Basic Principles of Response to Selection Jack Dekkers

Response to selection = (mean BV of progeny) – (mean BV parental generation)

Predicting Mean BV of Progeny Generation

Guiding principle of genetic improvement: parents with high BV tend to have progeny with high BV

Single progeny: $g_o = \frac{1}{2}g_s + \frac{1}{2}g_d + g_m$ $g_m =$ Mendelian sampling terms $E(g_o) = \frac{1}{2}g_s + \frac{1}{2}g_d$ because $E(g_m) = 0$

Progeny generation: $E(\overline{g}_o) = \frac{1}{2}\overline{g}_s^* + \frac{1}{2}\overline{g}_d^*$

Average BV of progeny * refers to selected individuals \overline{g}_s = ave. all males

$$E(\overline{g}_{o}) = \frac{1}{2}(\overline{g}_{s}^{*} - \overline{g}_{s} + \overline{g}_{s}) + \frac{1}{2}(\overline{g}_{d}^{*} - \overline{g}_{d} + \overline{g}_{d})$$

$$= \frac{1}{2}(\overline{g}_{s} + \overline{g}_{s}^{*} - \overline{g}_{s}) + \frac{1}{2}(\overline{g}_{d} + \overline{g}_{d}^{*} - \overline{g}_{d})$$

$$= \frac{1}{2}(\overline{g}_{s} + S_{s}) + \frac{1}{2}(\overline{g}_{d} + S_{d})$$

S = genetic superiority of the selected parents $S_s = \overline{g}_s^* - \overline{g}_s$

$$E(g_o) = \frac{1}{2}(g_s + g_d) + \frac{1}{2}(S_s + S_d)$$

mean parental average genetic sur

nean parentalaverage genetic superioritygenerationof selected parents

Response = $R = \Delta G$ = (mean BV progeny generation) – (mean BV parental generation)

$$E(R) = \overline{g}_{o} - \overline{g}_{p} \quad \text{with } \overline{g}_{p} = \frac{1}{2}(\overline{g}_{s} + \overline{g}_{d})$$
$$E(R) = \frac{1}{2}(\overline{g}_{s} + \overline{g}_{d}) + \frac{1}{2}(S_{s} + S_{d}) - \frac{1}{2}(\overline{g}_{s} + \overline{g}_{d})$$
$$= \frac{1}{2}(S_{s} + S_{d})$$

 \rightarrow expected response to selection = average genetic superiority of selected parents

For <u>current generation</u>, genetic superiority of selected parents can be estimated based on their EBV:

If EBV are unbiased:	E(g)	= <i>g</i>
Then – for an individual:	$E(g_o)$	$= \frac{1}{2}g_{s} + \frac{1}{2}g_{d}$
– for progeny generation:	$E(\overline{g}_o)$	$= \frac{1}{2} \overline{\hat{g}}_{s}^{*} + \frac{1}{2} \overline{\hat{g}}_{d}^{*}$
		$= \frac{1}{2} (\bar{\hat{g}}_{s} + \hat{S}_{s}) + \frac{1}{2} (\bar{\hat{g}}_{d} + \hat{S}_{d})$
٨		٨

 \hat{S} = estimated genetic superiority of the selected parents $\hat{S} = \overline{\hat{g}}^* - \overline{\hat{g}}$

→ Expected response =
$$E(R) = \frac{1}{2}(\hat{S}_s + \hat{S}_d)$$

Predicting Response per Generation into the Future

g are not available for future generations or for alternative designs

- → need to predict genetic superiority of selected parents by other means
 - do this based on the linear relationship between the selection criterion, I, and g •

Predict g_i given I_i :

Predict the mean BV of a group of selected animals:

 $\overline{\hat{g}}^* = \overline{g} + b_{gI} (\overline{I}^* - \overline{I})$ $\hat{S} = \bar{g}^* - \bar{g} = b_{gI} (\bar{I}^* - \bar{I})$

 $\hat{g}_i = \overline{g} + b_{oI} (I_i - \overline{I})$

Predict the genetic superiority of selected parents:

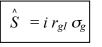
 $i = (\overline{I}^* - \overline{I}) / \sigma_I$ Define intensity of selection:

How many SD (for the selection criterion) is the selected group better than all candidates

Using

From regression:

 $(\overline{I}^* - \overline{I}) = i\sigma_I$ $\hat{S} = b_{g,I} i \sigma_I$



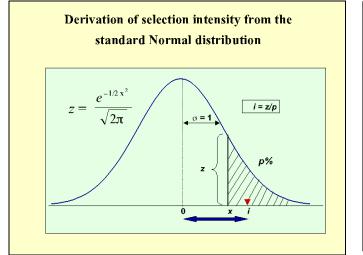
 $\hat{S} = i r_{gI} \sigma_g$ is general equation to predict genetic superiority of selected parents applies whenever selection criterion (I) is linearly related to the BV (g)

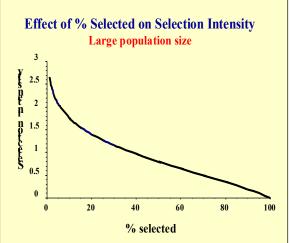
Use $S = i r_{gI} \sigma_g$ to model the genetic mean of the next generation recursively:

$$\overline{g}_o = \frac{1}{2}(\overline{g}_s + S_s) + \frac{1}{2}(\overline{g}_d + S_d)$$

or predict response per generation: $R = \frac{1}{2}(S_s + S_d) = \frac{1}{2}(i_s r_s \sigma_g + i_d r_d \sigma_g)$

Selection Intensity with Truncation Selection



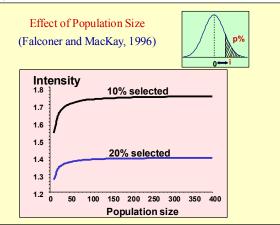


 r_{gI} = accuracy of selection

Adjustments to standard (large unrelated population) selection intensities:

- small populations: i < z/p٠
 - order statistics
 - approximation: $p = \frac{(s + \frac{1}{2})}{n + \frac{s}{2n}}$ s = # selected n = population size $i^* = \frac{z^*}{*}$

use p^* rather than p to derive intensity



Correct intensities for correlated EBV among selection candidates due to:

- 1) genetic relationships between candidates of selection
- 2) use of the same information in calculating the EBV
- e.g. n_{fs} full sib families with n_w individuals per family and selection on pedigree

$$(\Rightarrow g_o = \frac{1}{2}g_s + \frac{1}{2}g_d)$$
 Correlation between EBV of full sibs = 1

→

select n_c/n_w families out of n_{fs} \rightarrow related to effect of pop. size instead of:

Approximations to account for effect of correlated EBV on intensity:

Rawlings (1976)

$$i^* = \sqrt{1 - t_{av}} i$$

 t_{av} = average correlation between the selection criterion across all possible pairs of selection candidates

 $t_{av} = t_{fs} \frac{n_w - 1}{n_w n_{fs} - 1}$ Unrelated full sib families

 t_{fs} = correlation between selection criterion of full sibs

Full sib families nested within half sib families (Meuwissen 1991): n_{hs} sires mated with n_{fs} dams each producing n_w offspring

> Correlation between half sibs $= t_{hs}$ Correlation between full sibs $= t_{fs}$ Correlation between non-relatives = 0

$$t_{av} = \frac{t_{fs}(n_w - 1) + t_{hs}n_w(n_{fs} - 1)}{n_w n_{fs} n_{hs} - 1}$$

Correlations between EBV of relatives based on selection index theory :

$$t_{i,j} = \operatorname{corr}(I_i, I_j) = \operatorname{corr}(\mathbf{b}^* \mathbf{x}_i, \mathbf{b}^* \mathbf{x}_j) = \frac{\mathbf{b}^{\mathsf{cov}}(\mathbf{x}_i, \mathbf{x}_j)\mathbf{b}}{\mathbf{b}^{\mathsf{cov}} \mathbf{P}\mathbf{b}} = \frac{\mathbf{b}^{\mathsf{c}} \mathbf{R}\mathbf{b}}{\mathbf{b}^{\mathsf{c}} \mathbf{P}\mathbf{b}}$$

 $\mathbf{R} = m \ge m$ x m matrix with covariances between information sources on the relatives

Asymptotic Response per Unit Time

Equal selection in males and females:

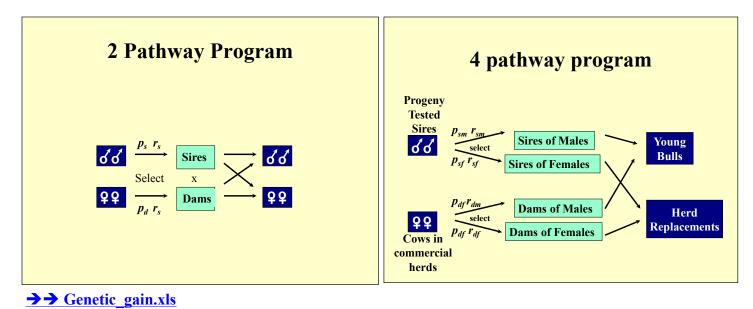
Response per generation:

$$R = S = i r_{gI} \sigma_g$$
$$R_{yr} = \frac{S}{L}$$

Response per year:

Generation interval = L = average age of the parents when their progeny are born = average time between birth of the parents and birth of progeny

Unequal selection in males and females: Figure 3.3 Example of predicted annual versus asymptotic responses Starting from an unselected population Response per generation: $R = \frac{1}{2}(S_s + S_d)$ $S = i r_{gI} \sigma_g$ 5.5 $R_{yr} = \frac{S_s + S_d}{L_s + L_d}$ 5.0 Response per year: 4.5 Annual Response 4.0 = 'steady state' or 3.5 'asymptotic' response 3.0 Responses from year to year obtained 2.5 recursively based on mean of selected 2.0 parents: 1.5 $\overline{g}_{o} = \frac{1}{2}(\overline{g}_{s} + S_{s}) + \frac{1}{2}(\overline{g}_{d} + S_{d})$ 1.0 18 19 20 10 11 12 13 14 15 16 17 Year $R_{yr} = \frac{S_s + S_d}{L_s + L_d}$ Derivation of asymptotic response: When response constant at R_{vr}/yr : Figure 3.4 Asymptotic response to selection for breeding programs $g_s = g_o - L_s R_{yr}$ with overlapping generations $\overline{g}_d = \overline{g}_o - L_d R_{yr}$ $\overline{g}_{o} = \frac{1}{2}(\overline{g}_{s} + S_{s}) + \frac{1}{2}(\overline{g}_{d} + S_{d})$ Substituting we get: $\overline{g}_{o} = \frac{1}{2}(\overline{g}_{o} - L_{s}R_{vr} + S_{s}) + \frac{1}{2}(\overline{g}_{o} - L_{d}R_{vr} + S_{d})$ $= \overline{g}_{o} - \frac{1}{2}R_{vr}(L_s + L_d) + \frac{1}{2}(S_s + S_d)$ Rearranging $\rightarrow R_{yr} = \frac{S_s + S_d}{L_s + L_d}$ 1 yr Sires Dams Offspring Birth year

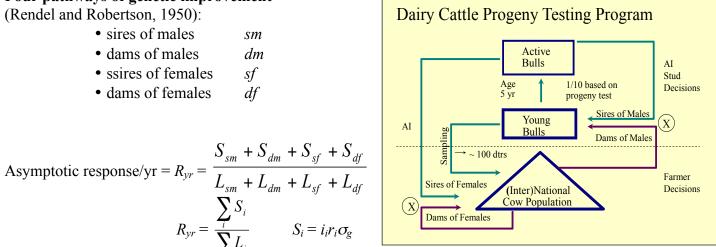




Four pathways of genetic improvement

(Rendel and Robertson, 1950):

- sires of males sm
- dams of males dm
- ssires of females sf
- dams of females df



$$R_{yr} = \frac{\sum_{i}^{i} S_{i}}{\sum_{i}^{i} L_{i}} \qquad S_{i} = i_{i}r_{i}\sigma_{g}$$

Table 1 Intensity and accuracy of selection and generation interval in a highly efficient hypothetical progeny-testing program for improving milk yield in dairy cattle.

	Proportion			Genetic	Generation
	Selected	Intensity	Accuracy	Superiority	Interval (yr)
Pathway	(p_i)	(i_i)	(r_i)	$(S_i = i r_i \sigma_g)$	(L_i)
Sires of males	2 %	2.42	0.90	2.178 σ_{g}	6
Sires of females	10 %	1.75	0.90	$1.575 \sigma_{g}$	7
Dams of males	0.5 %	2.89	0.60	1.743 σ_{g}	5
Dams of females	90 %	0.19	0.60	$0.114 \sigma_{g}$	6
TOTAL				$\Sigma S = 5.601 \sigma_g$	$\Sigma L = 24$

$$R_{yr} = \frac{(2.42 \times 0.9 + 1.75 \times 0.9 + 2.89 \times 0.6 + 0.19 \times 0.6)}{6 + 7 + 5 + 6}\sigma_g = 0.233 \sigma_g \text{ per yr}$$

Selection Across Multiple Age Groups

	Relative	Gene-	Mean	Accuracy of	Fraction	Genetic	Genetic mean
Age	number of	ration	within	selection	selected	superiority	selected
group	candidates	interval	group	within group	within group	within group	individuals
1	w_1	L_1	\overline{g}_1	r_1	p_1	$S_1 = i_1 r_1 \sigma_g$	$\overline{g}_1^* = \overline{g}_1 + S_1$
2	w_2	L_2	\overline{g}_{2}	r_2	p_2	$S_2 = i_2 r_2 \sigma_g$	$\overline{g}_{2}^{*} = \overline{g}_{2} + S_{2}$
3	<i>W</i> 3	L_3	\overline{g}_3	<i>r</i> ₃	p_3	$S_3 = i_3 r_3 \sigma_g$	$\overline{g}_3^* = \overline{g}_3 + S_3$
	$\Sigma w_i = 1$						

E.g. three age groups:

Total proportion selected is:

Genetic mean of selected individuals across groups is:

 $P = p_1 w_1 + p_2 w_2 + p_3 w_3$ $\bar{g}^* = \frac{1}{P} \{ p_1 w_1 \bar{g}_1^* + p_2 w_2 \bar{g}_2^* + p_3 w_3 \bar{g}_3^* \}$ $\bar{g}_i^* = \bar{g}_i + S_i = i_i r_i \sigma_g$

Applied to separate selection of males and females:

Genetic mean of selected sires:

Genetic mean of selected dams:

Genetic mean of progeny:

$$E(\overline{g}_o) = \frac{1}{2}\overline{g}_s^* + \frac{1}{2}\overline{g}_d^*$$

 $\overline{g}_{s}^{*} = \frac{1}{P_{s}} \sum p_{si} w_{si} (\overline{g}_{si} + S_{si})$

 $\overline{g}_{d}^{*} = \frac{1}{P_{d}} \sum p_{di} w_{di} (\overline{g}_{di} + S_{di})$

For asymptotic gain/yr: Compute average within-group genetic superiority and generation interval across

age classes:	For sires:	$S_s = \frac{1}{P_s} \sum p_{si} w_{si} S_{si}$	$L_s = \frac{1}{P_s} \sum p_{si} w_{si} L_{si}$	$B = S_s + S_d$
	For dams	$S_d = \frac{1}{P_d} \sum p_{di} w_{di} S_{di}$	$L_d = \frac{1}{P_d} \sum p_{di} w_{di} L_{di}$	$K_{yr} = \frac{1}{L_s + L_d}$

Genetic

Superiority

 $ir\sigma_g$

707.9

946.2

1001.9

Selection Across Age Groups

 Pooled Generation Interval L_{dm} = 50% * 2 	 Pooled Genetic Superiority S_{dm} = 50% * 707.9
+ 30% * 3	+ 30% * 946.2
+ 20% * 4	+ 20% * 1001.9
= 2.7 yr	= 838.2 kg

Selection Across Age Group

%

Selected

2.5%

1.5%

1.5%

i

2.34

2.53

2.53

r

.55

.68

.72

e.g. Selection of Bull Dams $\sigma_g = 550 \text{ kg}$

% of Bull

Dams

50%

30%

20%

Age at Birth of

Progeny

2 yr

3 yr

4 yr

Age Group

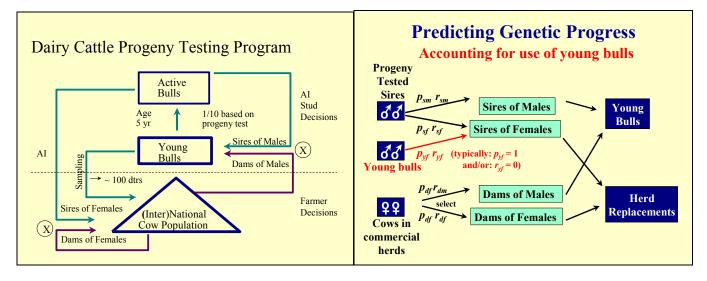
Heifers

1st Lact.

2nd Lact.

Accounting for the use of young bulls

y = proportion of females produced from young bulls



Genetic superiority sires of females

$$S_{sf} = y S_{yb,f} + (1-y) S_{pb,f}$$

 $L_{sf} = y L_{vb,f} + (1-y) L_{pb,f}$

Without MAS/GS

 $S_{vb,f} = 0$ because $p_{vb,f} = 1 \implies i_{vb,f} = 0$ or $r_{vf} = 0$

Generation interval of sires of females

Table 2. Intensity and accuracy of selection and generation interval in a highly efficient hypothetical progeny-testing program for improving milk yield in dairy cattle with accounting for 20% use of young bulls to breed female replacements.

	Proportion			Ge	netic	Gene	ration
	Selected	Intensity	Accuracy	Superiority		Interval (yr)	
Pathway	(p_i)	(i_i)	(r_i)	$(S_i = i r_i \sigma_g)$		(L_i)	
Sires of males	2 %	2.42	0.90	$2.178\sigma_g$		6	
Sires of - Young	100 %	0	0.50	0	1	2	
females - Proven	10 %	1.75	0.90	1.575	$1.260\sigma_g$	7	6
Dams of males	0.5 %	2.89	0.60	$1.734\sigma_g$		4	5
Dams of females	90 %	0.19	0.60	$0.114\sigma_g$		(5
TOTAL				$\Sigma S = 1$	$5.268\sigma_g$	ΣL	=23

Now response per year becomes:

$$R = \frac{5.268}{23} \sigma_g = 0.230 \sigma_g \text{ per yr}$$

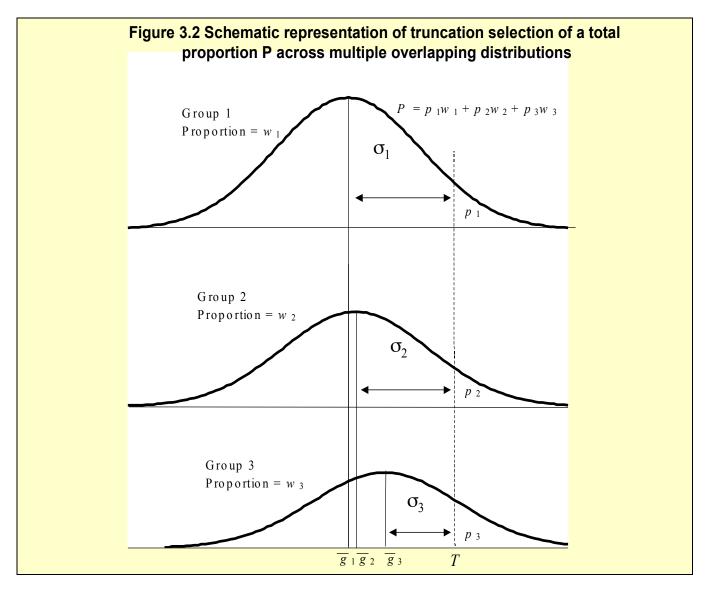
→→ Genetic_gain.xls

Optimizing selection across (age) groups

Optimize proportions to select from each group to maximize the average genetic value of the selected group (for total fraction selected P).

Assume that selection criterion is unbiased for each age group: $E(g_i) = I_i$

- \rightarrow truncation selection across distributions of *I*
- → find the truncation point where selection across all distributions yields a total proportion selected of P
 Various algorithms can be used
 Bisection
 - gradient algorithms
 - Genetic algorithms



→ Multrunc.xls
→ truncselDE.xls

Balancing Accuracy vs Generation Interval

Selection on EBV Across Age Groups

