Phenotypic selection: elaborations

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Preliminaries

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  - ▶ the sex-specific Lande equation
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- ▶ Sexually antagonistic selection
  - ▶ the sex-specific Lande equation
  - ▶ a cool new re-formulation
- ▶ Selection and age structure
  - ▶ overlapping generations
  - ▶ senescence and selection across ages
  - ▶ "Aster" models (how to make your own)
  - ▶ IPMs (don't believe the hype)

- ▶ Results from meta-analyses of natural selection
  - ▶ how strong is selection?
  - ▶ how variable is selection?

Selection via helping your offspring

Clutton-Brock 1988:

- *lifetime breeding success, LBS*: number of offspring born to a female throughout her life
- *lifetime reproductive success, LRS*: number of offspring raised to recruitment (canonically, to one year of age)

This has become deeply entrenched; has no specific theoretical basis as a measure of fitness that will work in
$\Delta\bar{z} = f(genetics,\ selection)$ equations.

QG, fitness, and the zygote-to-zygote boundary

Careful quote from Walsh and Morrissey (2019):

> *It is typical to view lifetime reproductive success as an 'ultimate' measure of fitness (Clutton-Brock, 1988). However, this view is unfortunate: the practice of using numbers of offspring raised to independence in formal quantitative genetic studies of selection and evolution is likely to obscure, rather than illuminate, the roles played by parental performance in the evolutionary process (Hadfield, 2012; Thompson and Hadfield, 2017). Critically, evolutionary quantitative genetics is not blind to parental effects, and a variety of models exist to formally handle the evolutionary consequences of cross-generational effects (see especially Willham, 1963, 1972; Kirkpatrick and Lande, 1989). These models are reviewed in Walsh and Lynch (2018, Chapter 22) and in Hadfield (2012).*

zygotes and fitness does not mean we must ignore kin selection

Of course helping kin (especially offspring) is a good way to increase your genetic representation in future generations.
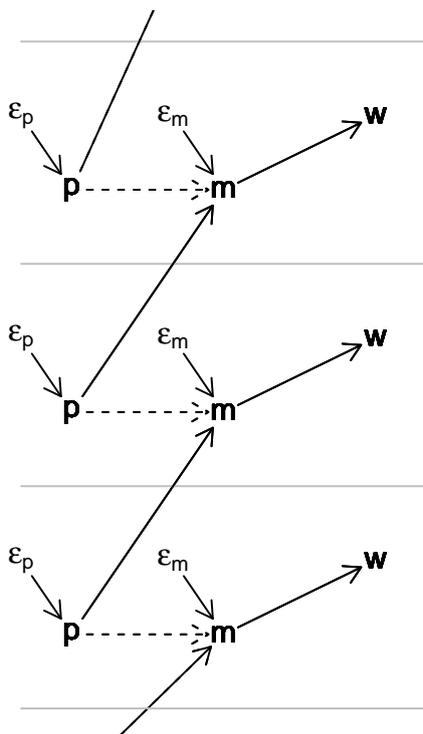
From Hamilton, altruism evolves if

$$c < rb$$

where

- c: cost of altruistic behaviour to self
- b: benefit of altruistic behaviour to recipient
- r: relatedness of actor and recipient

A Lande-like equation for parent-offspring effects in relation to Hamilton's rule

analogue to Hamilton's "cost", the non-social extended selection gradient

$$\boldsymbol{\eta} = \begin{bmatrix} b_{pm}b_{mw} \\ b_{mw} \end{bmatrix} = \begin{bmatrix} -ive \cdot +ive \\ +ive \end{bmatrix}$$

analogue of Hamilton's "benefit", the social extended selection gradient

$$\boldsymbol{\eta} = \begin{bmatrix} b_{p_s m}b_{mw} \\ b_{mw} \end{bmatrix} = \begin{bmatrix} +ive \cdot +ive \\ 0 \end{bmatrix}$$

$$\Delta\bar{\boldsymbol{\epsilon}} = \mathbf{G}_\epsilon \left(\boldsymbol{\eta} + \frac{1}{2}\boldsymbol{\eta}_s \right)$$

The two-sex Lande equation

$$\begin{bmatrix} \Delta\bar{\mathbf{z}}_m \\ \Delta\bar{\mathbf{z}}_m \end{bmatrix} = \frac{1}{2} \begin{bmatrix} \mathbf{G}_m & \mathbf{B} \\ \mathbf{B}^t & \mathbf{G}_f \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}_m \\ \boldsymbol{\beta}_f \end{bmatrix}$$
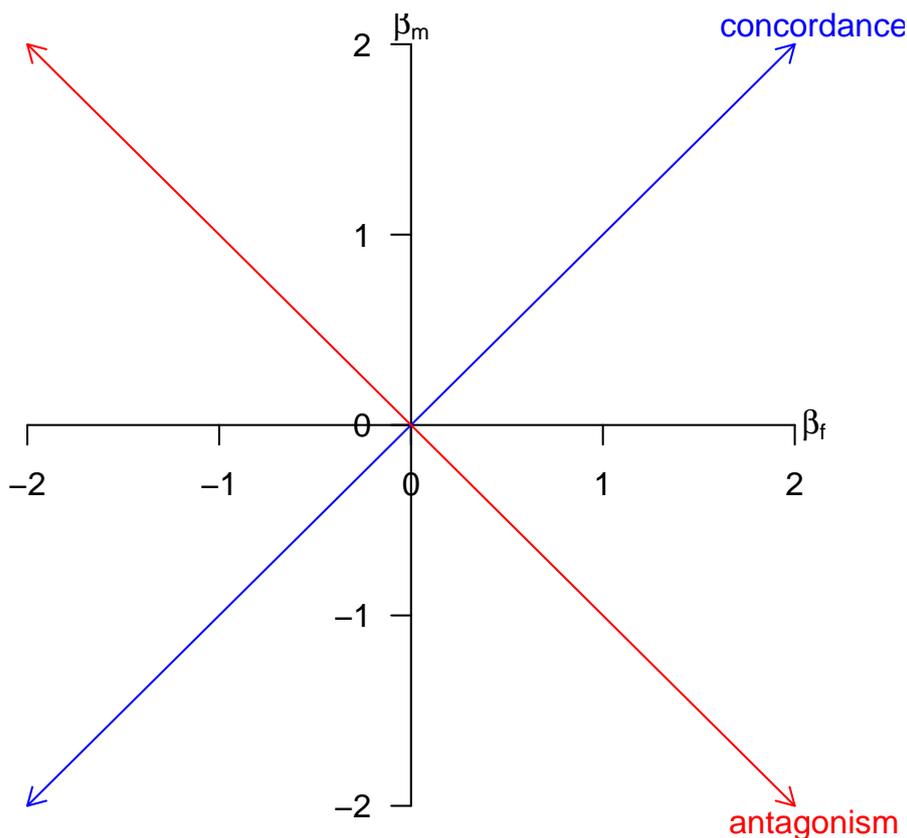
▶ $\frac{1}{2}$: each sex-specific β pertains only to half of the parents

▶ $\boldsymbol{\beta}_m$, $\boldsymbol{\beta}_f$: sex-specific selection gradients

▶ $\mathbf{G}_m$, $\mathbf{G}_f$: $\mathbf{G}$ matrices of traits as expressed in each sex separately

▶ $\mathbf{B}$: genetic correlations between the sexes

Cheng & Houle's reparameterisation
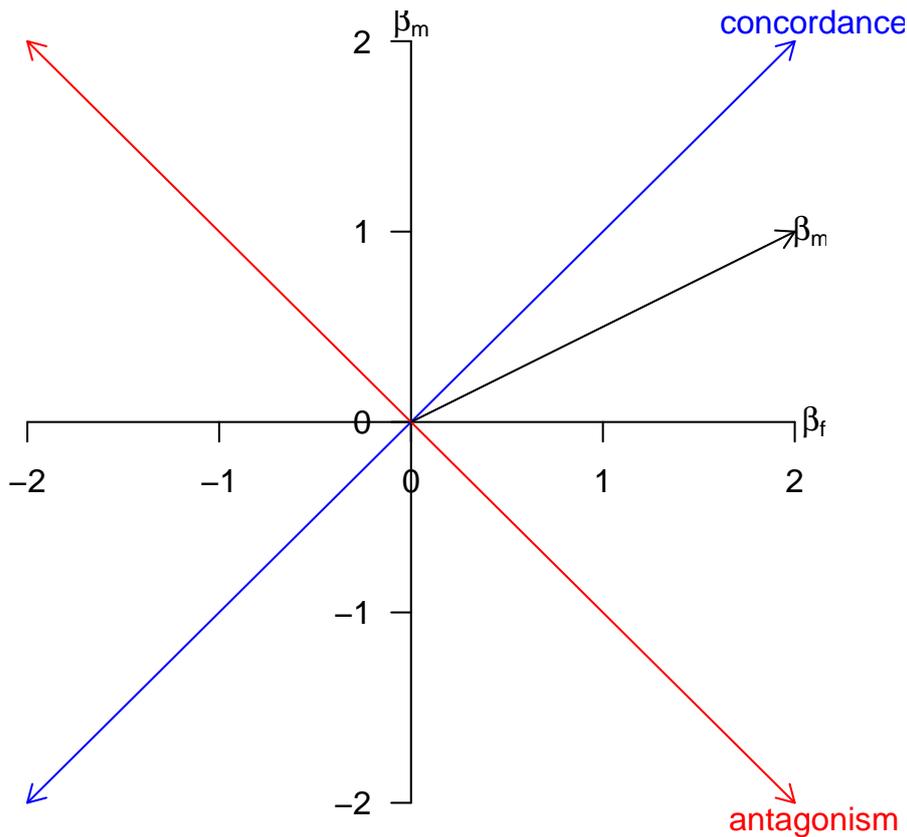
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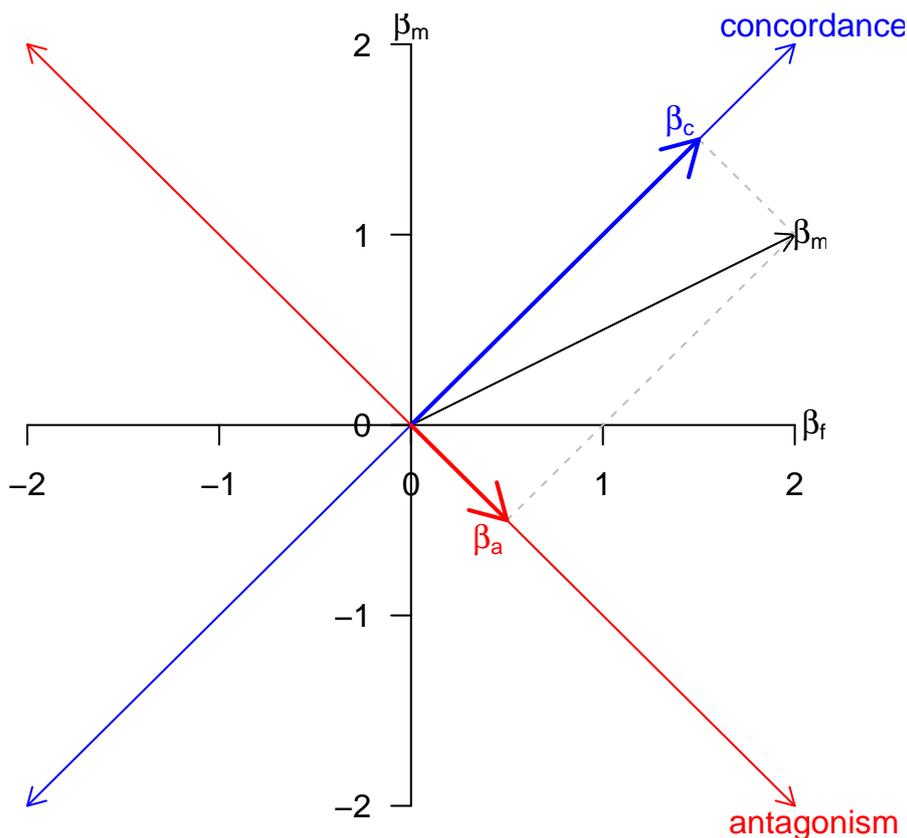
$$\boldsymbol{\beta}_{ac} = \begin{bmatrix} \beta_a \\ \beta_c \end{bmatrix} = \mathbf{Q}_{mf \to ca} \begin{bmatrix} \beta_m \\ \beta_f \end{bmatrix}$$

where

$$\mathbf{Q}_{mf \to ca} = \frac{1}{2} \begin{bmatrix} \mathbf{I} & \mathbf{I} \\ \mathbf{I} & -\mathbf{I} \end{bmatrix}$$

Cheng & Houle's reparameterisation

This reparameterisation has a gratifying
$evolution = f(genetics, \ selection)$ justification.

$$\begin{bmatrix} \Delta\bar{\mathbf{z}}_c \\ \Delta\bar{\mathbf{z}}_a \end{bmatrix} = \begin{bmatrix} \mathbf{G}_c & \mathbf{G}_{ca} \\ \mathbf{G}_{ca}^t & \mathbf{G}_a \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}_c \\ \boldsymbol{\beta}_a \end{bmatrix}$$

- $\boldsymbol{\beta}_m$, $\boldsymbol{\beta}_f$: sex-specific selection gradients
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Estimates of SA selection and genetic variation

Genetic correlation between the sexes

Sex-specific selection gradients
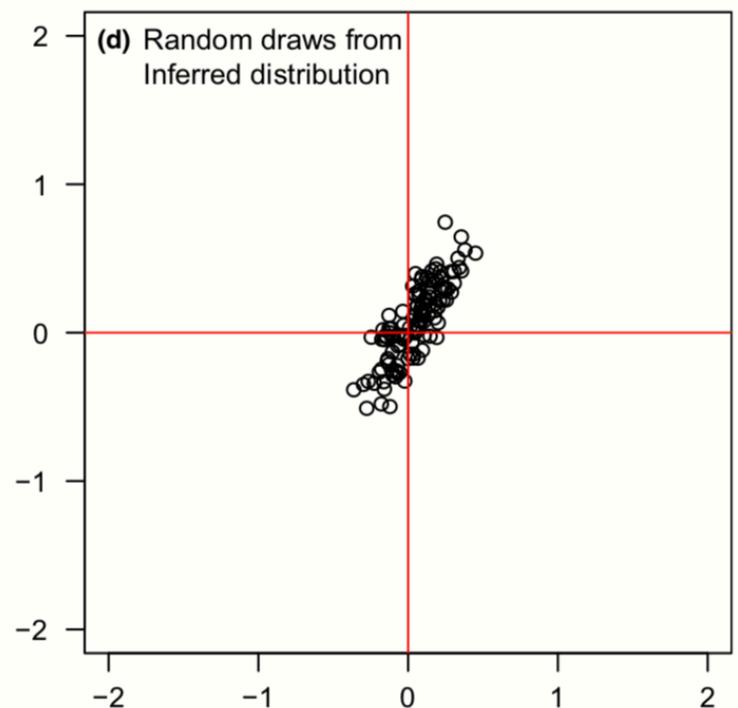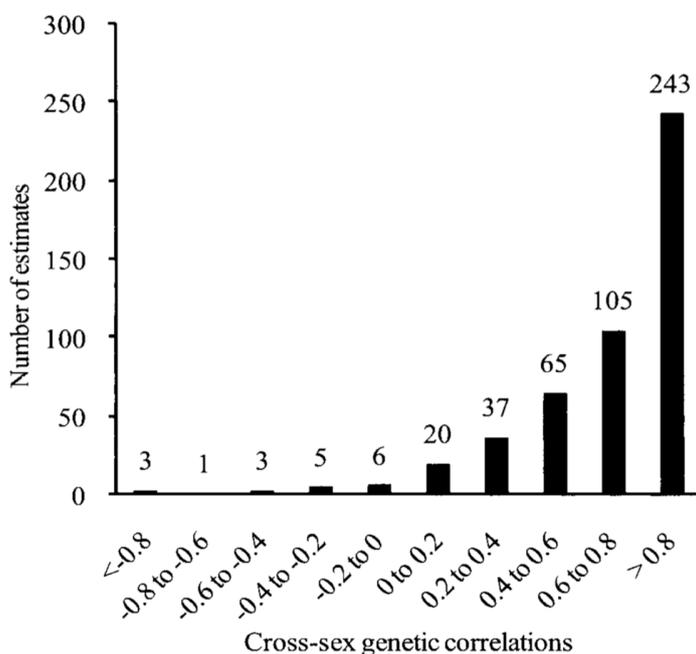
Lande equation for an age-structured population

Any given projection matrix, $\mathbf{A}$:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$$

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & f_1 s_1 & f_2 s_1 & \cdots \\ s_2 & 0 & 0 & \\ 0 & s_3 & 0 & \\ \vdots & & & \ddots \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \end{bmatrix}_t$$

defines a rate of increase λ.

$$\Delta \bar{\mathbf{z}} = \frac{1}{\lambda} \mathbf{G} \nabla | \boldsymbol{\lambda}$$

at the stable age distribution, where

$$\nabla | \boldsymbol{\lambda} = \begin{bmatrix} \frac{\partial \lambda}{\partial \bar{z}_1} \\ \frac{\partial \lambda}{\partial \bar{z}_2} \\ \vdots \end{bmatrix}$$

Age-structured Lande equation example

P and G matrices for deer life history traits
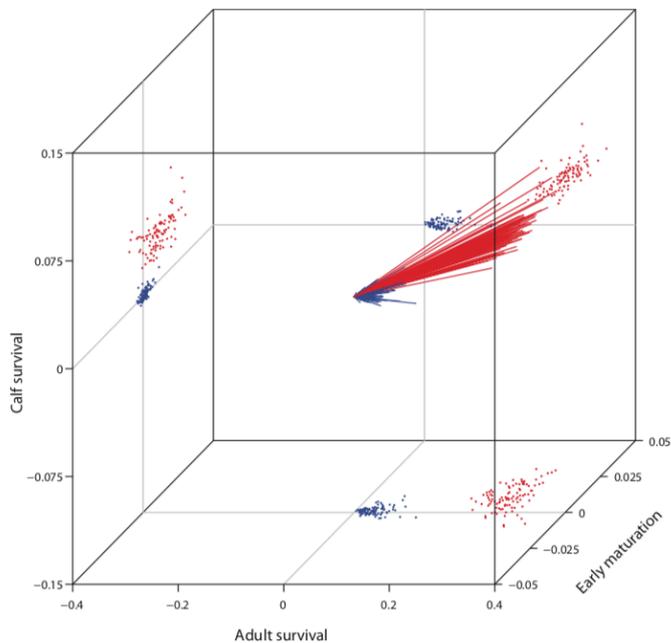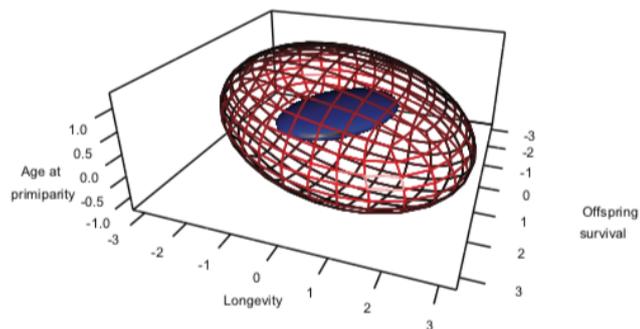
Predicted life history evolution from the age-structured Lande equation
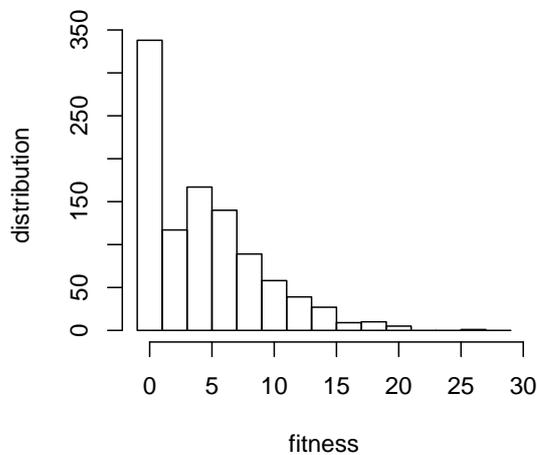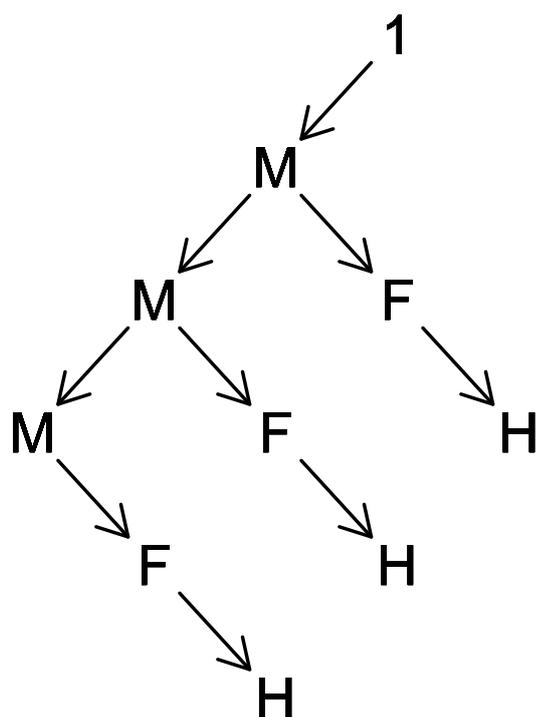
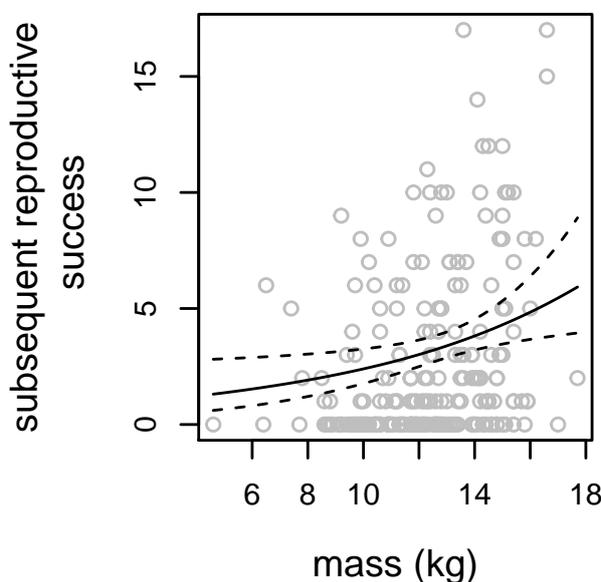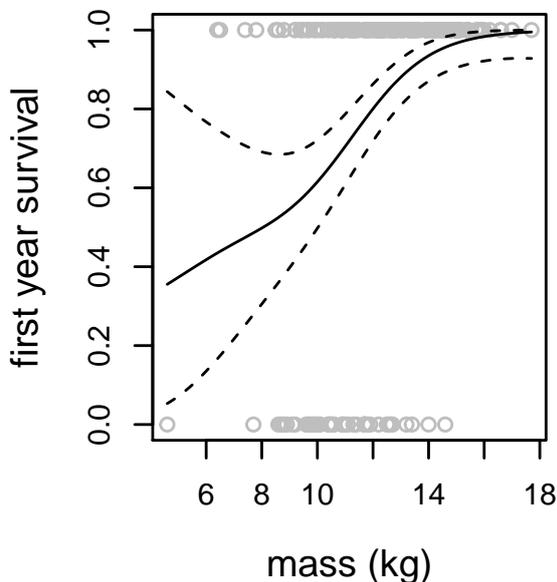# Aster models

do your own aster models
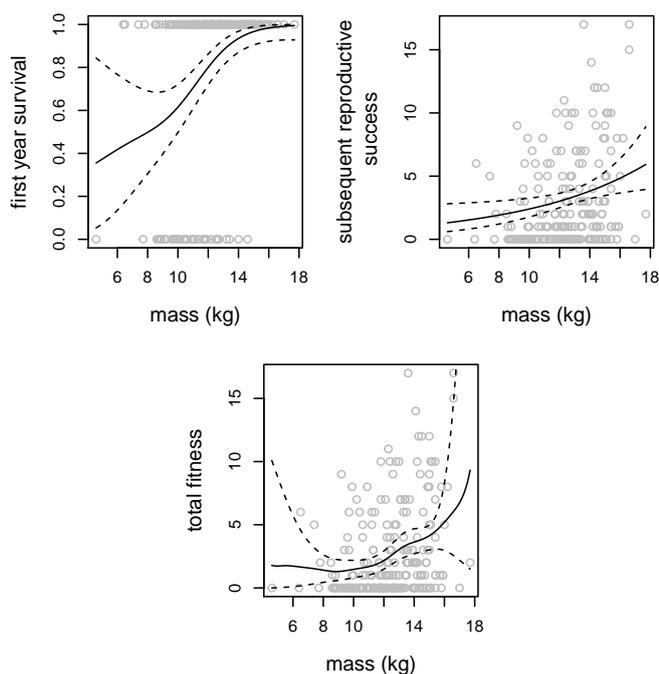
Option 1: study the known mechanics of episodes of selection
Option 2 (not exclusive of 1): combine estimates as appropriate
to your system and question

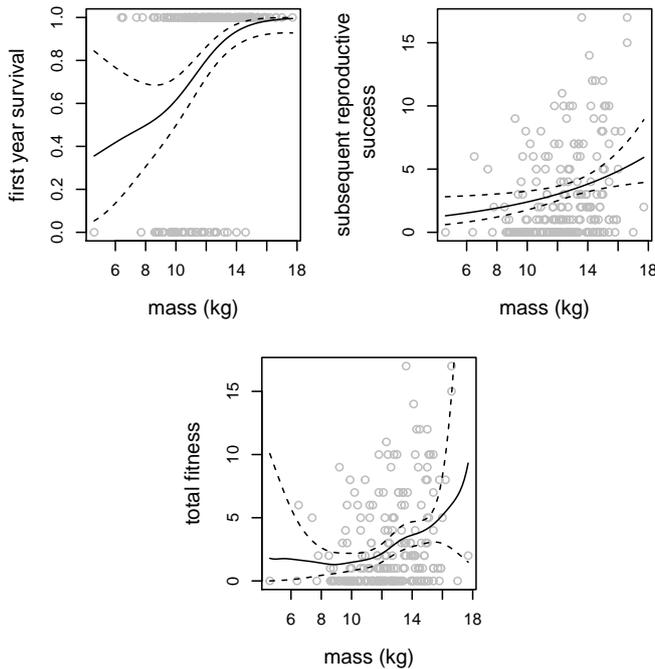$$E[W|z] = E[S|z] \cdot E[LRS|z, S == 1]$$

Do your own joint fitness models

β from average derivative of the total fitness function:

$$\beta_{average\ derivative} = 0.187(0.089 - 0.337)$$
(bootstrap CI)

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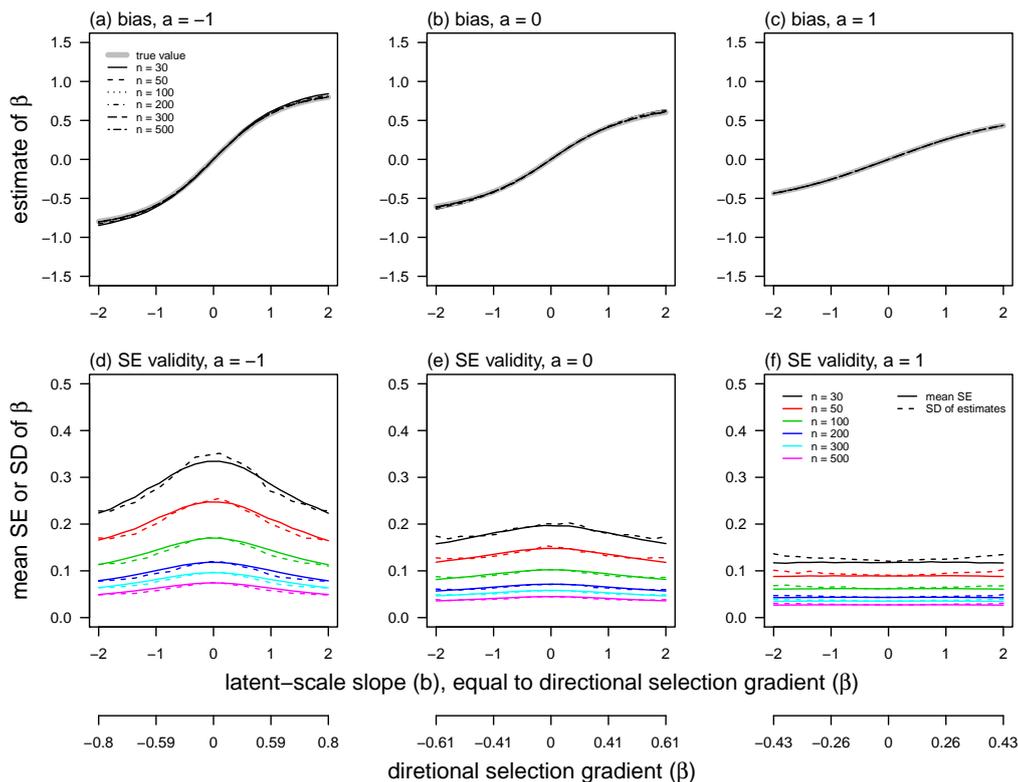$\beta_{average\ derivative} = 0.187(0.089 - 0.337)$ (bootstrap CI)

β from standard OLS analysis:
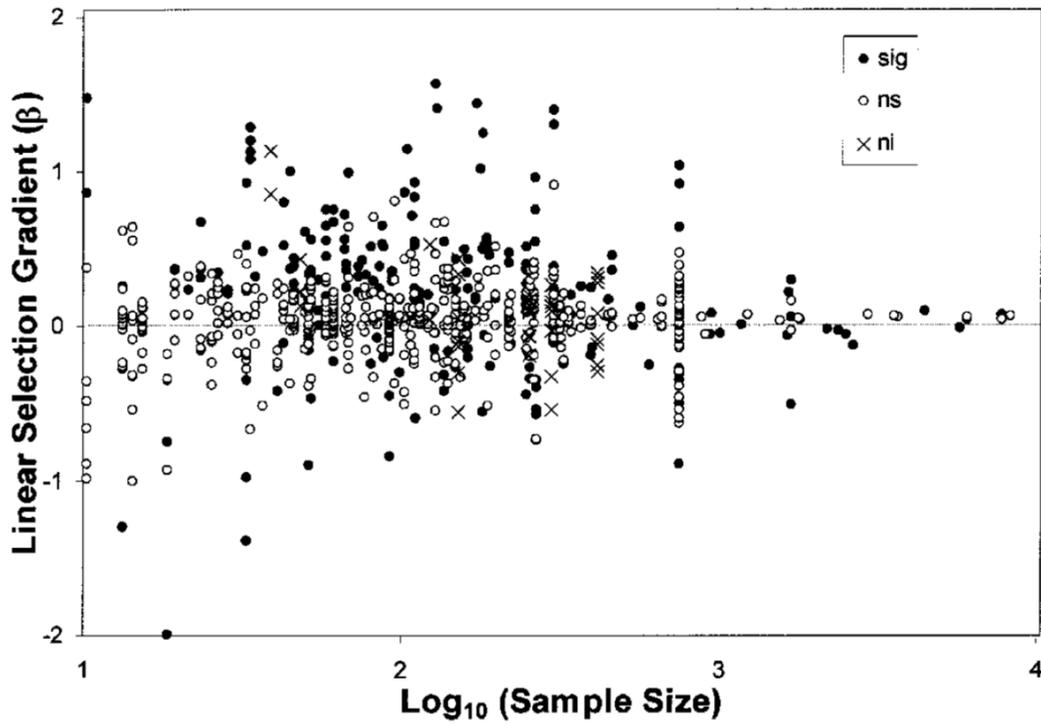
$\beta_{ols} = 0.184(0.105 - 0.263)$ (Wald CI)

Do (Can) we need to do better than OLS?
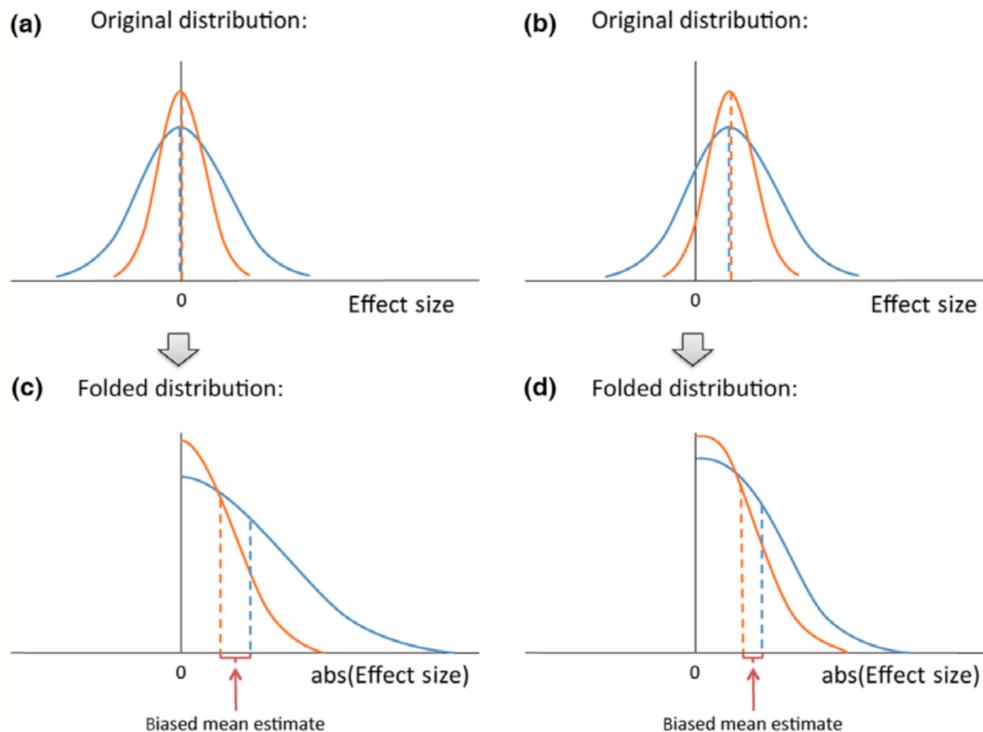
How strong is selection?

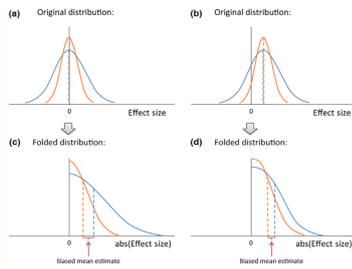▶ Mean of $|\hat{\beta}| = 0.21$ (variance standardised)

How strong is selection?

(a) Original distribution:

(b) Original distribution:

(c) Folded distribution:

(d) Folded distribution:

How strong is selection?

$$\hat{\beta}_i = \mu_\beta + m_i + e_i$$

- ▶ $\hat{\beta}_i$ selection gradient estimates
- ▶ model for statistical noise: $m_i \sim N(0, SE[\hat{\beta}_i]^2)$
- ▶ mean selection gradient: μ_β
- ▶ variation in selection: $e_i \sim N(0, \sigma_e^2)$

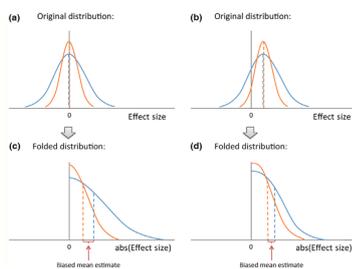# How strong is selection?

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Average magnitude of selection:

$$E[|\beta|] = E_{folded\ normal}(m = \mu_\beta, s^2 = \sigma_e^2)$$

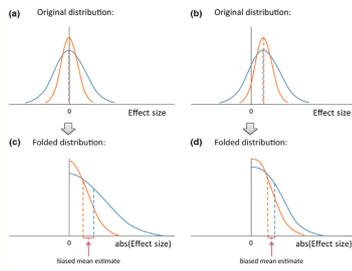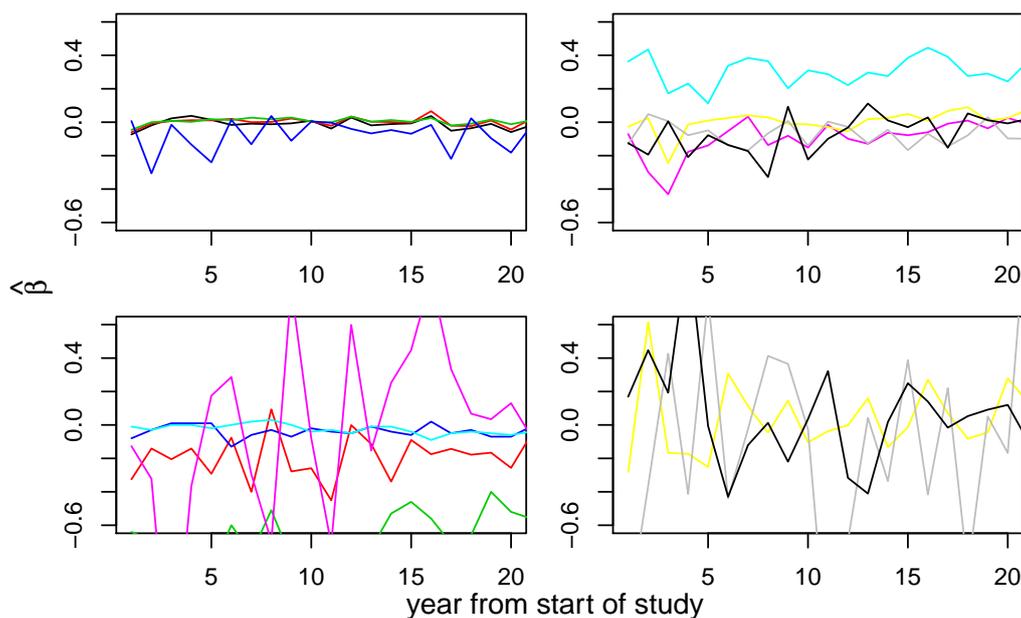# How strong is selection?

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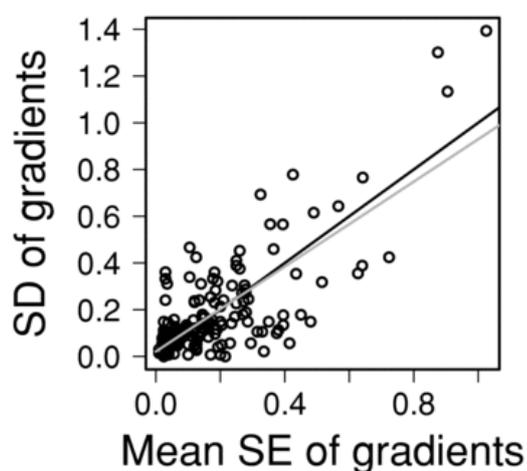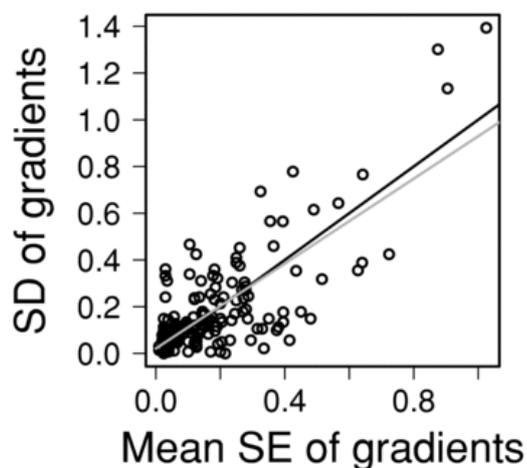

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$$E[|\beta|] = E_{folded\ normal}(m = \mu_\beta, s^2 = \sigma_e^2) = 0.10\ (0.09 - 0.12)$$

How variable is selection?

My (with Jarrod Hadfield) re-analysis

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$$\hat{\beta}_{ij} = \mu + u_j + m_{ij} + e_{ij}$$

- ▶ $\hat{\beta}_{ij}$: individual estimates of β
- ▶ variation among studies:
  $u_j \sim N(0, \sigma_u^2)$
- ▶ statistical noise:
  $m_{ij} \sim N(0, SE[\hat{\beta}_{ij}]^2)$
- ▶ variation within studies:
  $e_{ij} \sim N(0, \sigma_e^2)$
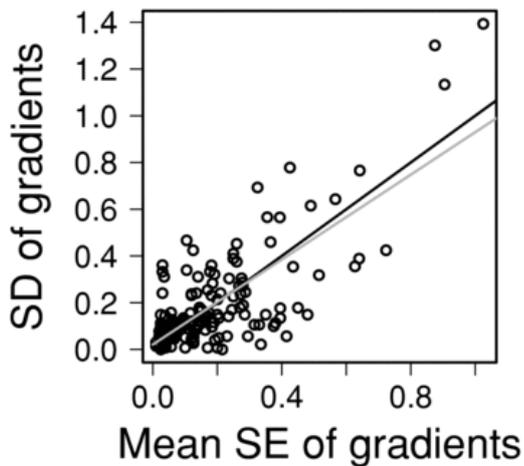
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How much does selection bounce around?

$$repeatability = \frac{\sigma_u^2}{\sigma_u^2 + \sigma_e^2}$$

My (with Jarrod Hadfield) re-analysis

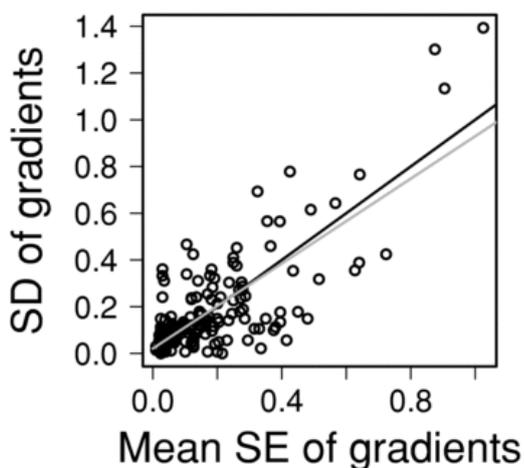$$\hat{\beta}_{ij} = \mu + u_j + m_{ij} + e_{ij}$$

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How much does selection bounce around?

$$repeatability = \frac{\sigma_u^2}{\sigma_u^2 + \sigma_e^2} = 0.88 \ (0.82 - 0.91)$$

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- ▶ Thank you!
- ▶ Back to the practicals
  - ▶ should feel free to re-assort (disassortatively!) according to `R` confidence!

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  - ▶ should feel free to re-assort (disassortatively!) according to `R` confidence!
- ▶ We've now been through a lot together!
  - ▶ no way to remember all the details
  - ▶ principles matter: e.g., the difficult issue of standardisation and judging the strength of selection
  - ▶ distrust biostats dogma
  - ▶ stats-on-stats is dangerous
  - ▶ most key concepts here are greatly elaborated in Walsh and Lynch 2018