Best Linear Unbiased Prediction properties of BLUP EBVs

BLUP properties

- Correction for mates and selection over generations.
- Allows estimation of genetic trend
- Selection across age classes
- Accuracy and linkage between herds/CGs
- BLUP and inbreeding

From data to BLUP EBV

Information

Phenotypic data and fixed effects

ID	*herd*	*age*	*weight*
1	*1*	*-1.5*	*494*
2	*2*	*1.5*	*556*
3	*1*	*-0.5*	*542*
4	*1*	*-2.5*	*473*
5	*2*	*3.5*	*632*
6	*2*	*-0.5*	*544*

→ X , Z, y

Pedigree Data

ID	*Idsire*	*IDdam*
1	*0*	*0*
2	*0*	*0*
3	*1*	*2*
4	*1*	*2*
5	*1*	*3*
6	*4*	*0*

→ A-inverse

Genetic parameters

→ $\lambda = (1-h^2)/h^2$

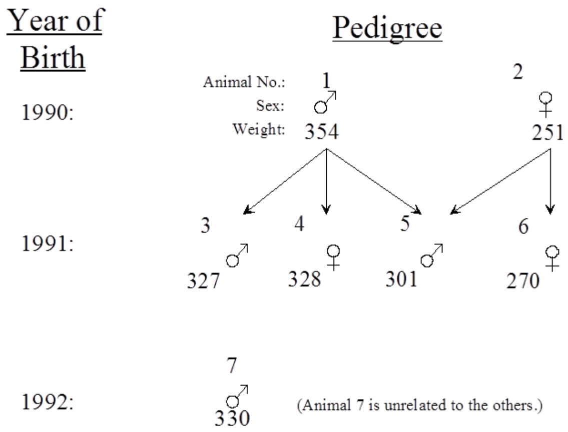
Mixed Model Equations

$$\begin{pmatrix} \hat{b} \\ \hat{u} \end{pmatrix} = \begin{pmatrix} X'X & X'Z \\ Z'X & Z'Z + \lambda A^{-1} \end{pmatrix}^{-1} \begin{pmatrix} X'y \\ Z'y \end{pmatrix}$$

→ EBV = $\hat{u}$

Properties of BLUP solutions

Solutions	A
311.94	
-9.15	
-8.90	
28.26	
-28.85	
18.34	
18.77	
-0.87	
-22.40	
0.00	



EBV of animals 1 and 2 are (close to) zero – on average

EBV of animals 3-6 are above zero +3.46 on average   Why?

→ BLUP provides genetic trend

Properties of BLUP

How are individual EBV’s estimated?
How does BUP account for genetic trend?

- Look at equations for individual animals

Coefficient matrix

RHS

μ

$$
\begin{pmatrix}
7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\
1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\
3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\
1 & 1 & 5 & \frac{19}{6} & \frac{1}{2} & -\frac{2}{3} & -\frac{2}{3} & -1 & 0 & 0 \\
1 & 1 & 0 & \frac{1}{2} & \frac{17}{6} & 0 & 0 & -1 & -\frac{2}{3} & 0 \\
1 & 0 & 0 & -\frac{2}{3} & 0 & \frac{7}{3} & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & -\frac{2}{3} & 0 & 0 & \frac{7}{3} & 0 & 0 & 0 \\
1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\
1 & 0 & 1 & 0 & -\frac{2}{3} & 0 & 0 & 0 & \frac{7}{3} & 0 \\
1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2
\end{pmatrix}
\begin{pmatrix}
\hat{b}_{mean} \\ \hat{b}_{2000} \\ \hat{b}_{2001} \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7
\end{pmatrix}
=
\begin{pmatrix}
2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330
\end{pmatrix}
$$

Look at animal 6

$$\mu + b_{1991} - {}^{2}\!/_{3}\,\hat{u}_2 + {}^{7}\!/_{3}\,\hat{u}_6 = 270$$

Look at animal 6

$$\mu + b_{1991} - \frac{2}{3}\hat{u}_2 + \frac{7}{3}\hat{u}_6 = 270$$

$$\hat{u}_6 = \frac{3}{7}(270 - \mu - b_{1991}) + \frac{2}{7}\hat{u}_2$$

$$\hat{u}_6 = \frac{3}{7}\underbrace{\left(270 - \mu - b_{1991} - \frac{1}{2}\hat{u}_2\right)}_{\text{This is own performance as deviation from expected, given its dam}} + \underbrace{\frac{1}{2}\hat{u}_2}_{\text{This comes from dam}}$$

Selection index weight:

¾ VA / (¾VA+VE) = 3/7

$$\begin{pmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\ 1 & 1 & 5 & \frac{19}{6} & \frac{1}{2} & -\frac{2}{3} & -\frac{2}{3} & -1 & 0 & 0 \\ 1 & 1 & 0 & \frac{1}{2} & \frac{17}{6} & 0 & 0 & -1 & -\frac{2}{3} & 0 \\ 1 & 0 & 0 & -\frac{2}{3} & 0 & \frac{7}{3} & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -\frac{2}{3} & 0 & 0 & \frac{7}{3} & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & -1 & 0 & 0 & 3 & 0 & 0 \\ 1 & 0 & 1 & 0 & -\frac{2}{3} & 0 & 0 & 0 & \frac{7}{3} & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{pmatrix} \begin{pmatrix} \hat{b}_{mean} \\ \hat{b}_{2000} \\ \hat{b}_{2001} \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{pmatrix} = \begin{pmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{pmatrix}$$

Look at animal 5

$$\mu + b_{1991} - \hat{u}_1 - \hat{u}_2 + 3\hat{u}_5 = 301$$

For animal 5

$$\mu + b_{1991} - \hat{u}_1 - \hat{u}_2 + 3\hat{u}_5 = 301$$

$$\hat{u}_5 = \tfrac{1}{3}\underbrace{(301 - \mu - b_{1991} - \tfrac{1}{2}(\hat{u}_1 + \hat{u}_2))}_{\text{This is own performance as deviation from expected, given its sire and dam}} + \underbrace{\tfrac{1}{2}(\hat{u}_1 + \hat{u}_2)}_{\text{Mean of parents}}$$

Selection index weight:

½ VA /(½VA+VE)= 1/3

$$\begin{pmatrix} 7 & 1 & 3 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 3 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & -1 \\ 3 & 1 & 5 & 0 & 0 & 1 & 1 & 1 & 1 & -1 \\ 1 & 1 & 5 & \frac{19}{6} & \frac{1}{2} & -\frac{2}{3} & -\frac{2}{3} & -1 & 0 & 0 \\ 1 & 1 & 0 & \frac{1}{2} & \frac{17}{6} & 0 & 0 & 0 & -\frac{2}{3} & 0 \\ 1 & 0 & 0 & -\frac{2}{3} & 0 & \frac{7}{3} & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & -\frac{2}{3} & 0 & 0 & \frac{7}{3} & 0 & 0 & 0 \\ 1 & 0 & 1 & -1 & 1 & 0 & 0 & 3 & 0 & 0 \\ 1 & 0 & 1 & 0 & -\frac{2}{3} & 0 & 0 & 0 & \frac{7}{3} & 0 \\ 1 & -1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \end{pmatrix} \begin{pmatrix} \mu \\ b_{1990} \\ b_{1991} \\ \hat{u}_1 \\ \hat{u}_2 \\ \hat{u}_3 \\ \hat{u}_4 \\ \hat{u}_5 \\ \hat{u}_6 \\ \hat{u}_7 \end{pmatrix} = \begin{pmatrix} 2161 \\ 275 \\ 896 \\ 354 \\ 251 \\ 327 \\ 328 \\ 301 \\ 270 \\ 330 \end{pmatrix}$$

Look at animal 2

$$\mu + b_{1990} + \tfrac{1}{2}\hat{u}_1 + \tfrac{17}{6}\hat{u}_2 - \hat{u}_5 - \tfrac{2}{3}\hat{u}_6 = 251$$

For animal 2

$$\mu + b_{1990} + {}^{1}\!/_{2}\,\hat{u}_1 + {}^{17}\!/_{6}\,\hat{u}_2 - \hat{u}_5 - {}^{2}\!/_{3}\,\hat{u}_6 = 251$$

$$\hat{u}_2 = {}^{6}\!/_{17}\underbrace{(251 - \mu - b_{1990})}_{\text{This is own performance as deviation from expected,}} - {}^{6}\!/_{17}\underbrace{(\hat{u}_5 - {}^{1}\!/_{2}\,\hat{u}_1)}_{\text{Prog 1, corrected for sire}} + \underbrace{{}^{4}\!/_{17}\,\hat{u}_6}_{\text{Prog 2, no sire known}}$$

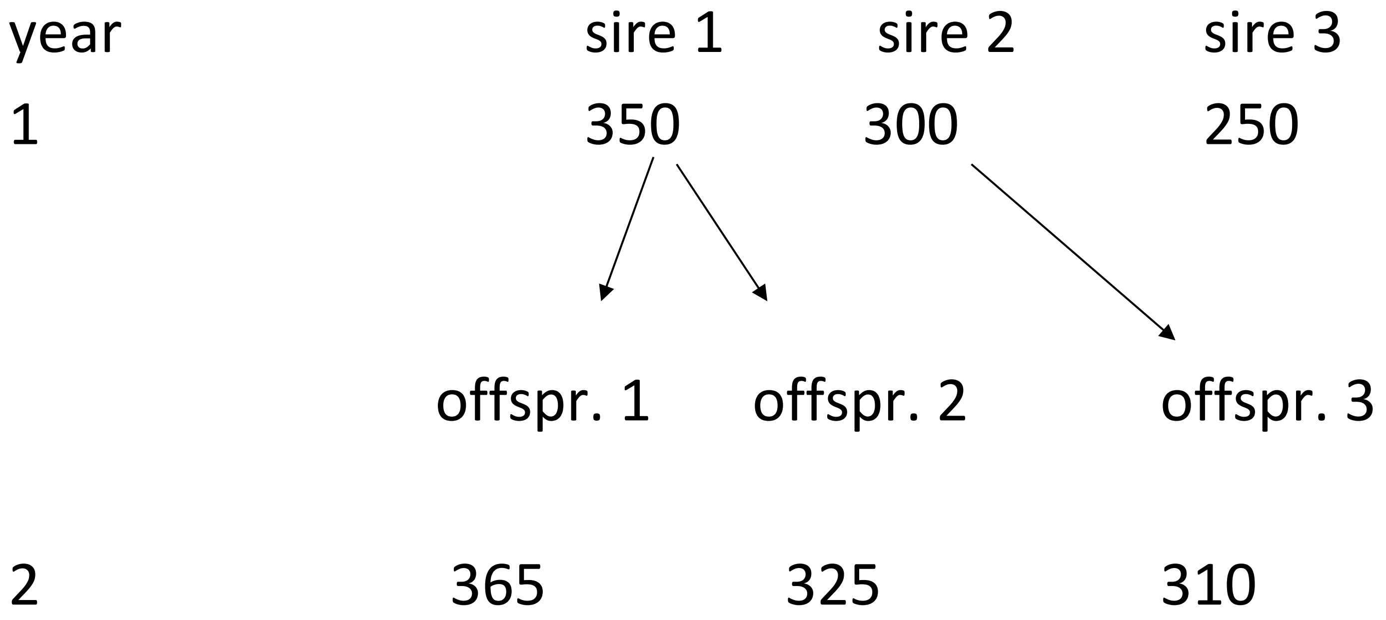
Parents themselves estimated based on:

- own record
- progeny records
- correction for mates

Weights are same as in selection index BLUP accounts for selection!!

Possible bias in genetic evaluation:

Animals are from selected parents



year sire 1 sire 2 sire 3

1 350 300 250

offspr. 1 offspr. 2 offspr. 3

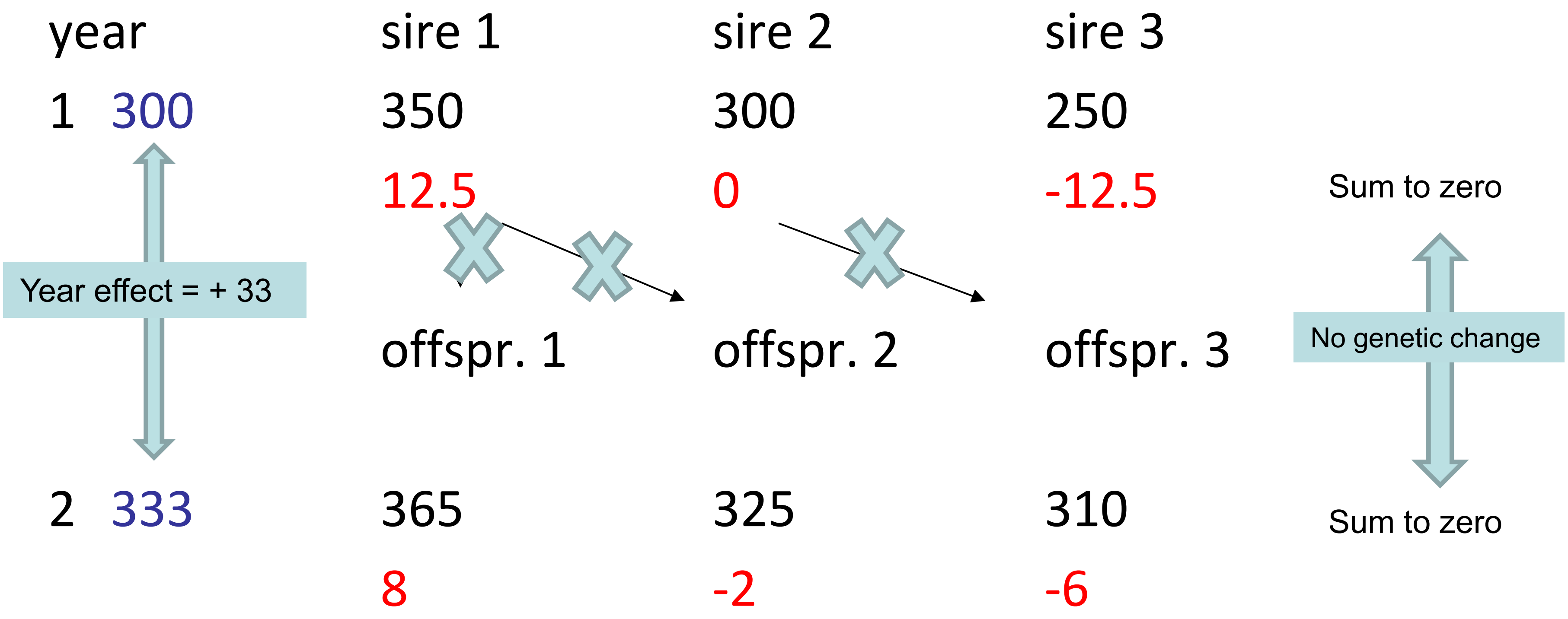
2 365 325 310

as years/generations go by, the genetic mean changes

- need to account for selection (evaluate jointly)
- calculate genetic trend from increase in EBV over years

Blup
accounts
for this

EBV’s without BLUP (within year)



year	sire 1	sire 2	sire 3
1 300	350	300	250
	12.5	0	-12.5
	offspr. 1	offspr. 2	offspr. 3
2 333	365	325	310
	8	-2	-6

Year effect = + 33

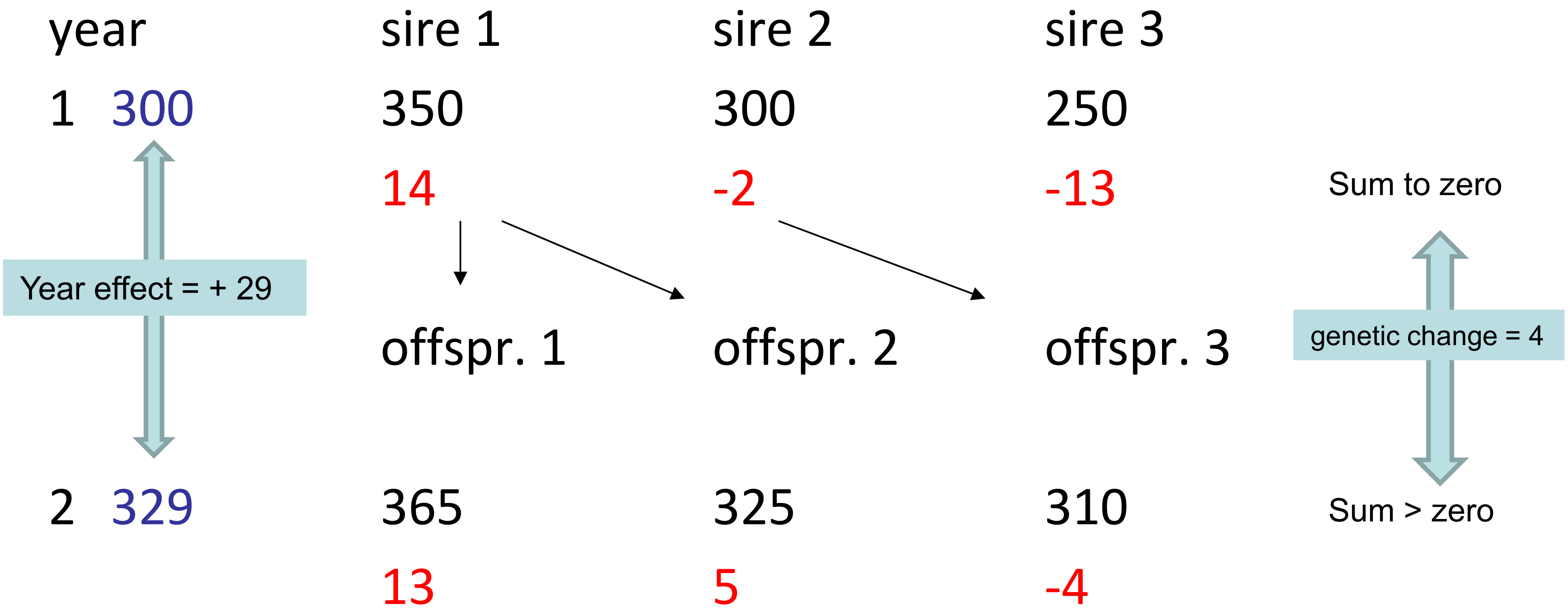
Sum to zero

No genetic change

Sum to zero

- No links between years
- Breeding vales are zero on average each year, no trend in average EBV over years
- Year solutions comprise genetic as well as environmental trend

EBV's with BLUP (across year)



year		sire 1	sire 2	sire 3
1	300	350	300	250
		14	-2	-13
		offspr. 1	offspr. 2	offspr. 3
2	329	365	325	310
		13	5	-4

Year effect = + 29

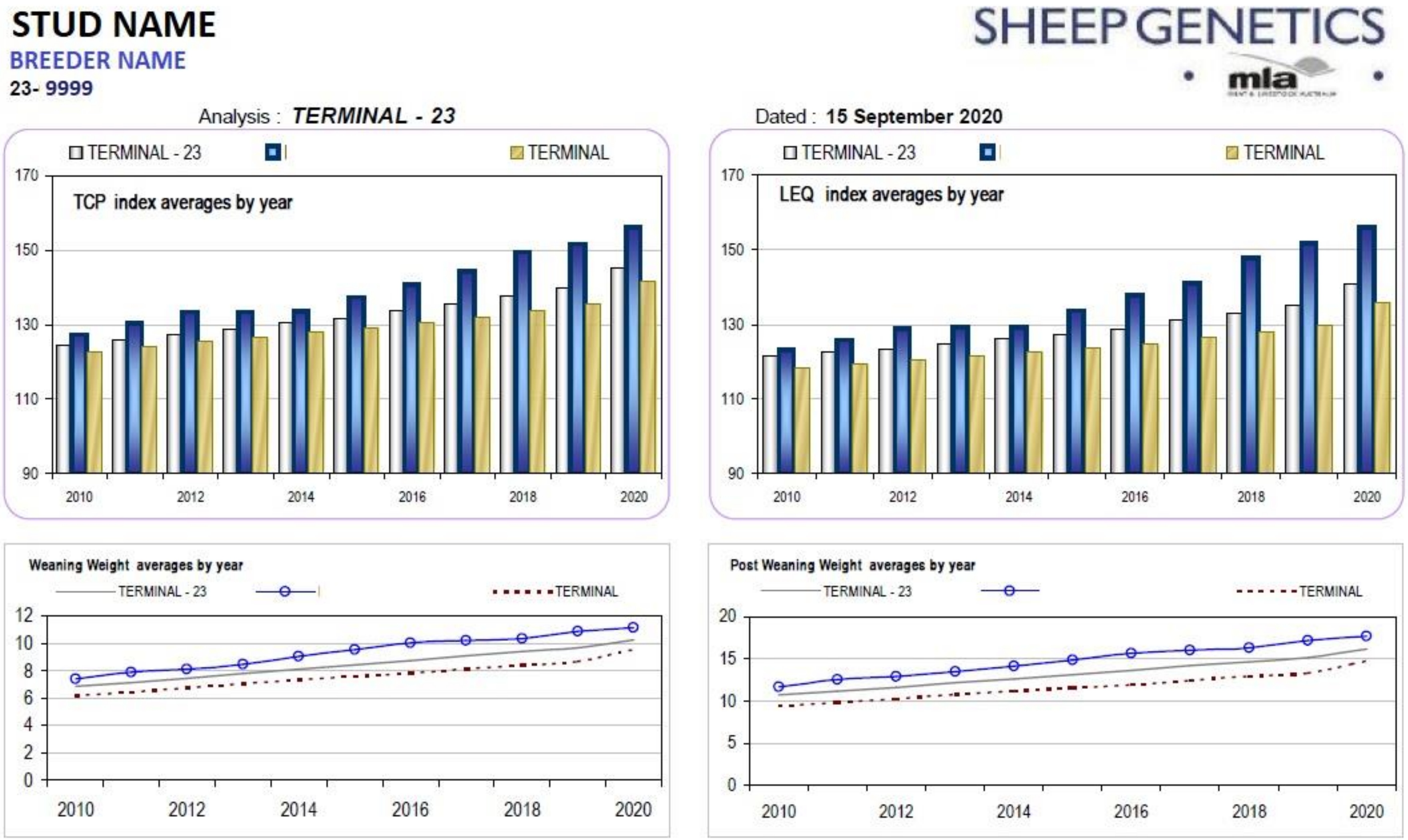
Sum to zero

genetic change = 4

Sum > zero

- BLUP accounts for selection (need a joint evaluation of all animals)
- Pedigree links between years
- Average EBV increases over years → genetic trend captured in EBV
- Year solutions only represent environmental trend

Genetic trends are published by Sheep Genetics



STUD NAME

BREEDER NAME

23- 9999

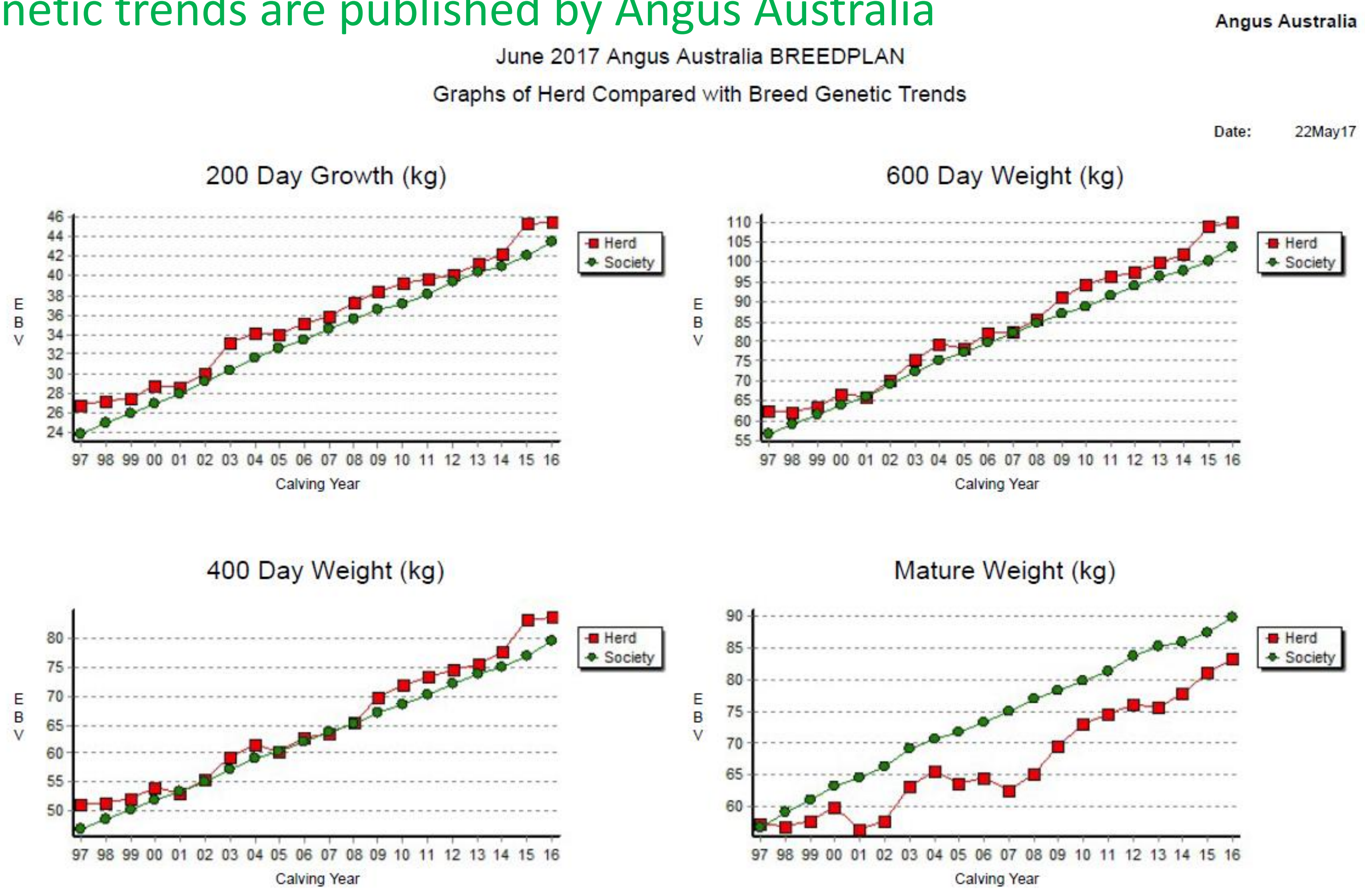
SHEEP GENETICS

mla

Analysis : ***TERMINAL - 23***

Dated : **15 September 2020**

Genetic trends are published by Angus Australia



Angus Australia

June 2017 Angus Australia BREEDPLAN

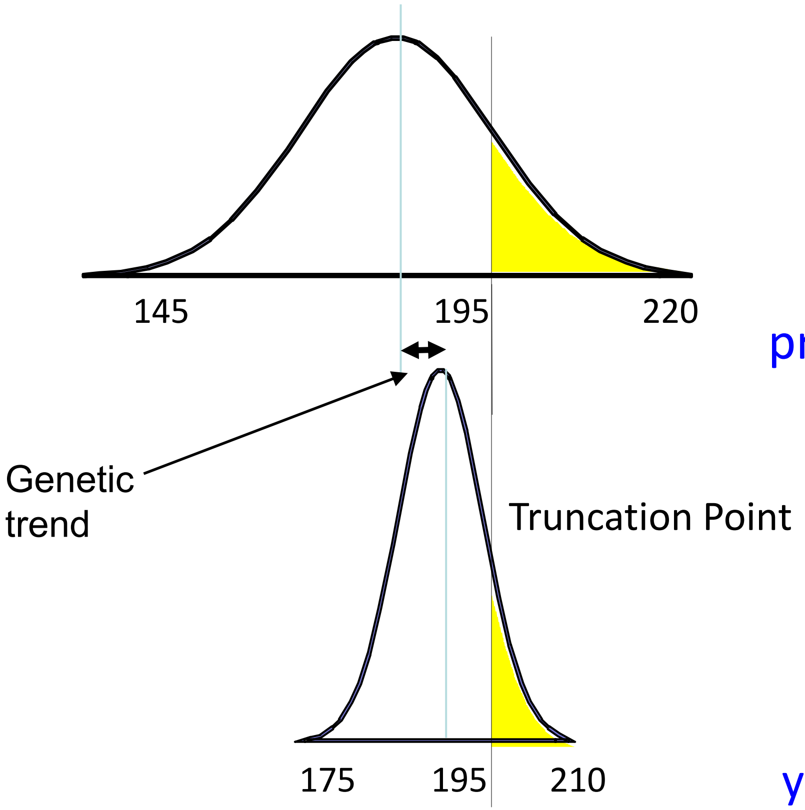
Graphs of Herd Compared with Breed Genetic Trends

Date: 22May17

Slide courtesy of C. Duff

BLUP helps selecting between old and young bulls

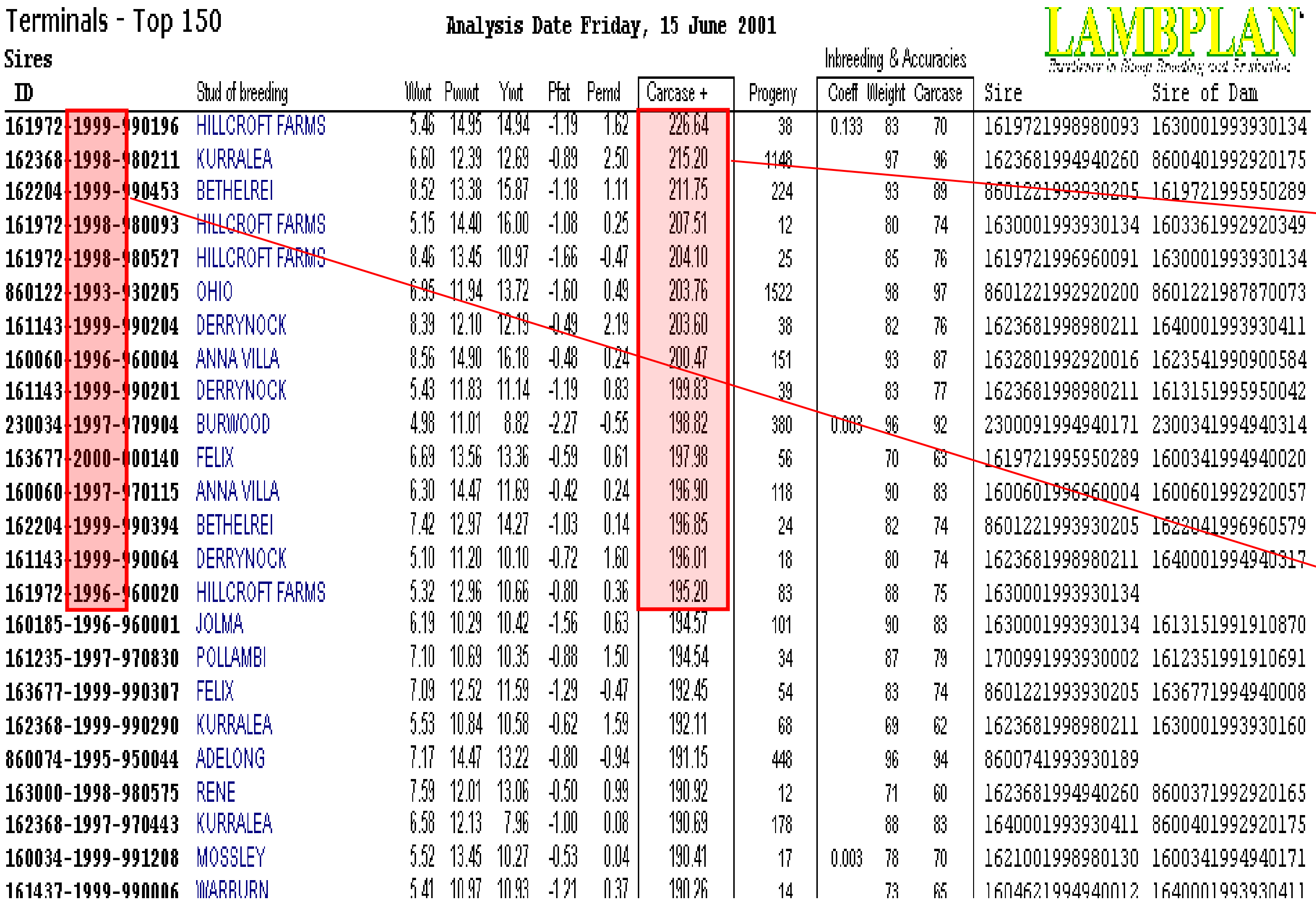
- EBVs can be compared directly over age classes
- Selection on BLUP EBVs optimizes generation interval



proven sires

young sires

Example of BLUP selection (truncation)



Terminals - Top 150

Analysis Date Friday, 15 June 2001

LAMBPLAN

Sires

									Inbreeding & Accuracies				
ID	Stud of breeding	Wwt	Pwwt	Ywt	Pfat	Pemd	Carcase +	Progeny	Coeff	Weight	Carcase	Sire	Sire of Dam
161972-1999-990196	HILLCROFT FARMS	5.46	14.95	14.94	-1.19	1.62	226.64	38	0.133	83	70	1619721998980093	1630001993930134
162368-1998-980211	KURRALEA	6.60	12.39	12.69	-0.89	2.50	215.20	1148		97	96	1623681994940260	8600401992920175
162204-1999-990453	BETHELREI	8.52	13.38	15.87	-1.18	1.11	211.75	224		93	89	8601221993930205	1619721995950289
161972-1998-980093	HILLCROFT FARMS	5.15	14.40	16.00	-1.08	0.25	207.51	12		80	74	1630001993930134	1603361992920349
161972-1998-980527	HILLCROFT FARMS	8.46	13.45	10.97	-1.66	-0.47	204.10	25		85	76	1619721996960091	1630001993930134
860122-1993-930205	OHIO	6.95	11.94	13.72	-1.60	0.49	203.76	1522		98	97	8601221992920200	8601221987870073
161143-1999-990204	DERRYNOCK	8.39	12.10	12.19	-0.49	2.19	203.60	38		82	76	1623681998980211	1640001993930411
160060-1996-960004	ANNA VILLA	8.56	14.90	16.18	-0.48	0.24	200.47	151		93	87	1632801992920016	1623541990900584
161143-1999-990201	DERRYNOCK	5.43	11.83	11.14	-1.19	0.83	199.83	39		83	77	1623681998980211	1613151995950042
230034-1997-970904	BURWOOD	4.98	11.01	8.82	-2.27	-0.55	198.82	380	0.003	96	92	2300091994940171	2300341994940314
163677-2000-000140	FELIX	6.69	13.56	13.36	-0.59	0.61	197.98	56		70	63	1619721995950289	1600341994940020
160060-1997-970115	ANNA VILLA	6.30	14.47	11.69	-0.42	0.24	196.90	118		90	83	1600601996960004	1600601992920057
162204-1999-990394	BETHELREI	7.42	12.97	14.27	-1.03	0.14	196.85	24		82	74	8601221993930205	1622041996960579
161143-1999-990064	DERRYNOCK	5.10	11.20	10.10	-0.72	1.60	196.01	18		80	74	1623681998980211	1640001994940317
161972-1996-960020	HILLCROFT FARMS	5.32	12.96	10.66	-0.80	0.36	195.20	83		88	75	1630001993930134	
160185-1996-960001	JOLMA	6.19	10.29	10.42	-1.56	0.63	194.57	101		90	83	1630001993930134	1613151991910870
161235-1997-970830	POLLAMBI	7.10	10.69	10.35	-0.88	1.50	194.54	34		87	79	1700991993930002	1612351991910691
163677-1999-990307	FELIX	7.09	12.52	11.59	-1.29	-0.47	192.45	54		83	74	8601221993930205	1636771994940008
162368-1999-990290	KURRALEA	5.53	10.84	10.58	-0.62	1.59	192.11	68		69	62	1623681998980211	1630001993930160
860074-1995-950044	ADELONG	7.17	14.47	13.22	-0.80	-0.94	191.15	448		96	94	8600741993930189	
163000-1998-980575	RENE	7.59	12.01	13.06	-0.50	0.99	190.92	12		71	60	1623681994940260	8600371992920165
162368-1997-970443	KURRALEA	6.58	12.13	7.96	-1.00	0.08	190.69	178		88	83	1640001993930411	8600401992920175
160034-1999-991208	MOSSLEY	5.52	13.45	10.27	-0.53	0.04	190.41	17	0.003	78	70	1621001998980130	1600341994940171
161437-1999-990006	WARBURN	5.41	10.97	10.93	-1.21	0.37	190.26	14		73	65	1604621994940012	1640001993930411

Consider top 15 sires, truncation point = 195

Sires in top are from various age classes

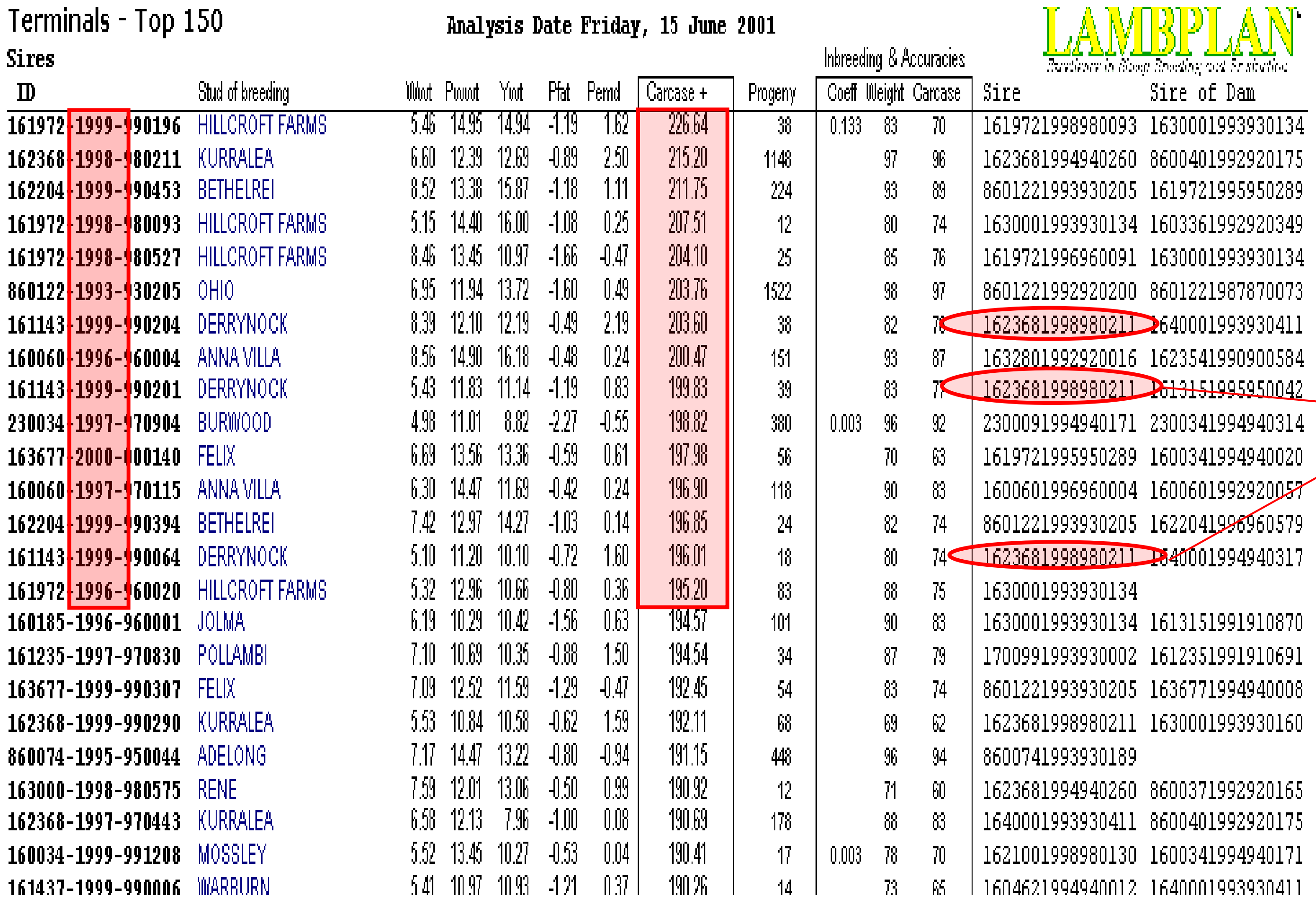
Another feature of BLUP

- BLUP uses family information (and more so at lower heritabilities)

- Selection on BLUP EBVs can thus result in higher inbreeding than selection on phenotypes alone

- Best strategy: Balance merit and genetic diversity
  - Start selecting from top, but leave an animal out if sibs have been selected already

Example of BLUP selection



Terminals - Top 150

Analysis Date Friday, 15 June 2001

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860074-1995-950044	ADELONG	7.17	14.47	13.22	-0.80	-0.94	191.15	448		96	94	8600741993930189	
163000-1998-980575	RENE	7.59	12.01	13.06	-0.50	0.99	190.92	12		71	60	1623681994940260	8600371992920165
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161437-1999-990006	WARBURN	5.41	10.97	10.93	-1.21	0.37	190.26	14		73	65	1604621994940012	1640001993930411

These are sibs so might not select all of them as flock sire

Advantages BLUP EBVs

- Optimal weights for all information sources
- Flexible: Lots of different sets exist of optimal weighting factors, BLUP does it automatically
- Allows comparisons of EBV's of animals in different herd (possibly with different genetic means)
  - *But links need to exist in the data!*
- Accounts for culling and selection, non-random mating
  - *But non selected animals need to be included in analysis!*
- Allows selection across age classes
- Provides an estimate of genetic trend

Consequences of BLUP selection

- Maximize genetic response in next generation

- Can compare animals over age classes
  → BLUP optimises generation interval

- Tend to select more related animals
  the more so with lower heritability
  → Simple selection on BLUP leads to more inbreeding

- Optimal selection uses BLUP + restricted inbreeding

See lecture 12

- BLUP only optimises next generation merit!

Accuracy of BLUP EBV's

The accuracy of an EBV depends on: 'the amount of information used'

The value of information (say a phenotype) depends on

1) the heritability,
2) the additive genetic relationship (if measured on another animal)
3) the genetic correlation (if measured on another trait)

Selection index can calculate these

4) the <u>effective number</u> of records, own or on relatives.

But not these

Effective number of records

a record has less value when in a small contemporary group

- A single observation is effectively worth

$$n_e = 1- (1/N)$$

where N is the number of animals
in the contemporary group

- Sire with n progeny in Contemp Grp of N:

$$n_e = \frac{n*(N-n)}{N}$$

Examples effective number of records

Contemporary group size (N)	1 record is effectively
1	0
2	0.5
4	0.75
20	0.95

$n_e = 1 - (1/N)$

Contemporary group size (N)	# sire A(n)	effective # sire A
1	1	0
10	10	0
10	9	0.9
10	1	0.9
10	5	2.5

$$n_e = \frac{n^*(N-n)}{N}$$

How is Accuracy (r) of BLUP-EBV's calculated?

- Use *inverse* of coefficient matrix of mixed model equations (MME)

$$\begin{pmatrix} \mathbf{X'X} & \mathbf{X'Z} \\ \mathbf{Z'X} & \mathbf{Z'Z} + \lambda\mathbf{A}^{-1} \end{pmatrix}^{-1}$$

independent of data values !!!!

Diagonal of Coeff. Matrix is basically the number of records per class/animal (N) + added relationships

Inverse of Coeff. Matrix is basically 1/(N+ added relationships)

- Use diagonal for animal i: C^{ii}
- Prediction Error Variance: $PEV = C^{ii}.var(e)$ (~ "σ^2/N")

Remember $PEV = (1-r^2_{IA}).V_A$

$$\rightarrow \quad r^2_{IA} = (V_A - PEV)/V_A$$

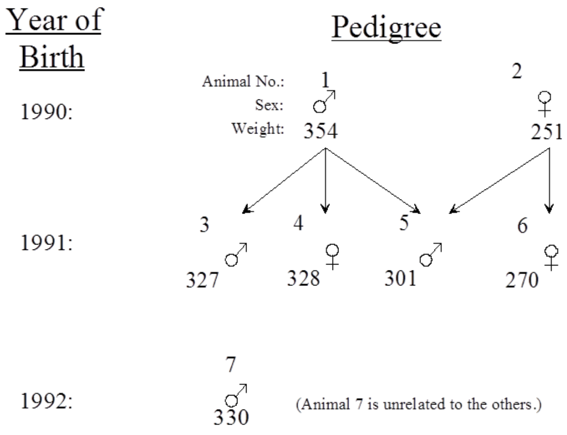
$$r^2_{IA} = 1 - \lambda C^{ii}$$

Accuracy = $r_{IA} = \sqrt{(1 - \lambda C^{ii})}$

C^{ii} is diagonal for animal "i" in MME

Accuracy of BLUP solutions

Solutions	Accuracy
311.94	
-9.15	
-8.90	
28.26	0.54
-28.85	0.56
18.34	0.56
18.77	0.56
-0.87	0.50
-22.40	0.58
0.00	0.00



Are these different from ‘selection index’?

Note accuracy of animal 7

BLUP EBV accuracy depends also on the model used!

Q: why are EBVs less accurate in Model 4?

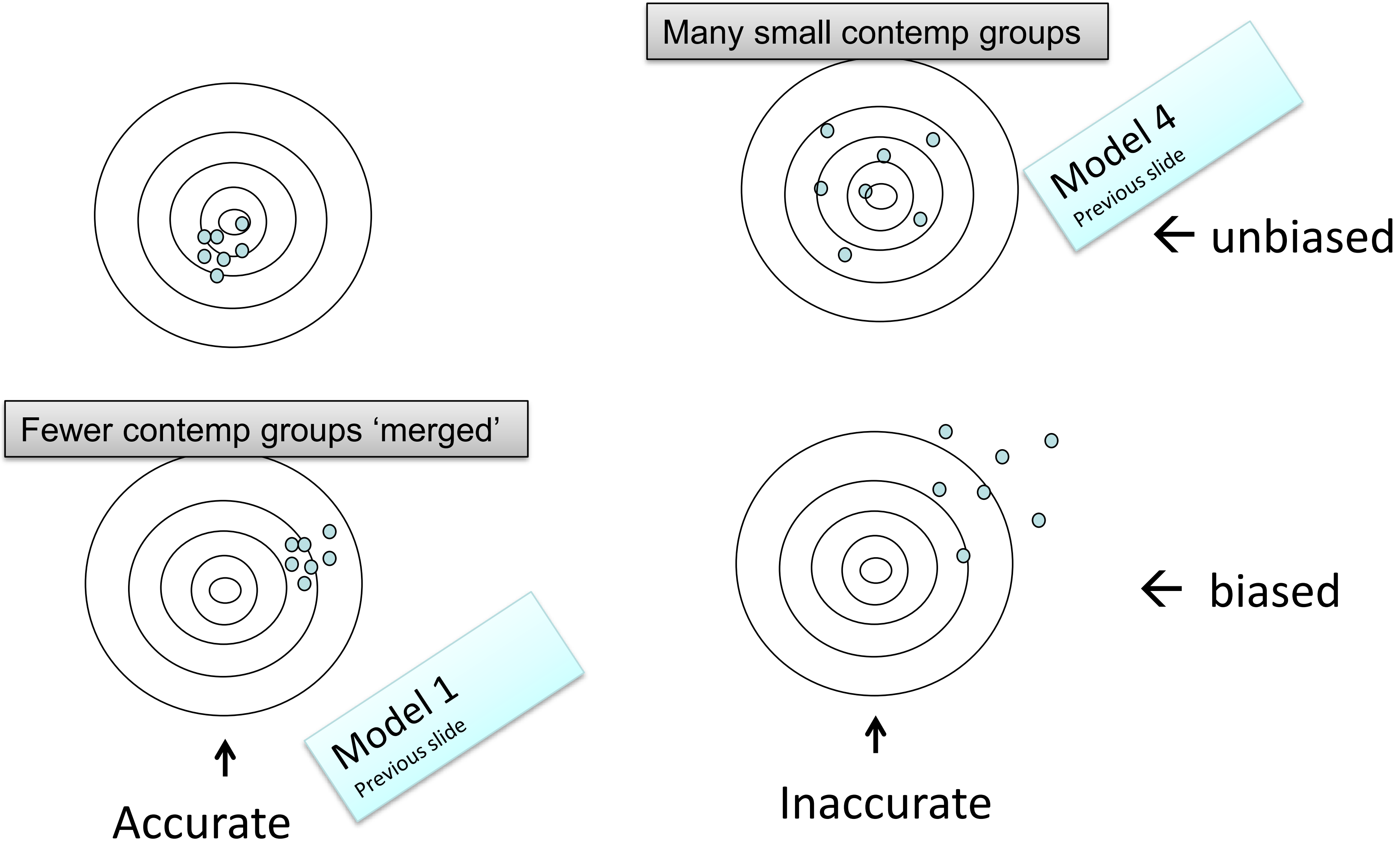
	model			
animal	1	2	3	**4**
1	0.7683	0.6082	0.5404	0.3809
2	0.7516	0.6264	0.5561	0.5181
3	0.7335	0.609	0.5647	0.4164
4	0.7335	0.609	0.5647	0.5554
5	0.7612	0.5664	0.504	0.4243
6	0.7321	0.6175	0.5788	0.5124
7	0.7071	0.6304	0	0

model 1 y = animal (mean is known)
m2: y = mean + animal
m3: y = mean + year + animal
m4: y = mean + year + sex + animal

Need to find a balance between accuracy and bias

Note that model 1 gives “selection index” accuracies

The balance between accuracy and bias



Many small contemp groups

Model 4
Previous slide

← unbiased

Fewer contemp groups ‘merged’

Model 1
Previous slide

← biased

↑ Accurate

↑ Inaccurate

Conclusion

Need to find a balance between

unbiasedness

> many (i.e. small)
fixed effect classes

and

accuracy

> few (i.e. large)
fixed effect classes

An observation is more worth when compared with many others

In progeny testing designs, we don’t need necessarily many progeny of the same sire tested in same flock/herd,

in fact better spread across as many flocks as possible

Evaluation of animals in practice

- Need proper data (centralized database)
  - recording system (management groups)
  - correct animal identification
  - Non-selective data reporting
  - other issues?

- Need proper model
  - Account for bias and selection
  - Account for other effects (maternal, permanent environment, multiple trait, different breeds)

The simple mixed model expanded

- Simple mixed model

  y = contempgrp + animal + residual

- More general

  y = fixed effects + random effects + residual

y:

- One trait
- More traits

fixed effects:

- cg
- age
- …..
- …..

random effects:

- animal
- maternal
- permanent env.
- sire x herd

residual:

homogeneous

heterogeneous

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

Reasons for multiple trait genetic evaluation

- Increased accuracy
  - Information from correlated traits

    (can check with selection index)

- To avoid selection bias
  - Sequential selection
  - Contemporary selection

Example of multiple trait model

Individual	Herd	Weaning Weight	Yearling Weight
1	1	160	-
2	1	180	320
3	1	210	330
4	2	190	-
5	2	228	360
6	2	210	350

Those two were culled after weaning

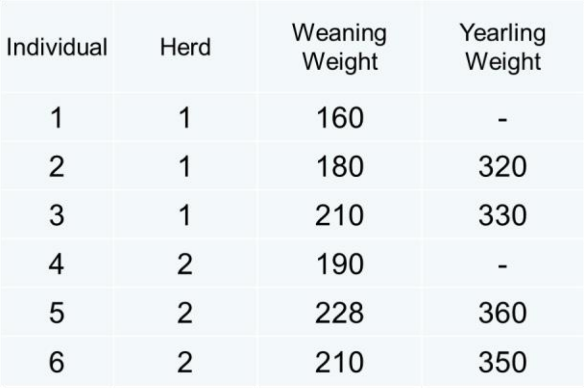
Genetic Parameters

$\sigma_{p1 = 20}$ $h^2{}_1 = .42$

$r_g = .8$; $r_e = 0.6$

$\sigma_{p2 = 40}$ $h^2{}_2 = .39$

Example of multiple trait model



Individual	Herd	Weaning Weight	Yearling Weight
1	1	160	-
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3	1	210	330
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5	2	228	360
6	2	210	350

		Single Trait Model Soln's		Multiple Trait Model Soln's	
		WW	YW	WW	YW
herd	b1	183	325	183	309
herd	b2	209	355	209	342
animal	u1	-9.86	0	-9.86	-14.58
animal	u2	-1.41	-1.95	-1	2.87
animal	u3	11.27	1.95	10.86	11.72
animal	u4	-8.17	0	-8.17	-12.08
animal	u5	7.89	1.95	7.7	9.35
animal	u6	0.28	-1.95	0.47	2.73

Herd effect on YW overestimated in ST

Animals without YW records get an EBV for YW

Average of selected animals >0 in MT

Differences in EBV2 are larger in MT

Advantages of Multiple Trait BLUP evaluation

- increase in accuracy of EBV's overall
- Also EBVs if no record (use correlated trait)
- correct for selection on correlated trait

- The accuracy increase depends on
  - *the information available on each animal*
  - *Information from correlated trait is more useful if limited information on trait itself*
  - *Heritability of traits and correlations between them*

Genetic groups, e.g. breed effects

Consider them as a (fixed) effect in the model

But add those to breeding values……..

$\text{EBV}_{\text{across}} = \text{EBV}_{\text{within}} + \text{group\_solution}$

Grouping needed whenever there is a genetic difference in base animals

(to account for selection: breeds, origin,….)

Only need to group the unknown parents

Remember that relationships matrix accounts for other selection

Example of genetic groups

Michael Angus	315	Mean Angus	300
Whiskey Hereford	315	Mean Hereford	320

if own performance ($h^2 = 0.4$)	$\text{EBV}_{\text{within}}$	$\text{EBV}_{\text{across}}$
Michael Angus	+ 6	+ 6
Whiskey Hereford	- 2	+ 18

if values are progeny means (“h^2 “= 0.9)	$\text{EBV}_{\text{within}}$	$\text{EBV}_{\text{across}}$
Michael Angus	+ 13.5	+ 13.5
Whiskey Hereford	- 4.5	+ 15.5

Genetic group (pedigree) becomes less important with more information and confidence in performance of the sire itself