Response to selection in variance

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- Effect of mass selection on Ve
- Response to selection and breeding goal
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  - Selection experiments
- Practical
  - Mass selection
  - Information of relatives and breeding goal

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Learning outcomes

- To understand and calculate the response to mass selection in mean and variance

- To calculate economic values for mean and variance

- To understand and calculate the response to index selection in mean and variance using information of relatives

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Effect of mass selection on Ve

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Response to selection in normal cases

- Mass selection = selection on phenotype
- $\Delta a = b\Delta x = bS$
- Δa = selection response
- Δx = S= selection differential
- b = regression coefficient of Δa on $\Delta x = \frac{\text{cov(a,x)}}{\text{var(x)}} = h^2$
- $\Delta a = b\Delta x = h^2 S$
- For directional truncation selection
- $\Delta a = b\Delta x = h^2 S = ih^2 \sigma_P \rightarrow$ breeders equation
- General breeders equation: $\Delta a = ir_{IH}\sigma_a$
- r_{IH} = accuracy of selection

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Quantitative genetic model: the additive model

$$P_i = \mu + A + E = \mu + A_{m,i} + \chi\sqrt{\sigma_E^2 + A_{v,i}}$$

$$\begin{pmatrix} A_m \\ A_v \end{pmatrix} \sim N\left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \mathbf{G} \otimes \mathbf{A} \right) \qquad \mathbf{G} = \begin{bmatrix} \sigma_{A_m}^2 & \text{cov}_{A_{mv}} \\ \text{cov}_{A_{mv}} & \sigma_{A_v}^2 \end{bmatrix}$$

$$\chi \sim N(0,1)$$

$A_{m,i}$ = breeding value of i for mean
$A_{v,i}$ = breeding value of i for environmental variance

σ_E^2 = the mean environmental variance

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Single phenotype, stochastic simulations

Mulder et al. 2007; Genetics 175:1895-1910
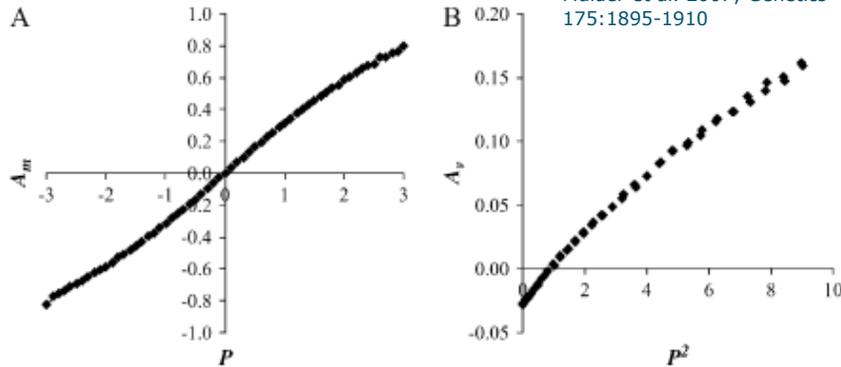
When $r_A = 0$, then

- P relates nearly linearly to A_m
- P^2 relates nearly linearly to A_v

If we want to predict A_m and A_v from a single phenotypic observation, then it makes sense to use an index of P and P^2

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Estimation of breeding values and selection responses

- Start simple: only a phenotype is available, e.g. mass selection

- $E(Am|P) \approx h^2*(P-P_{mean})$

- $E(Av|P^2) = b * (P^2 - P^2_{mean})$

Mulder et al. 2007; Genetics 175:1895-1910

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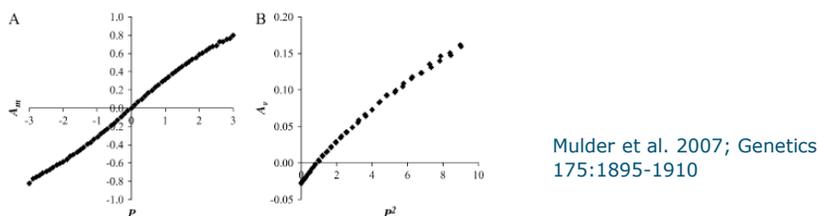
Single phenotype, selection index with P and P^2

Info: $x_1 = P - \mu, \quad x_2 = (P-\mu)^2 - \overline{(P-\mu)^2}$

$$\mathbf{x} = \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} P - \mu \\ (P-\mu)^2 - \overline{(P-\mu)^2} \end{bmatrix}$$

Index: $\hat{A}_m = b_{m,1}(P-\mu) + b_{m,2}\left[(P-\mu)^2 - \overline{(P-\mu)^2} \right]$

$$\hat{A}_v = b_{v,1}(P-\mu) + b_{v,2}\left[(P-\mu)^2 - \overline{(P-\mu)^2} \right]$$

Use both info sources for both traits, because A_m and A_v can be correlated

Selection index in matrix-vector notation

$$\hat{A}_m = \begin{bmatrix} b_{m,1} & b_{m,2} \end{bmatrix} \mathbf{x} = \mathbf{b}_m' \mathbf{x}$$
$$\hat{A}_v = \begin{bmatrix} b_{v,1} & b_{v,2} \end{bmatrix} \mathbf{x} = \mathbf{b}_v' \mathbf{x}$$

$$\hat{\mathbf{a}} = \begin{bmatrix} \hat{A}_m \\ \hat{A}_v \end{bmatrix} = \begin{bmatrix} b_{m,1} & b_{m,2} \\ b_{v,1} & b_{v,2} \end{bmatrix} \begin{bmatrix} P - \mu \\ (P-\mu)^2 - \overline{(P-\mu)^2} \end{bmatrix} = \mathbf{B}'\mathbf{x}$$

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Mulder et al. 2007; Genetics 175:1895-1910

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Single phenotype, selection index with P and P^2 = multiple regression

- Solve the index weights
  - $\mathbf{B} = \mathbf{P}^{-1}\mathbf{G}$, $\mathbf{P} = Var(\mathbf{x})$, $\mathbf{G} = Cov(\mathbf{x},\mathbf{a})$
  - Use moments of the normal distribution $\rightarrow$

$$\mathbf{P} = Var(\mathbf{x}) = \begin{bmatrix} \sigma_P^2 & 3\sigma_{A_{mv}} \\ 3\sigma_{A_{mv}} & 2\sigma_P^4 + 3\sigma_{A_v}^2 \end{bmatrix}$$

$$\mathbf{G} = Cov(\mathbf{x},\mathbf{a}) = \begin{bmatrix} Cov(x_1, A_m) & Cov(x_1, A_v) \\ Cov(x_2, A_m) & Cov(x_2, A_v) \end{bmatrix}$$

$$= \begin{bmatrix} \sigma_{A_m}^2 & \sigma_{A_{mv}} \\ \sigma_{A_{mv}} & \sigma_{A_v}^2 \end{bmatrix}$$

Mulder et al. 2007; Genetics 175:1895-1910

- This allows you to estimate breeding values for mean and variance when you know the phenotype of the individual
- From those selection index equations, you can also derive the accuracy for each trait

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Monte Carlo simulation

- To evaluate goodness of fit

$$h_m^2 = 0.3 \qquad \sigma_P^2 = 1 \qquad \sigma_{Av}^2 = 0.05 \qquad r_A = 0.5$$

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Mulder et al. 2007; Genetics
175:1895-1910

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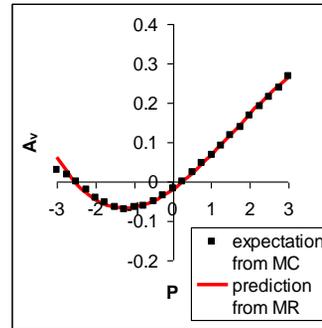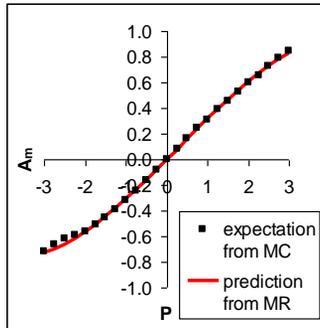
Intermezzo, The Moment Generating Function (MGF)

- The MGF is a function that allows you to derive "moments" of distributions
- First moment: $E(X)$ = mean
- Second moment: $E(X^2)$
    - Variance = $E(X^2) - \text{mean}^2$
- n^{th} moment: $E(X^n)$
- Really handy for derivations of variances and covariances
- For the nth moment:
    - Take the nth derivative of $M_X(t)$ with respect to t
    - Calculate its value for $t = 0$

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$$E(X^n) = M_X^n(t=0) = \frac{d^n M_X}{dt^n}(t=0)$$

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Moments of the normal distribution

Or, if you don't like derivatives, look-up the moments at Wikipedia

Number	Raw moment	Central moment
0	1	1
1	μ	0
2	$\mu^2 + \sigma^2$	σ^2
3	$\mu^3 + 3\mu\sigma^2$	0
4	$\mu^4 + 6\mu^2\sigma^2 + 3\sigma^4$	$3\sigma^4$
5	$\mu^5 + 10\mu^3\sigma^2 + 15\mu\sigma^4$	0
6	$\mu^6 + 15\mu^4\sigma^2 + 45\mu^2\sigma^4 + 15\sigma^6$	$15\sigma^6$
7	$\mu^7 + 21\mu^5\sigma^2 + 105\mu^3\sigma^4 + 105\mu\sigma^6$	0
8	$\mu^8 + 28\mu^6\sigma^2 + 210\mu^4\sigma^4 + 420\mu^2\sigma^6 + 105\sigma^8$	$105\sigma^8$

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Those things are used in the derivations in Mulder et al.

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Single phenotype, selection index with P and P^2

- Response to selection in mean and variance
    - $\mathbf{a} = \mathbf{B}'\mathbf{x} \rightarrow \Delta\mathbf{a} = \mathbf{B}'\Delta\mathbf{x}$
    - If you know the selection index weights in **B**, and the selection differentials in **x**, you can calculate response
- **Directional truncation selection on P**
    - Selection differentials in mean and variance (e.g. Tallis, 1961)

$$\Delta x_1 = \Delta\overline{P} = i\sigma_P$$

Selection intensity for the variance

$$\Delta x_2 = \Delta\overline{(P-\mu)^2} - \sigma_P^2 = \widehat{(ix)}\sigma_P^2$$

where x is the standardized truncation point

Selection for the mean also generates a positive selection differential in the variance!

Directional truncation selection
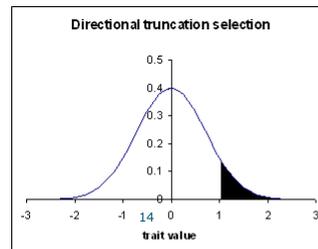
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Response to directional mass selection

$$h_m^2 = 0.3 \qquad \sigma_P^2 = 1 \qquad \sigma_{Av}^2 = 0.05 \qquad r_A = 0$$

p	ΔA_m	ΔA_v	σ_E^2	Ratio $\Delta A_v / \Delta A_m$
20%	0.42	0.03	0.73	0.06
5%	0.60	0.08	0.78	0.13
1%	0.73	0.14	0.84	0.20
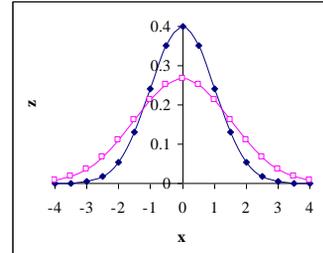
Animals with larger variance have larger probability of selection
→ Directional mass selection increases the environmental variance

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Mulder et al. 2007; Genetics 175:1895-1910

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Single phenotype, selection index with P and P²

- Can we increase uniformity using info on a single phenotype?
- Try **stabilizing selection**
- Again we can use $\Delta \mathbf{a} = \mathbf{B}' \Delta \mathbf{x}$

$$\Delta x_1 = \Delta \overline{P} = 0$$
$$\Delta x_2 = \Delta \overline{(P - \mu)^2} = \left[1 - 2 p^* i^* x^* / (1 - 2 p^*) \right] \sigma_P^2$$
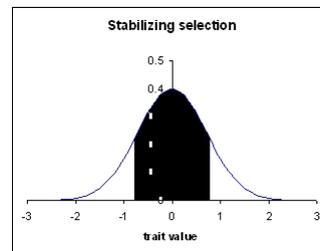
where p* is the proportion in one of the tails

Mulder et al. 2007; Genetics 175:1895-1910

Doing those calculations tells us whether we can select for uniformity by taking a group of average animals

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Single phenotype, selection index with P and P²

- What selection differentials are feasible for P² ?

Standardized selection differentials of $\overline{P_s^2}$ for directional, stabilizing, and disruptive selection by truncation on a normal distribution corrected for the expectation of P^2 (= 1) for different selected proportions (p)

	Selected proportion (p)						
Type of selection	0.80	0.40	0.20	0.10	0.05	0.01	0.001
Directional	−0.29	0.24	1.18	2.25	3.39	6.20	10.41
Stabilizing	−0.56	−0.91	−0.98	−0.99	−1.00	−1.00	−1.00
Disruptive	0.24	1.18	2.25	3.39	4.58	7.45	11.70

You can select strongly for greater P², but not for smaller P² ☹

The selection differential limits the potential to reduce variability with mass selection. Stabilizing selection on own performance is not promising

The usual directional selection has the effect to increase variability! ☹

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Response of A_v to mass selection
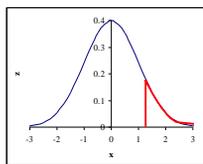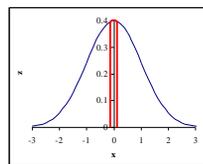
Directional selection   Stabilizing selection   Disruptive selection
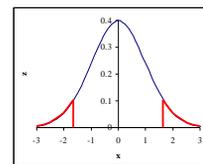
$$h_m^2 = 0.3 \quad \sigma_P^2 = 1 \quad \sigma_{Av}^2 = 0.05 \quad r_A = 0 \quad \sigma_{E,0}^2 = 0.70$$

p	Directional	Stabilizing	Disruptive
20%	0.03	-0.02	0.05
5%	0.08	-0.02	0.11
1%	0.14	-0.02	0.17

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Mulder et al. 2007; Genetics 175:1895-1910

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Heritability of environmental variance

- In analogy of the normal heritability of the mean

- Regression of Av on P[2]

$$h_v^2 = b_{A_V,P^2} = Cov(A_V, P^2)/Var(P^2)$$

$$h_v^2 = \sigma_{A_V}^2 / Var(P^2)$$

$$h_v^2 = \frac{\sigma_{A_V}^2}{2\sigma_P^4 + 3\sigma_{A_V}^2}$$

- Accuracy of BV = $\sqrt{h_v^2}$

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Mulder et al. 2007; Genetics 175:1895-1910

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Conclusions mass selection

- Opportunities to change the variance with info on single phenotypes is limited
  - Accuracy is low ($\sqrt{h_v^2}$)
  - The selection differential for stabilizing selection is small

- Traditional truncation selection has the tendency to increase variability

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Response to selection using information of relatives

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Selection based on relatives

- Use a group of relatives of a single sire and/or dam
  - E.g. progeny
- Within family variance is a measure for A_v
  - HS-Progeny of a single sire $\rightarrow$
  - $Var_W = \frac{3}{4}Var(A) + [Var(E) + \frac{1}{2}A_{v,sire}]$
- E.g. find the sire with the most uniform progeny, using 100 progeny per sire
- This yields much higher accuracies than own performance info

- The procedure is the same, but …
- The mathematics becomes more tedious (Mulder et al., 2007)

Mulder et al. 2007; Genetics 175:1895-1910

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Accuracy of selection based on relatives

- Selection based on the within family variance
  - Variance within a group of sibs or progeny

- Exact expression is complex → approximation

- Classical expression for selection on relatives

- $r_{IH} = ah\sqrt{\dfrac{n}{1+(n-1)t}}$ a = additive genetic relationship between candidate and group of relatives
t = intraclass correlation among the relatives
t = $a_w h^2$, a_w = additive genetic relationship among the group of relatives

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Mulder et al. 2007; Genetics 175:1895-1910
Hill and Mulder, 2010; Genetics Res. 92:381-395

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Accuracy of selection based on relatives

- Expression for selection on the variance (vEBV)

- $r_{IH,vEBV} \approx ah\sqrt{\dfrac{n}{1+(n-1)t}}$
  - a = additive genetic relationship between candidate and group of relatives
  - t = intraclass correlation among the relatives
  - $t = a_w h_v^2$, a_w = additive genetic relationship among the group of relatives

- This is the same as for classical traits
  - Limiting accuracies are 0.5 for HS, 0.71 for FS and 1 for progeny

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Comparison approximation with simulation

Table 6. Realized (MC) and predicted accuracy of $\hat{A}_v$ for different numbers of half-sib progeny per sire and $\sigma^2_{A_m}$ using either the exact prediction (MR exact) or the approximate prediction (MR approx)[a,b].   Mulder et al. 2007; Genetics 175:1895-1910

Accuracy $\hat{A}_v$

Number of progeny

		10			100	
$\sigma^2_{A_m}$	MC	MR exact	MR approx	MC	MR exact	MR approx
0	0.235	0.235	0.235	0.607	0.607	0.607
0.1	0.236	0.236	0.235	0.615	0.615	0.607
0.3	0.243	0.244	0.235	0.633	0.633	0.607
0.6	0.251	0.260	0.235	0.648	0.663	0.607

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Accuracy of vEBV

$h^2_m = 0.3$ $\sigma^2_P = 1$ $h^2_v = 0.023$ $r_A = 0$

Number of records	Mass	FS	HS progeny
Own phenotype	0.15	-	-
10	-	0.25	0.24
50	-	0.47	0.50
100	-	0.55	0.63

- With phenotype only, accuracy is small and relies on the mean when $r_A \neq 0$
- Using 100 progeny yields meaningful accuracies

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Mulder et al. 2007; Genetics 175:1895-1910   26

Numerical results for accuracy

TABLE 7

Predicted accuracy of $\hat{A}_v$ based on a single phenotype or different numbers of full-sibs or half-sib progeny for different values of $\sigma^2_{A_v}$ and r_A

Information	No. of progeny	$r_A = 0$: $\sigma^2_{A_v}$			$r_A = 0.5$: $\sigma^2_{A_v}$		
		0.01	0.05	0.10	0.01	0.05	0.10
			Predicted accuracy $\hat{A}_v$				
Phenotype	—	0.070	0.152	0.209	0.279	0.299	0.319
Full-sibs	10	0.123	0.252	0.327	0.299	0.348	0.388
	50	0.267	0.468	0.544	0.394	0.505	0.560
	100	0.355	0.553	0.610	0.442	0.570	0.617
Half-sib	10	0.115	0.244	0.325	0.346	0.386	0.424
Progeny	50	0.257	0.499	0.618	0.490	0.597	0.671
	100	0.353	0.633	0.745	0.545	0.693	0.772
	1000	0.768	0.933	0.962	0.798	0.936	0.963

$\sigma^2_{A_m} = 0.3$; $\sigma^2_E = 0.7$; $\sigma^2_P = \sigma^2_{A_m} + \sigma^2_E = 1.0$. $h_v^2 \approx 0.5\%, 2.5\%$ and 5%

- With phenotype only, accuracy is small and relies on the mean when $r_A \neq 0$

- Using 100 progeny yields meaningful accuracies

Mulder et al. 2007; Genetics 175:1895-1910

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The accuracy of vEBV (approximation)

heritability = 0.03

clones
full-sibs
half-sib progeny

accuracy vEBV

Number of relatives

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The accuracy of vEBV (approximation)

heritability = 0.01
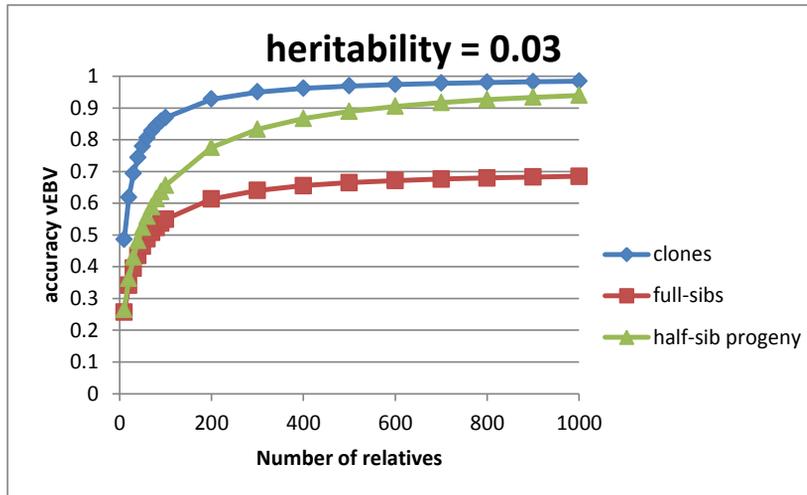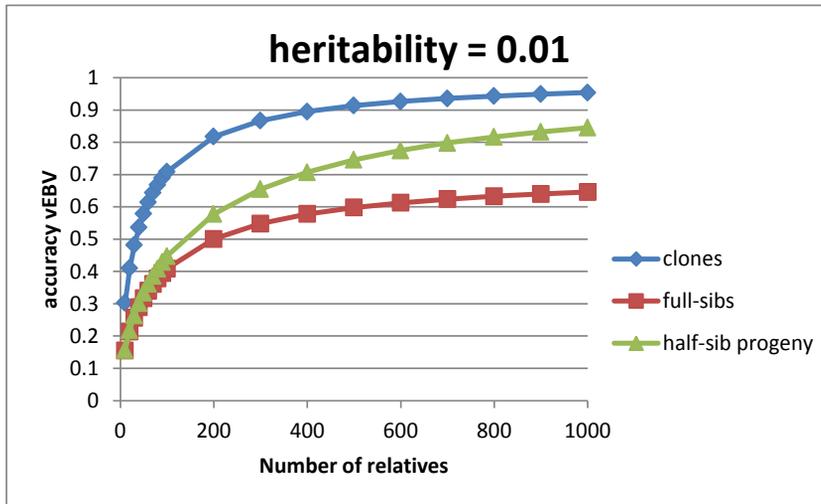
Large number of clones or half-sib progeny needed to approach accuracy = 1.0

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Selection to increase uniformity expressed in standard deviations

- Selected proportions: 5% in sires, 20% in dams
- sires progeny tested, dams sib tested

n	$\sigma^2_{A_v}$	h^2	acc sire	acc dam	%SDE	%SDP
50	0.05	0.3	0.36	0.18	-5.45	-3.78
100	0.05	0.3	0.48	0.24	-7.18	-4.97
200	0.05	0.3	0.61	0.31	-9.06	-6.25

- %SDE = change (%) in environmental standard deviation
- %SDP = change (%) in phenotypic standard deviation

Large families needed!!!

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Selection to improve uniformity expressed in standard deviations

▪ Selected proportions: 5% in sires, 20% in dams

▪ sires progeny/sib tested, dams sib tested

n	$\sigma^2_{A_v}$	h^2	%SDE		%SDP	
			sib	progeny	sib	progeny
100	0.05	0.1	-5.40	-8.48	-4.85	-7.60
100	0.05	0.3	-4.56	-7.18	-3.17	-4.97
100	0.05	0.5	-2.58	-5.54	-1.28	-2.73

- **Progeny testing gives larger response**
- **More response for traits with low heritability**

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Summary response to selection

▪ With info on relatives we can reach high accuracies despite low heritability
  ● Limiting accuracies are the same as in classical theory
  ● Clones would be ideal system to study genetics of Ve

▪ Combined with the high GCV, this yields high potential response to selection

$$\frac{\Delta\mu}{\mu} = ir_{IH}\frac{\sigma_A}{\mu}$$

▪ Selection to reduce Ve is promising, especially for traits with a low heritability of the phenotype

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Some extensions

Some extensions

- What is the heritability of the log-variance/standard deviation of repeated observations?

    - Within-litter variance of birth weight

    - Log-variance of repeated records for egg color/egg weight/milk yield

- Response to selection with the exponential model

    - Relationship response and GCV

Heritability litter variance

- We can use the classical equation

- $r_{IH} = \sqrt{\dfrac{nh^2}{1+(n-1)r}}$

- r = repeatability

- If $r = h_v^2 = 0.01$ and n=15 piglets:

- $h_{v,litter}^2 = 0.14$

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Heritability repeated observations

- Egg color in purebred laying hens
- $h_v^2 = 0.01$ and $r = 0.046$

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Mulder et al. 2016; GSE 48:39
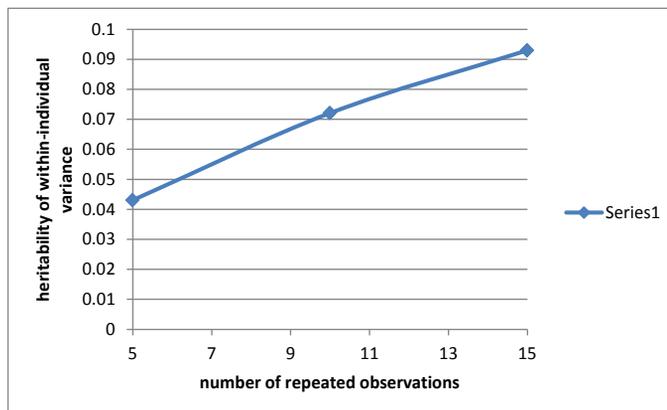
Response to selection with exponential model

- Remember: average Ve depends on genetic variance in Ve

- $\sigma_E^2 = \sigma_{E,exp}^2 \exp(0.5\sigma_{Av}^2)$

- $\Delta a_v = i r_{IH} \sigma_{Av}$

- $\Delta \sigma_E^2 = \sigma_{E,t}^2 (\exp(\Delta a_v) - 1)$
- $\sigma_{E,t+1}^2 = \sigma_{E,t}^2 + \Delta \sigma_E^2 = \sigma_{E,t}^2 (\exp(\Delta a_v))$

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Response under additive and exponential model
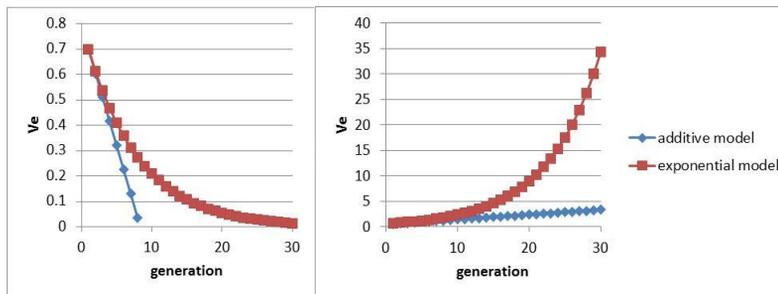
- Response to selection approximately the same in the first generations
- Additive model can be considered as a linear approximation of the exponential model
- No biological evidence which model is better

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Response to selection: use of GCV

- In exponential model: $GCV_{\sigma_E^2} \approx \sigma_{av}$

- $\frac{\Delta a_v}{\sigma_E^2} = i r_{IH} \frac{\sigma_{av}}{\sigma_E^2} \approx i r_{IH} \sigma_{av}$

- The response in the exponential model is the proportion of change in Ve

Selection response in standard deviations

- $GCV_{\sigma_e} \approx \frac{1}{2} \sigma_{av}$
- $GCV_{\sigma_P} \approx \frac{1}{2} \sigma_{av} \frac{\sigma_E^2}{\sigma_P^2}$
- $\frac{\Delta a_v}{\sigma_P} \approx i r_{IH} \frac{1}{2} \sigma_{av} \frac{\sigma_E^2}{\sigma_P^2}$

- Example: $i = 1.0$, $r_{IH} = 0.6$; $\sigma_{av}^2 = 0.05$; $\frac{\sigma_E^2}{\sigma_P^2} = 0.7$

- $\Delta a_v = 1.0 * 0.6 * \sqrt{0.05} = 13\%$

- $\frac{\Delta a_v}{\sigma_E} = 1.0 * 0.6 * \sqrt{0.05} * 0.5 = 6.7\%$

- $\frac{\Delta a_v}{\sigma_P} = 1.0 * 0.6 * \sqrt{0.05} * 0.5 * 0.7 = 2.3\%$

Summary

- Classical equations can be used to calculate accuracy of selection using heritability of Ve

- Many offspring/sibs needed to obtain reasonable accuracy

- The additive model is easier for selection response than the exponential model

- Genetic coefficient of variation parameters are easy parameters to know the change in standard deviation or variance

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Breeding goal and deriving economic values

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When do we want to select on variance?

- Optimum traits: bring population close to the optimum
- How could we determine it more precisely?
- Take the derivative with respect to the variance

$$v_{A_v} = \frac{d\overline{M}}{d\sigma_P^2} \neq 0$$ ● M=profit equation

- Only non-zero economic value for non-linear profit equations!!!

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Mulder et al. Genet. Sel. Evol. 40:37-59.

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Different cases of non-linear profit

- Quadratic profit equation
    - Age at first calving
    - Some conformation traits in cattle

- Animals between thresholds
    - Carcass weight in pigs
    - pH of meat in pigs
    - Egg weight in laying hens

profit=0 | profit=1 | profit=0

Optimum range

-3 -2 -1 0 1 2 3
P

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Mulder et al. Genet. Sel. Evol. 40:37-59.   44
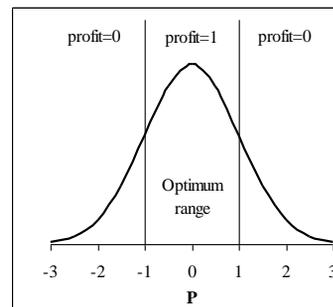
Non-linear profit: Risk aversion

- Risk aversion
- Higher profit increases utility less than lower profit decreases utility

- $U = 1 - \exp(-aY)$
- Y is yield

Eskridge, K. M. and B. E. Johnson. 1991. Expected utility maximization and selection of stable plant cultivars. Theor. Appl. Genet. 81:825-832.
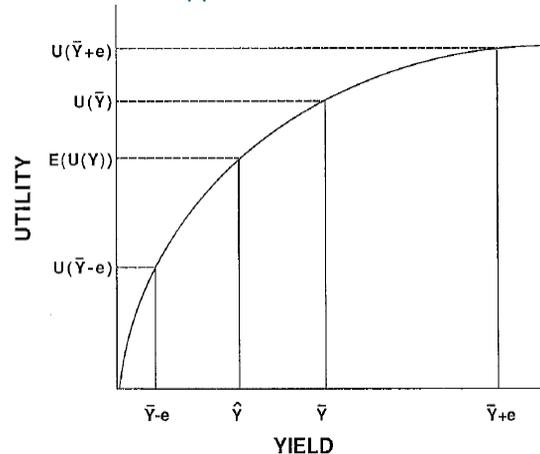
Fig. 1. Utility function of a risk-averse plant breeder

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Case non-linear profit: derivation of economic values (quadratic profit)

- Animal level

$$M = a_1(P-O)^2 + a_2$$

- Population level

$$\overline{M} = \int_{-\infty}^{\infty} Mf(P)dP = a_1\mu^2 - 2a_1\mu O + a_1 O^2 + a_2 + a_1\sigma_P^2$$

- Economic values

$$v_{A_m} = \frac{d\overline{M}}{d\mu} = 2a_1(\mu - O)$$

$$v_{A_v} = \frac{d\overline{M}}{d\sigma_P^2} = a_1$$

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Case non-linear profit
derivation of economic values (thresholds)

$$v_{A_m} = \frac{z_l - z_u}{\sigma_P} \qquad v_{A_v} = \frac{\frac{1}{2}(z_l t_l - z_u t_u)}{\sigma_P^2}$$

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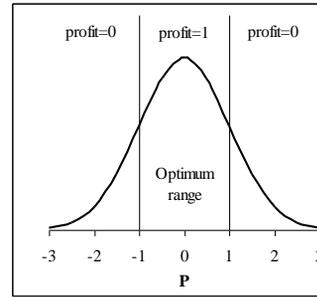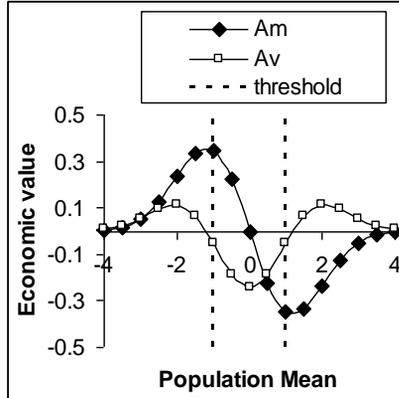
Case non-linear profit
mean and phenotypic variance

Mulder et al. Genet. Sel. Evol. 40:37-59.

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Multi-trait selection on mean and variance

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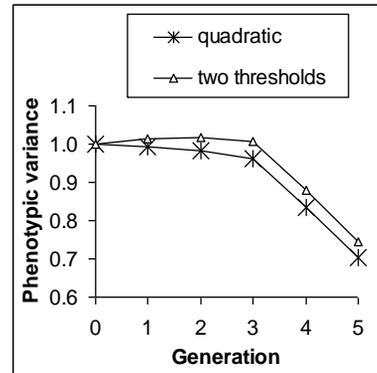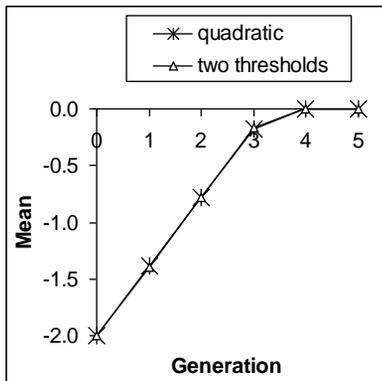
Multi-trait selection: selection index theory

- $H = v_{Am}A_m + v_{Av}A_v = \mathbf{v}'\mathbf{a} \quad \mathbf{v}' = [v_{Am} \quad v_{Av}]; \ \mathbf{a} = \begin{bmatrix} A_m \\ A_v \end{bmatrix}$

- Suppose we have information on the mean performance and the within-family variance of half-sibs (either as sibs or as offspring of selection candidate)

- $I = b_1\bar{P} + b_2 varW = \mathbf{b}'\mathbf{x} \quad \mathbf{b}' = [b_1 \quad b_2]; \ \mathbf{x} = \begin{bmatrix} \bar{P} \\ varW \end{bmatrix}$

- $\mathbf{b} = \mathbf{P}^{-1}\mathbf{G}\mathbf{v}$ index weights to maximize genetic gain in H

- $\mathbf{P} = \text{var}(\mathbf{x}) = \begin{bmatrix} \text{var}(\bar{P}) & \text{cov}(\bar{P}, varW) \\ \text{cov}(\bar{P}, varW) & \text{var}(varW) \end{bmatrix}$

- $\mathbf{G} = \begin{bmatrix} cov(A_m, \bar{P}) & cov(A_v, \bar{P}) \\ cov(A_m, varW) & cov(A_v, varW) \end{bmatrix}$

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Response to selection

- $\Delta A = [\Delta A_m \quad \Delta A_v] = \dfrac{i\, \mathbf{b'G}}{\sqrt{\mathbf{b'Pb}}}$ i : selection intensity;

- $\sqrt{\mathbf{b'Pb}}$ = standard deviation of index

- Use classical equations for P and G and h_v^2 and additive model for Ve (approximation)

- $\mathbf{P} = \begin{bmatrix} \mathrm{var}(\bar{P}) & \mathrm{cov}(\bar{P}, varW) \\ \mathrm{cov}(\bar{P}, varW) & \mathrm{var}(varW) \end{bmatrix} =$

- $\begin{bmatrix} [\sigma_p^2(1 + (n-1)ah^2)]/n & [\{3 + a(n-3)\}cov_{amv}]/n \\ symmetric & [(2\sigma_p^4 + 3\sigma_{av}^2)(1 + (n-1)ah_v^2)]/n \end{bmatrix}$

- a = additive genetic relationships between family members

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Response to selection

- $\mathbf{G} = \begin{bmatrix} cov(A_m, \bar{P}) & cov(A_v, \bar{P}) \\ cov(A_m, varW) & cov(A_v, varW) \end{bmatrix} = \begin{bmatrix} a_j\sigma_{am}^2 & a_j cov_{amv} \\ a_j cov_{amv} & a_j\sigma_{av}^2 \end{bmatrix}$

- a_j = additive genetic relationship between the animal to be evaluated and the group of relatives
    - 0.5 parent-offspring
    - 0.25 when selection candidate is a half-sib

- Exact elements in Mulder et al. Genet. Sel. Evol. 40:37-59.

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What does nature say with respect to selection on variance?

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What is the relationship between fitness and Ve?

- What is the best Ve from a fitness point of view?
- Are there any trade-offs of a high or low variance?

- What is the regression of fitness on trait values or on within-family variance?

- We performed an analysis in Great Tits at the Veluwe, a nature reservation close to Wageningen

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Fitness and Ve in Great Tit
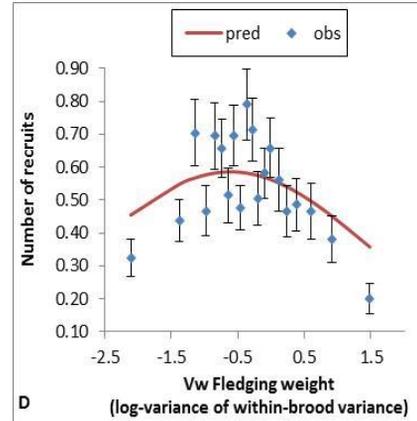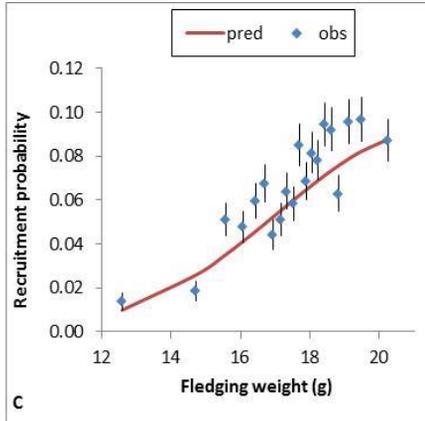
- Results show stabilizing selection on Ve
- Ve is maintained

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Mulder et al., Evolution 70:2004-2016

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Selection experiments

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Selection experiments

- Selection experiments with laboratory animals, e.g. Drosophila

- Selection experiment in rabbits

- Need for more selection experiments

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Selection experiment in rabbits
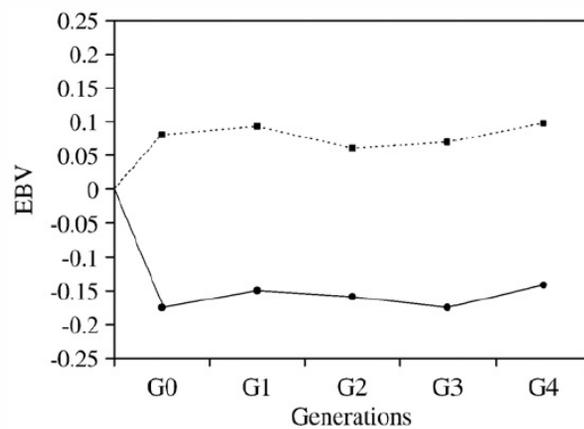
Garreau et al. 2008;
Livest. Sci. 119:55-62.

Fig. 1. Estimated breeding values (ν) of environmental variability over the four generations of selection in heterogeneous (··■··) and homogeneous lines (—●—).

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Experiment in rabbits

Garreau et al. 2008;
Livest. Sci. 119:55-62.
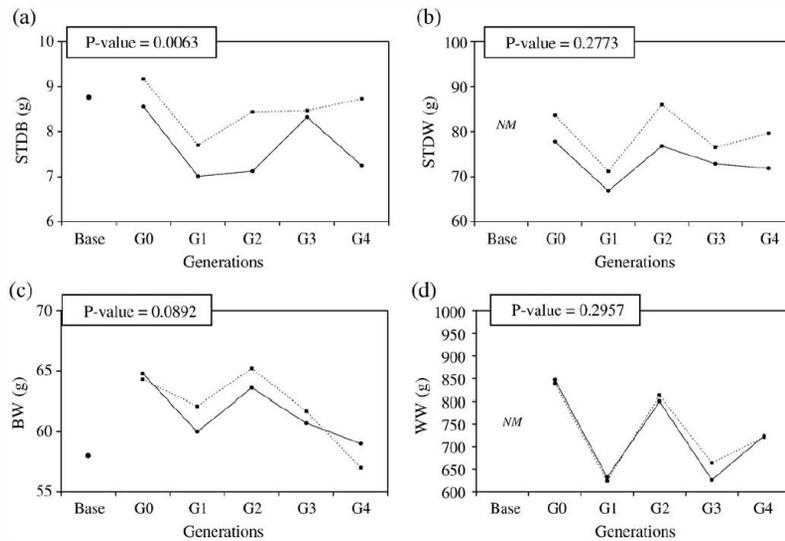
Fig. 2. Phenotypic least-squares means of the four generations of selection and phenotypic mean of the base population for standard deviation of birth weight (STDB) (a), standard deviation of weaning weight (STDW) (b), individual birth weight (BW) (c), individual weaning weight (WW) (d) in heterogeneous (···■···) and homogeneous lines (─●─). *P* value of the line effect. (NM: Not measured in the base population).

Summary

- Selection index theory can be used to predict responses to selection
- Selection to change the variance is important when the profit equation is non-linear
  - Selection to improve uniformity is of importance when having an optimum
- Need for knowledge on relationships between Ve and fitness (traits)
- More selection experiments are needed to learn more about genetic architecture of Ve

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