Analysis of multivariate phenotypic selection

Michael Morrissey
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Preliminaries 2

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  - Key concepts in methods and theory to support solid empirical work (as before)

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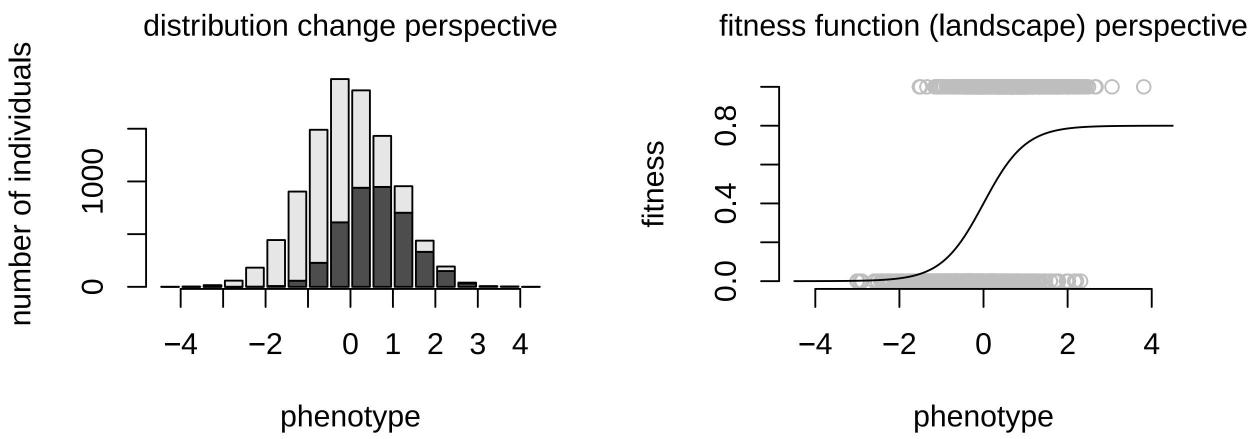
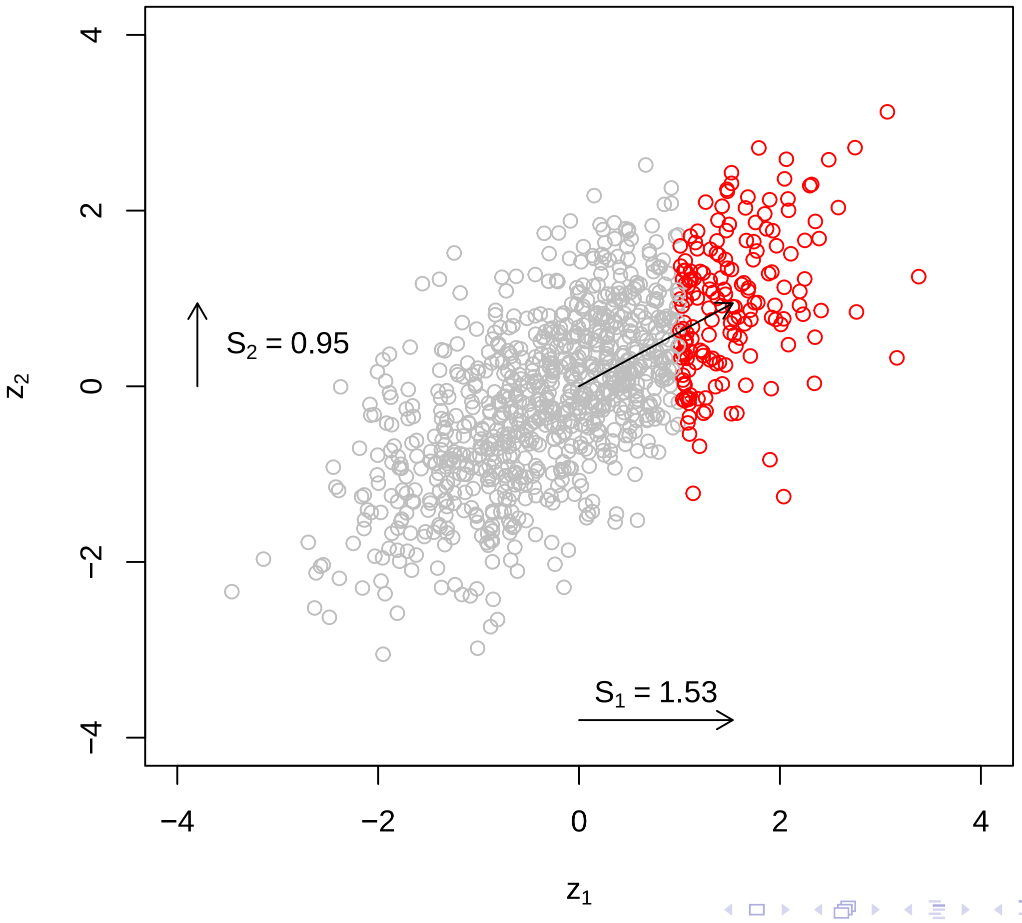
  - Key concepts in methods and theory to support solid empirical work (as before)
- Structure
  - What happens when selection acts on more than one trait at a time?
  - The selection gradient concept really comes into its own.
- Set up for following lectures
  - Many of the most useful concepts in modern selection analysis are elaborations of the basic multivariate case we focus on in this lecture.

Two views, univariate (from lecture 1)

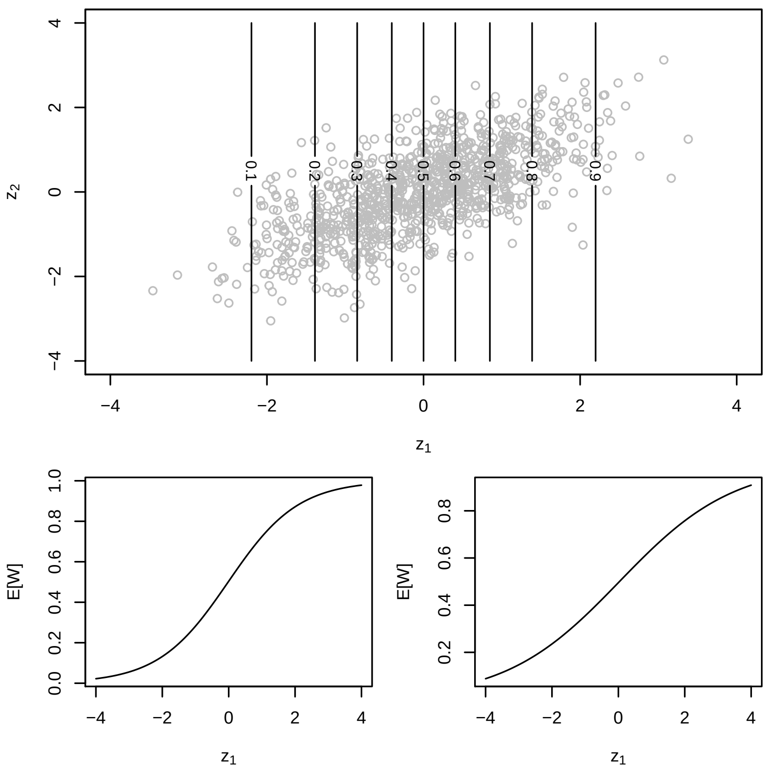
Two complimentary ways of thinking about natural selection:



The multivariate distributional view

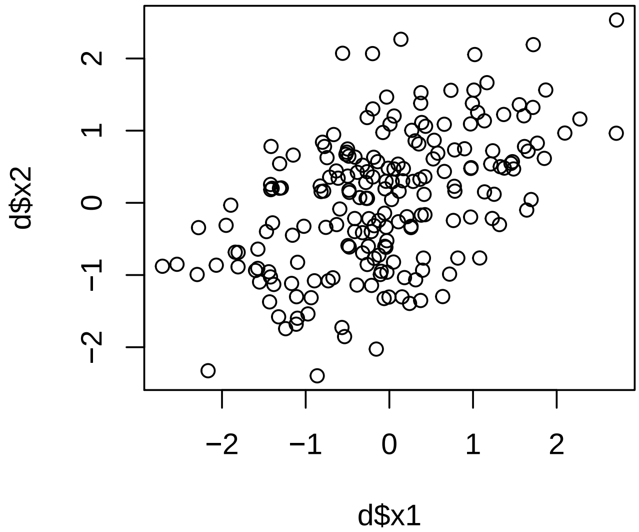


The multivariate function view



Dispensing with misunderstandings about collinearity 1

```
> S <- matrix(c(1,0.5,0.5,1),2,2)
>
> x <- rmvnorm(200,c(0,0),S)   # from pkg mvtnorm
>
> d <- data.frame(x1=x[,1],x2=x[,2])
>
> plot(d$x1,d$x2)
```



Dispensing with misunderstandings about collinearity 1

```
> d$y <- rnorm(200,0.5*d$x1,1)
```

Dispensing with misunderstandings about collinearity 1

```
> d$y <- rnorm(200,0.5*d$x1,1)
> summary(lm(y~x1,data=d))$coefficients
```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> summary(lm(y~x1,data=d))$coefficients
              Estimate Std. Error   t value     Pr(>|t|)
(Intercept) 0.03284569 0.07174432 0.4578159 6.475867e-01
x1          0.53123048 0.06472664 8.2072930 2.849766e-14
>
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> summary(lm(y~x2,data=d))$coefficients
```


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> summary(lm(y~x2,data=d))$coefficients
```


```
             Estimate Std. Error  t value     Pr(>|t|)
(Intercept) 0.0828077 0.08010253 1.033771 0.3025040808
x2          0.2734574 0.07188813 3.803930 0.0001896892
>
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>
> summary(lm(y~x1+x2,data=d))$coefficients
```


Dispensing with misunderstandings about collinearity 1

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> summary(lm(y~x1+x2,data=d))$coefficients
```


```
               Estimate Std. Error    t value     Pr(>|t|)
(Intercept)  0.03036372 0.07222198  0.4204222 6.746353e-01
x1           0.54704737 0.07798616  7.0146722 3.610191e-11
x2          -0.02831862 0.07750379 -0.3653838 7.152170e-01
```

The multivariate breeder's equation

Univariate breeder's equation

$$\Delta \bar{z} = \frac{V_a}{V_p} S$$

Multivariate breeder's equation

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

where

$$\mathbf{G} = \begin{bmatrix} \sigma^2_a z_1 & \sigma_a(z_1, z_2) & \dots \\ \sigma_a(z_1, z_2) & \sigma^2_a z_2 & \\ \vdots & & \ddots \end{bmatrix}, \quad \mathbf{P} = \begin{bmatrix} \sigma^2_p z_1 & \sigma_p(z_1, z_2) & \dots \\ \sigma_p(z_1, z_2) & \sigma^2_p z_2 & \\ \vdots & & \ddots \end{bmatrix}, \quad \mathbf{S} \begin{bmatrix} S_1 \\ S_2 \\ \vdots \end{bmatrix}$$

Regression parameterisations of the multivariate breeder's equation

If we define the regression of an offspring trait vector on a mid-parent trait vector, we ge

$$\mathbf{H} = \mathbf{G}\mathbf{P}^{-1}$$

and so

$$\Delta \bar{\mathbf{z}} = \mathbf{H}\mathbf{S}$$

But what turns out to be really fun is to note that the multiple regression of fitness on traits is

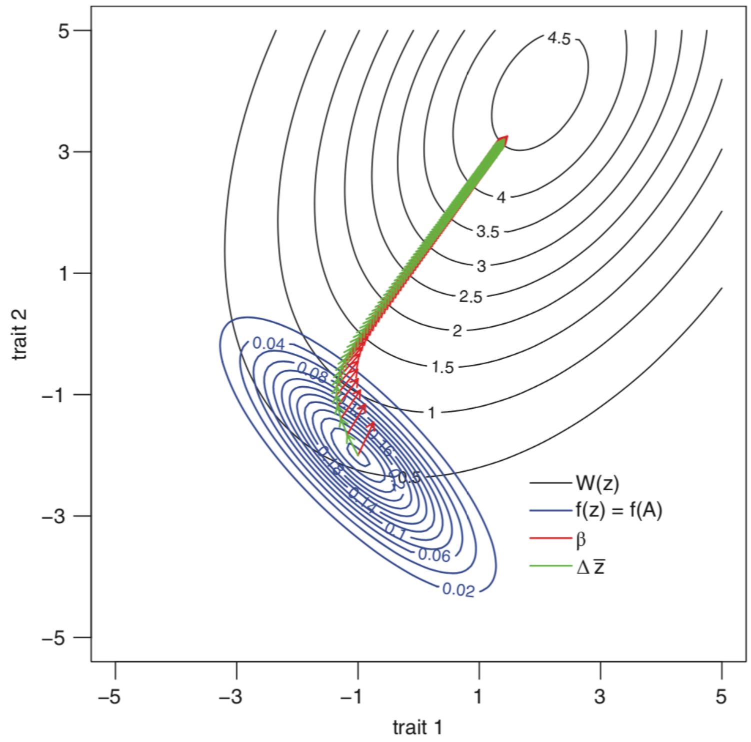
$$\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{S}$$

and so

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

This is referred to as the *multivariate Lande equation*.

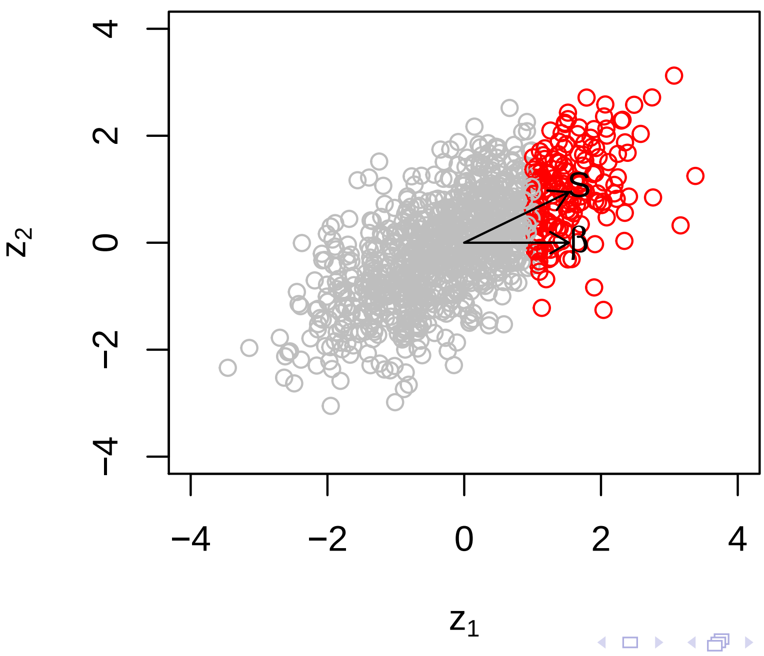
β points in the direction of most rapidly increasing fitness



The duality of covariances: phenotypic and genetic correlations and their effects 1

Phenotypic covariances map fitness function (surface) geometry onto changes in the multivariate distribution of phenotype.

$$\mathbf{S} = \mathbf{P}\beta$$



The duality of covariances: phenotypic and genetic correlations and their effects 1

Let's break that down...

- direct selection

$$S_{i,direct} = \sigma^2_{z_i}\beta_i$$

- indirect selection

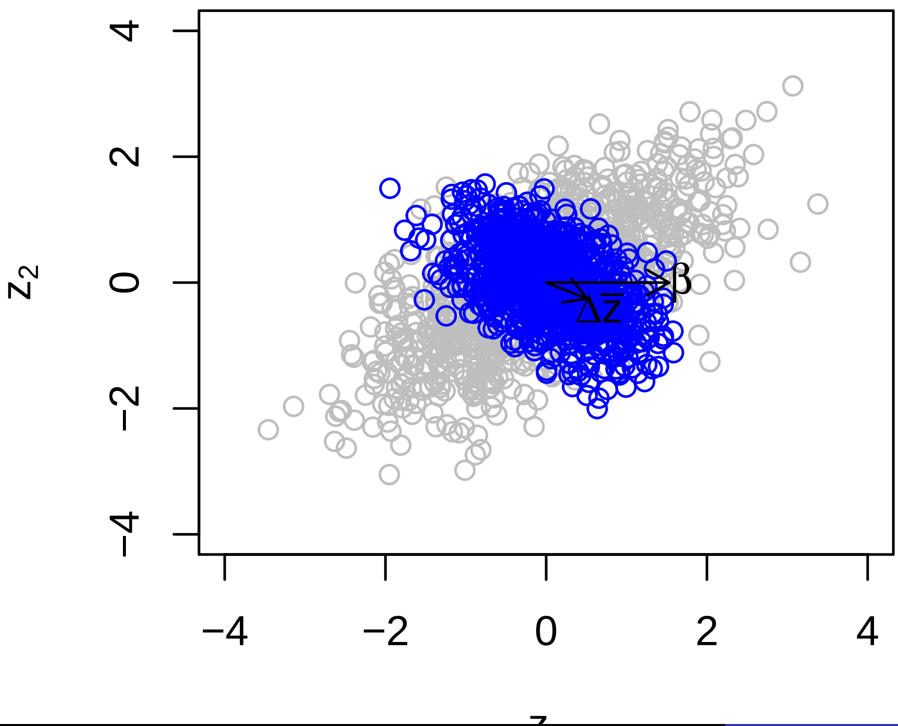
$$S_{i,indirect} = \Sigma_{j \neq i}\sigma_{z_j,z_i}\beta_j$$

- total multivariate selection

$$\mathbf{S} = \mathbf{P}\boldsymbol{\beta}$$

The duality of covariances: phenotypic and genetic correlations and their effects 2

Genetic covariances map the response to selection onto the selection gradient vector



for e.g., if

$$\mathbf{G} = \begin{bmatrix} \frac{1}{3} & -\frac{1}{6} \\ -\frac{1}{6} & \frac{1}{3} \end{bmatrix}$$

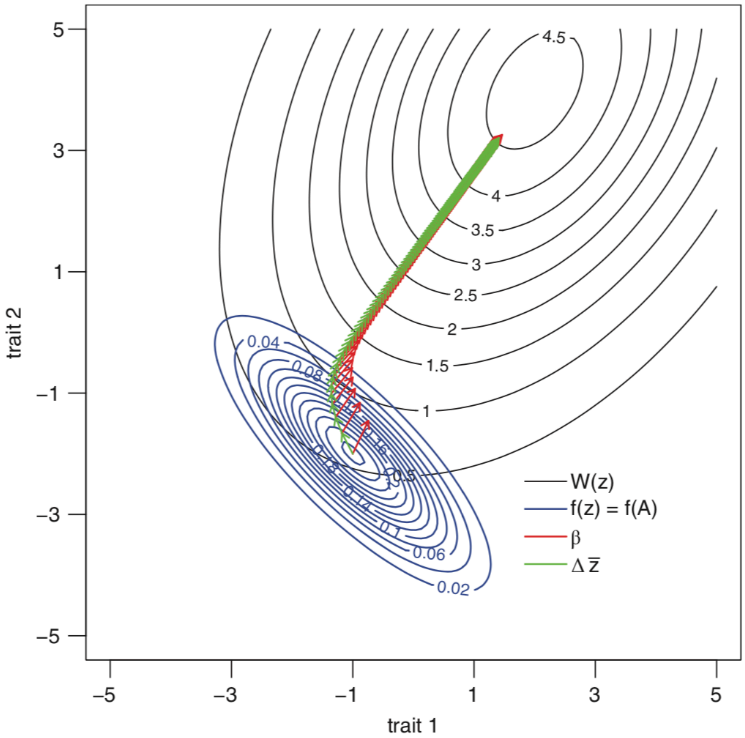
and

$$\boldsymbol{\beta} = \begin{bmatrix} 1.5 \\ 0 \end{bmatrix}$$

then

$$\Delta\bar{\mathbf{z}} = \begin{bmatrix} 0.5 \\ -0.25 \end{bmatrix}$$

The MV response over generations



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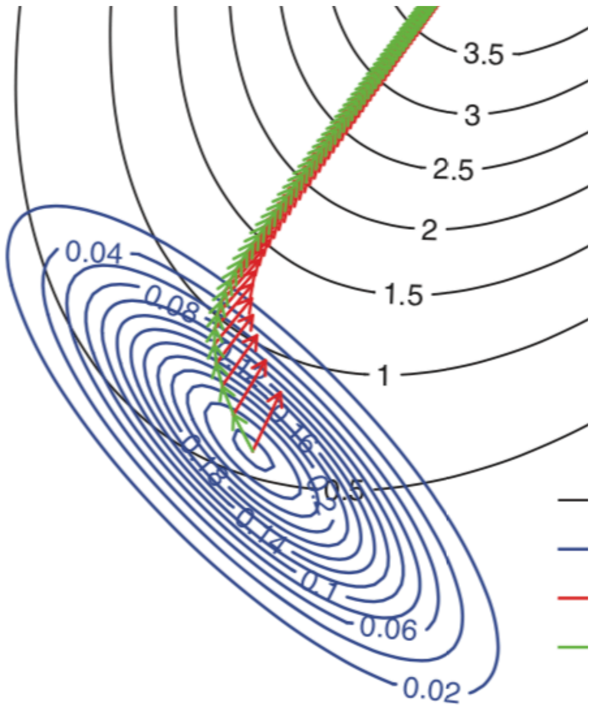

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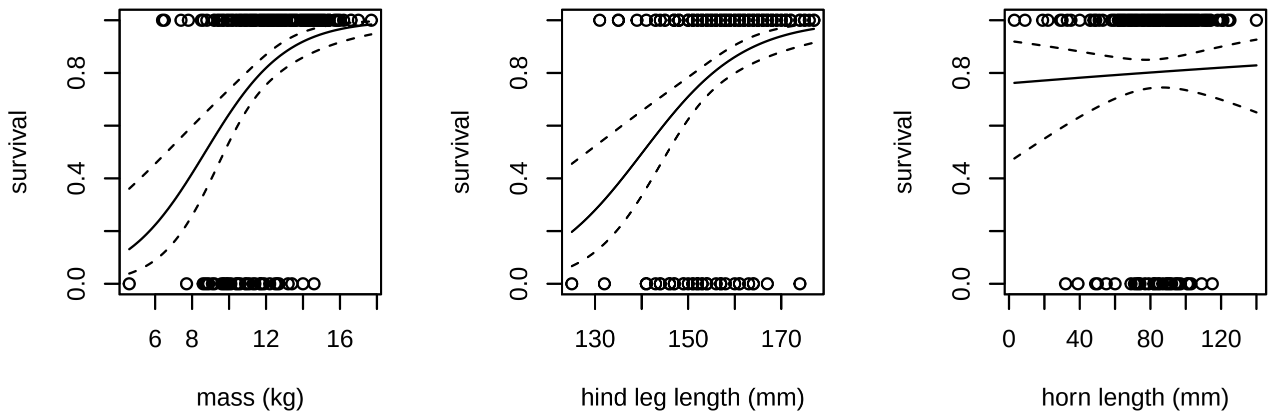
Estimation: the multivariate Lande-Arnold regression

$$\begin{aligned} w_i = \; & \alpha \\ & + \Sigma_j \beta_j z_{ij} && \textit{directional} \\ & + \frac{1}{2}\Sigma_j \gamma_j (z_{ij} - \bar{z}_j)^2 && \textit{quadratic} \\ & + \Sigma_{j=2}^{t} \Sigma_{k=j+1}^{k} \gamma_{jk} (z_{ij} - \bar{z}_j)(z_{ik} - \bar{z}_k) && \textit{correlational} \\ & + e_i \end{aligned}$$

This is an extension of the univariate Lane-Arnold regression from lecture 1 to multiple regression.
We will continue in this lecture with the directional component only.
Multivariate quadratic selection will be treated separately.

Multivariate selection in Soay lambs

First we'll back-track and do univariate analyses



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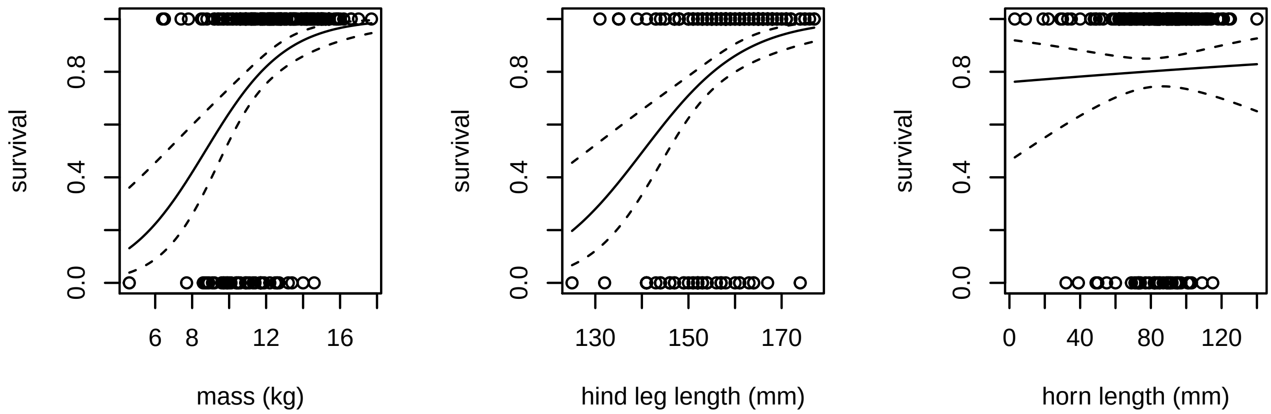
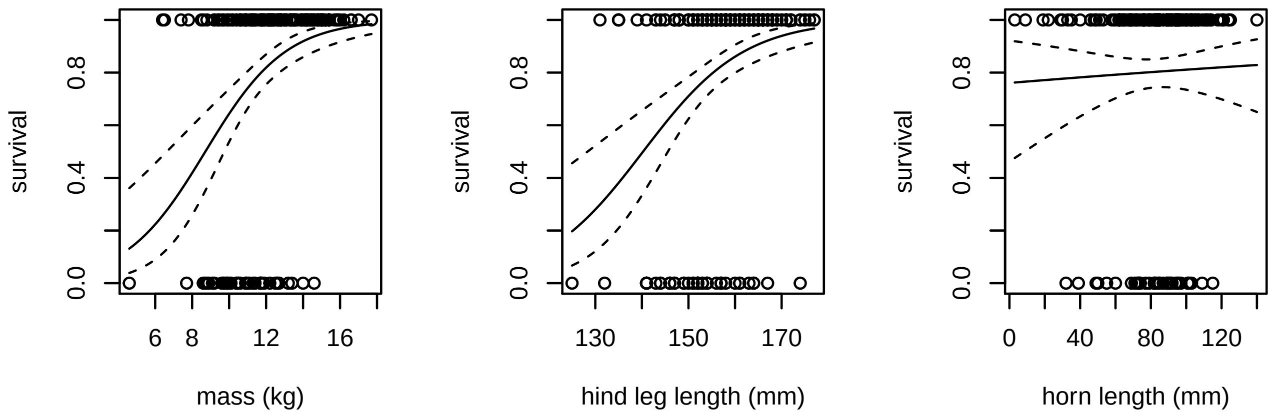


trait	S	$SE[S]$	β_{univ}	$SE[\beta_{univ}]$
mass (kg)	0.394	0.070	0.082	0.014
hind leg length (mm)	1.525	0.300	0.017	0.003
horn length (mm)	0.281	0.740	0.000	0.002

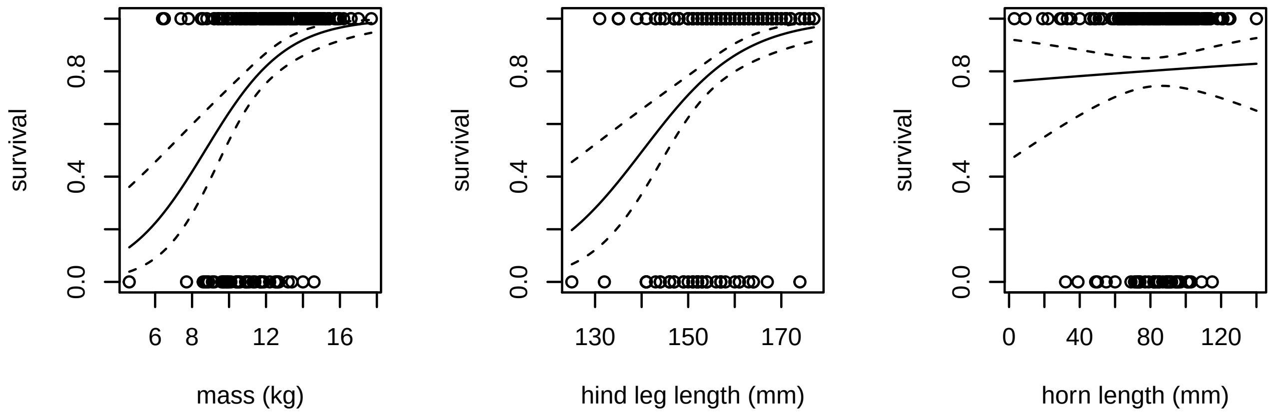
Multivariate selection in Soay lambs



Multivariate directional selection OLS model

$$w_i = \alpha + \beta_{mass} mass_i + \beta_{leg} leg_i + \beta_{horn} horn_i + e_1$$

Multivariate selection in Soay lambs



Multivariate directional selection OLS model

$$w_i = \alpha + \beta_{mass} mass_i + \beta_{leg} leg_i + \beta_{horn} horn_i + e_1$$

trait	β_{univ}	$SE[\beta_{univ}]$	β	$SE[\beta]$
mass (kg)	**0.082**	0.014	**0.087**	0.029
hind leg length (mm)	**0.017**	0.003	0.004	0.007
horn length (mm)	0.000	0.002	**−0.004**	0.001

Direct and indirect selection in Soay lambs

$$\mathbf{S} = \mathbf{P}\boldsymbol{\beta}$$

$\mathbf{P}$ =

	mass	leg	horn
mass	5	18	22
leg	18	86	85
horn	22	85	468

, $\boldsymbol{\beta}$ =

mass	0.087
leg	0.004
horn	-0.004

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Direct selection of horn length:

$$S_{direct} = \sigma^2_{horn} \cdot \beta_{horn} = 468 \cdot -0.0043 = -2.01$$

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$$S_{indirect} = \sigma_{horn,mass} \cdot \beta_{mass} + \sigma_{horn,leg} \cdot \beta_{leg} = 22 \cdot 0.087 + 85 \cdot 0.0004 = 2.25$$

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Total selection differential:

$$S = S_{direct} + S_{indirect} = -2.01 + 2.25 = 0.24$$

Estimation: average partial gradients

The average gradient concept applies to multivariate analysis also.

Scheme:

1. estimate $W \;\; f(z_1, z_2, ...)$
2. predict individual fitness, calculate $\bar{W(z)}$
3. add a small amount h to each value of z_1, holding all other traits constant
4. calculate $\bar{W(z)}^*$, i.e., predictions with the modified $z_1 + h$ values
5. estimate gradient of $\bar{W}$ (finite differences), and scale to w

$$\hat{\beta}_1 = \frac{\bar{W(z)}^* - \bar{W(z)}}{h} \frac{1}{\bar{W}}$$

6. restore values of z_1; repeat for other traits

Multivariate selection and variation in fitness

We saw earlier that the combined effect of direct and indirect selection sum up to the covariance according to

$$\mathbf{S} = \mathbf{P}\boldsymbol{\beta}$$

This is simply the covariance o a linear transformation; when $\mathbf{P}$ is transformed according to $\boldsymbol{\beta}$ the covariances of $\mathbf{z}$ and w that result are $\mathbf{S}$.

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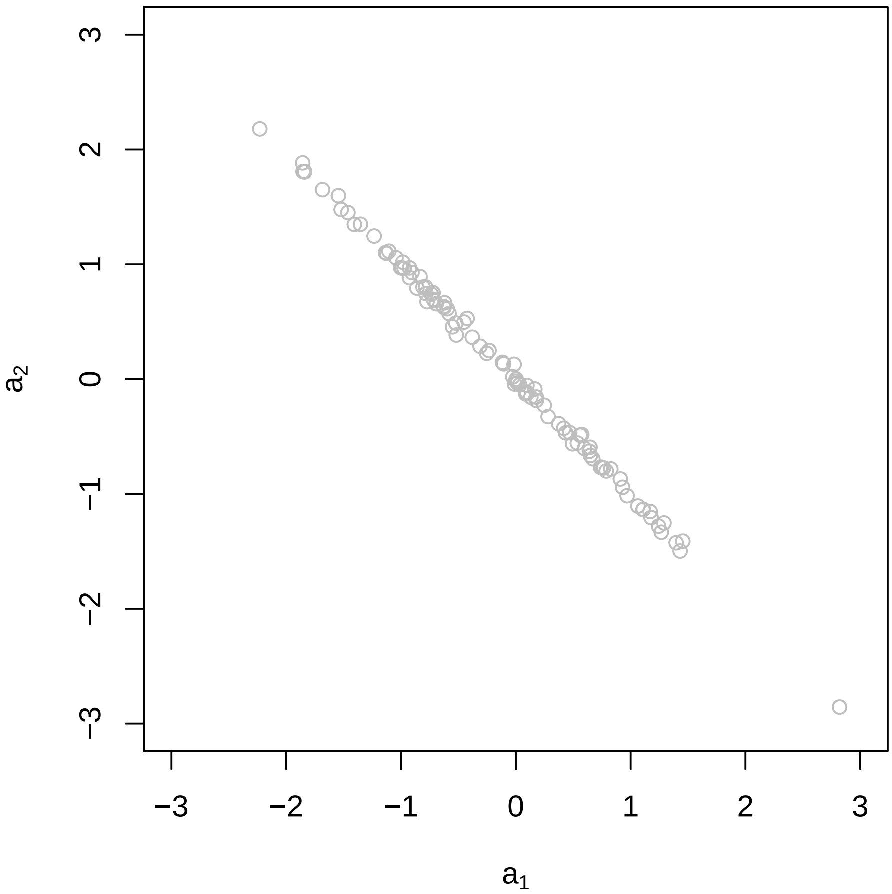
The variance of a linear transformation ($\boldsymbol{\beta}$) of a random vector ($\mathbf{z}$) is similar:

$$VAR[w] = \boldsymbol{\beta}^T\mathbf{P}\boldsymbol{\beta}$$

Absolute constraints can hide in multivariate space - 1



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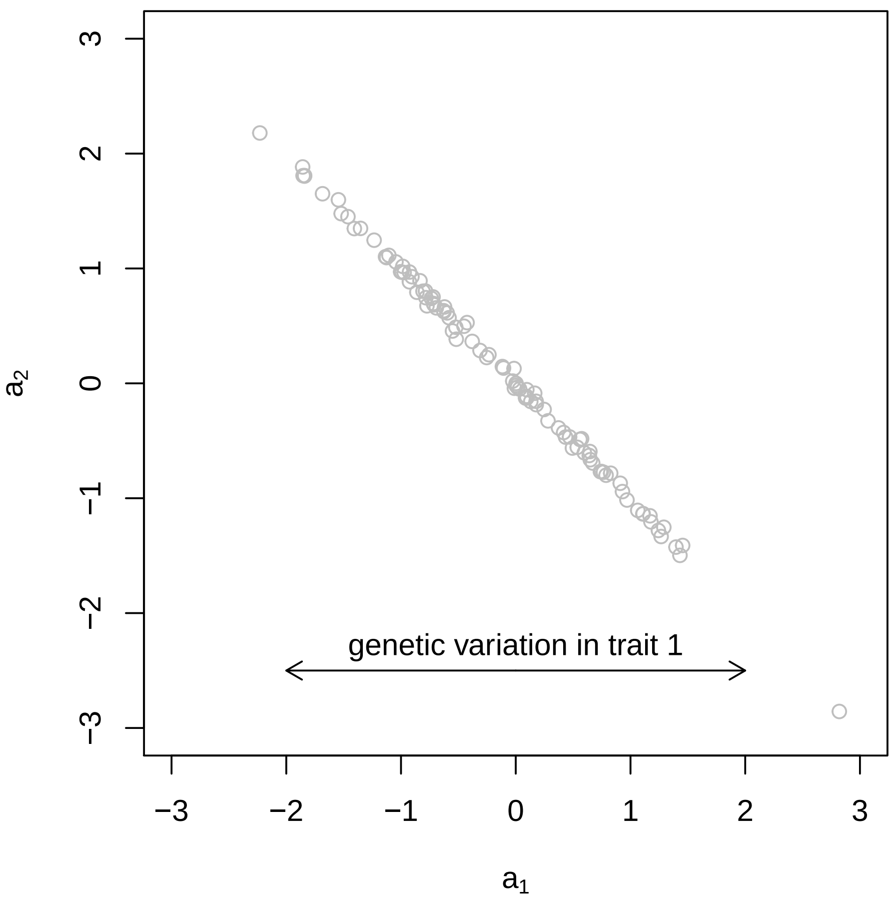

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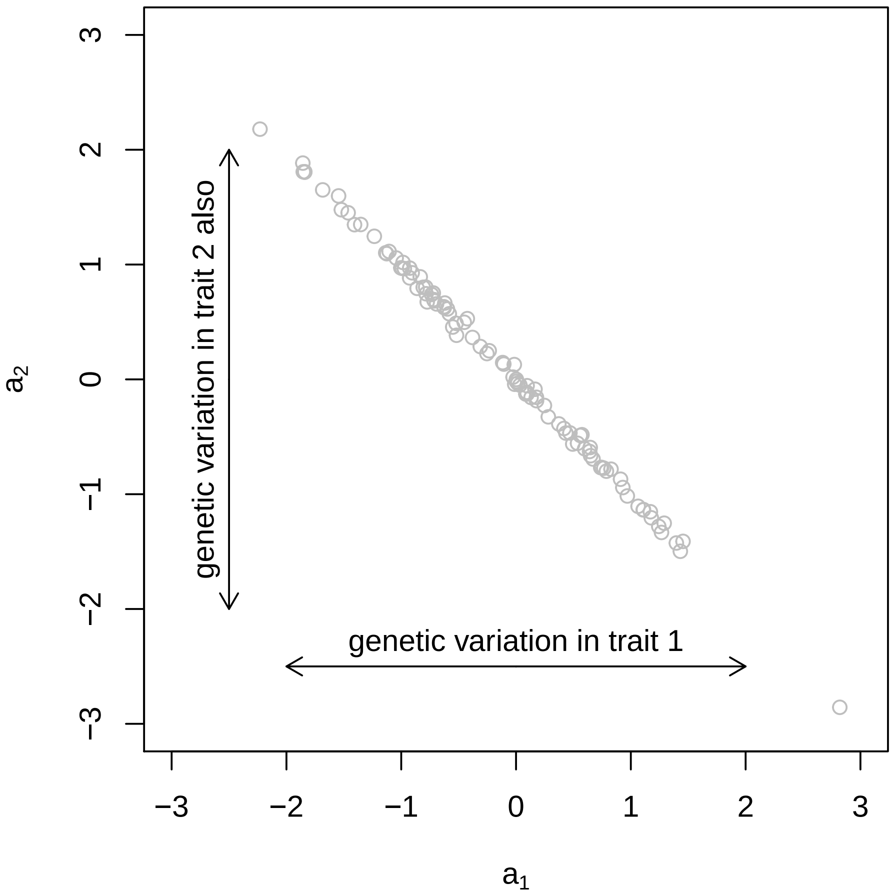

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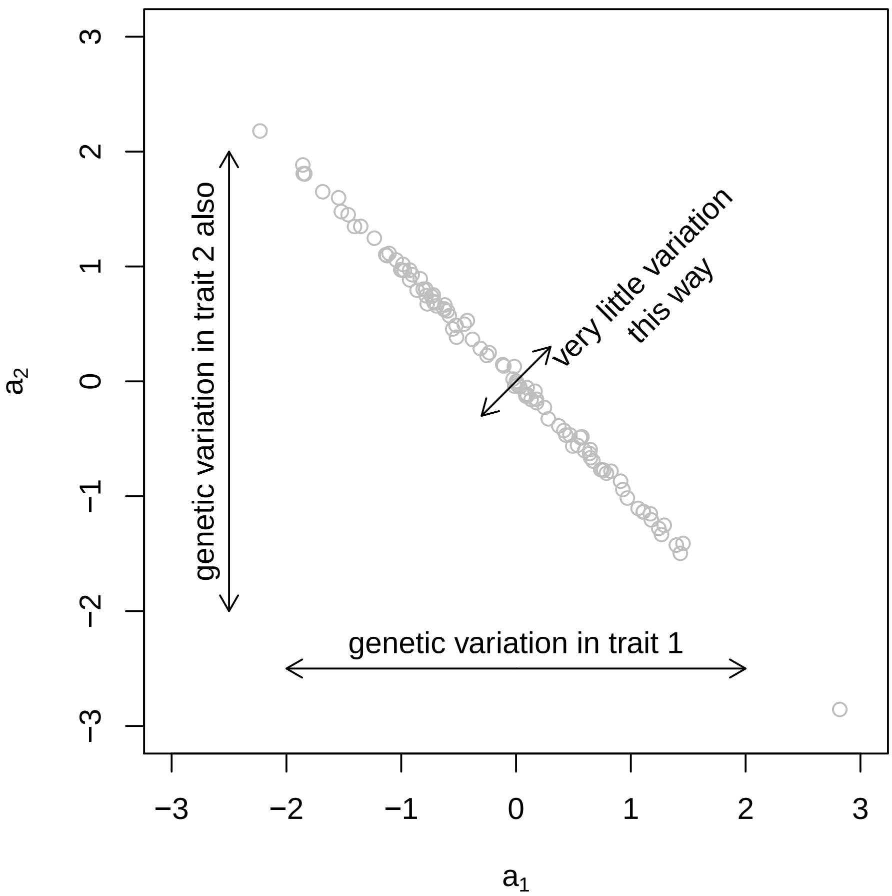
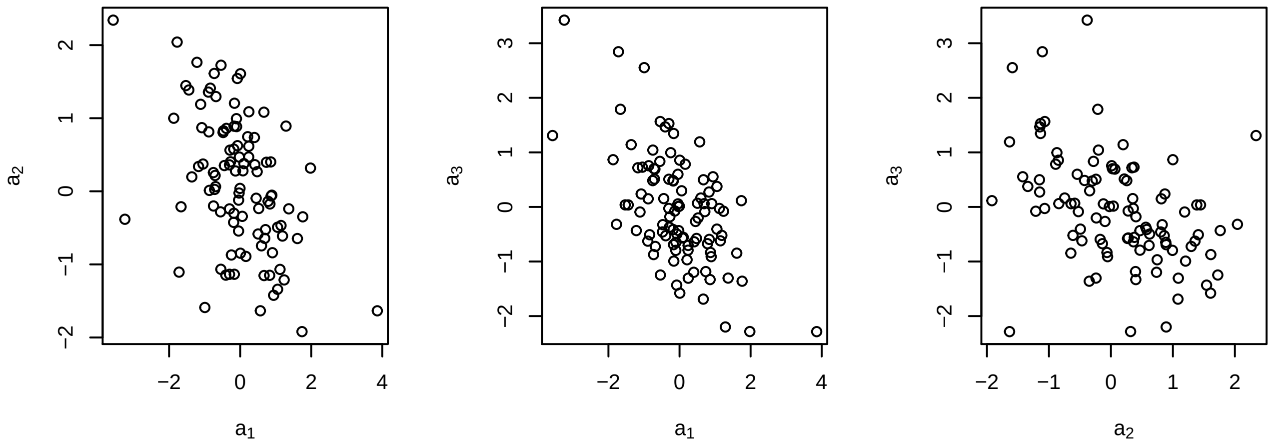


Absolute constraints can hide in multivariate space - 2



Interpretation: if more than two traits, some geometry makes it less mind-bending

Sorry - couldn't imbed my animation. I'll give it in the presentation.
The distribution depicted is for

$$\mathbf{G} = \begin{bmatrix} 1 & -0.5 & -0.5 \\ -0.5 & 1 & -0.5 \\ -0.5 & -0.5 & 1 \end{bmatrix}$$

and

$$\begin{bmatrix} 1 & -0.5 & -0.5 \\ -0.5 & 1 & -0.5 \\ -0.5 & -0.5 & 1 \end{bmatrix} \begin{bmatrix} b \\ b \\ b \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

Interpreting effect size

Which is more important to fitness: mass, skeletal size, or horn length?

trait	β	β_σ	β_μ
mass (kg)	0.087	0.190	1.074
hind leg length (mm)	0.004	0.040	0.671
horn length (mm)	-0.004	-0.094	-0.359