Phenotypic selection: elaborations

Michael Morrissey
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Preliminaries

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- Key concepts in methods and theory to support solid empirical work

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   - erroneous estimates of selection
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3. A closer look at non-linear selection
   - interpreting all those γ terms
4. Does the selection gradient measure what we really want?
   - what traits are materially relevant to fitness?

The additive partition of S

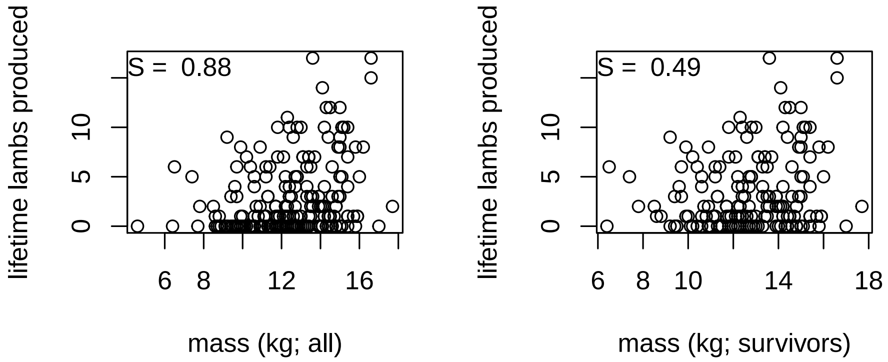
The total selection differential over k episodes is

$$S_T = \Sigma_j^k S_j$$

- From before, $S_1 = 0.39$ kg.
- Among survivors of the first winter, subsequent selection is $S_2 = 0.49$ kg.

So,

$$S = S_1 + S_2 = 0.88kg$$

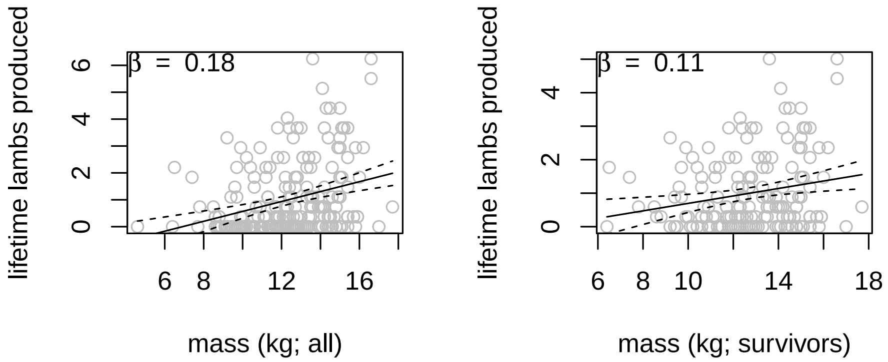


The additive partition of β

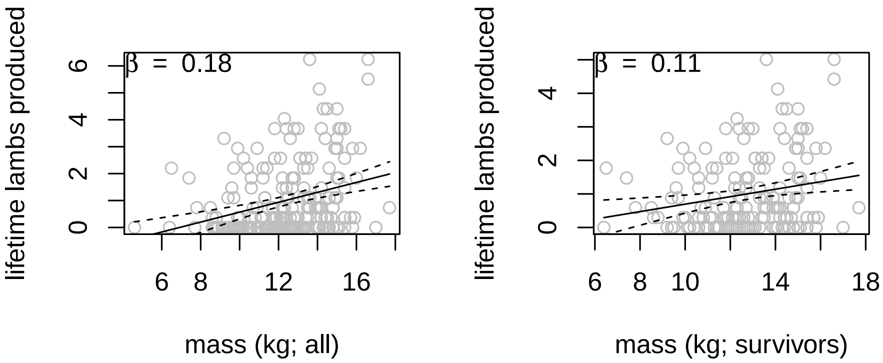
The total selection gradient over k episodes is

$$\beta_T = \Sigma_{j=1}^k \frac{\sigma_{j-1}^2}{\sigma_0^2} \beta_j$$

- this is a weighted additive partitioning of selection gradients.
- since viability selection changes the variance, and the variance is in the denominator of the formula for β, this change must be taken into account.



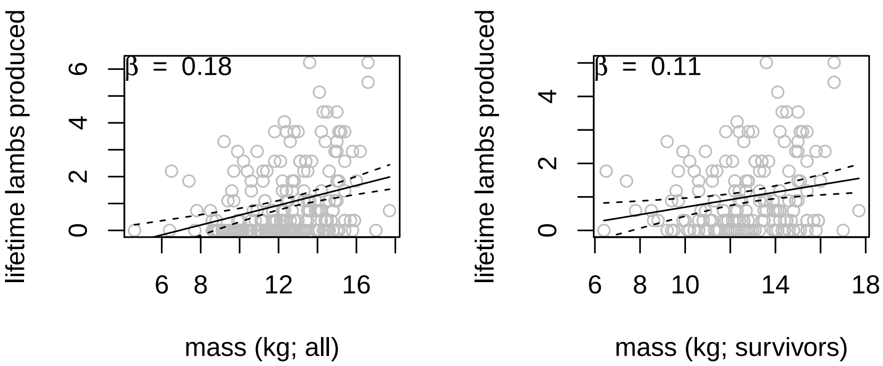
β_T for body mass



$\beta_1 = 0.082,\ \beta_2 = 0.111,\ \beta = 0.184$

$V_0 = 4.78,\ V_1 = 4.38$

β_T for body mass



$\beta_1 = 0.082,\ \beta_2 = 0.111,\ \beta = 0.184$

$V_0 = 4.78,\ V_1 = 4.38$

$\beta = \beta_1 + \frac{V_1}{V_0}\beta_2 = 0.082 + \frac{4.38}{4.78}0.111 = 0.184$

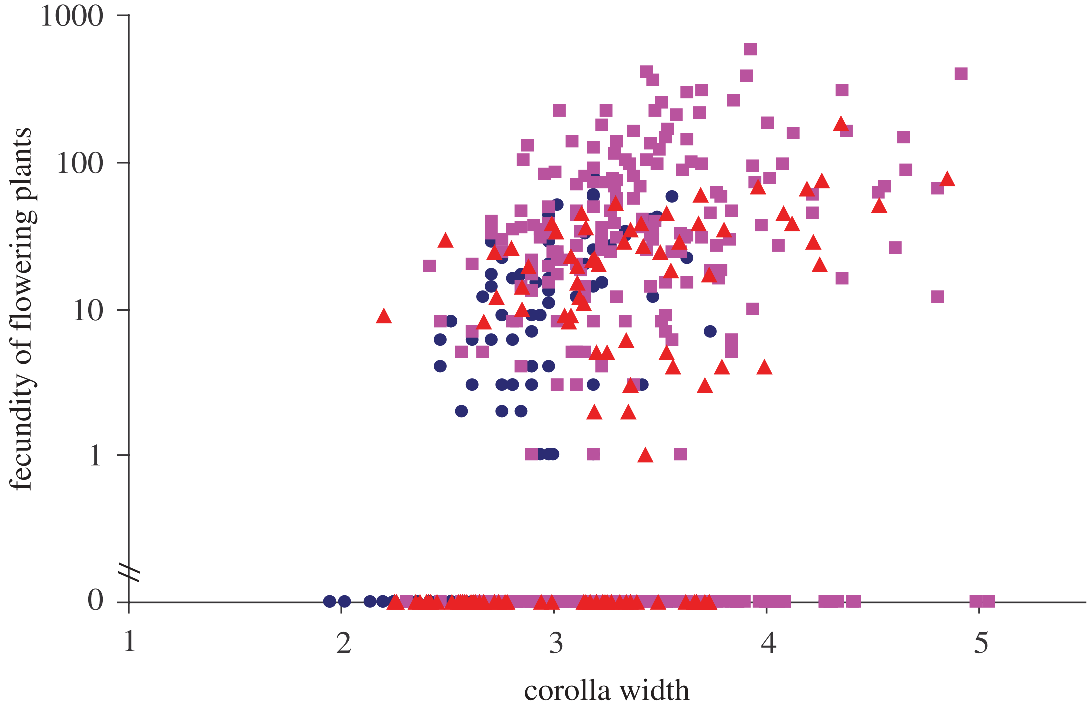
Is it worth partitioning selection?

If you have lifetime fitness, why break it down?

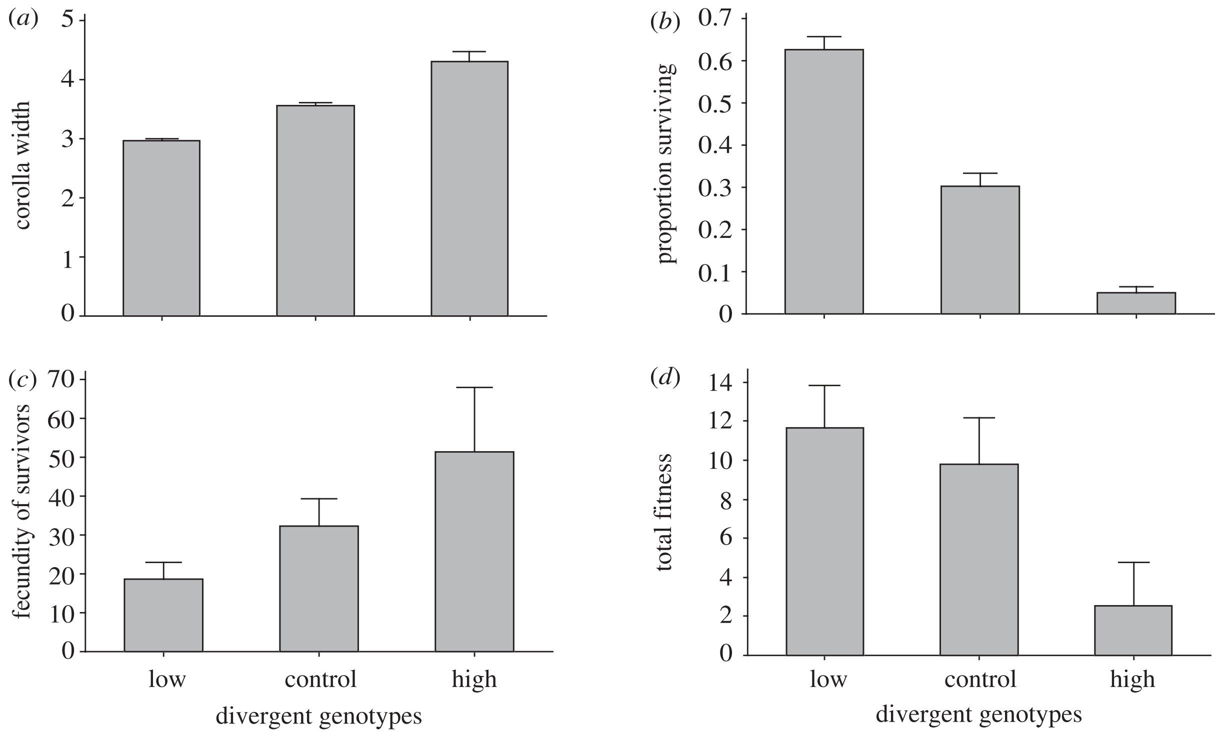
- It is worth knowing where in the life cycle selection arises
- It is statistically equally powerful, despite more stuff being calculated.
  for e.g., episodes of selection analysis for lamb mass:

gradient	estimate	standard error
S_1	0.394	0.091
S_1	0.488	0.183
S_{total}	0.881	0.215
$S_1 + S_1$	0.881	0.201

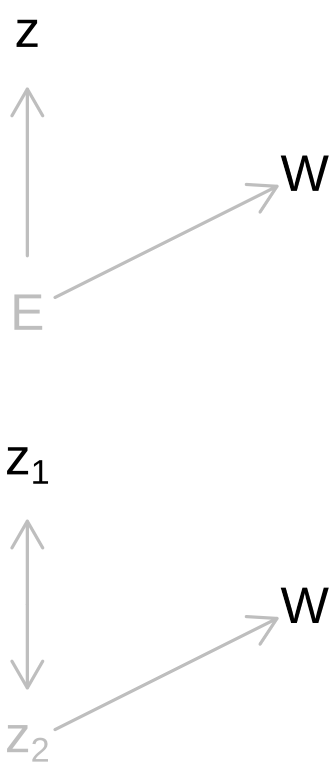
What about missing episodes of selection?



What about missing episodes of selection?

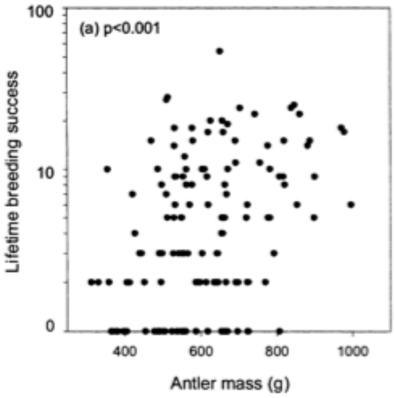


Missing traits



- Any trait or environmental variable that causes trait-fitness covariance will leave a mistaken signature of selection.
- Solution (part): do more multivariate analyses.
- Solution (other part): include environmental variables in regression-based selection analyses.
- This has been considered and prematurely rejected.

Signatures of missing traits: red deer



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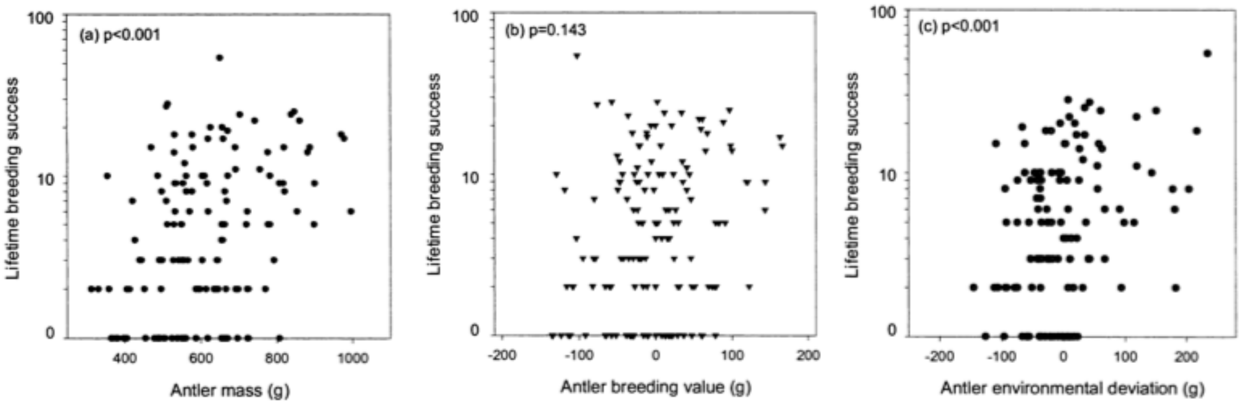

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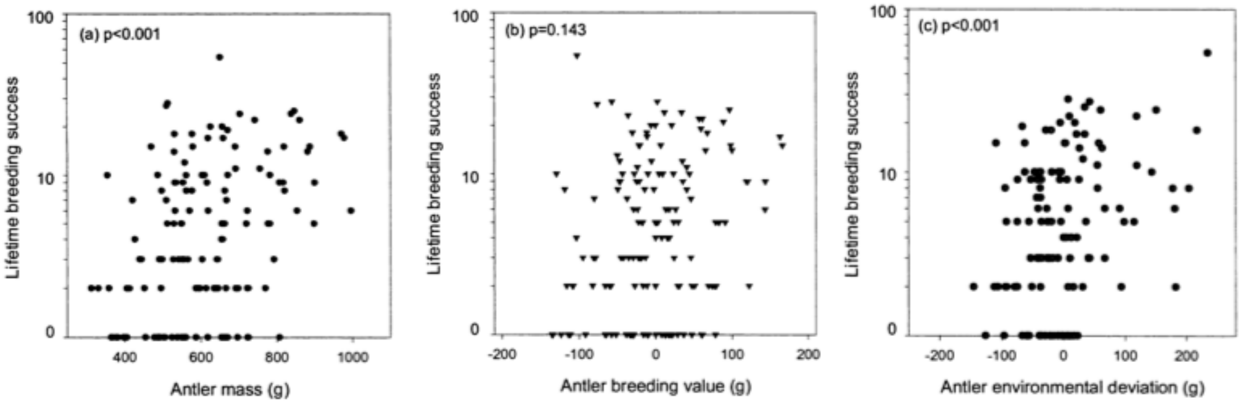
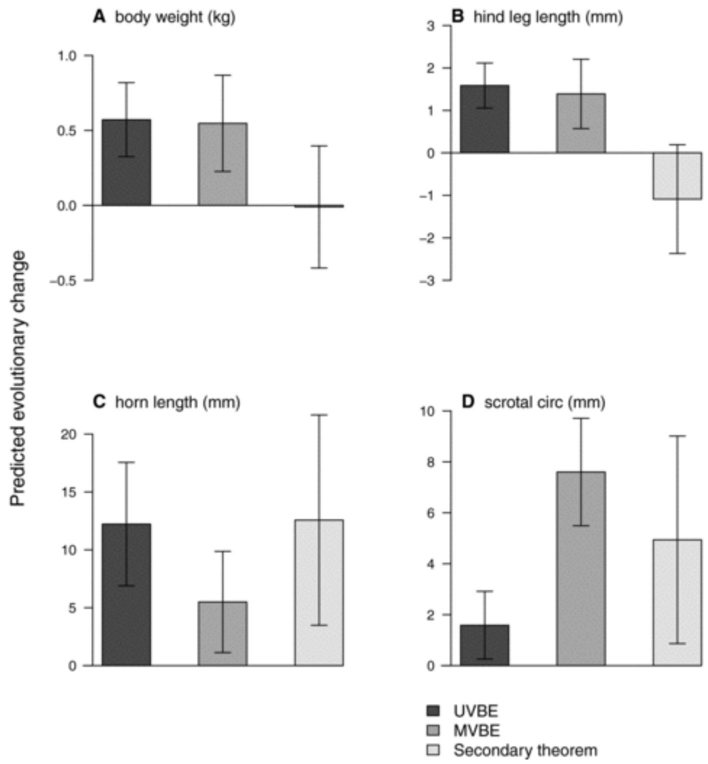


This amounts to applying the secondary theorem of selection

$$E[\Delta\bar{z}] = E[\Delta\bar{a}] = \sigma_{a,w}$$

Signatures of missing traits: Soay sheep



Empirical application of the STS without stats-on-stats 1

The secondary theorem (Robertson-Price equation applied to breeding values) is

$$\Delta\bar{z} = \sigma_a(z, w)$$

and the breeder's equation is

$$\Delta\bar{z} = h^2\sigma_p(z, w)$$

Set these to be equal:

$$\sigma_a(z, w) = \frac{\sigma_a^2(z)}{\sigma_p^2(z)}\sigma_p(z, w)$$

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$$\frac{\sigma_a(z, w)}{\sigma_a^2(z)} = \frac{\sigma_p(z, w)}{\sigma_p^2(z)}$$

$$\beta_a = \beta$$

Empirical application of the STS without stats-on-stats 1

The condition for the breeder's (Lande) equation to be predictive, namely equality of genetic and phenotypic (partial) regressions of traits on fitness, can be decomposed further:

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$$\frac{\sigma_a(z,w)}{\sigma_a^2(z)} = \frac{\sigma_a(z,w)+\sigma_e(z,w)}{\sigma_a^2(z)+\sigma_e^2(z)}$$

$$\frac{\sigma_a(z,w)}{\sigma_a^2(z)} = \frac{\sigma_e(z,w)}{\sigma_e^2(z)}$$

Thus, a corollary of the condition $\beta_a = \beta$, $\beta_a = \beta_e$

The numerators and denominators of β, β_a and β_e are all estimable by multi-response mixed model methods.

LMM and GLMM analysis of the STS and associated relationships

GLMM analysis seems most natural:

$$\begin{bmatrix} z_i \\ log(E[W])_i \end{bmatrix} = \mathbf{X}\beta + \begin{bmatrix} a_{z,i} \\ a_{W,i} \end{bmatrix} + ...$$

Where $\mathbf{a}_i$, and especially their covariance, is estimated using the pedigree.

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Where $\mathbf{a}_i$, and especially their covariance, is estimated using the pedigree. But what matters is relative fitness on the scale upon which it is expressed... ...but it turns out that the log-link GLMM has a cool justification:

$$x_i = log(E[W]_i)$$

FTNS analogue:

$$\Delta\bar{w} = e^{\sigma_a^2(x)} - 1$$

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FTNS analogue:

$$\Delta\bar{w} = e^{\sigma_a^2(x)} - 1$$

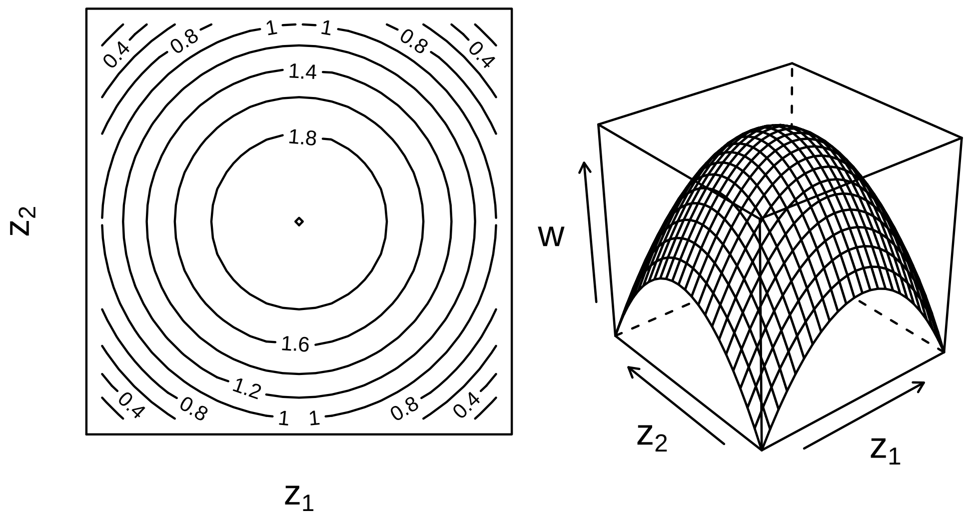
STS analogue:

$$\Delta\bar{z} = \sigma_a^2(z, x)$$

So, theGLMM consistency measure is:

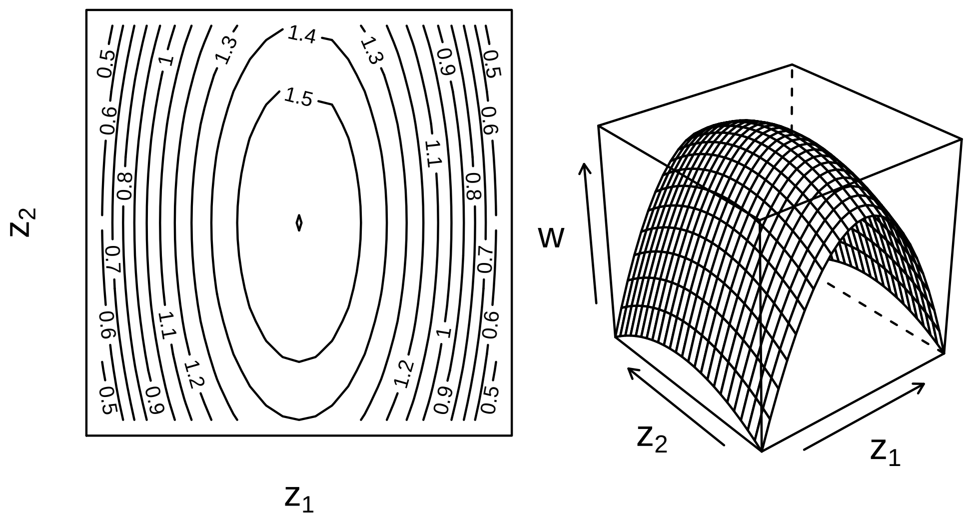
$$\mathbf{G}^{-1}\sigma_a(x, z) = \boldsymbol{\beta}$$

Non-linear selection, example 1



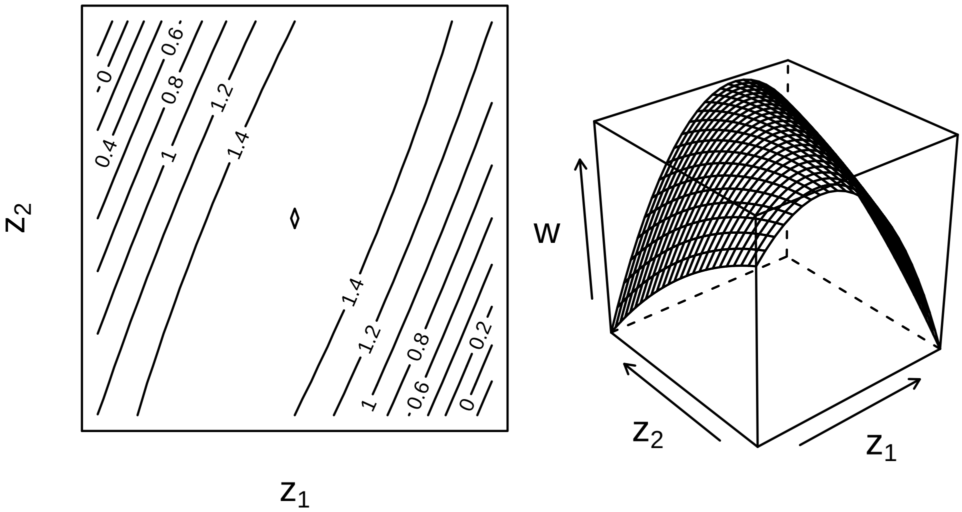
$$\gamma = \begin{bmatrix} -0.5 & 0 \\ 0 & -0.5 \end{bmatrix}$$

Non-linear selection, example 2



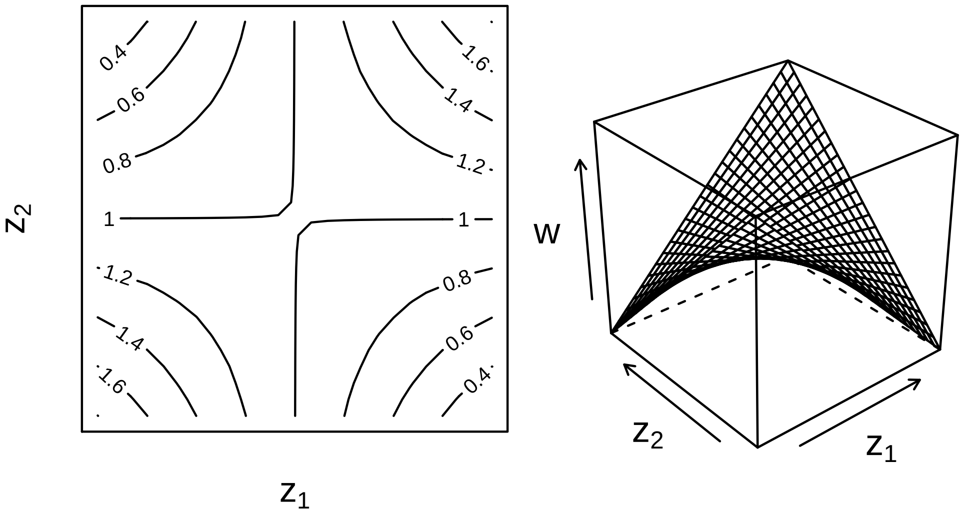
$$\gamma = \begin{bmatrix} -0.5 & 0 \\ 0 & -0.1 \end{bmatrix}$$

Non-linear selection, example 3



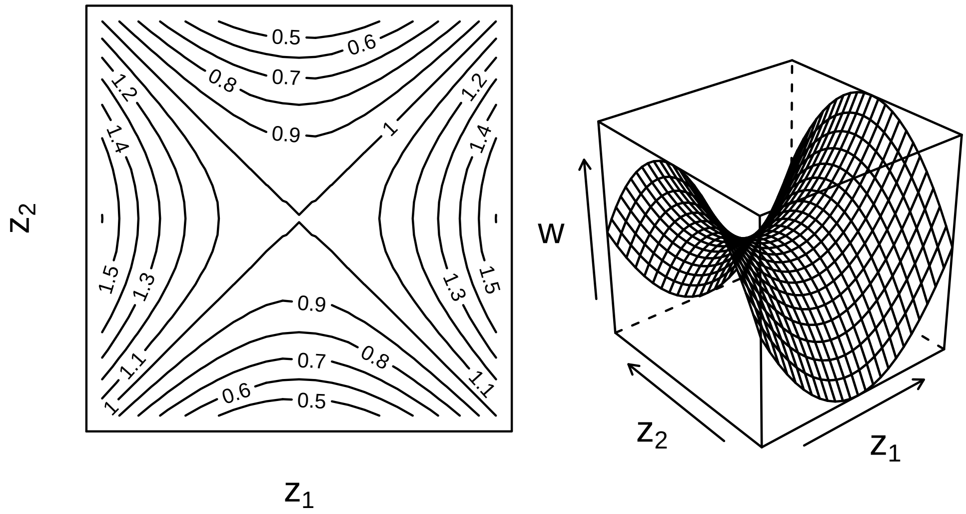
$$\gamma = \begin{bmatrix} -0.5 & 0.2 \\ 0.2 & -0.1 \end{bmatrix}$$

Non-linear selection, example 4



$$\gamma = \begin{bmatrix} 0 & 0.2 \\ 0.2 & 0 \end{bmatrix}$$

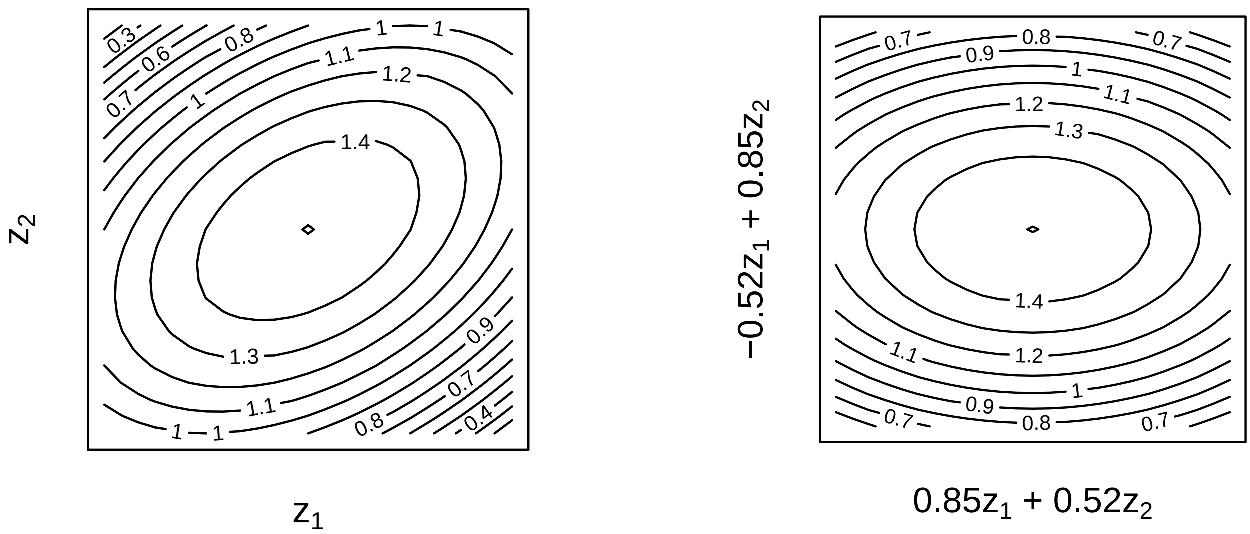
Non-linear selection, example 5



$$\gamma = \begin{bmatrix} 0.3 & 0 \\ 0 & -0.3 \end{bmatrix}$$

Major axes of non-linear selection

The γ matrix can be rotated so that it can be described in a new set of axes, which experience no correlational selection.



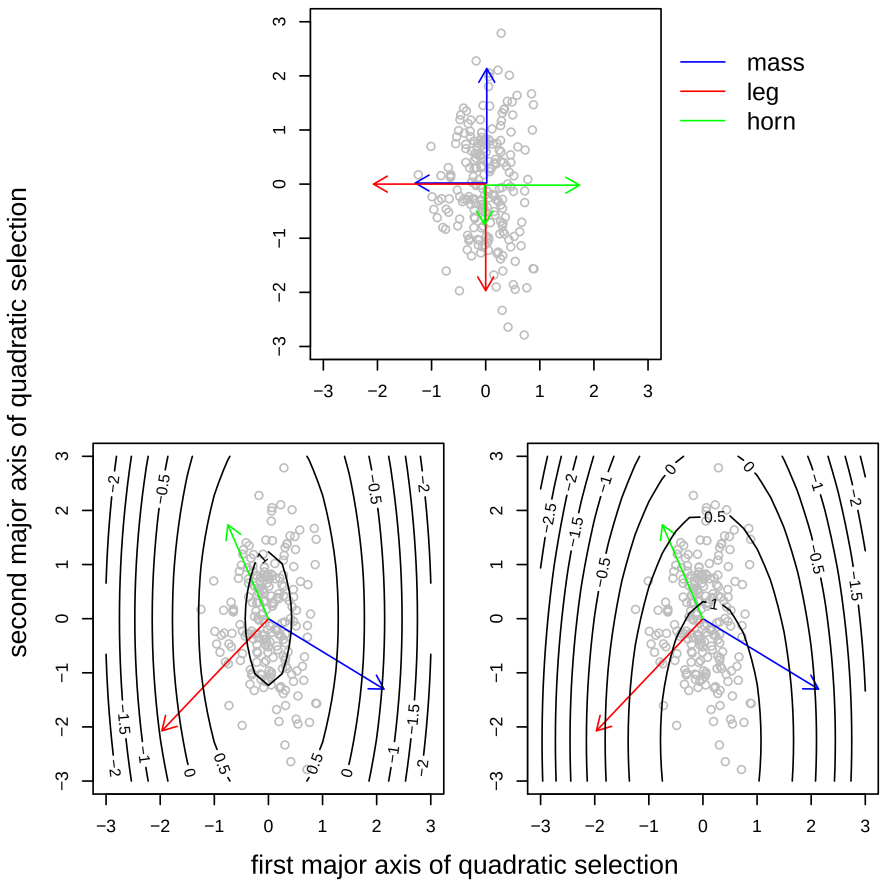
Care in inferring the shape of (MV) non-linear selection

- traits: mass, leg length, horn length
- variance-standardised analysis

$$\boldsymbol{\beta} = \begin{bmatrix} 0.16 \\ 0.08 \\ -0.12 \end{bmatrix}$$

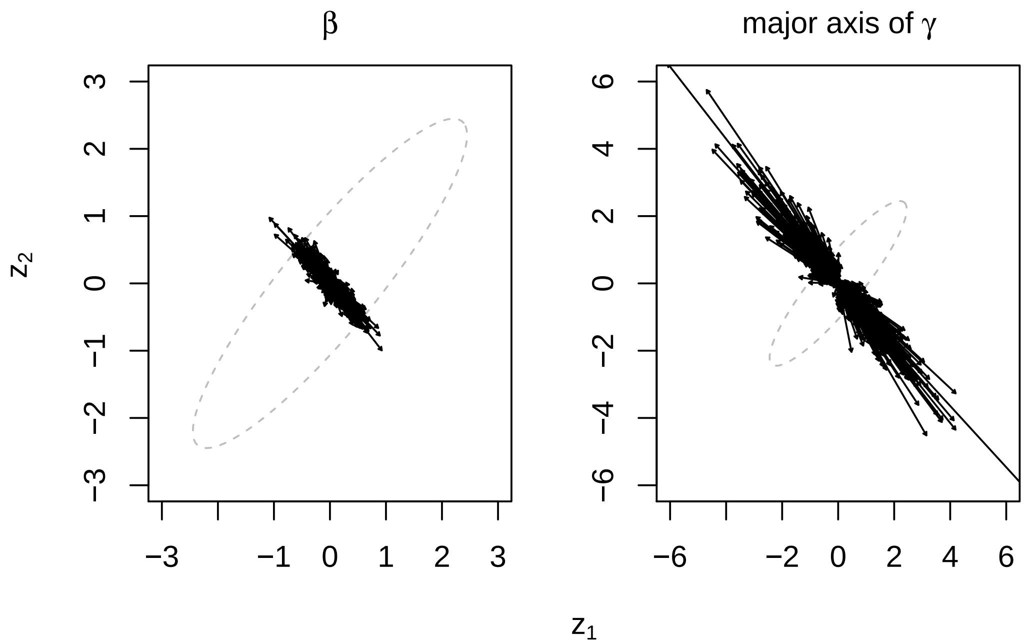
$$\boldsymbol{\gamma} = \begin{bmatrix} -0.35 & 0.30 & 0.15 \\ 0.30 & -0.33 & -0.07 \\ 0.15 & -0.07 & -0.05 \end{bmatrix}$$

Care in inferring the shape of (MV) non-linear selection

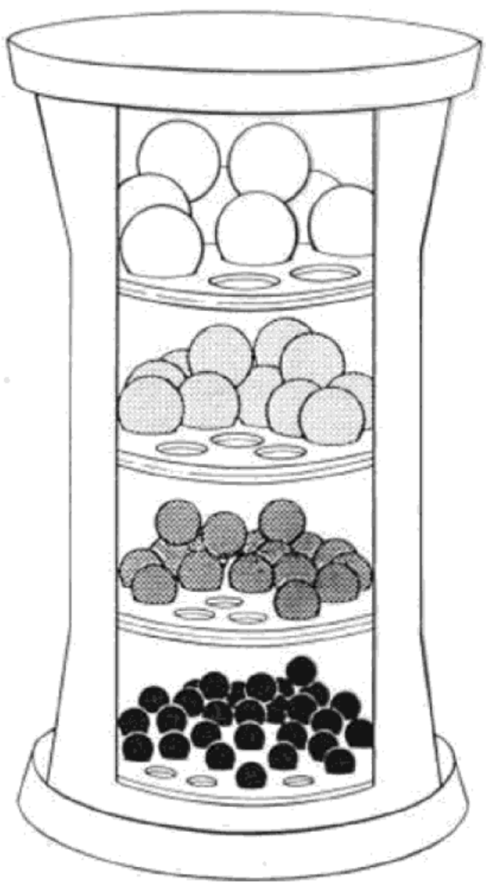


Bias in directions of selection relative to axes of phenotype

- simulated bivariate selection gradient analysis
- no relationship between trait and fitness



Does β reflect the relevance of traits to fitness?



Do black balls make it to the bottom?

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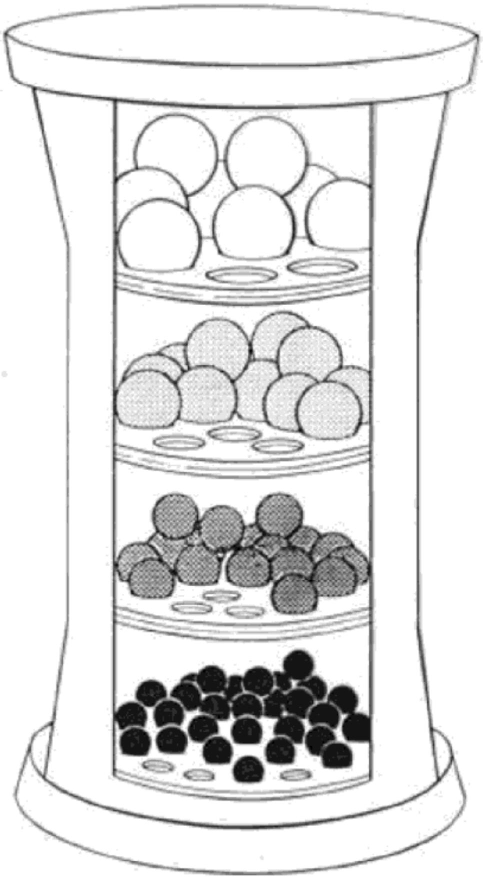

Do black balls make it to the bottom?
Yes. There is *selection of* black colour

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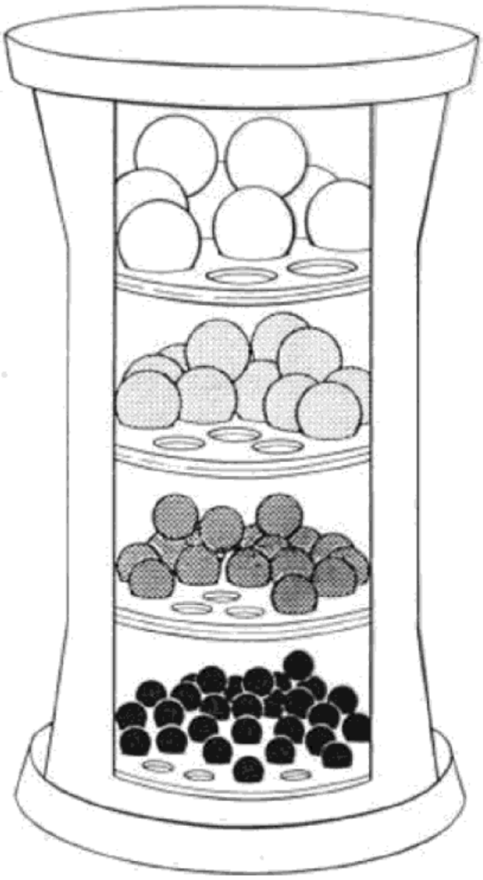

Do black balls make it to the bottom?
Yes. There is *selection of* black colour; it is *associated* with passage through the toy.

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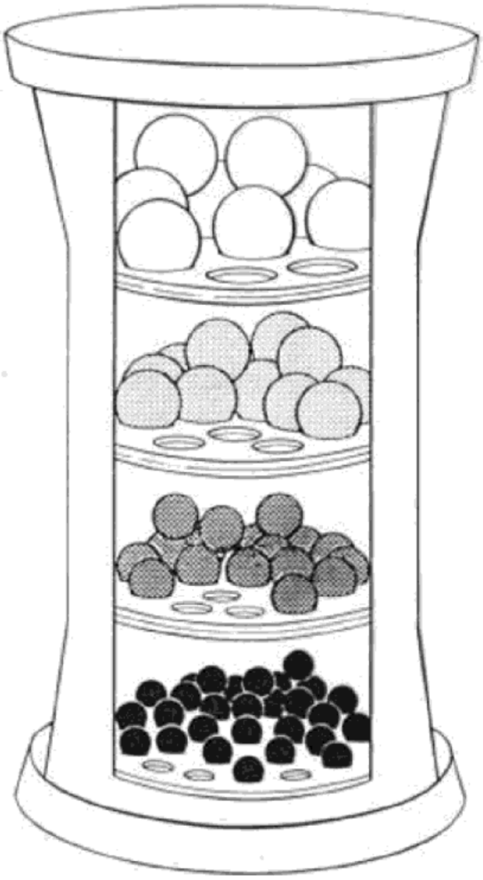

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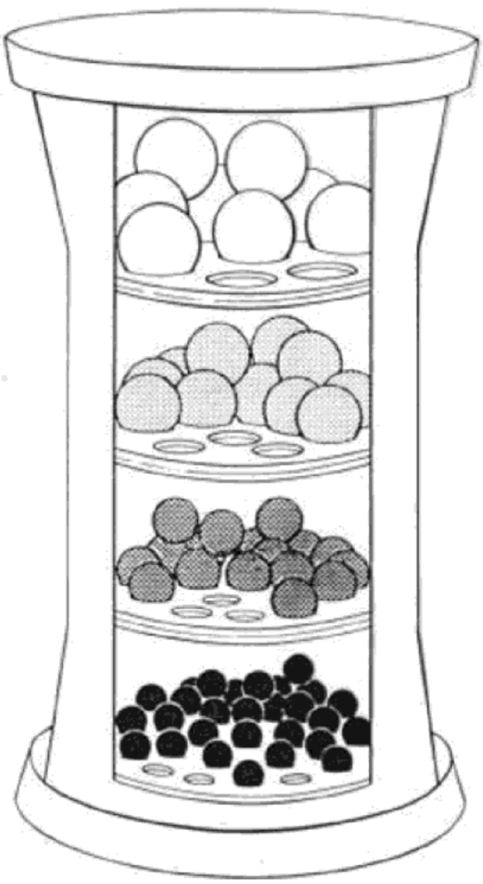

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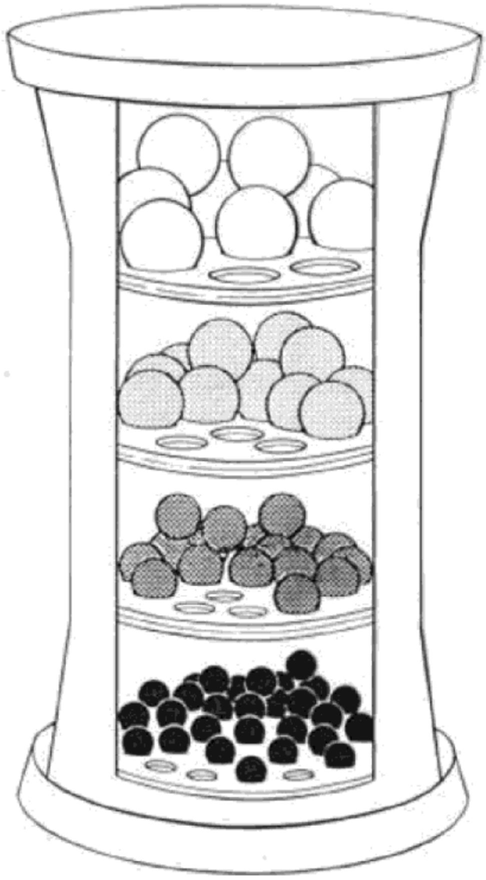

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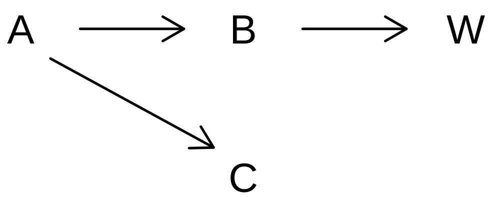
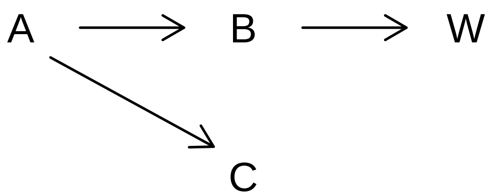
S is widely interpreted as representing total selection, something like *selection of*.
β is erroneously interpreted as representing something like *selection for*; however, it is something rather more specific.

The $A \to B \to W$ toy model



A
B
C

The $A \rightarrow B \rightarrow W$ toy model



	S
A	✓
B	✓
C	✓

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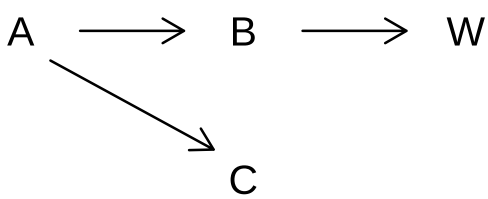

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C	✓	✗

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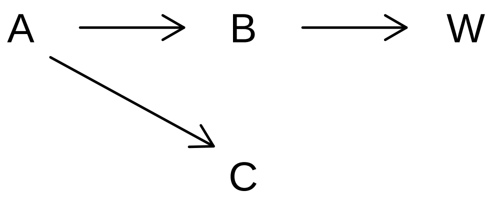

	S	β	η
A	✓	✗	✓
B	✓	✓	✓
C	✓	✗	✗

η, genetic variation, and evolution 1

- a Greek letter (η) does not a selection coefficient make!
- does η have a role in a $\Delta\bar{z} = f(genetics,\ selection)$ equation?

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Total effects of traits on one another are given by

$$\mathbf{\Phi} = (\mathbf{I} - \mathbf{b})^{-1}$$

where **b** is a matrix containing a certain arrangement of effects of traits on one another.
It then turns out, if $\mathbf{G}_\epsilon$ contains genetic variation that is independent of effects in the path model, then

$$\mathbf{G} = \mathbf{\Phi}\mathbf{G}_\epsilon\mathbf{\Phi}^T$$

and

$$\boldsymbol{\eta} = \mathbf{\Phi}^T\boldsymbol{\beta}$$

η, genetic variation, and evolution

Key facts from the previous slide:

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So, from the Lande equation

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

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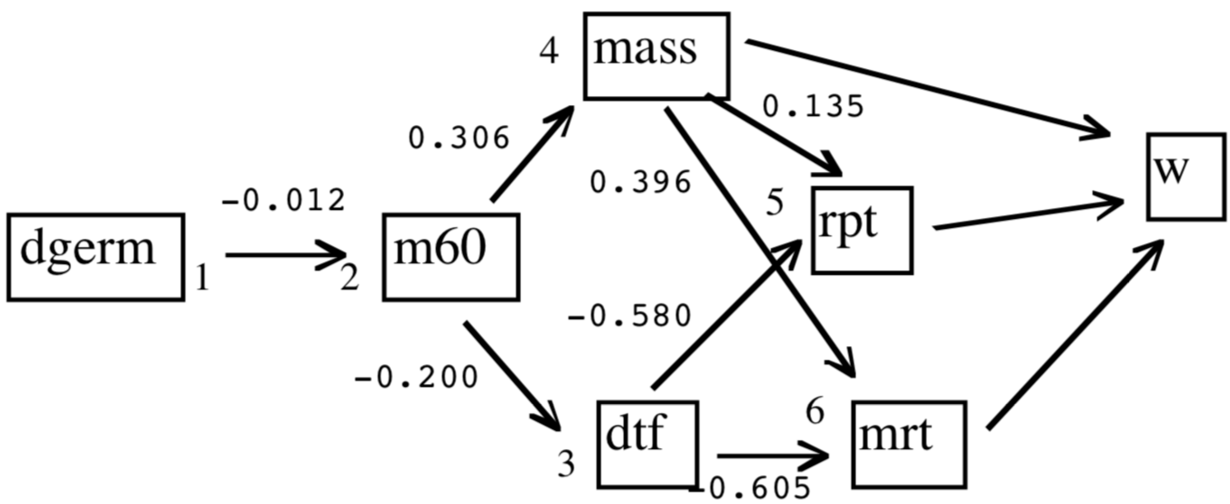
$$\Delta\bar{\mathbf{z}} = \mathbf{\Phi}\mathbf{G}_\epsilon\boldsymbol{\eta}$$

Example of estimation of η



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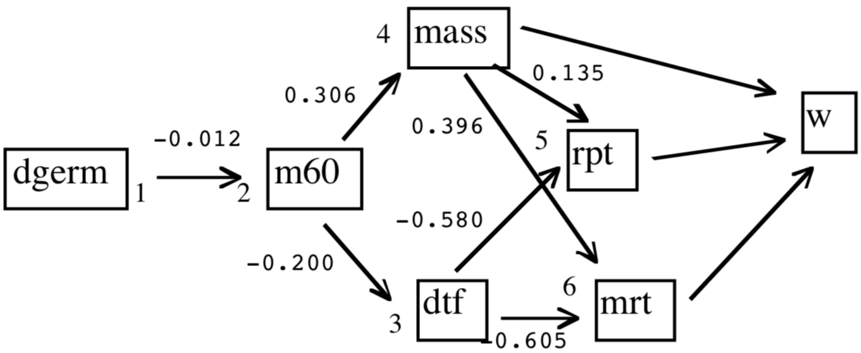

$$
\begin{aligned}
m60 &\sim dgerm \\
mass &\sim m60 \\
dtf &\sim m60 \\
rpt &\sim mass + dtf \\
mrt &\sim mass + dtf \\
w &\sim mass + rpt + mrt
\end{aligned}
\qquad
\mathbf{b} = \begin{bmatrix} 0 & -0.01 & 0 & 0 & 0 & 0 \\ 0 & 0 & -0.20 & 0.30 & 0 & 0 \\ 0 & 0 & 0 & 0 & -0.58 & -0.60 \\ 0 & 0 & 0 & 0 & 0.13 & 0.39 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}
$$

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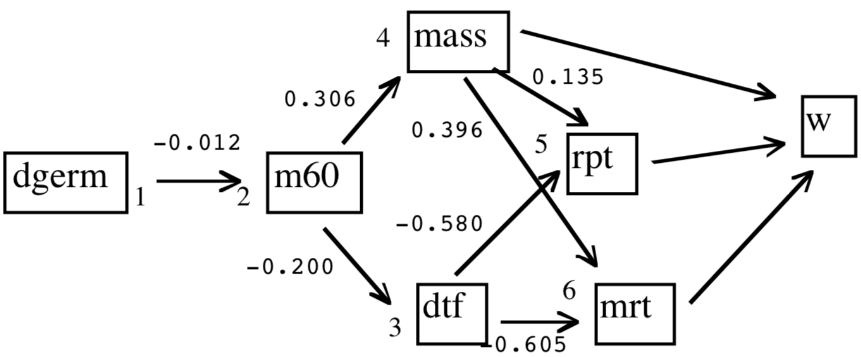

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\qquad
\boldsymbol{\beta} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ -0.03 \\ 0.15 \\ 0.21 \end{bmatrix}
$$

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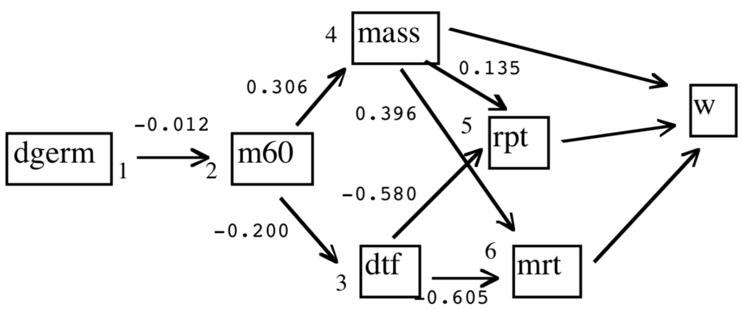
$$\mathbf{\Phi} = (\mathbf{I} - \mathbf{b})^{-1} = \begin{bmatrix} 1 & -0.01 & 0.02 & -0.003 & -0.002 & -0.003 \\ 0 & 1 & -0.20 & 0.30 & 0.157 & 0.242 \\ 0 & 0 & 1 & 0 & -0.580 & -0.605 \\ 0 & 0 & 0 & 1 & 0.135 & 0.396 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

Example of estimation of η



$$\boldsymbol{\beta}_{path} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ -0.0333 \\ 0.157 \\ 0.207 \end{bmatrix} \qquad \boldsymbol{\beta}_{ols} = \begin{bmatrix} 0.009 \\ 0.004 \\ 0.040 \\ -0.028 \\ 0.142 \\ 0.207 \end{bmatrix} \qquad \boldsymbol{\eta} = \begin{bmatrix} -0.001 \\ 0.065 \\ -0.216 \\ 0.070 \\ 0.157 \\ 0.207 \end{bmatrix}$$