Response to selection

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Response to selection

• Interest is in:

• Response in mean level of trait in each environment

• Response in environmental sensitivity
Environmental Sensitivity

- Change of mean trait value of a genotype with a change in environment

\[ s = \mu_H - \mu_L \]

Scaled response in sensitivity:
\[ s^* = \frac{\mu_H^* - \mu_L^*}{\mu_H - \mu_L} \] (WL38.5)

- A measure of sensitivity: \( s = \mu_H - \mu_L \)
- Scaled response in sensitivity: \( s^* = \frac{\mu_H^* - \mu_L^*}{\mu_H - \mu_L} \)

\( s^* \) = relative response in the difference
\( s^* > 1 \) → increase in sensitivity due to selection
\( s^* < 1 \) → decrease in sensitivity due to selection

If \( E \) is quantitative (i.e. a value):
\[ n = \frac{\mu_H - \mu_L}{E_H - E_L} = \text{Slope of the reaction norm} \]
Trends observed in response

- Jinks-Connoly rule
  - Antagonist selection reduces sensitivity
  
  ![Graph showing antagonistic selection reduces sensitivity]

- Synergistic selection increases sensitivity
  
  ![Graph showing synergistic selection increases sensitivity]

- A trend, not an absolute truth
  - Falconer’s rule:
    - Sensitivity is less after antagonistic than after synergistic selection: holds more generally

Conclusion

With GxE-interaction, the environment and direction of selection matter for the change in environmental sensitivity
Models for GxE-interaction:

Character state model
(multitrait model)

Reaction norm model
(random regression model)

Character State Model (Via and Lande)

- Multitrait approach (Falconer)
  - Population is split into discrete environments
  - Phenotype and genotype in each environment “is” a trait.
  - The different traits (environments) may have different genetic means, genetic (co)variances, and there is a genetic correlation between traits in different environments
  - Vector of breeding values in each environment: \( \mathbf{g}_i' = [g_{1,i}, g_{2,i}, \ldots, g_{m,i}] \)
  - \( i \) = individual, \( m \) = no. of environments

- Applicable when you can split the environment into discrete classes
  - Captures all the GxE-interaction between these environments, in contrast to the reaction norm model.
  - Examples: purebreds vs crossbreds, temperate vs tropical climates, location, herd
Character state model: example

Yield of dairy cows in New Zealand vs. Australia

Two traits:
- Milk-yield in Australia
- Milk-yield in New Zealand

Key parameter:
Genetic correlation between both traits \( r_g \)
\[ r_g < 1 \rightarrow \text{GxE-interaction} \]

Reaction norm model

- Trait expression is on a continuous environmental scale (x)
  - BV and genetic parameters change gradually along the environmental scale
  - At different locations on the environmental scale, traits may have different means and (co)variances, and there is a genetic correlation between trait expression at different points of the environmental scale

- Applicable when you have a continuous environmental variable that explains (part of) the GxE interaction
  - Temperature, average herd milk yield, HYS effect, Pasture contamination

- Note: Captures only the part of the GxE-interaction due to the environmental variable (the x-axis).

- Advantage RN-model:
  - Explicit model for environmental sensitivity (slope)
  - Prediction in other (non-recorded) environments.
Reaction norm model: basics

- Breeding value is a function of the environment \( \rightarrow g(x) \)
  - For example \( g_i(x) = g_{0,i} + g_{1,i}x + g_{2,i}x^2 + g_{3,i}x^3 + \ldots \)
  - \( g_{0,i} \) = breeding values of individual \( i \) for environment \( x \)
  - \( x = \) value of the environment
  - \( g_{0,i}, g_{1,i}, g_{2,i}, \ldots \) are breeding values of individual \( i \)

- Vector notation: \( \mathbf{g}_i(x) = g_{0,i} + g_{1,i}x + g_{2,i}x^2 + g_{3,i}x^3 + \ldots \)

- \( \mathbf{g}_i(x) = \) breeding value of individual \( i \) for environment \( x \)

- Phenotype
  - Analogy of \( P = G + E \rightarrow P(x) = g(x) + e \)
  - Expected phenotype equals breeding value, \( E[e] = 0 \)
  - Breeding value predicts the phenotype

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Reaction norm model: example

Growth rate (GR) and worm egg pasture contamination (PC)

Idea:
- Sheep grow slower when pasture contamination is higher
- But not all sheep are equally sensitive to PC (=GxE)

Linear reaction norm:
\[
Y_{i,flock} = \text{HYS} + g_{0,i} + g_{1,i} PC_{flock} + e
\]

- \( g_{0,i} = \) breeding value for level
- \( g_{1,i} = \) breeding value for slope (with respect to PC)

Breeding value:
\[
\mathbf{g}_i(PC) = \begin{bmatrix} g_{0,i} \\ g_{1,i} \end{bmatrix} \mathbf{x} = \begin{bmatrix} 1 \\ PC_{flock} \end{bmatrix}
\]

\[
\mathbf{g}_i(PC) = \begin{bmatrix} g_{0,i} \\ g_{1,i} \end{bmatrix} \mathbf{x} = \begin{bmatrix} 1 \\ PC_{flock} \end{bmatrix} = g_{0,i} + g_{1,i} PC_{flock}
\]
The linear reaction norm

Breeding value: \( g_i(x) = g_{0,i} + g_{1,i} x \)

Two BV \( \rightarrow \) Three genetic parameters:
- Genetic variance in level: \( \text{var}(g_0) \)
- Genetic variance in slope: \( \text{var}(g_1) \)
- Genetic correlation between level and slope: \( r_{g01} \)

Q: What does the correlation between level and slope mean?

The correlation between level and slope

Linear reaction norm: \( g_i(x) = g_{0,i} + g_{1,i} x \)

Genetic correlation level-slope: \( r_{g01} = \text{corr}(g_0, g_1) \)

\( r_{g01} \) indicates whether animals that have better breeding values for level are also more \( (r_{g01}>0) \) or less \( (r_{g01}<0) \) environmentally sensitive

Indicates whether selection for level will increase or decrease environmental sensitivity

However:
RN: Meaning of the correlation between level and slope

- **Message:** Correlation depends on the location of the intercept on the environmental scale (i.e. where \( x = 0 \)).
  - General RN: \( g(x) = g_0 + g_1 x \), where \( g_0 \) and \( g_1 \) are correlated with \( r_{g01} \)
- **Problem:** Can we shift the intercept so that \( r_{g01} \) becomes zero?
  - Note: intercept is value of \( g(x) \) at \( x = 0 \). Hence, find \( x \) where \( g(x) \) is independent of \( g_1 \), and put the intercept there.
  - \( \text{Cov}[g(x), g_1] = \text{Cov}(g_0 + g_1 x, g_1) = 0 \)

\[
x = -r_{g01} \frac{\sigma_{g0}}{\sigma_{g1}}
\]

\( r_{g01} > 0 \rightarrow \text{shift intercept to the left (down)} \)
\( r_{g01} < 0 \rightarrow \text{shift intercept to the right (up)} \)

**Conclusion:** In itself, the correlation between level and slope is meaningless

*Suggested convention:* define the intercept in the mean environment

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**Modelling response to selection**
Selection Index Theory

- How to predict response to selection?
  - Selection is usually on an index of EBV
  - But we don’t have “genetic parameters” of EBV
  - However, EBV are predicted from phenotypes

- Hence, to predict response, we can mimic selection on EBV by selection on phenotypes

- Method: regress true breeding values on phenotypes

Selection index: response to selection (R)

- Selection is on an index: $I = b_1 P_1 + b_2 P_2 + .. + b_n P_n = b' p$
  - $p$ are phenotypes, $b$ are weights.
  - We can use any $b$ or find the optimum $b$.

- Interest is in response to selection in multiple traits
  - $g' = [g_1, g_2, ..., g_m]$, a vector of breeding values

- Regression of $g$ on $I$ yields an expression for response:
  - Approximate normality is assumed

\[
R = \begin{bmatrix}
\Delta P_1 \\
\Delta P_2 \\
\vdots \\
\Delta P_m
\end{bmatrix} = G' b \frac{i}{\sigma_I}
\]

$G = \text{cov}(p, g)$ Phenotypes in rows, breeding values in columns

$\sigma_I = \text{standard deviation of the index}$

$i = \text{selection intensity}$
Response to Selection in the Character-state Model

Multi-environment selection with GxE

Selection may occur in multiple flocks
- GxE between flocks
- Mixing of flocks: exchange of rams

Full model is tedious → Illustration for 2-flock system
Character State Model: Response to Selection

• Analogy of the multitrait model
  – Two environments, A and B
    • Two traits, trait 1 expressed in A, trait 2 expressed in B
    • Each individual has a BV for both traits, but only one of those BV is expressed
  – Two groups of individuals: individuals in A, and individuals in B
    • Different (genetic) means between groups: \( \bar{x}_1, \bar{x}_2, \bar{y}_1, \bar{y}_2 \)

• Response to selection: 2 steps
  – Step 1: Calculate genetic level of selected parents for both traits in each environment
  – Step 2: Follow the flow of individuals/genes between environments
    • Contribution of each environment to selected individuals
    • Contribution of selected individuals to each environment (mixing)

Step 1: Genetic selection differential per environment

• Selection of individuals that are in Environment A
  – Selection criterion for environment A → \( I_A = b_{i,A} P_{i,A} + b_{j,A} P_{j,A} + \ldots \)
  – Intensity of selection for environment A → \( i_A \)
  – Covariances between \( P_A \) and true breeding values \( g_1 \) and \( g_2 \) → \( G_A \)
  – Response in both traits → vector \( \Delta \bar{g}_A \)

Genetic selection differential:
\[
\Delta \bar{g}_A = \begin{bmatrix} \Delta \bar{g}_{A,1} \\ \Delta \bar{g}_{A,2} \end{bmatrix} = G_A' \hat{b}_A \frac{i_A}{\sigma I_A}
\]

For environment B, the equation is analogous
Step 1: Genetic mean of selected in each environment

Genetic mean of selected indiv. in environment A:

$$\bar{g}_{A, selected} = \begin{bmatrix} \bar{g}_{1,A, selected} \\ \bar{g}_{2,A, selected} \end{bmatrix} = \begin{bmatrix} \bar{g}_{1,A} \\ \bar{g}_{2,A} \end{bmatrix} + \Delta \bar{g}_{1,A}$$

Genetic mean of selected indiv. in environment B:

$$\bar{g}_{B, selected} = \begin{bmatrix} \bar{g}_{1,B, selected} \\ \bar{g}_{2,B, selected} \end{bmatrix} = \begin{bmatrix} \bar{g}_{1,B} \\ \bar{g}_{2,B} \end{bmatrix} + \Delta \bar{g}_{1,B}$$

Step 2: Flow of animals → genetic mean next generation

Breeding value offspring is mean of its parents:

$$\bar{g}_{A,t+1} = f_{A\rightarrow A} \bar{g}_{A, selected} + f_{B\rightarrow A} \bar{g}_{B, selected}$$

$$\begin{bmatrix} \bar{g}_{A,1,t+1} \\ \bar{g}_{A,2,t+1} \end{bmatrix} = f_{A\rightarrow A} \begin{bmatrix} \bar{g}_{A,1, selected} \\ \bar{g}_{A,2, selected} \end{bmatrix} + f_{B\rightarrow A} \begin{bmatrix} \bar{g}_{B,1, selected} \\ \bar{g}_{B,2, selected} \end{bmatrix}$$

$$f_{A\rightarrow A} + f_{B\rightarrow A} = 1$$

$$f_{A\rightarrow A} = \text{contribution of selected from A to offspring in A}$$

$$f_{B\rightarrow A} = \text{contribution of selected from B to offspring in A}$$
Simplest example: correlated response

- Mass selection in environment A, no selection in B
  - E.g. breeding nucleus and production environment
  - Flow of animals: $f_{B\rightarrow A} = 0, f_{B\rightarrow B} = 0, f_{A\rightarrow A} = 1, f_{A\rightarrow B} = 1$

Multi-environment selection with GxE

Selection in environment A

Producers in B get their rams from A

→ Response in both A and B
Simplest example: correlated response

- Mass selection in environment A, no selection in B
  - E.g. breeding nucleus and production environment
  - Flow of animals: \( f_{B \rightarrow A} = 0 \), \( f_{B \rightarrow B} = 0 \), \( f_{A \rightarrow A} = 1 \), \( f_{A \rightarrow B} = 1 \)
  - Interest in response in both environments: two traits

Suppose starting level is equal (say zero)

\[
\begin{pmatrix}
\bar{g}_{A,1,selected} \\
\bar{g}_{A,2,selected}
\end{pmatrix}
= f_{A \rightarrow A}
\begin{pmatrix}
\bar{g}_{A,1,selected} \\
\bar{g}_{A,2,selected}
\end{pmatrix}
+ f_{B \rightarrow A}
\begin{pmatrix}
\bar{g}_{B,1,selected} \\
\bar{g}_{B,2,selected}
\end{pmatrix}
= 1 \times
\begin{pmatrix}
\bar{g}_{A,1,selected} \\
\bar{g}_{A,2,selected}
\end{pmatrix}
+ 0
\]

\[
\begin{pmatrix}
\bar{g}_{1,A,selected} \\
\bar{g}_{2,A,selected}
\end{pmatrix}
= \begin{pmatrix}
\bar{g}_{1,1} \\
\bar{g}_{2,1}
\end{pmatrix}
+ \Delta \begin{pmatrix}
\bar{g}_{1,1} \\
\bar{g}_{2,1}
\end{pmatrix}
\]

Hence: We need selection differentials for both traits due to selection in environment A

Simplest application: correlated response

Selection differentials:

\[
\begin{pmatrix}
\Delta \bar{g}_{A,1,1} \\
\Delta \bar{g}_{A,2,1}
\end{pmatrix}
= G_A b_A \frac{f_A}{\sigma_A}
\]

Mass selection in environment A
  - Selection criterion: \( I = P_i (=1 \times P_i) \)
  - \( b = 1; \sigma_i = \sigma_{P_i} \)

Response in BV in environment B is the same (\( f_{A \rightarrow B} = 1 \), \( f_{B \rightarrow B} = 0 \))

(see e.g. Falconer & Mackaybook)
Simplest example: correlated response

- $h^2_1 = 0.30$, $h^2_2 = 0.25$, $\sigma^2_{p1} = 1$, $\sigma^2_{p2} = 1.33$, $r_g = 0.84$, selected proportion in env. $A = 20\% \rightarrow i_1 = 1.4$

\[
\frac{\Delta \mu_{A,1}}{\Delta \mu_{A,2}} = \frac{i_1 h_i \sigma_{g,1}}{i_1 h_i \sigma_{g,2}} = \frac{1.4 \times \sqrt{0.3} \times \sqrt{0.3 \times 1}}{1.4 \times \sqrt{0.3} \times 0.84 \times \sqrt{0.25 \times 1.33}} = 0.42 \frac{\Delta \mu_{B,1}}{\Delta \mu_{B,2}}
\]

Expressed

Question:
What does this mean for environmental sensitivity / plasticity?

Assignment 1: GxE in sheep breeding

- Breeding program for meat sheep (body weight)
  - Two flocks, one in each environment ($H_{hi}$ and $L_{lo}$)
  - Both environments have a breeding program, there is exchange of animals
  - Phenotypic means: $\mu_H = 60kg$, $\mu_L = 50kg$
  - In generation 0, both breeds are a random sample from a single breed imported from elsewhere
  - In each environment:
    - 50% of the selected parents come from the environment itself (e.g. the dams)
    - 50% come from the other environment (e.g. the sires)
  - Mass selection in both environments
    - Selected proportions in both sexes: $p_H = 20\%$, $p_L = 50\%$
    - $h^2_H = 0.4$; $h^2_L = 0.2$; $r_g = 0.7$; $\sigma_pH = 6kg$, $\sigma_pl = 5kg$,
  - Calculate the change of phenotypic means for 10 generations (e.g use Excel)
    - Consequences for environmental sensitivity?
    - Can you achieve zero change in environmental sensitivity? (using mass selection)
  - See Excelsheet “sheepbreeding GxE.xlsx”
Response to Selection in the Reaction Norm Model

$g_i(x) = g_{0,i} + g_{1,i} x$

$R(x) = \Delta g_i(x) = \Delta g_{0,i} + \Delta g_{1,i} x$

Reaction norm model: response to sel.

- Response is in the average parameters of the RN (mean values of the $g$'s)
- $\Delta g_0, \Delta g_1, \Delta g_2, \Delta g_3,...$
- Response in the $g$'s depends on the environment of selection
- Observed phenotypic response depends on the environment in which the offspring perform

$\Delta g(x)_{off} = \Delta g_0 + \Delta g_1 x_{off} + \Delta g_2 x_{off}^2 + \Delta g_3 x_{off}^3 + \ldots$

$E[\Delta g(x)_{off}] = \Delta g(x)_{off}$

$\Delta g_0 \rightarrow$ change in level
$\Delta g_1 \rightarrow$ change in slope
$\Delta g_{\geq 2} \rightarrow$ change in curvature

$\Delta g(x)$ depends on the changes in level, slope, quadratic, etc., and on the environment in which performance is expressed.
Reaction norm model: response to sel.

• Mass selection in a single environment $x_s$
  – Selection is for phenotype $P(x_s)$
  – Hence, the “index” is: $I = P(x_s) = g_0 + g_1 x_s + g_2 x_s^2 + ... + e$
  – Hence, the index weights are: $b^I = (1, x_s, x_s^2, ...)$
  • I ignore $e$ here, as it does not correlate with $g$
  – Response is in the average genetic coefficients of the reaction norm:
    $\Delta G = (\Delta g_0, \Delta g_1, \Delta g_2, ...)$

\[
\Delta G = \begin{bmatrix}
\Delta g_0 \\
\Delta g_1 \\
\vdots \\
\Delta g_n
\end{bmatrix} = G \cdot b \cdot \frac{i}{\sigma_I}
\]

where $\sigma_I = \sigma_P(x_s)$ the phenotypic standard deviation in the selection environment

Hence, selection on a reaction norm trait can be interpreted as index selection, the weights ($b$) being the powers of the environmental variable ($x$).

Reaction norm model: response to sel.

• Response to selection

\[
\Delta G = \begin{bmatrix}
\Delta g_0 \\
\Delta g_1 \\
\vdots \\
\Delta g_n
\end{bmatrix} = G \cdot b \cdot \frac{i}{\sigma_I}
\]

with $G = \text{cov}(g, g) = \text{var}(g) = \begin{bmatrix}
\sigma_{g_0}^2 & \sigma_{g_0-g_1} & \ldots & \sigma_{g_0-g_n} \\
\sigma_{g_0-g_1} & \sigma_{g_1}^2 & \ldots & \sigma_{g_1} \\
\vdots & \vdots & \ddots & \vdots \\
\sigma_{g_0-g_n} & \sigma_{g_1} & \ldots & \sigma_{g_n}^2
\end{bmatrix}$

and $b = \begin{bmatrix}
1 \\
x_s \\
x_s^2 \\
\vdots \\
x_s^n
\end{bmatrix}$ where $x_s$ is the selection environment.
Reaction norm: Example

• Linear reaction norm for milk yield, mass selection
  – Environmental variable \( x \) = mean milk yield in an environment
    • E.g. HYS = Finlay Wilkinson-regression
  – \( g(x) = g_0 + g_1x \)
    • \( \text{Var}(g_0) = 550^2; \text{Var}(g_1) = 0.05 \)
    • Meta-population mean milk yield = 7000kg
    • Genetic correlation mean milk yield and slope = -0.2

Q: How does the mean RN before selection look like?
- where to put the intercept?
- what is the mean slope?

Reaction norm: Example

• Linear reaction norm for milk yield, mass selection
  – Environmental variable = mean milk yield in an environment
    • E.g. HYS = Finlay Wilkinson-regression
  – \( g(x) = g_0 + g_1x \)
    • \( \text{Var}(g_0) = 550^2; \text{Var}(g_1) = 0.05, \text{Corr}(g_0,g_1) = -0.2 \)
    • Meta-population mean milk yield = 7000kg
  – Two environments
    • Selection environment 9000kg,
      \[
      I = P(x_s) = g_0 + g_1(9000 - 7000) + e = (1 \ 2000) \begin{pmatrix} g_0 \\ g_1 \end{pmatrix} + e
      \]
    – \( b' = (1, 2000) \)
    – \( \text{Var}(P_s) = 1308^2 \text{ kg}^2 \) (assumed given here)
    – Selected proportion = 20% \( \rightarrow i = 1.4 \)
    • Production environment 8000kg
      – \( x_{off} = (1, 1000) \)
Reaction norm: Example

\[ \Delta \mathbf{g} = \begin{bmatrix} \Delta g_0 \\ \Delta g_1 \\ \vdots \\ \Delta g_n \end{bmatrix} = \mathbf{g}' \mathbf{b} \begin{bmatrix} i \sigma_i \end{bmatrix} \]

\[ \Delta \mathbf{g} = \begin{bmatrix} \Delta g_0 \\ \Delta g_1 \\ \vdots \\ \Delta g_n \end{bmatrix} = \begin{bmatrix} \sigma^2_{g_0} & \sigma_{g_0} \sigma_{x_1} & \cdots & \sigma_{g_0} \sigma_{x_n} \\ \sigma_{g_1} \sigma_{x_1} & \sigma^2_{g_1} & \cdots & \sigma_{g_1} \sigma_{x_n} \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{g_n} \sigma_{x_1} & \sigma_{g_n} \sigma_{x_2} & \cdots & \sigma^2_{g_n} \end{bmatrix} \begin{bmatrix} i \\ \sigma_{x_1} \\ \vdots \\ \sigma_{x_n} \end{bmatrix} \]

\[ \Delta g(x_{ef}) = \Delta \mathbf{g}' \mathbf{x}_{ef} = \begin{bmatrix} 271 & 0.081 \end{bmatrix} \begin{bmatrix} 1 \\ 1000 \end{bmatrix} = 352 \text{kg} \]

\[ \Delta g(x_{e}) = \Delta \mathbf{g}' \mathbf{x}_e = \begin{bmatrix} 271 & 0.081 \end{bmatrix} \begin{bmatrix} 1 \\ 2000 \end{bmatrix} = 433 \text{kg} \]

- An increase in level (+271)
- An increase in slope (+0.081)

More response in better environments
Increased sensitivity
Despite \( r_{g0} = -0.2 \)

The Result:

Due to selection in a good environment, herds with good environments gain more, and environmental sensitivity increases.

Question: what are the consequences of simultaneous improvements in genetic merit and nutrition for environmental sensitivity of our livestock breeds?
Assignment 2: Selection for milk yield when GxE is modelled as a linear RN

- See word document: “Single trait selection on a linear reaction norm trait.docx”
- See R-code: “univariate reaction norm milk yield.R”
- Investigate:
  - Consequences of selection for environmental sensitivity
  - Effect of the selection environment