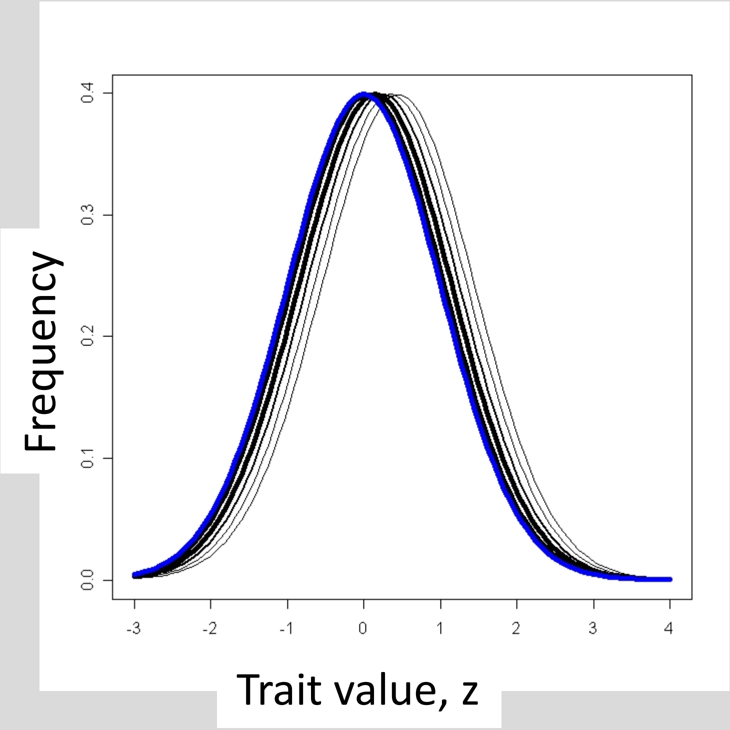
where w(z) is relative fitness of the z trait class

3. Surveys of selection differentials

a. The standardized linear selection differential, s', measures the shift in the mean

$$s' = (\bar{z}^* - \bar{z})/\sqrt{P}$$

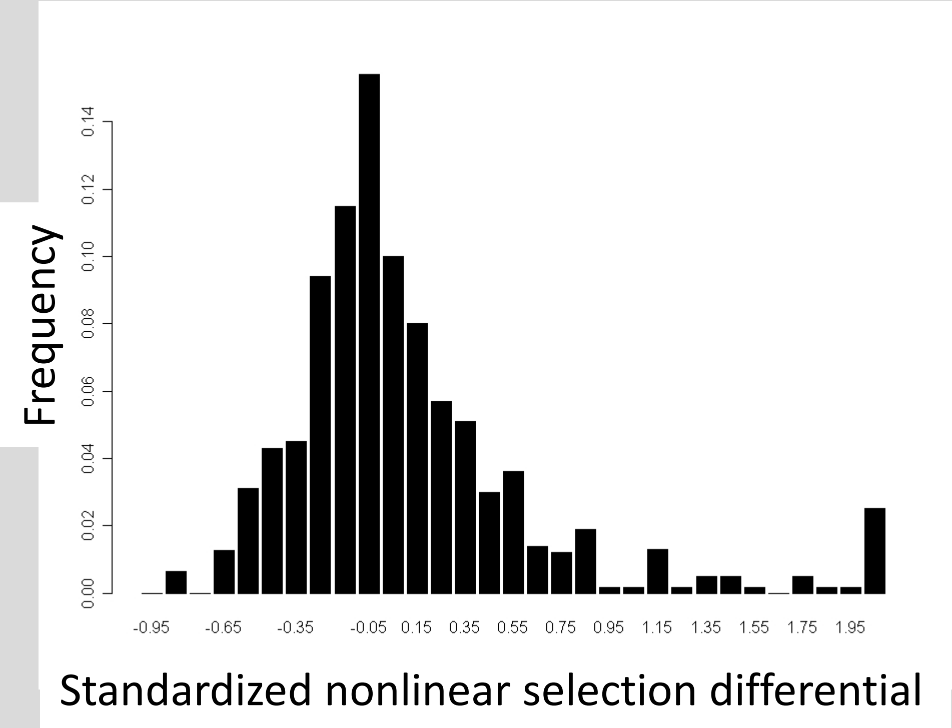


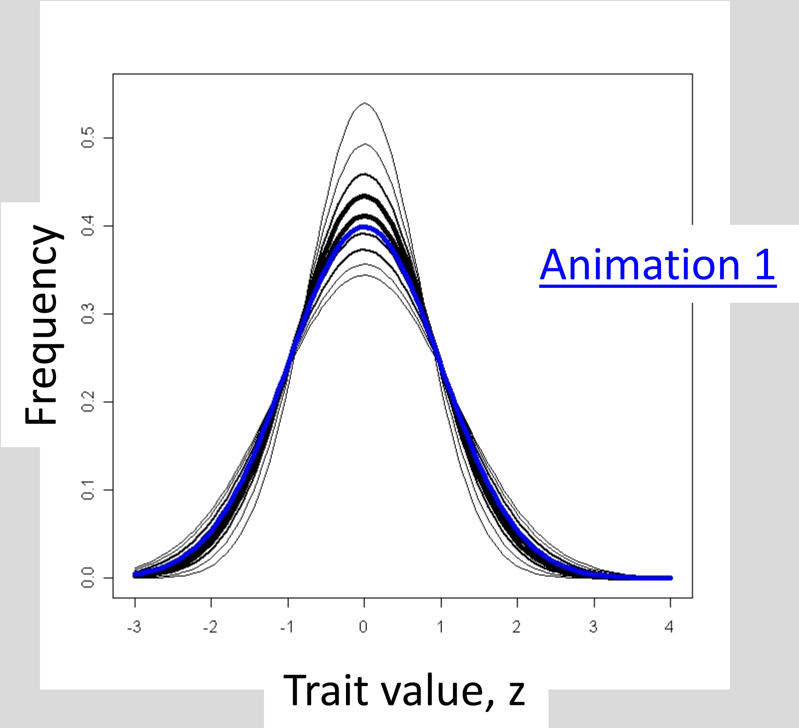


3. Surveys of selection differentials

b. The standardized nonlinear selection differential, C', measures change in the variance (or covariance)

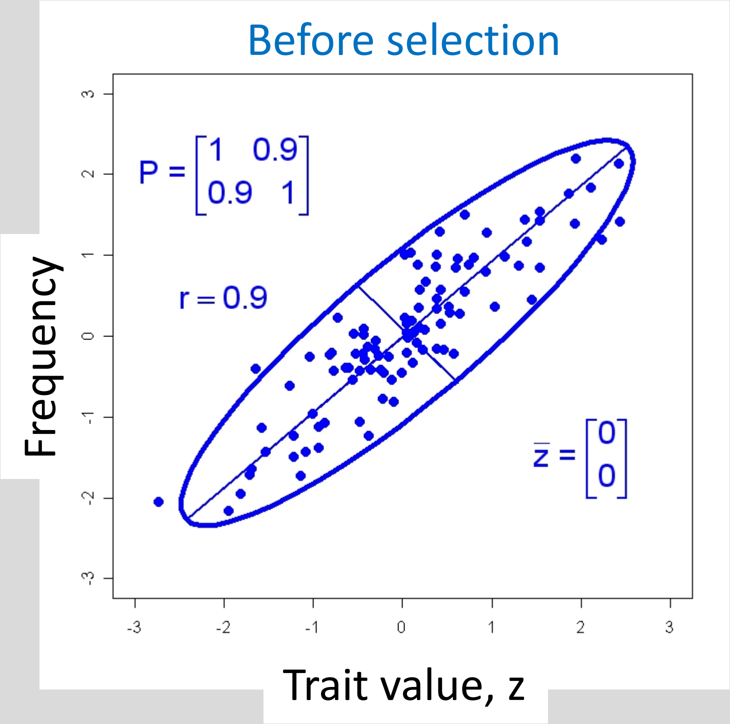
$$C' = (P^* - P + s^2)/P$$

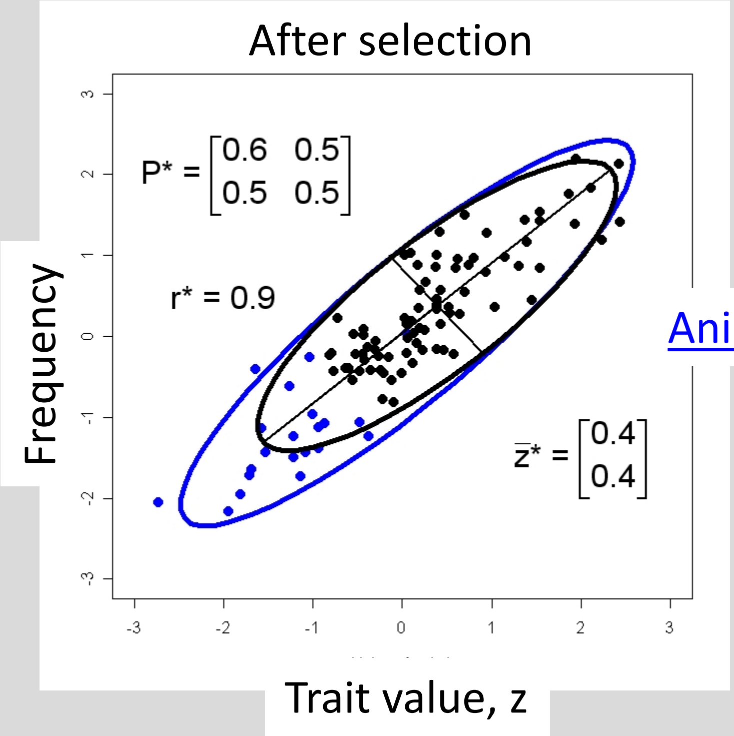




4. Selection changes the multivariate trait distribution

a. The contrast between distributions before and after selection



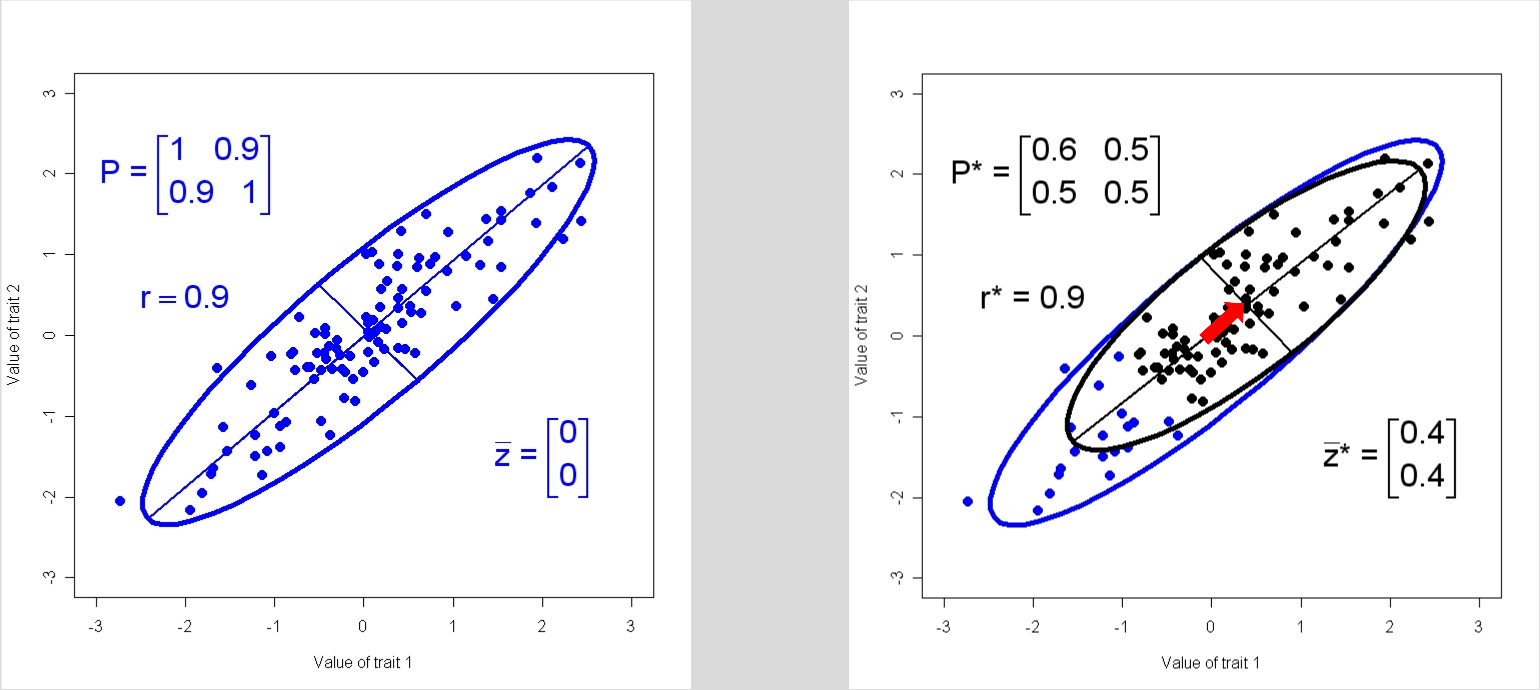


Animation 2

4. Selection changes the multivariate trait distribution

b. The directional selection differential, *s*, is a vector

$$s = Cov(w,z) = \begin{bmatrix} Cov(w,z_1) \\ Cov(w,z_2) \end{bmatrix} = \bar{z} - \bar{z}^* = \begin{bmatrix} \bar{z}_1 - \bar{z}_1{}^* \\ \bar{z}_2 - \bar{z}_2{}^* \end{bmatrix} = \begin{bmatrix} s_1 \\ s_2 \end{bmatrix}$$



4. Selection changes the multivariate trait distribution

c. The directional selection gradient, *β*, is related to s and measures the direct force of selection on a trait

$$\beta \equiv P^{-1}s = \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix}$$

Easier to understand if we rearrange terms

$$s = P\beta = \begin{bmatrix} P_{11} & P_{12} \\ P_{12} & P_{22} \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} = \begin{bmatrix} P_{11}\beta_1 + P_{12}\beta_2 \\ P_{12}\beta_2 + P_{22}\beta_2 \end{bmatrix} = \begin{bmatrix} s_1 \\ s_2 \end{bmatrix}$$

Direct effect of selection on trait 1 on trait 1 $P_{11}\beta_1$

Indirect effect of selection on trait 2 on trait 1 $P_{12}\beta_2$

4. Selection changes the multivariate trait distribution

d. Similarly, the nonlinear selection gradient, γ, is related to C

$$\gamma \equiv P^{-1}CP^{-1} = \begin{bmatrix} \gamma_{11} & \gamma_{12} \\ \gamma_{12} & \gamma_{22} \end{bmatrix}$$

Rearranging to see direct and indirect terms,

$$C = P\gamma P = \begin{bmatrix} P_{11} & P_{12} \\ P_{12} & P_{22} \end{bmatrix} \begin{bmatrix} \gamma_{11} & \gamma_{12} \\ \gamma_{12} & \gamma_{22} \end{bmatrix} \begin{bmatrix} P_{11} & P_{12} \\ P_{12} & P_{22} \end{bmatrix} =$$

$$\begin{bmatrix} P_{11}^2\gamma_{11} + 2P_{11}P_{12}\gamma_{12} + P_{12}^2\gamma_{22} & P_{11}P_{12}\gamma_{11} + P_{12}^2\gamma_{12} + P_{11}P_{12}\gamma_{12} + P_{12}P_{22}\gamma_{22} \\ P_{11}P_{12}\gamma_{11} + P_{12}^2\gamma_{12} + P_{11}P_{12}\gamma_{12} + P_{12}P_{22}\gamma_{22} & P_{12}^2\gamma_{11} + 2P_{12}P_{22}\gamma_{12} + P_{22}^2\gamma_{22} \end{bmatrix}$$

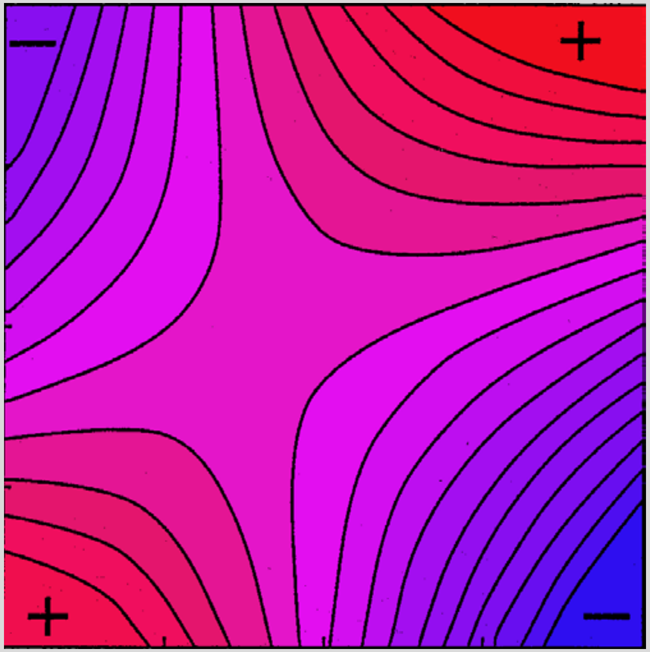
γ measures the direct force of selection on a trait

What have we learned?

1. The change in trait distributions before and after selection within a generation can be used to derive useful measures of selection.

2. Using those measures we can distinguish between the effects of directional and stabilizing selection.

Part 2. Selection as a Surface



Thesis

- We can think of selection as a surface.

- Selection surfaces allow us to estimate selection coefficients, as well as visualize selection.

- To visualize and estimate, we need to keep track of three kinds of surfaces:
  1. the individual selection surface
  2. our approximation of that surface
  3. the adaptive landscape.

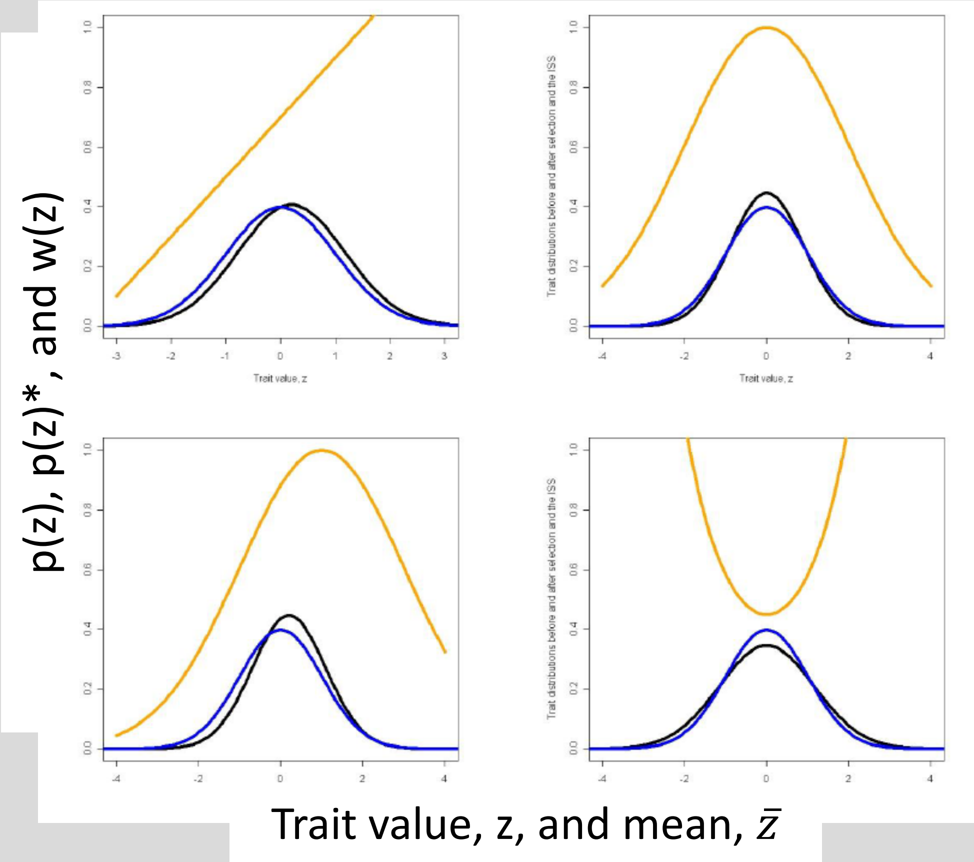
Outline

1. The individual selection surface, ISS.
2. Approximations to the ISS.
3. The adaptive landscape, AL.
4. Surveys.
5. The multivariate ISS.
6. Approximations to the multivariate ISS.
7. The multivariate AL.
8. Examples and surveys.

1. The Individual Selection Surface

Expected individual fitness, $w(z)$, as a function of trait value, z

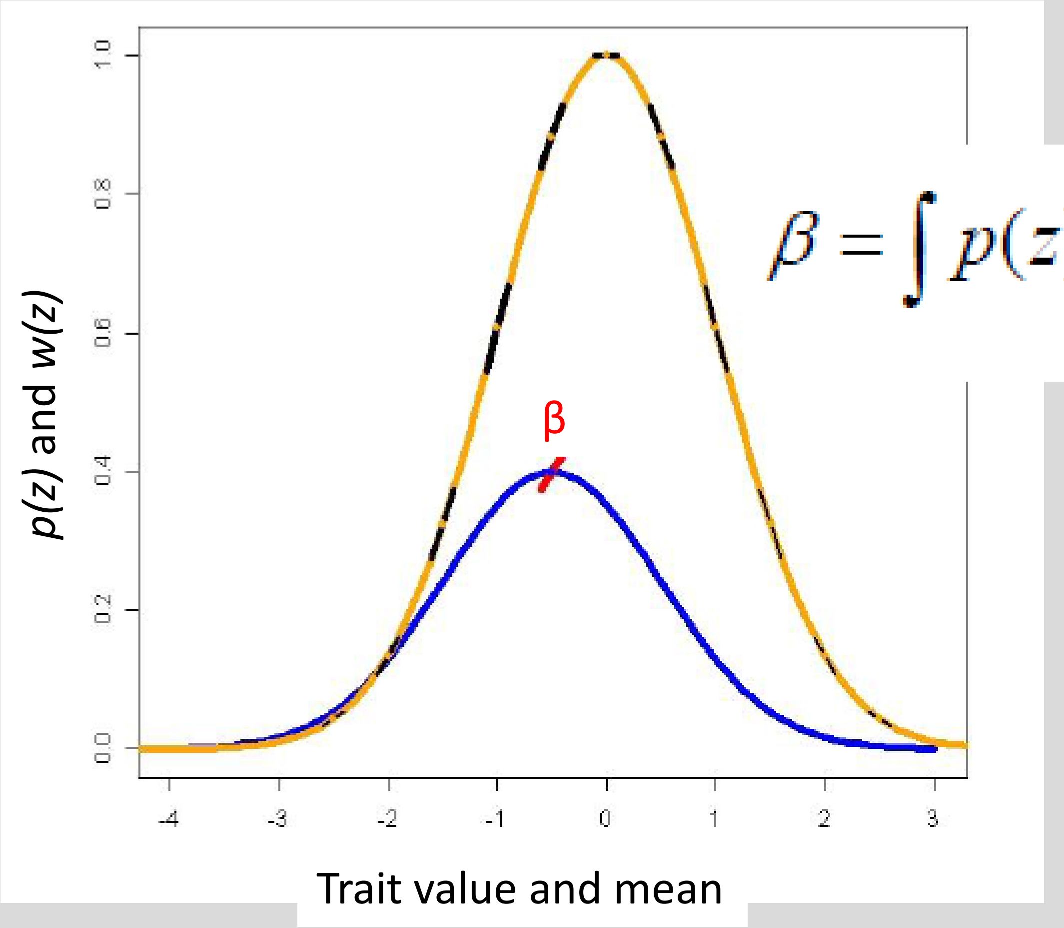
a. A model for how selection that changes trait means and variances



Animation 0

1. The Individual Selection Surface

b. β is the weighted average of the first derivatives of the ISS

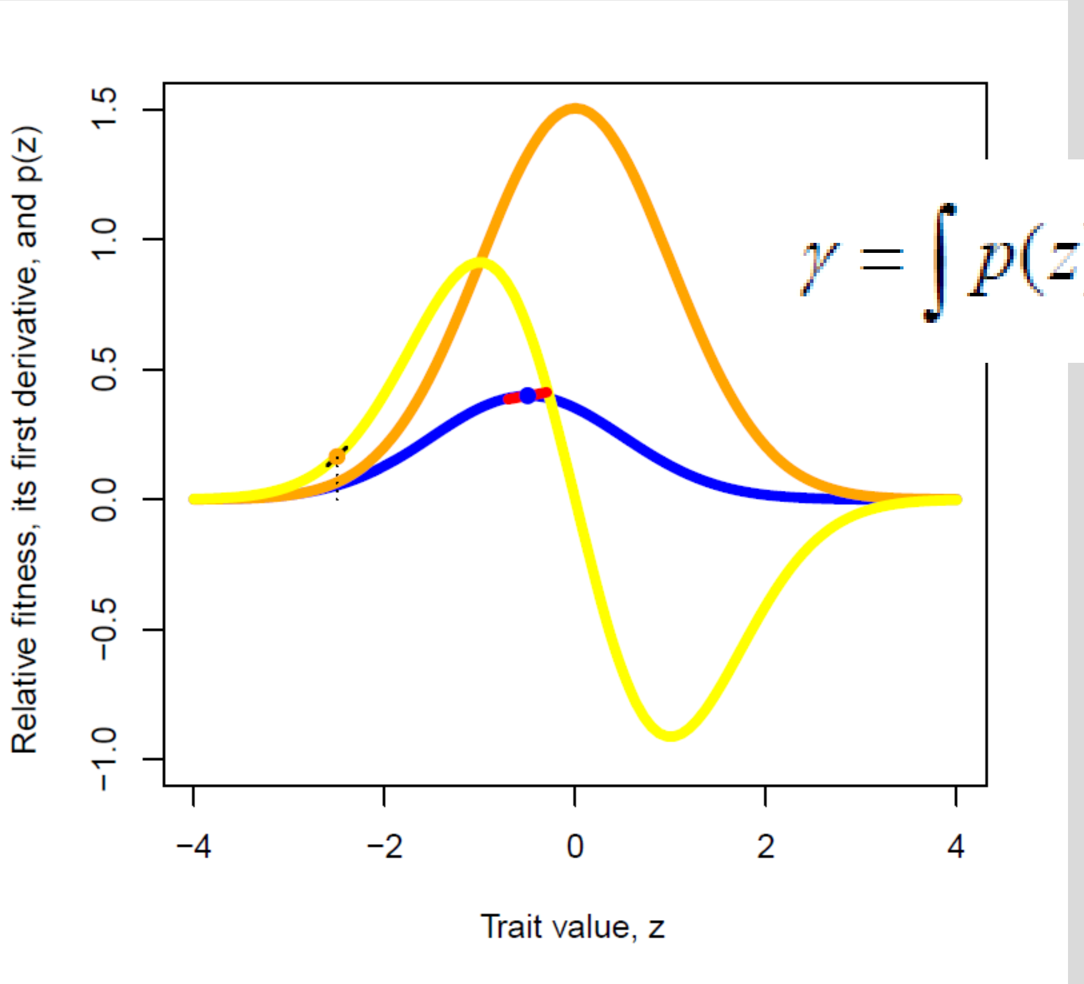


$$\beta = \int p(z) \frac{\partial w(z)}{\partial z} dz$$

Animation 1

1. The Individual Selection Surface

c. Similarly, γ is the weighted average of the second derivatives of the ISS



$$\gamma = \int p(z) \frac{\partial^2 w(z)}{\partial z^2} dz$$

Animation 2

2. Approximations to the ISS

a. Linear & quadratric approximations: a way to estimate β and γ

$$w(z) = \alpha + \beta z + \varepsilon$$ linear

$$w(z) = \alpha + \beta z + \tfrac{1}{2}\gamma z^2 + \varepsilon$$ quadratic*

* the factor of ½ makes γ a second derivative

2. Approximations to the ISS

b. When z is a vector of traits, β and γ account for correlations among traits and are known as selection gradients

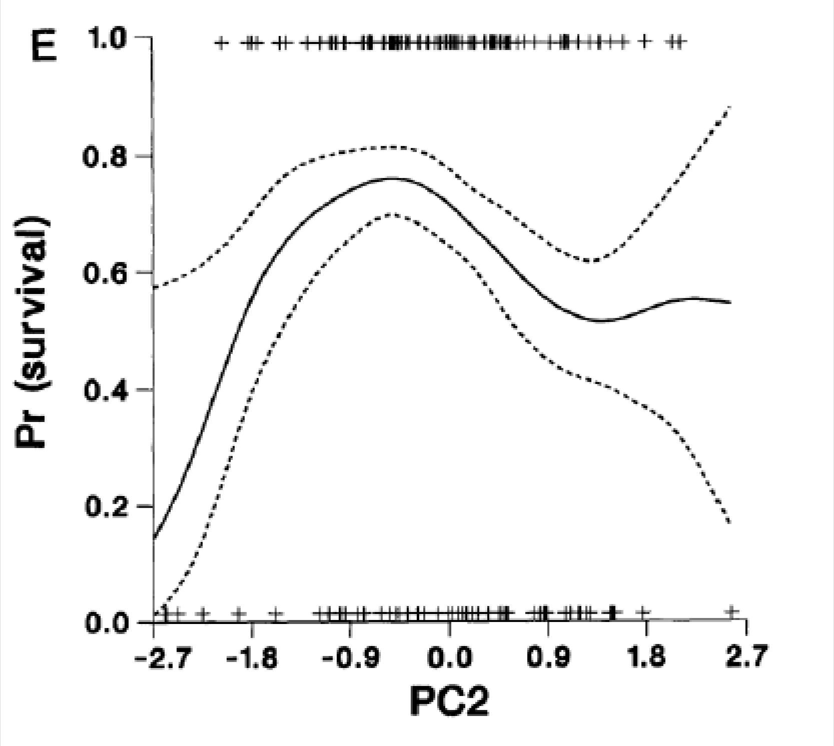
$$w(z) = \alpha + \beta z + \varepsilon$$ linear

$$w(z) = \alpha + \beta z + \tfrac{1}{2}\gamma z^2 + \varepsilon$$ quadratic*

* the factor of ½ makes *γ* a second derivative

2. Approximations to the ISS

c. Cubic spline approximation,
describes the surface but doesn't estimate β or γ



3. The adaptive landscape, AL, the surface on which $\bar{z}$ evolves

Mean fitness of the population, $\bar{W}$ or $ln\bar{W}$ as a function of the trait mean, $\bar{z}$

a. A window on the AL at the position of the trait mean

$$\beta = \frac{\partial \overline{W}}{\overline{W}\partial \overline{z}} = \frac{\partial \ln \overline{W}}{\partial \overline{z}}$$

$$\gamma - \beta^2 = \frac{\partial^2 \overline{W}}{\overline{W}\partial \overline{z}^2} = \frac{\partial^2 \ln \overline{W}}{\partial \overline{z}^2}$$

3. The adaptive landscape, AL, the surface on which $\bar{z}$ evolves

Mean fitness of the population, $\bar{W}$ or $ln\bar{W}$ as a function of the trait mean, $\bar{z}$

b. If *w(z)* is Gaussian, the AL takes a simple form

A normally-distributed trait before selection

$$p(z) = (\sqrt{2\pi P})^{-1} \exp\{\frac{-(z-\bar{z})^2}{2P}\}$$

A Gaussian ISS with optimum θ and width *ω*

$$w(z) = \exp\{\frac{-(z-\theta)^2}{2\omega}\}$$

A Gaussian AL with optimum θ and width *ω+P*

$$\bar{W} \propto \exp\{\frac{-(\bar{z}-\theta)^2}{2(\omega+P)}\}$$

3. The adaptive landscape, AL, the surface on which $\bar{z}$ evolves

Mean fitness of the population, $\bar{W}$ or $ln\bar{W}$ as a function of the trait mean, $\bar{z}$

b. and we can easily solve for first and second derivatives of the AL

First derivative, β

$$\frac{\partial \ln \overline{W}}{\partial \bar{z}} = (\omega + P)^{-1}(\theta - \bar{z})$$

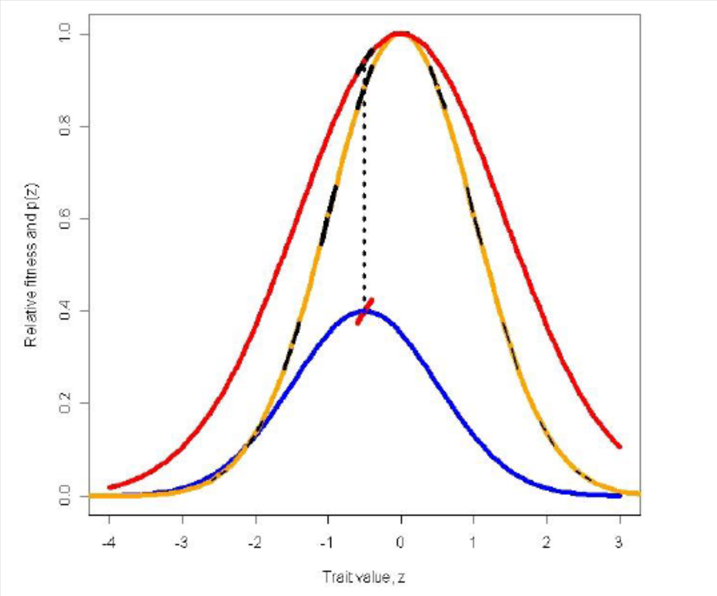
Second derivative

$$\frac{\partial^2 \ln \overline{W}}{\partial \bar{z}^2} = -(\omega + P)^{-1} = \gamma - \beta^2$$

3. The adaptive landscape, AL, the surface on which $\bar{z}$ evolves

Mean fitness of the population, $\bar{W}$ or $ln\bar{W}$ as a function of the trait mean, $\bar{z}$

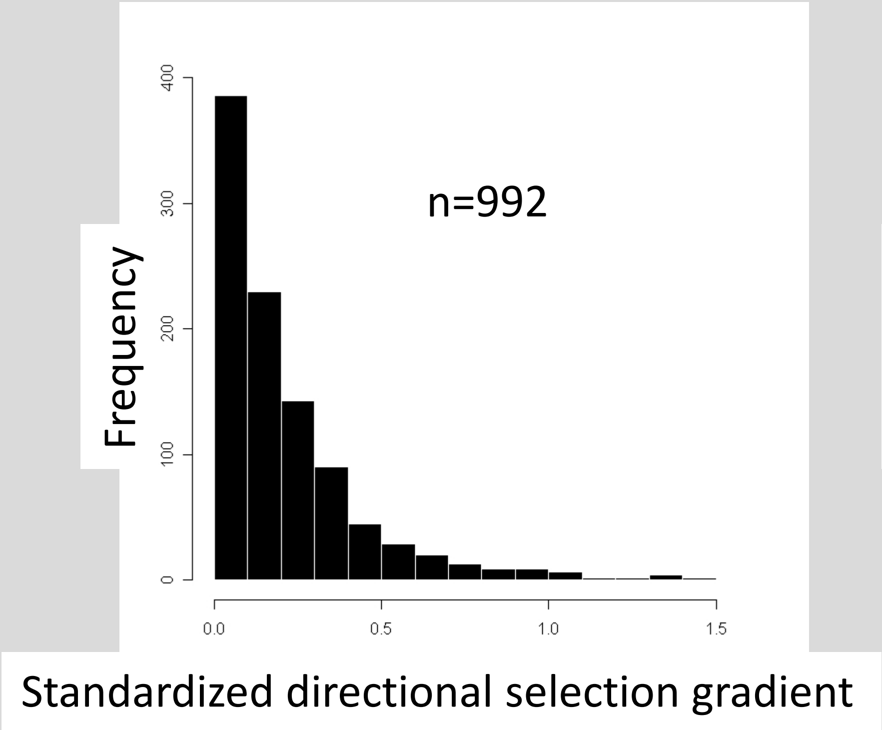
b. In the Gaussian case, the AL (red) has the same optimum as *w(z)* (orange) but is flatter

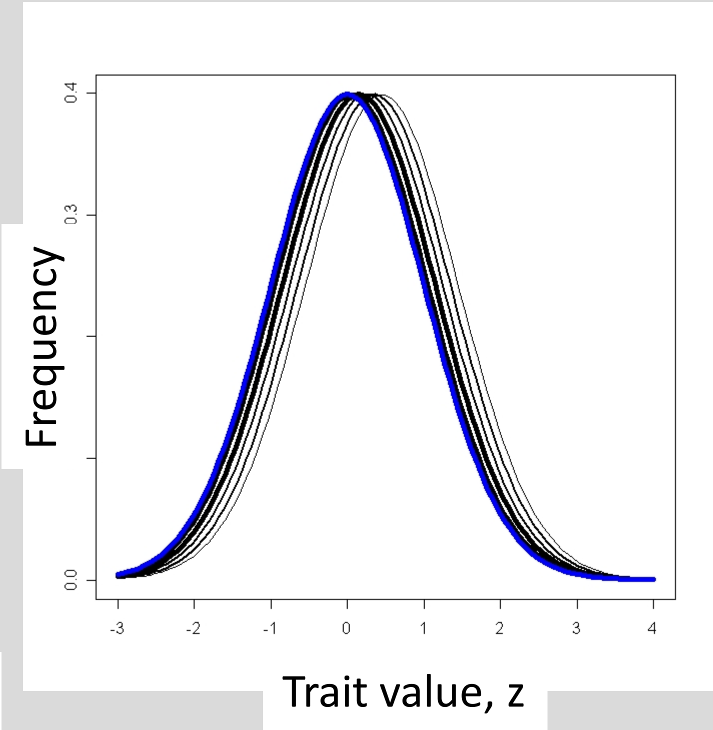


4. Survey of β estimates

Standardized directional selection gradients, β

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

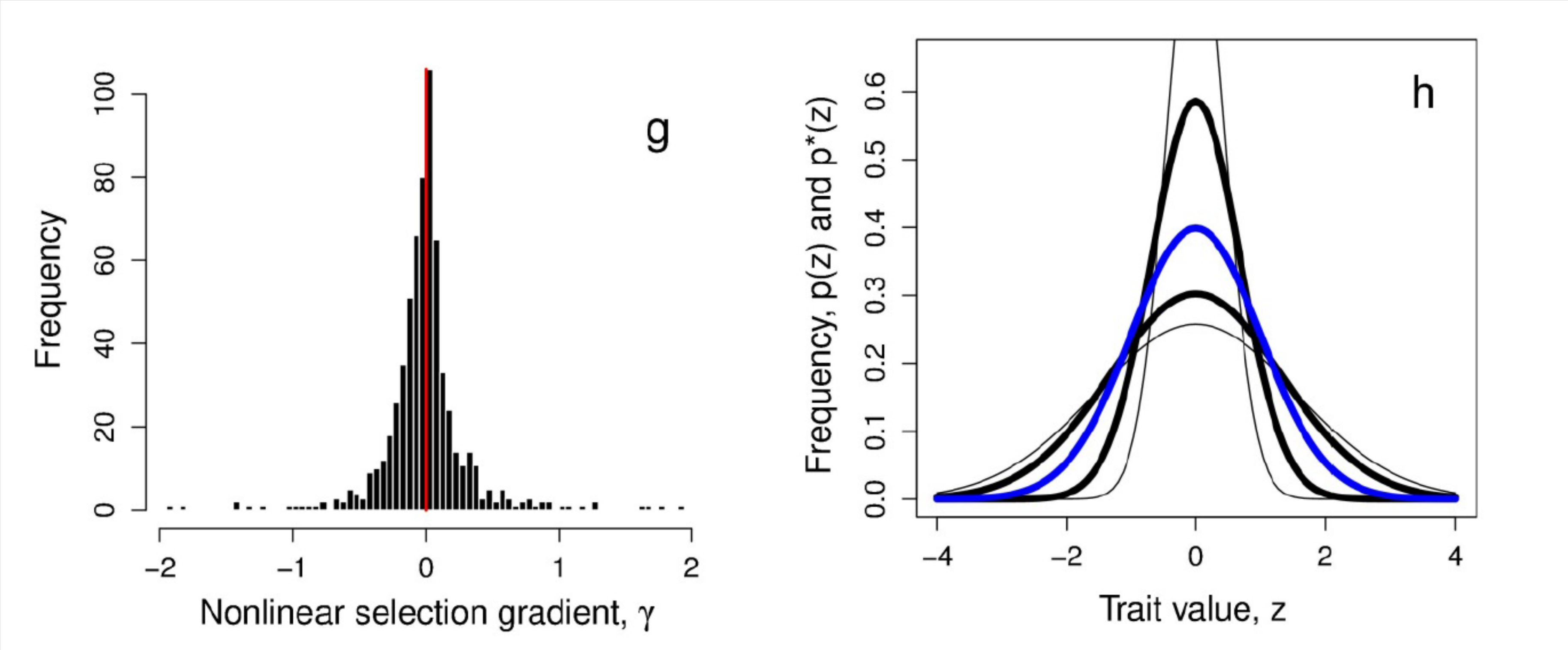




4. Survey of γ estimates

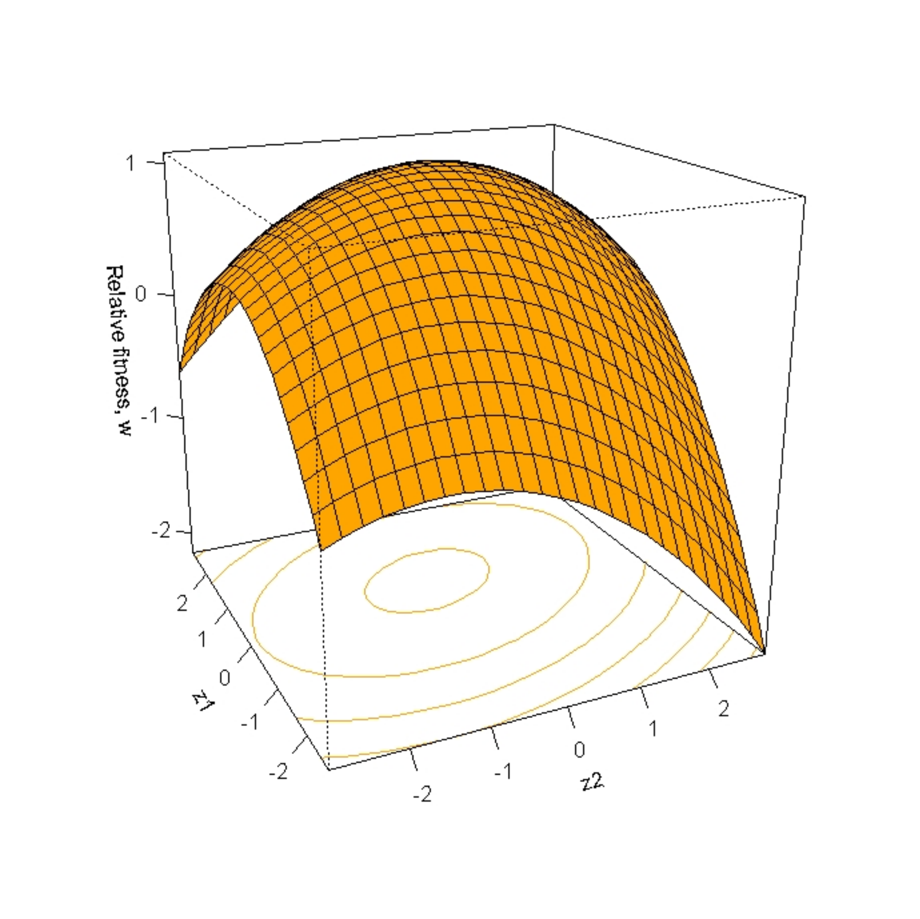
Standardized nonlinear selection gradients, γ

$$\gamma \equiv P^{-1}CP^{-1}$$



5. The multivariate individual selection surface, *ISS*

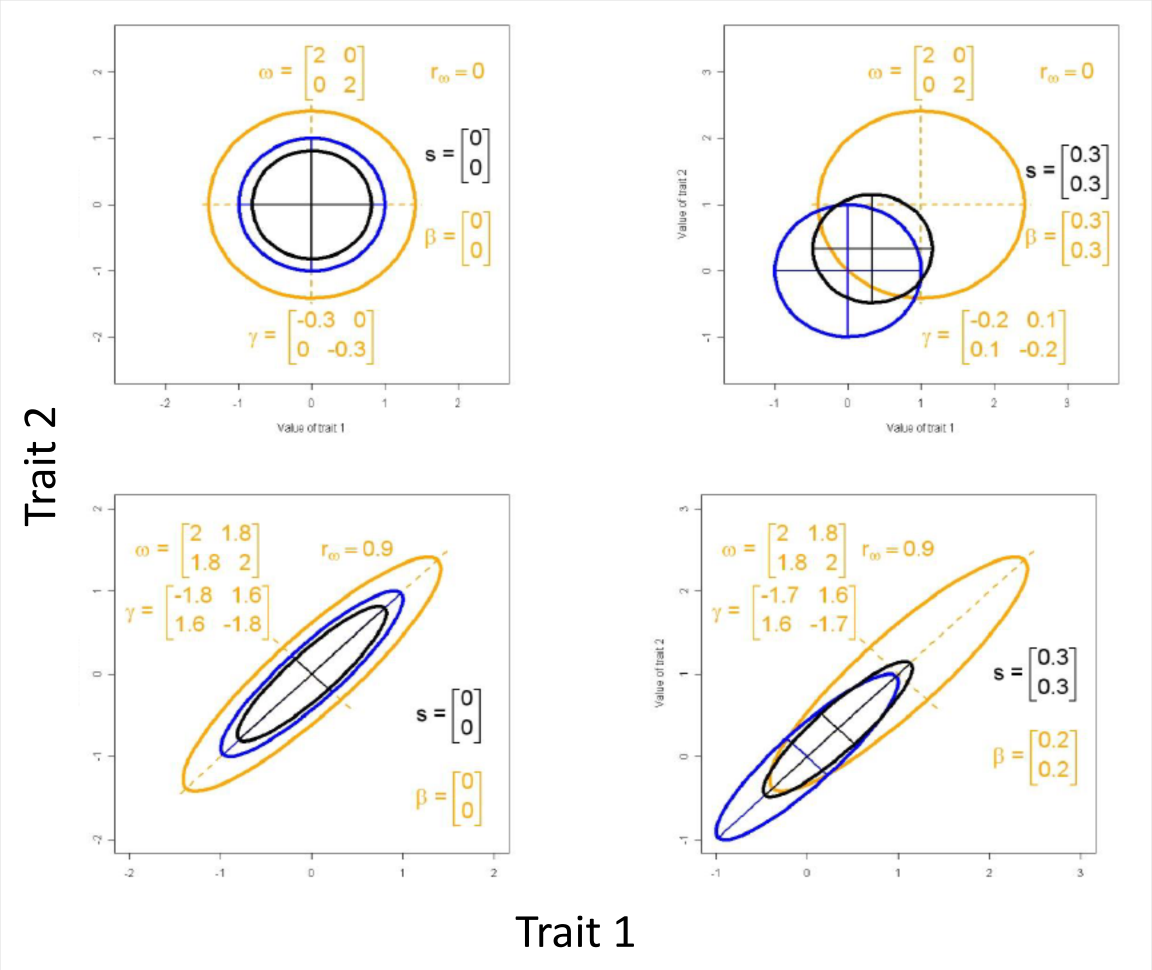
a. A hypothetical bivariate example



Animation 3

5. The multivariate individual selection surface, *ISS*

b. Some examples of bivariate ISSs and the selection they impose



Animation 4

5. The multivariate individual selection surface, *ISS*

c. Consider a point on the selection surface. The slope at that point is a vector and curvature is a matrix

First derivatives

$$\begin{bmatrix} \partial w(z)/\partial z_1 \\ \partial w(z)/\partial z_2 \end{bmatrix}$$

Second derivatives

$$\begin{bmatrix} \partial^2 w(z)/\partial z_1^2 & \partial^2 w(z)/\partial z_1 \partial z_2 \\ \partial^2 w(z)/\partial z_1 \partial z_2 & \partial^2 w(z)/\partial z_2^2 \end{bmatrix}$$

5. The multivariate individual selection surface, *ISS*

d. If we assume that *p(z)* is multivariate normal and the actual ISS is quadratic, then β and γ are, respectively, the average first and second derivatives of the surface.

$$\beta = \int p(z)\frac{\partial w(z)}{\partial z}dz = \begin{bmatrix} \int p(z)\frac{\partial w(z)}{\partial z_1}dz \\ \int p(z)\frac{\partial w(z)}{\partial z_2}dz \end{bmatrix}$$

$$\gamma = \int p(z)\frac{\partial^2 w(z)}{\partial z^2}dz = \begin{bmatrix} \int p(z)\frac{\partial^2 w(z)}{\partial z_1^2}dz & \int p(z)\frac{\partial^2 w(z)}{\partial z_1 \partial z_2}dz \\ \int p(z)\frac{\partial^2 w(z)}{\partial z_1 \partial z_2}dz & \int p(z)\frac{\partial^2 w(z)}{\partial z_2^2}dz \end{bmatrix}$$

6. Approximations to the multivariate ISS

a. Linear and quadratic approximations, a way to estimate β and γ

For simplicity, we consider the two-trait case

Linear approximation

$$w(z) = \alpha + \beta^T z + \varepsilon = \alpha + \beta_1 z_1 + \beta_2 z_2 + \varepsilon$$

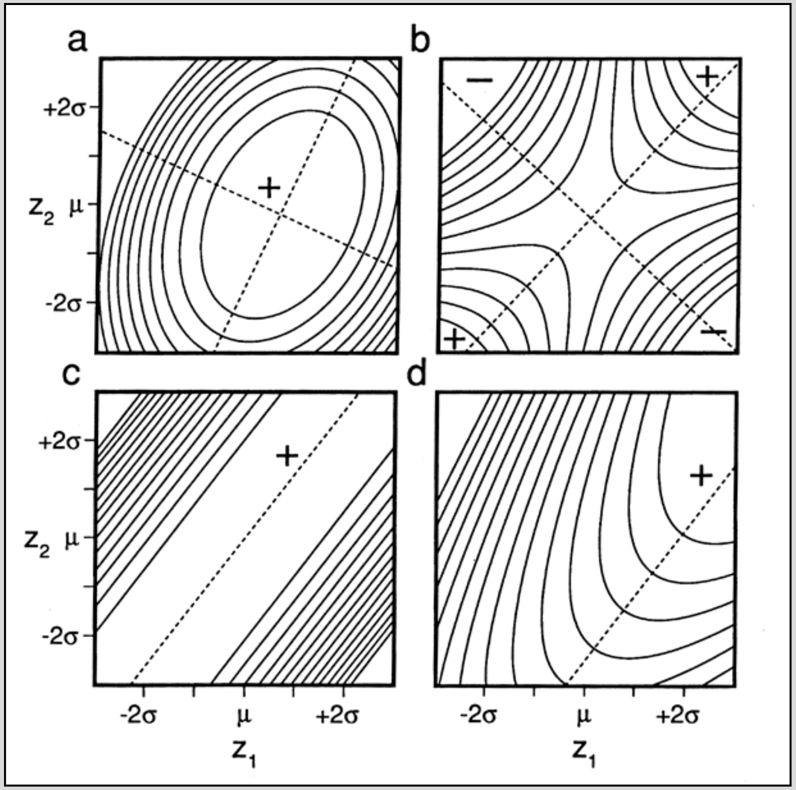
Quadratic approximation

$$w(z) = \alpha + \beta^T + \tfrac{1}{2} z^T \gamma z + \varepsilon = \alpha + \beta_1 z_1 + \beta_2 z_2 + \tfrac{1}{2}\gamma_{11} z_1^{\;2} + \tfrac{1}{2}\gamma_{22} z_2^{\;2} + \gamma_{12} z_1 z_2 + \varepsilon$$

6. Approximations to the multivariate ISS

a. Linear and quadratic approximations, a way to estimate β and γ

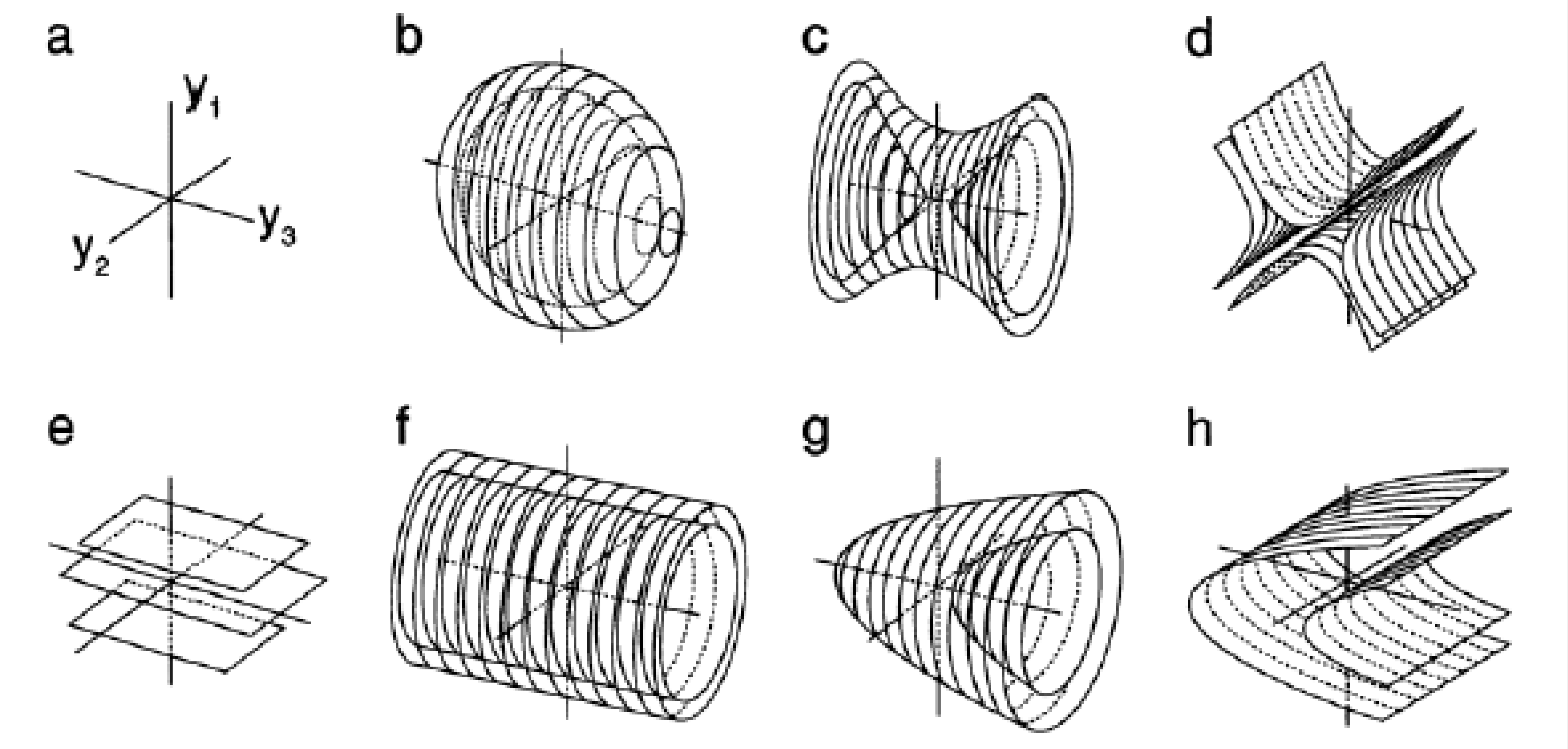
What can we approximate with a quadratic surface?



6. Approximations to the multivariate ISS

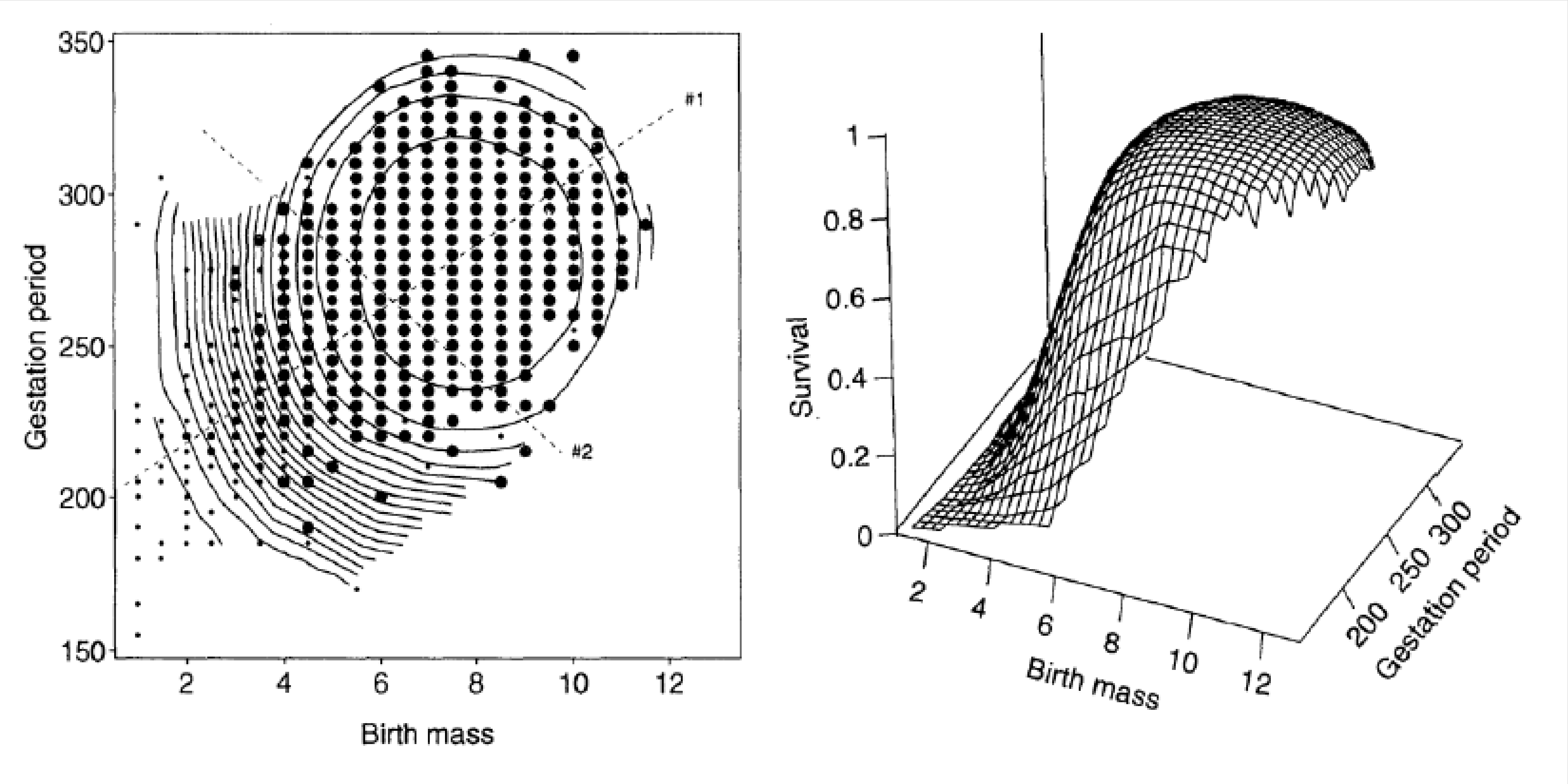
a. Linear and quadratic approximations, a way to estimate β and γ

What can we approximate with a quadratic surface?



6. Approximations to the multivariate ISS

b. Cubic spline approximation, describes the surface without estimating β and γ



7. The multivariate adaptive landscape, AL

a. The slope and curvature of the AL, evaluated at the trait mean are related to β and γ

A window on the adaptive landscape

$$\beta = \frac{\partial \overline{W}}{\overline{W}\partial \overline{z}} = \frac{\partial \ln \overline{W}}{\partial \overline{z}} = \begin{bmatrix} \partial \ln \overline{W} / \partial \overline{z}_1 \\ \partial \ln \overline{W} / \partial \overline{z}_2 \end{bmatrix} = \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix}$$

$$\gamma - \beta\beta^T = \frac{\partial^2 \overline{W}}{\overline{W}\partial \overline{z}^2} = \frac{\partial^2 \ln \overline{W}}{\partial \overline{z}^2} = \begin{bmatrix} \partial^2 \ln \overline{W} / \partial \overline{z}_1^2 & \partial^2 \ln \overline{W} / \partial \overline{z}_1 \partial \overline{z}_2 \\ \partial^2 \ln \overline{W} / \partial \overline{z}_1 \partial \overline{z}_2 & \partial^2 \ln \overline{W} / \partial \overline{z}_2^2 \end{bmatrix} = \begin{bmatrix} \gamma_{11} - \beta_1^2 & \gamma_{12} - \beta_1\beta_2 \\ \gamma_{12} - \beta_1\beta_2 & \gamma_{22} - \beta_2^2 \end{bmatrix}$$

7. The multivariate adaptive landscape, AL

b. If the ISS is multivariate Gaussian, the AL takes a simple Gaussian form

Gaussian ISS

$$W(z) = \exp\{-\tfrac{1}{2}(z-\theta)^T \omega^{-1}(z-\theta)\}$$

$$\omega = \begin{bmatrix} \omega_{11} & \omega_{12} \\ \omega_{12} & \omega_{22} \end{bmatrix}$$

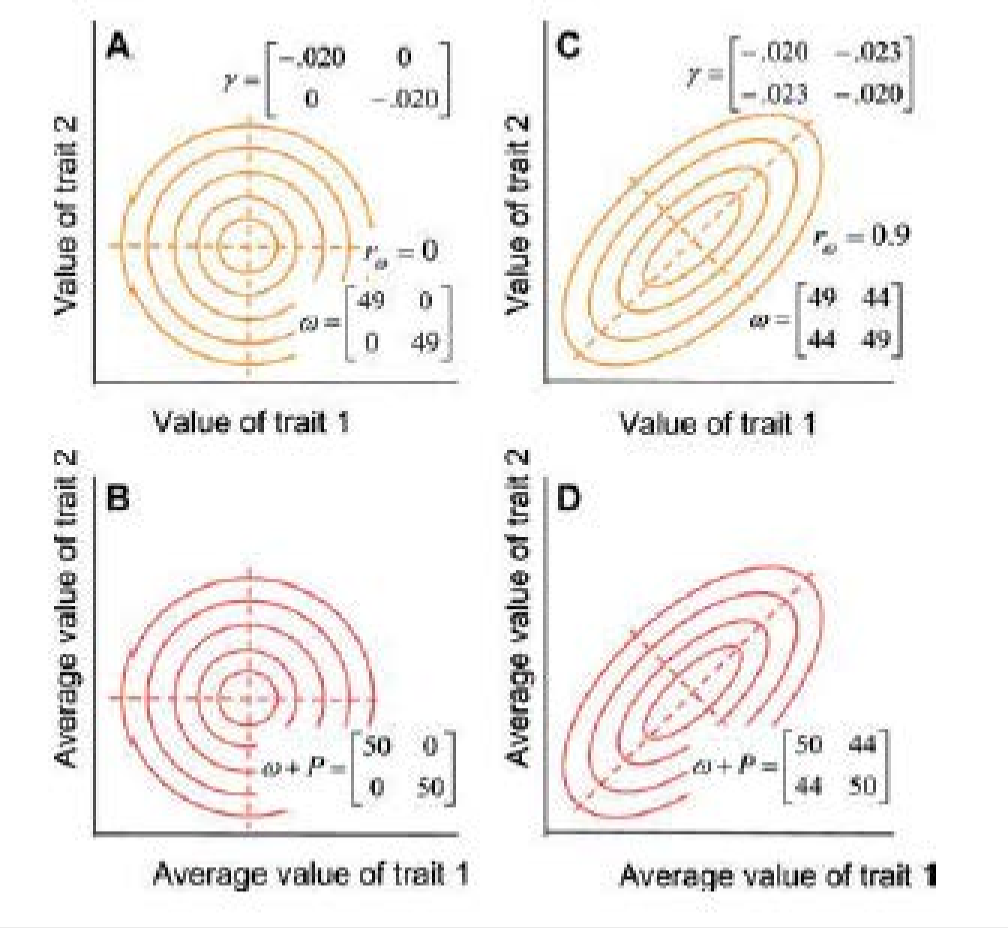
Gaussian AL

$$\overline{W} \propto \exp\{-(\bar{z}-\theta)^T(\omega+P)^{-1}(\bar{z}-\theta)\}$$

$$\omega + P = \begin{bmatrix} \omega_{11}+P_{11} & \omega_{12}+P_{12} \\ \omega_{12}+P_{12} & \omega_{22}+P_{22} \end{bmatrix}$$

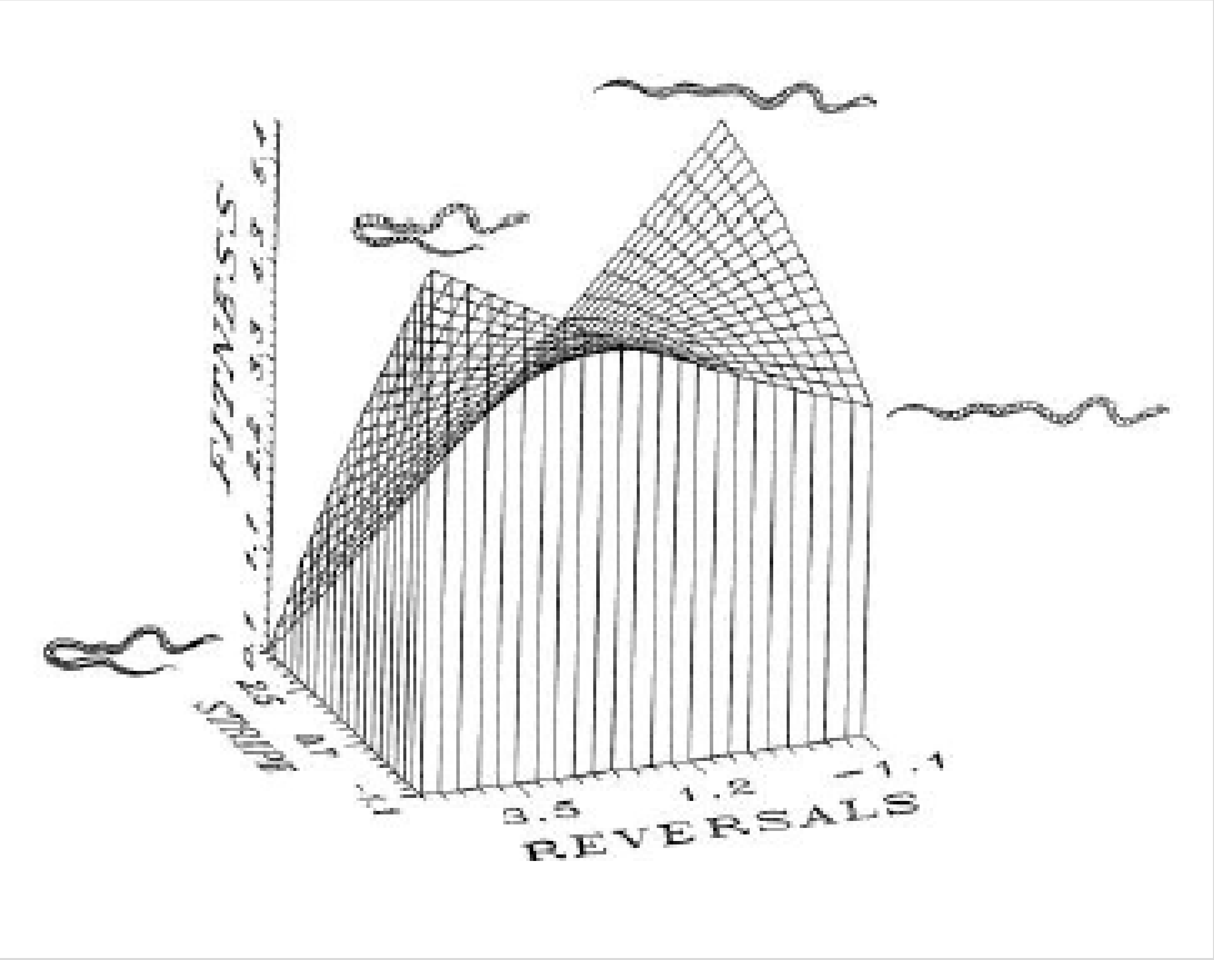
7. The multivariate adaptive landscape, AL

c. We can characterize the main axes of the ISS and AL by taking the eigenvectors of the ω - and ω+P matrices



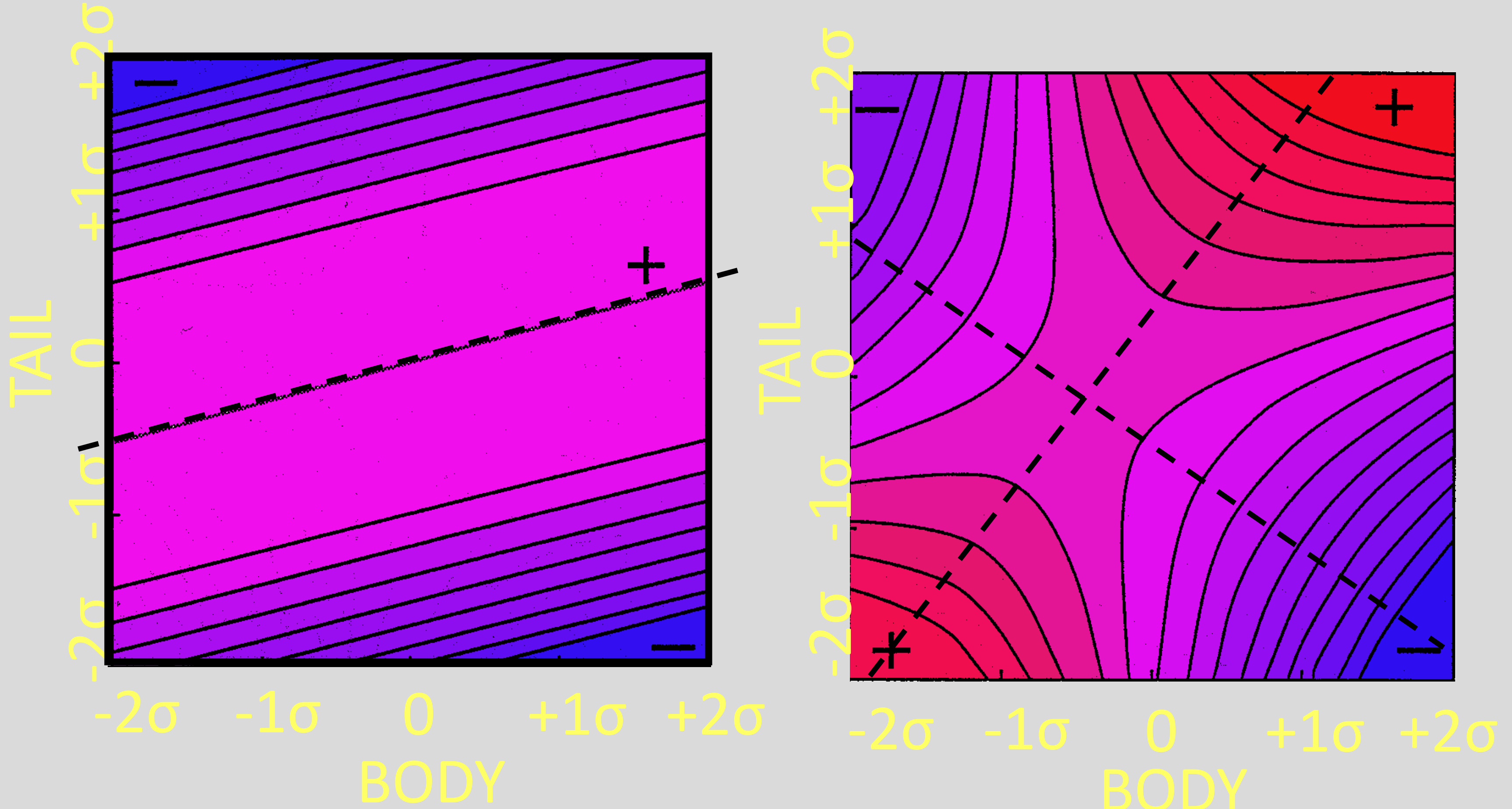
8. Examples and surveys

a. Bivariate selection on escape behavior and coloration pattern in a garter snake



8. Examples and surveys

b. Growth rate as a function of vertebral numbers (left) and crawling speed as a function of vertebral numbers (right) in garter snakes



8. Examples and surveys

c. A survey of quadratic approximations to ISSs shows that saddles are common

n	Largest γ_{ii}	λ	Type of surface	Type of selection	Reference
5	.044	.062	Saddle	O	Mitchell-Olds and Bergelsson 1990
4	−.457	−1.262	Saddle	F	Moore 1990
4	−.550	−.714	Saddle	M	Moore 1990
4	−.707	−1.093	Saddle	F	Moore 1990
4	−.498	−.729	Saddle	M	Moore 1990
4	.102	.155	Saddle	M	Moore 1990
4	−.538	−.650	Saddle	F	Moore 1990
4	−.122	−.273	Saddle	S	Brodie 1992
3	−.874	−.875	Saddle	F	Nunez-Farfan and Dirzo 1994
3	.370	.552	Saddle	F	O'Connell and Johnston 1998
3	1.180	1.709	Bowl	F	O'Connell and Johnston 1998
3	.770	1.124	Saddle	F	O'Connell and Johnston 1998
3	.260	.283	Saddle	F	O'Connell and Johnston 1998
3	.200	.305	Saddle	F	O'Connell and Johnston 1998
3	.23	.26	Saddle	F	O'Connell and Johnston 1998
5	.994	.999	Saddle	F	Simms 1990
3	−.019	−.021	Peak	S	Kelly 1992
4	.016	.027	Saddle	S	Kelly 1992
5	.112	.214	Saddle	F	Kelly 1992

What have we learned?

1. Selection can be described with surfaces.

2. Some approximations of selection surfaces allow us to estimate key measures of selection (β and γ).

3. Those key measures in turn tell us about the adaptive landscape.

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