1   GENERAL INTRODUCTION

Selection of sires and dams can be used to improve economically important carcase traits of subsequent generations of cattle. This selection is based on estimates of the genetic value of animals as parents. The physical expression of an animal for a particular trait - its phenotype, is a result of its genetic makeup and the environment to which it has been exposed to. Quantitative methods can be used to separate the effects of genes and the environment on animals phenotypes to estimate the genetic value of animals. The resulting estimated breeding values (EBVs) can then be used to select genetically superior sires and dams. Statistical analysis has developed over time and best linear unbiased prediction (BLUP) has been in common use for many years to estimate breeding values. For example, BLUP has been used since 1981 for beef cattle evaluation in Australia (Graser et al. 2005).

As carcase traits are not measurable on live animals, carcase trait records of progeny can be used to estimate sire breeding values. Groups of progeny may be sent to feedlots and for various reasons subsets of these original groups may be individually removed for slaughter. Animals are often non-randomly removed for slaughter over time according to market suitability for weight and fatness (Colditz et al. 2007). Other reasons for removing subsets of animals are the need to create space in feedlots for incoming cattle and the kill capacity of abattoirs. However, regardless of the reason, those animals assessed as meeting the carcase requirements of the market will be slaughtered first to maximise profit. Animals will be chosen based on live-animal indicators of carcase value.

It is expected that progeny of different sires will be genetically different for traits associated with the market specifications. The resulting difference in progeny performance could result in differential removal (i.e. harvesting) of progeny between sires, thus generating non-random subsets of progeny slaughtered. An issue arising from this harvesting is how carcase trait records are influenced by effects particular to a harvest group. It is from an understanding of these two issues that it can be appreciated how the carcase trait measurements between harvest groups may differ and how the statistical estimation of breeding values may be affected by them. The aims of this thesis are to explore these issues and find appropriate statistical methodology that can be applied to

harvested data to give unbiased and accurate estimated breeding values (EBVs) for carcase traits.

Methodology has been proposed to account for harvesting providing the history of selection is available from the data. Unbiased EBVs may result for a trait recorded on a subset of animals chosen based on the records of a previously measured trait if the two traits are correlated (Pollak et al. 1984; Schaeffer et al. 1998). Accurate EBVs resulted from a multivariate analysis of harvested data when the history of selection was contained in the data (Jopson et al. 2007). However, for the specific case of a progeny test to estimate sire carcase trait breeding values where progeny have been harvested over time, the history of selection in the form of records available for the harvesting criteria at the point of harvest may not be available.

Fitting inappropriate statistical models to this type of data may result in biased and inaccurate EBVs which can lead to reduced genetic gain through suboptimum choice of parents. This type of data results when records of harvested animals are only available at slaughter. This study explores the potential effects of harvesting over time on EBV prediction and aims to find appropriate statistical methodology including suitable models that result in unbiased and accurate EBVs for harvested data where the history of selection may not be directly known from the available data.

To achieve this, both simulated and field data was used. Simulation of harvested data provided data sets with known genetic parameters including true breeding values enabling calculation of EBV accuracy and bias from applying different models. Although appropriate harvested field data was not available, consideration of the structure of particular non-harvested field data provided a data set that could represent harvested data.

The study begins with a review of literature in Chapter 2. The effect of the market on harvesting is explored and explanation given how records taken on different slaughter days can differ due to many potential harvest day effects. Statistical background relevant to analysing harvested data is explored, particularly the use of best linear unbiased prediction (BLUP) and restricted (residual) maximum likelihood (REML) in the prediction of EBVs.

CHAPTER 1. GENERAL INTRODUCTION

Chapters 3, 4 and 5 explore the application of various models and trait adjustments to simulated harvested data. In Chapter 3, harvested data comprising the records of a single age-dependent trait which was also the criteria for harvesting is analysed, with and without harvest day effects added. This provides insight into the effect of harvesting on EBV accuracy and bias, as well as variance component estimation. This single trait simulation study is then extended in Chapter 4 by examining the potential use of normal distribution theory to adjust harvested records to the point of the first harvest. In Chapter 5, this single trait study is extended to the simulation of an age-dependent carcase trait correlated to the harvesting criteria. Different models were applied to predict EBVs of the carcase trait with varying levels of genetic correlation with the harvesting criteria. Variation in the magnitude of harvest day effects and number of progeny were explored.

A field data set was used in Chapter 6, providing evidence of the practical applicability of different statistical analyses to predict EBVs from harvested data. Finally, the General Discussion summarises major outcomes of the preceding studies, exploring the applicability of the results to the beef industry.

2   LITERATURE REVIEW

2.1   Introduction

In Australia, approximately 8 million adult cattle were slaughtered in the 2006-07 year, and of these one third were grainfed (MLA 2007). The beef cattle industry derives maximum profit by providing animals with carcase characteristics that meet the requirements of particular markets (Reverter et al. 2003b). This influences the prices cattle finishers are offered by abattoirs. Many carcase traits have been shown to be heritable (Burrow et al. 2001; Utrera and Van Vleck 2004). Having a genetic basis, several carcase traits have been incorporated into Australia's genetic evaluation system 'BREEDPLAN' (Johnston et al. 1999).

This thesis focuses on the problem of and possible solutions to estimating carcase trait breeding values for sires from harvested progeny. This section lays out market specifications that can lead to harvesting, introduces harvest group effects and their potential to affect genetic evaluation, and explores statistical methodology that may be used to account for harvesting.

2.2   Harvesting decisions are based on the market

Market demand for carcases meeting particular specifications can lead to harvesting of live animals from within an original contemporary group. In Australia there are numerous requirements for different markets as illustrated in Table 2.1. The two main carcase specifications for determining market eligibility are hot standard carcase weight and P8 fat depth (Pitchford et al. 2006).

Although it is likely that cattle are harvested primarily on live-animal indicators of carcase weight and fat depth, other carcase specifications may influence harvesting decisions. As examples, leanness and marbling have been indicated as important properties in Australia, and tenderness followed by flavour have been indicated as the most important eating qualities of cooked meat for Australian consumers (Egan et al. 2001). Marbling is one of the determining factors in Australia influencing the price paid for beef destined for the Japanese market, with a score of 2-4 on the 12 level grading system defined by the Australian Meat and Livestock Corporation (now Meat and Livestock Australia) being

4

used to line beef up with the grade most widely required by the Japanese marketing system (Baud et al. 1998b).

Table 2.1 Major and minor market specifications. Source: Andrews and Littler (2007)

Major	
Weight (live or carcase)	Sex
Fat (P8 fat depth or score)	Age (dentition)
Minor	
Breed	Hormonal growth promotant status
Lifetime traceability	Meat colour
Accreditation or other eligibility requirements (e.g. European Union market, Woolworths, Meat Standards Australia)	Fat colour
	Fat distribution
	Meat/carcase pH
Muscle score	Butt Shape

The two major carcase specifications for cattle entering major markets for Australia are fat depth and liveweight (LWT). Sometimes cattle must fall into quite narrow ranges for these characteristics to meet the specifications as Figure 2.1 illustrates. The large range in LWTs and fat depth for contemporary groups in one series of studies illustrates that it is likely original contemporary groups will be harvested over time to meet market specifications. For one study, with no harvesting, the standard deviation for LWT at the end of finishing for temperate breeds ranged from about 38 to 44 kg for different market weights and finishing regimes (Johnston et al. 2003). In this same series of papers, for temperate breeds, a multivariate analysis resulted in a standard deviation for P8 fat depth of 2.80 mm (Reverter et al. 2003b). In these studies, the two traits were adjusted to a constant age and constant carcase weight, respectively. These variability values are therefore likely to be much lower than the variability in the unadjusted measurements. With such large variation, animals within a contemporary group may be harvested over time to meet the specific requirements of the market for LWT and P8 fat depth as illustrated in Figure 2.1.
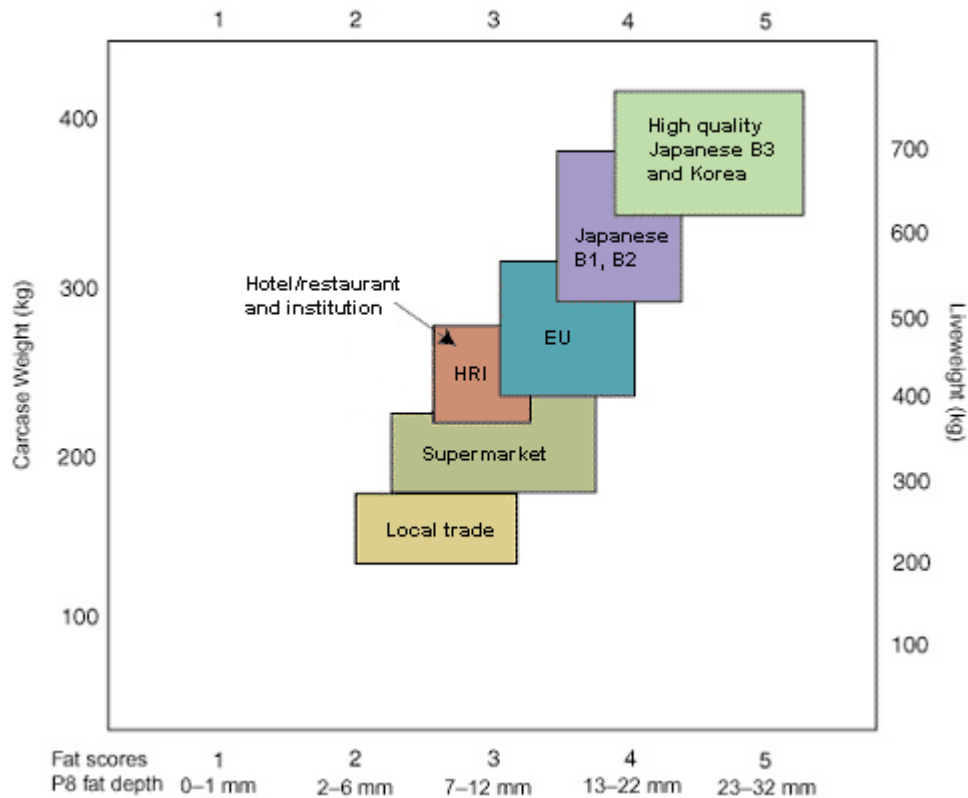
Figure 2.1 Basic weight and fat specifications for the major market segments. Source: Beer and Newsome (2004)

2.3   Definition of harvest group effects

Harvest group effects are influences on trait measurements particular to the individual harvest group. This thesis focuses on effects that influence all the records of a particular harvest group. As this thesis focuses on harvesting over time these effects have been referred to as specific harvest day effects. These effects are not limited to those occurring on a single day but are specific to the group of animals slaughtered on a particular day.

Harvest group effects also include influences that affect proportions of individual harvest groups, for example due to changes in staff or accuracy of scales during measurement of individual harvest groups. This thesis does not specifically address these within-harvest group effects, but assumes they occur randomly and become part of the residual error.

2.3.1   Examples of specific harvest day effects

There are many examples of specific harvest day effects. Significant differences in muscle glycogen levels were found between seasons for pasture fed cattle (Knee et al.

2004), leading to possible differences in meat quality traits. Ferguson *et al*. (2001) reported that the palatability of beef is influenced most by the conditions cattle are exposed to just prior to slaughter and the specific prevailing conditions in the first 24 hours post-slaughter.

An experiment carried out in Queensland, Australia (Wythes et al. 1981) showed that cows travelling for a longer distance and which had a greater time between mustering and slaughter had significantly greater LWT loss (13.6 vs. 10.4%) and significantly lower gross hot carcase weight (219 kg compared with 226 kg where initial LWT differences were accounted for). However, no significant differences were found between groups for muscle pH. In this experiment the management procedures at the abattoirs were standardized.

A Brazilian study involved 45 Nelore steers at an average age of 37 months (Ferreira et al. 2006) . After exposure to different combinations of transport times and resting periods (0 to 24 hours), they were slaughtered and electrically stimulated. When no rest was given before slaughter, the ultimate pH (taken 24h post-mortem) was significantly higher for animals transported for about 5 hours compared to up to 2 hours (pH 6.04 vs. 5.68, P<0.05). For higher rest periods no significant difference was found between ultimate pH values. A pH of 6.04 was considered to be moderately dry, firm and dark (DFD). This agrees with other literature (Ferguson et al. 2001; Locker 1989).

A study reported by Johnston et al. (2001) looking at beef tenderness as measured by Warner-Bratzler shear force in tropically adapted breeds found that the slaughter date effect within an abattoir accounted for 15.3% of the total variance for the M. Longissimus dorsi muscle. This did not include the electrical stimulation effect partitioned out as making up 1.1% of the total variance. However, the slaughter date effect also included the effect of intake group which were groups of animals in the same sex, season and year.

2.3.2 Potential influence of specific harvest day effects on genetic evaluation

To account for specific harvest day effects in a genetic evaluation of records resulting from harvesting over time, harvest group may be fitted as a fixed effect in the model. However, the effects of age and harvest group may be inseparable by particular models

causing predicted EBVs to be biased. Because age partially determines when animals are harvested, age may become confounded with harvest groups.

2.4 Accounting for harvesting over time through statistical methodology

Harvesting based on particular criteria such as weight and fatness can lead to non-random groups of cattle slaughtered over time. In a progeny test, it is likely that progeny of the genetically faster growing sires for these criteria will be slaughtered in earlier groups. Moreover, previous discussion established the reality and magnitude of possible specific harvest day effects. The issue of particular interest is whether statistical analysis can give accurate and unbiased EBVs and related variance components using harvested data.

2.4.1 Best linear unbiased prediction (BLUP)

EBVs are predicted random effects for individual animals subject to different environmental factors. Considering these as fixed effects, a statistical method is required that can predict EBVs taking these into account. Best linear unbiased prediction (BLUP) developed by Henderson (1949; 1950; 1973) is such a method and is now used extensively in animal industries internationally to predict EBVs (Mrode 2005).

The BLUP methodology is used to give best linear unbiased predictions of EBVs and best linear unbiased estimates (BLUE) of fixed effects. For prediction of random effects major properties of this methodology are that the random effects are a linear function of the data, they are unbiased as the expectation of the predictor is the true mean of the random effect, they are best as the variance of the estimated random effects less their true effects are minimised in this class of linear predictors, and interest is in predicting future records (Henderson 1984).

A basic linear model to describe data as a function of both fixed and random effects (a mixed model) can be defined as follows (Henderson 1984):

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Zu} + \mathbf{e} \tag{2.1}$$

where **y** is an nx1 vector of observations, **X** is a known nxp incidence matrix for fixed effects, **β** is a px1 vector of generally unknown fixed effects, **Z** is a known nxq incidence matrix for random effects, **u** is a qx1 vector of unknown random effects, and **e** is an nx1 vector of random residual effects.

The random u and e effects are assumed to have means of 0. The symmetric (co)variance matrix for **u** is denoted by **G** with dimensions qxq. The symmetric (co)variance matrix for **e** is denoted by **R** with dimensions nxn. It is assumed that the random u effects are independent of the random e effects, i.e., that cov(**u**,**e'**)=0.

Further, E(**y**) = **Xβ** and Variance(**y**) = **ZGZ' + R = V**

Solving the following simultaneous equations known as Henderson's mixed model equations (Henderson 1950) results in a generalised least squares solution for fixed effects (**β°**) and is often a simple way to calculate BLUP of **u** (**û**) (Henderson 1984):

$$\begin{bmatrix} \mathbf{X'R^{-1}X} & \mathbf{X'R^{-1}Z} \\ \mathbf{Z'R^{-1}X} & \mathbf{Z'R^{-1}Z+G^{-1}} \end{bmatrix} \begin{bmatrix} \mathbf{\beta^0} \\ \mathbf{\hat{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X'R^{-1}y} \\ \mathbf{Z'R^{-1}y} \end{bmatrix} \qquad [2.2]$$

For BLUP, **G** and **R** are assumed known. However, these must be estimated from available data. Inaccurate variance components can lead to larger prediction error variances of random effects. For example, Henderson (1975a) showed this effect when an incorrect **G** was used.

2.4.2 Accuracy of EBVs

The accuracy of EBVs may be determined as the correlation between EBVs and true breeding values (TBVs) as used by Tosh and Wilton (1994). The following equation for generational change in response to parental selection indicates that accuracy is an important determinant (Cameron 1997):

$R_n = I \times r_{TBV,EBV} \times \sigma_A$

Where i is the parental selection intensity, $r_{TBV,EBV}$ is the accuracy of EBVs and σ_A is the additive genetic standard deviation. Simulated data as used in this thesis provides known TBVs enabling direct calculation of EBV accuracy resulting from fitting different models.

2.4.3 Estimation of variance components

There are various methods available to estimate variance components. However, because of desirable statistical properties, restricted (or residual) maximum likelihood (REML) has become a standard in animal breeding for the estimation of variance components (Duangjinda et al. 2001). This section describes this method and the related method maximum likelihood (ML).

2.4.3.1 Maximum likelihood (ML)

Variance components may be estimated by assuming multivariate normality of the data and maximising the likelihood of the fixed effects **β** and the variance components for the mixed model given the set of observations **y**. This ML procedure however, does not take into account the degrees of freedom involved in estimation of fixed effects when estimating variance components and leads to biased estimators of variance components (Searle et al. 1992). This issue regarding accounting for degrees of freedom has been solved by the use of REML.

2.4.3.2 Restricted maximum likelihood (REML)

Methodology for REML was presented by Patterson and Thompson (1971). REML has become popular for the estimation of variance components for mixed models assuming normally distributed random effects (Gilmour et al. 1995). In presenting the modified maximum likelihood procedure REML, Patterson and Thompson (1971) describe maximising the likelihood of a set of selected error contrasts to estimate within- and between-block weights for the incomplete block design when blocks may be different sizes. The problem can be considered as estimating fixed effects and variance components in a general two-way classification dividing data into fixed and random effects. REML maximises the joint likelihood of all possible error contrasts where the expectations are zero. Contrasts between fixed effect totals are not included in the

likelihood function assuming they provide no information on error (Patterson and Thompson 1971).

REML can be described as estimating variance components based on the residuals determined after the fixed effects of the model have been fitted. These are linear combinations of observations not containing fixed effects and have been referred to as 'error contrasts' (Searle et al. 1992).

2.4.4 Best linear unbiased prediction under selection

Henderson (1990) describes selection assuming the model presented as [2.1] and multivariate normality. Selection is based on a random vector **w**. The mean and (co)variance matrix of **w** changes with selection from what it would have been without selection. It is assumed that **w** is correlated with **u** and **e**, with **u** only or **e** only. The following equations describe the model involving **w** when there is no selection:

$$E\begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \\ \mathbf{w} \end{bmatrix} = \begin{bmatrix} \mathbf{X\beta} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{d} \end{bmatrix}$$

$$V\begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \\ \mathbf{w} \end{bmatrix} = \begin{bmatrix} \mathbf{ZGZ'+R} & \mathbf{ZG} & \mathbf{R} & \mathbf{B_y} \\ & \mathbf{G} & \mathbf{0} & \mathbf{B_u} \\ \text{Symmetric} & & \mathbf{R} & \mathbf{B_e} \\ & & & \mathbf{H} \end{bmatrix}$$

where $\mathbf{B_y} = \mathbf{ZB_u} + \mathbf{B_e}$

Drawing on Pearson (1903), Henderson (1990) presented means and (co)variances conditional on linear selection functions - in this case when selection is based on **w**. In this case **w** is selected and under repeated sampling results in E(**w**) = **s** rather than **d** and var(**w**) = $\mathbf{H_s}$ rather than **H**.

w is equal to **L'y** where **L'** defines the rules of selection. It is shown that although the means and variances change with selection, the usual mixed model equations ([2.2]) can

result in the correct values for fixed effects and estimations for random values equal to the conditional means. This will occur when $\mathbf{L'X} = 0$, σ^2_a and σ^2_e are correct, and all data is used.

Further, unbiased estimators of $\boldsymbol{\beta}$ and predictors of $\mathbf{u}$ will result from the normal mixed model equations ([2.2]) when the distribution is multivariate normal, and selection is based on translation invariant linear functions where the functions will remain the same regardless of the fixed effects.

However, for the case of harvesting over time based on LWT, selection is not invariant to the fixed effect of age and genetic values may become confounded with age. An example was given by Henderson (1990) that considered this issue. A covariate was simulated but ignored in the selection process with culling based on the unadjusted phenotype. The covariate was included in the model and the normal mixed model equations gave biased results. For this example $\mathbf{L'X}$ did not equal zero. Modifying the normal mixed model equations to account for $\mathbf{L'X}$ not being equal to zero resulted in unbiased estimators and predictors.

For the selection model, modification of the normal mixed model equations ([2.2]) are given which result in BLUE of fixed effects and BLUP of random effects:

$$
\begin{bmatrix}
\mathbf{X'R^{-1}X} & \mathbf{X'R^{-1}Z} & \mathbf{X'R^{-1}B_e} \\
\mathbf{Z'R^{-1}X} & \mathbf{Z'R^{-1}Z + G^{-1}} & \mathbf{Z'R^{-1}B_e - G^{-1}B_u} \\
\mathbf{B'_eR^{-1}X} & \mathbf{B'_eR^{-1}Z - B'_uG^{-1}} & \mathbf{B'_eR^{-1}B_e + B'_uG^{-1}B_u}
\end{bmatrix}
\begin{bmatrix}
\boldsymbol{\beta}^{\circ} \\
\mathbf{u}^{\circ} \\
\mathbf{t}^{\circ}
\end{bmatrix}
=
\begin{bmatrix}
\mathbf{X'R^{-1}y} \\
\mathbf{Z'R^{-1}y} \\
\mathbf{B'_eR^{-1}y}
\end{bmatrix}
$$

The zero superscripts indicate that the solution may not be unique. Methods are given to check for estimability and predictability when the solution is not unique. Appropriately adjusting for fixed effects generally causes $\mathbf{L'X}$ to equal zero and therefore removes the need to write $\mathbf{L'}$ and use modified mixed model equations (Henderson 1990).

2.4.5 Estimation of variance components from selected data

Gianola et al. (1989) describe methods of estimating genetic variance components under selection, focussing on likelihood methods and selection where animals recorded at time

2 were a subset selected from the animals recorded at time 1. It was explained that theory given by Pearson (1903) and used by Henderson (1975b) was inadequate for this type of selection due to the principle being violated that there should be random sampling of animals at the first point of selection.

Gianola et al. (1989) describe three kinds of likelihoods to estimate parameters applicable to selection on observations as described above where the second set of measurements are on a selected subset of the animals measured previously. These are conditional, unconditional and partial likelihoods. In particular, for the unconditional likelihood, functions representing the joint densities of all observations (including observations at both measurement points) given a parameter vector, say θ, which ignore selection can be maximised to find the desired parameters. This provides a way to estimate variance components ignoring selection of this type, which can be extended to more rounds of selection. This is applicable to any distribution indexed by a given θ. Although with this type of selection, maximising the unconditional likelihood does not differ from when there is no selection, calculation of the (co)variability of the resulting estimates must change with selection and several authors have described possibilities (Cox and Hinkley 1974; Curnow 1961; Im et al. 1989; Thompson 1973).

For any likelihood based method inferences can be made ignoring selection if the history of selection is included in the data, regardless of the distribution and including when estimators are nonlinear and selection criteria change with fixed effects (Schaeffer et al. 1998). This suggests that for harvested data the history of selection should be contained in the available records to estimate variance components using REML.

2.4.6 Use of multiple-trait BLUP to account for sequential selection

Sequential selection involves the removal of some of the animals available based on particular criteria leading to a non-random sample of the original animals available for measurement of a subsequent trait. For example, estimation of breeding values for yearling LWT of cattle remaining after removal of the lightest animals at weaning. Multiple trait analysis can be used to analyse data subjected to sequential selection. Simulation studies have examined the use of multiple trait evaluation to remove bias caused by sequential selection and selection on correlated traits (Pollak and Quaas 1981; Pollak et al. 1984).

Multiple trait analysis has the potential to remove bias resulting from selection in estimation of breeding values (Pollak et al. 1984). In BLUP methodology described by Henderson (1973) the inverse of the relationship matrix is necessary to account for the relationships between relatives. A simple method of computing the inverse of the relationship matrix (**A**) from pedigree information was discovered (Henderson 1976). With the ability to easily compute $\mathbf{A}^{-1}$ and its known application in BLUP equations, multiple trait evaluation involving the relationships of many relatives became computationally feasible (Henderson and Quaas 1976). Henderson and Quaas (1976) present such methodology for multiple trait evaluation. The methods are based on the mixed linear model ([2.1]) and mixed model equations ([2.2]) described earlier. For these methods where **u** is a vector of unknown breeding values, the elements of **y** and **u** are ordered by animals within traits. Where there are no missing records, if n is the number of animals and q the number of traits, then **β** is subdivided into q vectors (i.e., $\boldsymbol{\beta}' = [\boldsymbol{\beta}'_1, \boldsymbol{\beta}'_2, \ldots , \boldsymbol{\beta}'_q]$) referring to the fixed effects for each trait, and **X** is partitioned into sub-matrices ($\mathbf{X}_1, \mathbf{X}_2, \ldots, \mathbf{X}_q$) to map animals to the corresponding fixed effects in **β** for each trait, i.e.

$$\mathbf{X} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} & \cdots & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 & \cdots & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{X}_q \end{bmatrix}$$

Z is an identity matrix (**I**) of order nqxnq.

The mixed model equations given in [2.2] expanded to include multiple traits, the (co)variances between them and the relationships between animals are then solved for $\boldsymbol{\beta}^o$ and $\hat{\mathbf{u}}$ using any generalised inverse of the coefficient matrix. Henderson and Quaas (1976) give specific calculation details which include the use of $\mathbf{A}^{-1}$.

Detailed methodology for calculating fixed effects and breeding values is also given in the case where some records are missing (Henderson and Quaas 1976). This includes a specific characterization for all the animals within a group of animals having the same pattern of missing values in the calculation of $\mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}$, which is needed for the mixed

model equations. Following the specific calculations set out, the best linear unbiased estimator of **Xβ** and BLUP of **u** results if there was no selection or selection was carried out within fixed effects.

Assuming known (co)variance components Pollak et al. (1984) illustrated bias resulting from analysis of a single trait affected by selection on a correlated trait. Drawing from the simulation work of Pollak and Quaas (1981), potential bias resulting from sequential selection was illustrated. The yearling weights of cattle left after culling on weaning weight were evaluated. Records on weaning weights for all animals and post-weaning gain for selected animals were available. Yearling weight was calculated as the sum of the weaning weight and post-weaning gain to yearling age. Heritabilities and genetic correlations were defined and several intensities of selection on weaning weight imposed. For one scenario, all animals with weaning weights less than the mean of their contemporary group were culled. Two methods were used to analyse yearling weight, the first a multiple trait analysis using weaning weight and post weaning gain ignoring weaning weights of culled animals, and the second a similar multiple trait analysis including the weaning weights of culled animals. In both analyses yearling weight was evaluated as the sum of the weaning weight and post-weaning gain evaluations for each animal.

It was expected that better sires would have more progeny left after selection at weaning. Selection at weaning caused the progeny of sires to be 22 kg heavier on average as yearlings compared to no selection. Also, the range in yearling weight between the 'worst' and 'best' sires reduced from 30 kg without selection to 9 kg with selection. The evaluation of yearling weight is summarised in Table 2.2 for sires arranged according to their number of progeny remaining after selection at weaning (averaged over 100 replicates). From 'worst' to 'best' sires, the true breeding values show a strong positive trend from -20.8 kg for the 'worst' to 17.9 kg for the 'best'. When only the selected weaning weights were included in the analysis the EBVs, particularly for the 'worst' and 'best' sires, showed large bias (error of prediction calculated as the estimated less the true breeding value). The trend was for 'poor' sires to have EBVs overestimated and 'better' sires to be underestimated. The bias ranged from 17.1 kg to -13.9 kg. Including all weaning records in the analysis removed this bias (Table 2.2).

Table 2.2 Summary of yearling weight evaluations for sires using selected data only and all weaning weights (Pollak et al. 1984)

Number of progeny remaining after selection	Mean true breeding value	Error of prediction (Estimated less true breeding value)	
		Selected weaning and selected gain records	All weaning and selected gain records
6	-20.8	17.1	1.1
7-9	-6.8	4.7	-0.6
10	0.8	-0.8	-0.3
11-13	6.9	-5.0	0.6
14	17.9	-13.9	0.3

By satisfying requirements of normality and selection invariant to fixed effects, and by using all weaning weight records upon which selection was based, multiple trait evaluation was able to remove the potential bias in estimation of yearling weight breeding values due to sequential selection (Pollak et al. 1984).

This example shows the benefit of using multiple trait evaluation to remove bias in EBVs when the records of the trait of interest are not random due to selection on a correlated trait. This could be very useful in removing potential bias caused by harvesting over time. For carcase traits correlated to LWT, the potential of biased EBVs for carcase traits due to harvesting over time based on LWT, may be removed by utilising multiple trait evaluation which includes LWTs for all animals available for selection at a point prior to selection beginning or at each point of selection.

A multiple trait analysis was also used by Jopson et al. (2007) on progeny test data to take account of harvesting lambs over time based on LWT. Breeding values of sires were estimated for the final LWT measured, the six-month LWT. LWTs of all lambs present at each harvest were recorded, and the multi-trait analysis of LWTs at the four harvest points resulted in sire six-month LWT EBV correlations between harvested data sets and the full data set where records were available for all animals at every harvest of 0.99. Knowing the history of selection was able to account for the harvesting. However, it is possible that measurements for the trait selection is based on may only be available for the animals slaughtered at each harvest point.

2.4.6.1 Genetic correlations between live-animal traits and carcase traits

Multiple-trait evaluation can include information on the history of selection and remove bias from traits correlated to the selection criteria. In a progeny test to estimate carcase trait EBVs, sire progeny may be harvested over time based on criteria such as LWT and fatness with carcase traits only measurable once as the progeny are killed. If the harvesting criteria is LWT, LWTs may be recorded for all animals at the first harvest and/or certain time points before harvesting, and even possibly for all remaining animals at each subsequent harvest point. For these LWT measurements impacting on the estimation of carcase trait EBVs, LWT and the carcase traits of interest must be genetically correlated. LWT is generally moderately to highly correlated to several carcase traits. Table 2.3 gives some examples of literature estimates of genetic correlations between different LWT measures and a selection of carcase traits. Therefore, if LWT is the criteria for harvesting over time, knowledge of LWT records for all animals at the first harvest is likely to provide useful information to remove bias in estimating EBVs for carcase traits.

Table 2.3 Estimates of genetic correlations between liveweight and carcase traits
CWT, carcase weight; P8, fat depth at P8 site; EMA, eye muscle area; IMF, intra-muscular fat content

Liveweight	Carcase trait						Reference[‡]
	CWT	P8	Fat thickness at 12/13th rib	EMA	Marbling score	IMF	
Birth weight	0.535*	-0.227		0.477		-0.454	1
	0.57	-0.53	-0.57	-0.37		-0.51	3
Weaning weight	0.66	-0.53	-0.44	-0.24		-0.33	3
	0.13		-0.28[#]	0.33	-0.01		2
Yearling weight	0.67	-0.42	-0.28	-0.19		-0.31	3
	0.61		-0.19	0.60			6
	-0.03		-0.13[#]	-0.06	0.20		2
Final weight	0.70	-0.46	-0.33	-0.23		-0.37	3

*Hot standard carcase weight

[#]For backfat

[‡]References are:

1 Pitchford et al. (2006) for crossbred cattle

2 Arnold et al. (1991) for Hereford cattle

3 Meyer et al. (2004) for Australian Hereford cattle

6 Moser et al. (1998) for Brangus cattle

Other traits assessed on live animals apart from LWT may also be used as selection criteria for harvesting, such as fatness. Ultrasound measurements of fatness or other live-animal indicator-measures of carcase traits may be used, possibly in addition to LWT data, in estimating breeding values for carcase traits.

Table 2.4 Estimates of genetic correlations between live animal measures and carcase traits
See Table 2.3 for trait definitions; [approximate standard errors]; (standard errors)

Live-animal ultrasound measure	Carcase trait						Reference[‡]
	CWT	P8	Fat thickness at 12/13th rib	EMA	Marbling score	IMF	
P8*	0.06	0.80				0.39	4
P8[#]	0.21 [0.46]	1.08 [0.16]		-0.72 [0.61]			5
EMA[#]	1.20 [0.54]	0.03 [0.65]		0.94 [0.54]			5
EMA**	0.41 (0.12)		0.12 (0.17)	0.66 (0.14)			6
Bull EMA**				0.80 (0.11)			7
	0.07 (0.10)		0.09 (0.06)	0.66 (0.07)	-0.67 (0.03)		8
Heifer EMA**				0.54 (0.12)			7
Fat thickness at 12th rib**	-0.15 (0.17)		0.69 (0.18)	0.15 (0.19)			6
Bull fat thickness at 12/13th rib**			0.79 (0.13)				7
	0.28 (0.09)		0.88 (0.03)	-0.07 (0.08)	0.54 (0.06)		8
Heifer fat thickness at 12/13th rib**			0.83 (0.12)				7
Bull IMF**					0.74 (0.11)		7
Heifer IMF**					0.69 (0.13)		7
Bull IMF**	-0.55 (0.07)		0.08 (0.03)	-0.22 (0.10)	0.80 (0.06)		8

* Measured at start of finishing period

[#] Measured at feedlot exit

** Measured on yearlings

[‡]References are:

4 Reverter et al. (2003a) for temperate breeds

5 Baud et al. (1998a) for steers of temperate breeds

6 Moser et al. (1998) for Brangus cattle

7 Crews et al. (2003) for Simmental cattle

8 Devitt and Wilton (2001) for mixed breeds

Some examples of literature estimates of genetic correlations between some live-animal ultrasound measures and carcase traits are given in Table 2.4. Ultrasound and carcase measurements of the same trait tend to be very highly genetically correlated, and therefore when animals are harvested, ultrasound measures taken on all animals at the first harvest may be very useful in removing bias from their corresponding carcase traits. However, measures on the live animal may not be genetically correlated to certain carcase traits, for example ultrasound fat thickness at the 12/13th rib with carcase eye muscle area (see Table 2.4).

2.4.7   Data augmentation

Multiple trait evaluation can be useful for removing EBV bias from a carcase trait correlated to the harvesting criteria when there are records available for all animals for the harvesting criteria at the point of selection. However, records for the harvesting criteria may not be available for all animals at the point of selection. In this situation, missing records at the point of selection may be estimated based on the known selected records and assuming normality as described by Appel et al. (1998).

2.4.8 Non-zero covariance between random residual effects and other random effects

It is usually assumed that the covariances between the random effects $\mathbf{u}$ and $\mathbf{e}$ are zero. This however is generally invalid for field data in the biological sciences (Schaeffer and Henderson 1983). In the case where animals are harvested over time based on particular criteria, the residual error becomes correlated with genetic effects. For example, if the harvesting criteria is LWT, then it is likely that animals with large positive values for their LWT residuals and breeding values will be harvested together. This results in a correlation between random residual and genetic effects within harvest groups. If the magnitude of the correlation could be quantified or estimated, this knowledge could be useful in genetic evaluation of this type of data, removing bias from breeding values.

Schaeffer and Henderson (1983) describe methodology to account for covariances between the residual random effects and the other random effects in the model using mixed model equations. This is done by defining an equivalent model to the basic linear

model presented as [2.1], so that the covariance between the random vectors and residual vectors remains zero.

Based on [2.1], expectations and co(variances) are defined as follows:

$$E \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{X\beta} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}$$

$$V \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{V} & \mathbf{CG} & \mathbf{F} \\ \mathbf{GC'} & \mathbf{G} & \mathbf{S'} \\ \mathbf{F'} & \mathbf{S} & \mathbf{R} \end{bmatrix}$$

where

$$\mathbf{C} = \mathbf{Z} + \mathbf{SG^{-1}}$$

$$\mathbf{F} = \mathbf{ZS'} + \mathbf{R}$$

$$\mathbf{V} = \mathbf{ZGZ'} + \mathbf{ZS'} + \mathbf{SZ'} + \mathbf{R}$$

$$= \mathbf{CGC'} + \mathbf{R} - \mathbf{SG^{-1}S'} \qquad [2.3]$$

Usually, **S** is assumed to be zero and **R** is taken to be $\mathbf{I}\sigma^2$. Schaeffer and Henderson (1983) assumed **G**, **R** and **S** were known. An equivalent model is defined as one that has the same expectation of **y** and results in the same (co)variance matrix of **y**. Such an equivalent model to [2.1] can be defined as:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Cu} + \boldsymbol{\varepsilon}$$

with expectations and (co)variances as follows:

$$E \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \boldsymbol{\varepsilon} \end{bmatrix} = \begin{bmatrix} \mathbf{X\beta} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}$$

$$V \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \boldsymbol{\varepsilon} \end{bmatrix} = \begin{bmatrix} \mathbf{V} & \mathbf{CG} & \mathbf{B} \\ \mathbf{GC'} & \mathbf{G} & \mathbf{0} \\ \mathbf{B} & \mathbf{0} & \mathbf{B} \end{bmatrix}$$

and **B** was defined as **R - SG⁻¹S'**

and for this model **V = CGC' + B** which is the same as [2.3]. This is an equivalent model to one with covariances between **u** and **e** but which has covariance(**u**,**ε**) = 0.

The mixed model equations given in [2.2] can be used to solve this equivalent model. The specific mixed model equations for this model are:

$$
\begin{bmatrix} \mathbf{X'B^{-1}X} & \mathbf{X'B^{-1}C} \\ \mathbf{C'B^{-1}X} & \mathbf{C'B^{-1}C} + \mathbf{G^{-1}} \end{bmatrix} \begin{bmatrix} \mathbf{\beta^0} \\ \mathbf{\hat{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X'B^{-1}y} \\ \mathbf{C'B^{-1}y} \end{bmatrix}
$$

where variance components involving the fixed and random effects can be calculated using a generalised inverse of the left hand side coefficient matrix. Alternative mixed model equations were presented that avoid the need to invert **B**.

To utilise this methodology the covariance must be defined between the residual and other random effects in the model (**S**). This may be a multiple of **Z** involving the genetic variance. Returning to the case of harvesting over time, it may be possible based on prior knowledge of the population being studied and selection policy to estimate **S**. It is possible however, that **S** is not constant for every harvest group. For example if the animals in the last slaughter group were killed based on a less stringent requirement for the selection criteria then it would be expected that **S** would be less for this harvest group than previous ones.

2.4.9 Accounting for selection bias through distribution of subclass numbers

The number of animals in different subclasses could be related to genetic merit. For example, the number of progeny a sire has through artificial insemination may be assumed to be positively correlated to the sire's breeding value for milk yield (Henderson 1973). In the case of harvesting over time it may be assumed that the number of progeny a sire has in different harvest groups is related to its genetic merit for the harvesting criteria and correlated traits. However, this approach may be difficult to apply (Henderson 1973).

2.4.10 Comparison of different genetic evaluation methods

True breeding values are unknown for field or experimental data, therefore there is no defining test of breeding value accuracy for the predictors from different genetic evaluation methods. Three ways to compare different genetic evaluation methods are theoretical determination, simulation and application to actual data. Theoretical determination is based on assumed parameters of the model and experimental design or sampling process to mathematically define the properties of the method. Where this is not practical, simulation provides an alternative and can provide data when actual data is not available. This however requires a lot of computing time to examine many different combinations of design and parameter values. Applying alternative methods to actual data may result in differences, however, because the true underlying effects are unknown, the best method is uncertain. Results are also specific to the particular population and design from which the data was taken (Henderson 1975a).

The aim of this thesis was to find appropriate models applicable to harvested data with varying population parameters that result in accurate and unbiased EBVs. To do this various models were applied to simulated and field data. Simulating populations subjected to harvesting over time provided data in the absence of appropriate actual data and knowledge of the underlying true parameters including true breeding values enabling evaluation of EBVs. Results from simulation studies were also compared to theoretical expectations based on the parameters used. Alternative models were also fitted to field data considered to be representative of harvested data, where sire EBVs from harvested data were compared to EBVs resulting from non-harvested data. This allowed some testing of the validity of particular models to practical application, acknowledging that results were based on particular populations and sampling design.

3 UNIVARIATE ESTIMATION OF LIVEWEIGHT BREEDING VALUES WHEN LIVEWEIGHT IS THE CRITERION FOR SELECTIVE SLAUGHTER– A SINGLE-TRAIT SIMULATION STUDY

3.1 Introduction

Suppliers of beef to consumers in a demand driven economy will aim to satisfy consumer desire to maximise profit by increasing market share or increasing the price they can ask for their product. Therefore customer desire will be reflected in the price offered to cattle finishers for different carcase specifications. In order to maximise the money received for their cattle, finishers will aim to have cattle fall into the particular grades which offer the best price. In the commercial situation, because individuals within groups of cattle entering feedlots reach optimum finish over time and not concurrently, feedlot cattle are commonly selectively removed for slaughter (i.e. harvested) over time.

When a progeny test is implemented to estimate carcase-trait breeding values for sires, the progeny may be sent to commercial feedlots and harvested over time. Harvesting the progeny based on particular criteria such as weight and fatness will not result in random samples of the progeny selected at each harvest. It is expected that a greater proportion of progeny from genetically superior sires for the harvesting criteria will be in the earlier harvests. Inequitable comparisons between sires may result due to differences in progeny age across harvest days, for example, a fast growing animal may have been killed at a younger age than a slower growing animal that was older when it was harvested. Therefore, fitting a simple model to estimate liveweight (LWT) breeding values not accounting for harvesting is likely to give biased estimated breeding values (EBVs).

Apart from age differences between harvests, there could be non-random influences on LWT phenotypes specific to the harvest group slaughtered on a particular day. In this thesis these influences are called specific harvest day effects.

The aim of this study was to assess the effect of harvesting on the accuracy and bias of EBVs considering the single trait LWT as the harvesting criteria, and to find appropriate methods of analysis for such data. The influence and treatment of specific harvest day effects are also examined.

3.2 Materials and methods

Stochastic simulations of populations, all with the same pedigree and age structure, provided data to investigate harvesting. Sire progeny were harvested based on LWT and at each harvest LWTs were recorded. Various models were fitted to this data to estimate sire and progeny breeding values.

3.2.1 Population structure

To quantify the effect of harvesting and compare different models of analysis a population of fixed structure was created based on the half-sib design. There were 125 sires with 40 male offspring each, each dam having only one offspring, giving a total of 5,000 progeny.

For 100 replicates, each animal's phenotype, including the genetic and environmental components, was variable, but the pedigree structure remained the same, as did the birth dates for progeny. Apart from the division of animals into slaughter groups caused by harvesting, and specific harvest day effects, no additional fixed effects were simulated. All 5,000 progeny were therefore directly comparable before harvesting.
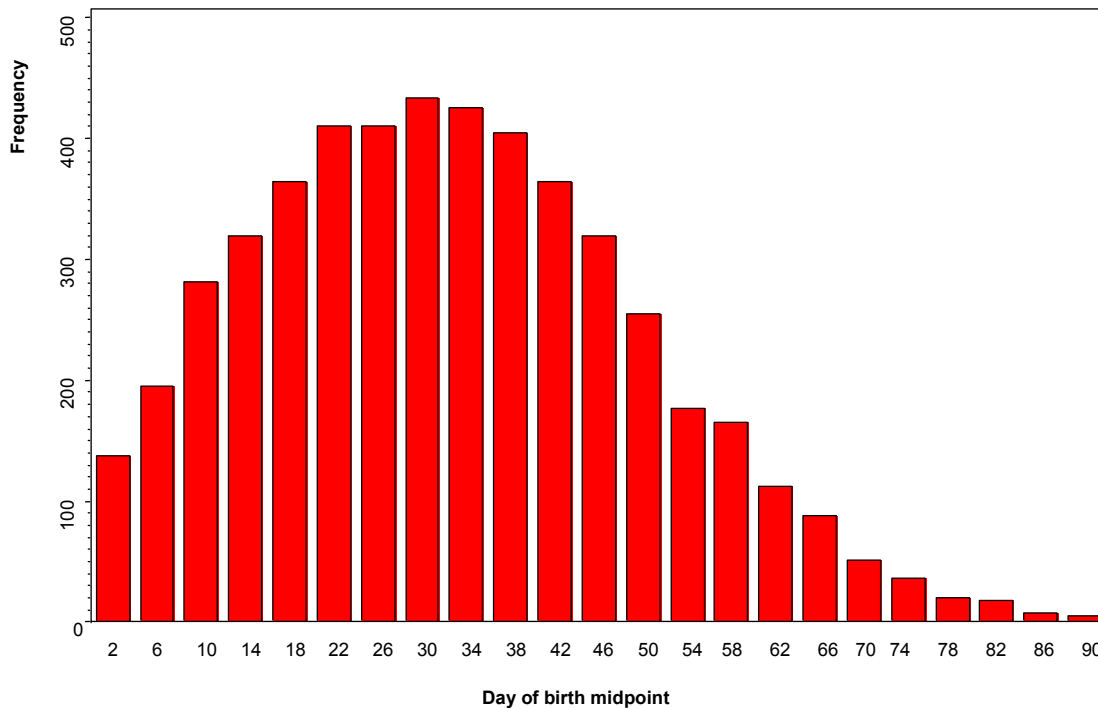

Figure 3.1 Example distribution of simulated birth dates for half-sib design

3.2.2 Progeny birth dates

All progeny were assumed born in a single year, and Durham Shorthorn data (Australian Shorthorn database extract, December 2005) was used to provide an estimate of the spread of birth dates. Birth dates were sampled from a truncated normal distribution with an original standard deviation of 20.1 days and a spread of 90 days. An example of the resulting distribution of birth dates is given in Figure 3.1.

3.2.3 RRGibbs simulation

The RRGibbs random regression program was used to create LWT records for the sires and their progeny (Meyer 2002). Running the RRGibbs program in simulation mode required providing a parameter file, a pedigree file, and a data file. This data file contained three fields: a field for animal identifications, a LWT field containing arbitrary placeholders, and a field for the ages that the LWTs were to be simulated for. Although not subject to harvesting, sires were also specified in the data file to enable extraction of their TBVs for statistical analysis.

For this study, the first simulated LWT was on the 200th day after the average birth date. LWTs for progeny were simulated for 590 consecutive days, enabling harvesting of the progeny based on the specific harvesting criteria imposed.

Input parameters included the upper triangle of the symmetric matrix of covariances between random regression coefficients for the additive-genetic random effect (Table 3.1) and animal permanent-environmental effect (Table 3.2), as well as specific temporary environmental variances for given age ranges (Table 3.3). These values were from Angus cattle (Meyer 2005), with the temporary environmental variances scaled down to make temporary environmental variance about 2% of the total variance, and the covariances between random regression coefficients scaled up for the permanent-environmental effect to repartition the variance removed from the temporary environmental variance into the permanent-environmental variance. This information available on Angus cattle provided a convenient source of parameters for a common beef breed. The proportion of environmental variance attributed to the temporary component was reduced to make the daily changes in LWT due to the environment less volatile and more realistic (Graser, H.-U. and Johnston, D. 2006, pers. comm.). Legendre

polynomials of order 3 were fitted for the additive-genetic and animal-permanent-environmental random effects. The random environmental deviation for each record was a random number drawn from a multivariate normal distribution with mean zero and variance as specified in Table 3.3 for the given age. The phenotypic deviations for each animal were calculated as the sum of the additive-genetic, permanent-environmental and temporary environmental effects for each age.

Table 3.1 Covariances between random regression coefficients β0, β1 and β2, for the additive-genetic random effect

	β0	β1	β2
β0	748.93	340.63	-41.65
β1		186.74	2.76
β2			18.37

Table 3.2 Covariances between random regression coefficients β0, β1 and β2, for the animal permanent-environmental effect

	β0	β1	β2
β0	737.48	371.41	-29.42
β1		311.18	75.91
β2			70.83

Output files were created from RRGibbs containing fields for animal identification, age, temporary environmental effect, additive-genetic effect (TBV), permanent-environmental effect and phenotypic deviation. These phenotypic deviations were centred on zero and were added to mean LWT values for each age to give actual phenotypes. The mean LWT for each age was determined from a linear regression of LWT on age using steer data from an extract taken from the Australian Shorthorn database in December 2005:

LWT (kg) = 100.2610 + 0.6266 age (d)   [3.1]

Table 3.3 Simulated temporary environmental variance values for specific age ranges

Age range		Environmental variance
Minimum	Maximum	
0	0	0.04
1	60	7.34
61	90	10.21
91	120	8.82
121	150	10.92
151	180	12.37
181	210	13.72
211	240	16.54
241	270	19.31
271	300	12.67
301	360	15.96
361	420	18.22
421	480	19.73
481	540	23.05
541	600	19.02
601	660	16.83
661	720	21.37
721	780	51.29
781	820	29.98

3.2.4 Data sets

One hundred populations were simulated using RRGibbs. These 100 replicates were subjected to 3 different harvesting schemes and the addition of harvest day effects creating 4 datasets for analysis.

3.2.4.1 Data set 1: Data not harvested

All progeny were slaughtered when the average age of the animals was 580 days.

3.2.4.2 Data set 2: Randomly harvested data

Progeny were randomly harvested at three time points. The three points were determined by non-randomly harvesting the data from one replicate as described for Data set 3 below. The data were therefore randomly harvested at average ages of 531, 580, and 624 days.

3.2.4.3 Data set 3: Non-randomly harvested data

For this dataset progeny records were harvested based on LWT. Cattle were harvested on 3 weighing days, the first two determined by consecutive thirds of the cattle reaching the minimum target LWT of 445 kg, and the final third was harvested when 7/12ths of the remaining cattle reached the minimum target LWT. Harvesting on 3 days was a simple scenario that provided substantially selected data sets to analyse.

Based on the supermarket market in Australia, cattle are slaughtered between 17 and 22 months of age (~520 – 670 days) at 240 to 280 kg carcase-weight (~445-520 kg LWT) (Upton, W. 2006, pers. comm.), possibly involving several drafts. Therefore a minimum harvest LWT of 445 kg was used.

3.2.4.4 Data set 4 : Non-randomly harvested data with specific harvest day effects

For each replicate, three specific harvest day effects were simulated, one for each harvest day, simulated with N(0, 16.6 kg). If these specific harvest day effects were treated as random effects, they would account for 20% of the phenotypic variance.

3.2.5 Statistical analyses

The statistical package ASReml, which uses restricted maximum likelihood (Gilmour et al. 2002), was used to apply various mixed animal models to non-harvested and harvested data to quantify the effect of harvesting on the bias and accuracy of EBVs and to find the analysis giving the greatest accuracy of EBVs. Each analysis was fitted to data sets from 100 simulations and results summarised. Each set of 100 replicates used the same series of random-number seeds. Comparisons were made between TBVs simulated at a standard age of 580 days and the breeding values estimated from applying the various models. 580 days corresponded to the approximate average age of slaughter when

harvesting on LWT (see Figure 3.3). All fitted models used the pedigree and included additive-genetic and residual random effects.

3.2.5.1 Data set 1

Two univariate models were fitted:

$$y_i = \mu + a_i + e_i \hspace{4cm} \text{Analysis 1.1}$$
$$y_i = \mu + age_i + a_i + e_i \hspace{3.3cm} \text{Analysis 1.2}$$

where y_i represents the simulated LWT of the ith animal, μ the mean harvest LWT, age_i the linear age effect of the animal, a_i the random additive-genetic effect, and e_i the random residual effect. It was assumed that the random additive-genetic and residual effects were independently distributed with cov(a,e) = 0, with a residual variance of σ_e^2.

3.2.5.2 Data set 2

Two univariate models were fitted:

$$y_i = \mu + age_i + a_i + e_i \hspace{3.3cm} \text{Analysis 2.1}$$
$$y_{ij} = \mu + harvest\_day_j + age_i + a_i + e_{ij} \hspace{1.2cm} \text{Analysis 2.2}$$

where the effects are as above with the addition of a harvest day fixed effect to take account of differences between harvest days.

3.2.5.3 Univariate analyses of LWT involving data set 3

Four univariate models were fitted:

$$y_i = \mu + a_i + e_i \hspace{4cm} \text{Analysis 3.1}$$
$$y_i = \mu + age_i + a_i + e_i \hspace{3.3cm} \text{Analysis 3.2}$$
$$y_{ij} = \mu + harvest\_day_j + age_i + a_i + e_{ij} \hspace{1.2cm} \text{Analysis 3.3}$$
$$y_{ij} = \mu + harvest\_day_j + age_i(harvest\_day_j) + a_i + e_{ij} \hspace{0.6cm} \text{Analysis 3.4}$$

where the effects are as above with the addition of $age_i(harvest\_day_j)$, the linear age effect of the animal nested within harvest day.

3.2.5.4 Univariate analyses of pre-adjusted LWT involving data set 3

The harvest LWTs were pre-adjusted for age according to the following equation:

$$\text{Adj.LWT}_i = \frac{\text{harvest LWT}_i - \text{birth LWT}_i}{\text{age}_i} * \text{standard age}(580d) \qquad [3.2]$$

where Adj.LWT_i is the harvest LWT pre-adjusted for age for the ith animal, harvest LWT_i is the harvest LWT for the ith animal and age_i is the age at slaughter for the ith animal. Birth LWT was set at 35 kg.

Two univariate models were fitted:

$\text{Adj.lwt}_i = \mu + a_i + e_i$	Analysis 3.5
$\text{Adj.lwt}_{ij} = \mu + harvest\_day_j + a_i + e_{ij}$	Analysis 3.6

where the effects are as above.

3.2.5.5 Univariate analyses involving data set 4

Three univariate models were applied to this data:

$\text{Adj.lwt}_i = \mu + a_i + e_i$	Analysis 4.1
$\text{Adj.lwt}_{ij} = \mu + harvest\_day_j + a_i + e_{ij}$	Analysis 4.2
$y_{ij} = \mu + harvest\_day_j + a_i + e_{ij}$	Analysis 4.3

where the variables are as above.

3.2.5.6 Multivariate analyses involving data set 4

Two trivariate models were fitted using ASReml (Gilmour et al. 2006), taking the LWT or Adj.LWT at each of the three harvest days as separate traits. For the analyses all

animals had LWT records at harvest 1, but for harvests 2 and 3 only those animals selected for harvest on those harvest days had LWT records. All records for each harvest included a specific harvest day effect. When Adj.LWT was modelled, only one the mean was fitted as fixed effect (Analysis 4.4). When modelling LWT the fixed effects also included an age-of-slaughter covariable (Analysis 4.5).

The analyses fitted with observations separated into the three traits were of the following form:

$$
\begin{bmatrix} \mathbf{y_1} \\ \mathbf{y_2} \\ \mathbf{y_3} \end{bmatrix} = \begin{bmatrix} \mathbf{X_1} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{X_2} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{X_3} \end{bmatrix} \begin{bmatrix} \mathbf{b_1} \\ \mathbf{b_2} \\ \mathbf{b_3} \end{bmatrix} + \begin{bmatrix} \mathbf{Z_1} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z_2} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{Z_3} \end{bmatrix} \begin{bmatrix} \mathbf{u_1} \\ \mathbf{u_2} \\ \mathbf{u_3} \end{bmatrix} + \begin{bmatrix} \mathbf{e_1} \\ \mathbf{e_2} \\ \mathbf{e_3} \end{bmatrix}
$$

where $\mathbf{y}_i$ (i = 1 to 3 for traits 1 to 3) are the vectors of observations for traits 1 to 3, $\mathbf{X}_i$ are the incidence matrices for fixed effects, $\mathbf{b}_i$ are the vectors of fixed effects, $\mathbf{Z}_i$ are the incidence matrices for random effects, $\mathbf{u}_i$ are the vectors of random effects, and $\mathbf{e}_i$ are the vectors of random residual effects.

It was assumed that

$$
\mathrm{var} \begin{bmatrix} \mathbf{u_1} \\ \mathbf{u_2} \\ \mathbf{u_3} \end{bmatrix} = \begin{bmatrix} g_{11}\mathbf{A} & g_{12}\mathbf{A} & g_{13}\mathbf{A} \\ g_{21}\mathbf{A} & g_{22}\mathbf{A} & g_{23}\mathbf{A} \\ g_{31}\mathbf{A} & g_{32}\mathbf{A} & g_{33}\mathbf{A} \end{bmatrix}
$$

where g_{ij} are the animal additive-genetic (co)variances between traits i and j and $\mathbf{A}$ is the relationship matrix between animals. Three residual structures were assumed for the different number of records on an animal:

i) Harvest one LWT only

$$
\mathrm{var}[\mathbf{e_1}] = [r_{11}]
$$

ii) Missing harvest three LWT

$$
\mathrm{var} \begin{bmatrix} \mathbf{e_1} \\ \mathbf{e_2} \end{bmatrix} = \begin{bmatrix} r_{11} & r_{12} \\ r_{21} & r_{22} \end{bmatrix}
$$

iii) Missing harvest two LWT

$$\text{var}\begin{bmatrix} e_1 \\ e_3 \end{bmatrix} = \begin{bmatrix} r_{11} & r_{13} \\ r_{31} & r_{33} \end{bmatrix}$$

where r_{ij} are the residual (co)variances between traits i and j. Because there were no animals in common between harvests 2 and 3, no residual covariance was required.

3.2.6 Analysis comparison

To examine the ability of each analysis to estimate breeding values the results were summarised. The heritability, additive variance and phenotypic variance are presented indicating how the variance was partitioned by fitting each model to the various data sets. Four statistics were calculated using SAS software (SAS 1999), namely EBV variance, EBV accuracy, EBV bias, and the standard error of prediction (SEP).

Variation of estimated breeding values

The standard deviation, minimum and maximum of the EBVs resulting from fitting each model were calculated; it is expected that greater EBV accuracy will lead to greater variation in EBVs. Based on the BLUP methodology used, the mean of EBVs for all models fitted was by definition equal to zero.

Accuracy of estimated breeding values

The accuracy of EBVs was calculated as the Pearson correlation between the TBVs (at the standard age of 580 days) and the EBVs estimated from each of the analyses. The Pearson product-moment correlation was calculated as

$$r_{TBV,EBV} = \frac{\sum_{i=1}^{n}\left(TBV_i - \overline{TBV}\right)\left(EBV_i - \overline{EBV}\right)}{\sqrt{\sum_{i=1}^{n}\left(TBV_i - \overline{TBV}\right)^2 \sum_{i=1}^{n}\left(EBV_i - \overline{EBV}\right)^2}}$$

where n is the total number of sires or the total number of progeny, and $\overline{TBV}$ and $\overline{EBV}$ are the sample means of the respective TBVs and EBVs.

The results presented for each analysis include the mean accuracy over 100 replicates and the minimum and maximum accuracy obtained within the 100 replicates.

Bias of estimated breeding values

For each analysis, the bias of the EBVs was calculated as

$$\text{bias}_{\text{EBVs}} = \frac{\sum\limits_{i=1}^{n}\left(\text{EBV}_i - \text{TBV}_i\right)}{n}$$

where n is the total number of sires or the total number of progeny. The bias for each analysis was calculated for all sires; all progeny; and for the top and bottom third of sires ranked on EBV. Based on the simulation and modelling, the TBVs and EBVs of sires are both expected to sum to zero for any replicate. Therefore the expectation is no EBV bias for sires. However, ranking sires by EBV as outlined above highlighted trends in bias across the range of EBVs.

Standard error of prediction (SEP)

SEP was determined as follows:

$$\text{SEP} = \sqrt{\frac{\sum\limits^{n}\left[\left(\text{EBV} - \text{TBV}\right) - \left(\overline{\text{EBV} - \text{TBV}}\right)\right]^2}{n-1}}$$

where n is the total number of sires or the total number of progeny.

The SEP can be calculated deterministically as follows (Mrode 2005):

$$\text{SEP} = \sqrt{\left(1 - r^2\right)\sigma_a^2}$$

where r^2 is reliability, the accuracy squared, and σ_a^2 is the additive-genetic variance.

Replication

Four statistics, EBV variance, EBV accuracy, EBV bias and SEP, were calculated for sires and progeny separately, and the following results present the mean and standard deviation of these statistics over 100 replicates. Variance components are also presented as the mean and standard deviation over 100 replicates.

For all the simulation work of this thesis, the simulated TBVs of animals at 580 days of age were used to calculate EBV accuracy. The average age of harvested animals was 574.67 days for this single-trait study and 574.63 days for the two-trait study in Chapter 5. For analyses when records were not adjusted to an age of 580 days, there could therefore have been a discrepancy from the true EBV accuracy and analyses that did and did not adjust records to 580 days may not have been completely comparable. However, the additive-genetic correlation simulated between either 574 or 575 days and 580 days was greater than 0.9999 for both the traits used in the simulation work, specifically, the harvesting criteria LWT and the correlated trait EMA. Therefore, no difference from the EBV accuracies presented in the simulation work were expected had TBVs at 574.67 or 574.63 days been used rather than at 580 days.

Similarly, variance components used in comparisons were those simulated at 580 days. However, the simulated heritability did not differ between 574, 575, or 580 days of age for either LWT or EMA. For LWT, the largest differences between 580 days and 574 or 575 days were only 11, 12, and 0 kg^2 for the additive variance, permanent-environmental variance and temporary environmental variance. For EMA, the corresponding values were only 0.1, 0.0, and 0.0 cm^4.

Similarly, it is expected that the EBV bias presented for analyses when records were not adjusted to 580 days of age may have been slightly different to the bias values that would have resulted if TBVs were taken at 574.67 or 574.63 days of age. However, as given above, the genetic correlations between these ages and 580 days were greater than 0.9999 and it is expected that there were not large differences in TBVs between these ages.

Significance testing

To determine whether the sample means of 100 replicates were significantly different from the simulated values, theoretical expectations or zero, the *t* distribution was used. For a single random sample of size n, to test whether the sample mean $\bar{x}$ was significantly different from the null hypothesis of the mean μ_0, the probability of a value less than or equal to the following *t* test statistic was calculated.

$$t = \frac{\bar{x} - \mu_0}{s/\sqrt{n}}$$

where s is the sample standard deviation. This *t* statistic follows a *t* distribution with n-1 degrees of freedom (Moore and McCabe 2006). An online calculator was used (2007b).

The difference between means of 100 replicates for each statistic was determined to be statistically significant when the difference was larger than twice the sum of the standard errors. Standard errors were calculated as the standard deviation over the 100 replicates for the statistic divided by the square root of the number of replicates (i.e. divided by 10).

Variances of different runs were determined to be significantly different if 2 times the probability of a greater value for the following *F* test statistic was less than 0.05.

$$F = \frac{\text{larger } s^2}{\text{smaller } s^2}$$

where s^2 are the sample variances. This *F* statistic follows an *F* distribution defined by the degrees of freedom for the numerator and denominator sample variances (Moore and McCabe 2006). An online calculator was used (2007a).

3.3 Results and discussion

3.3.1 No harvesting

3.3.1.1 Analyses 1.1 & 1.2

Analyses 1.1 and 1.2 fitted to non-harvested data provide a basis to compare the results of analyses fitted to harvested data.

Variance partitioning

The only fixed effect affecting the observations was age. The mean phenotypic variance under Analysis 1.2 which fitted an age covariate was 1,250.2 kg^2 (Table 3.4). This was not significantly different from the simulated value of 1,247.0 kg^2 (P=0.31, two-sided test). However, the mean phenotypic variance under Analysis 1.1, where the age covariate was not fitted, was significantly greater than this simulated value at 1,364.5 kg^2 (P=0.0). This shows that Analysis 1.1 did not fit the data as well as Analysis 1.2.

Analyses 1.1 and 1.2 partitioned 602.66 kg^2 and 601.73 kg^2 to additive variance respectively (Table 3.4). Neither of these values were significantly different from the simulated additive variance at 580 days of 612.4 kg^2 (P>0.2, two-tailed test).

Table 3.4 Variance components for univariate analyses fitted to data not harvested (all progeny slaughtered at an average age of 580 d) and data randomly harvested (standard deviation of 100 replicates in brackets)

Analyses	Heritability	Additive variance	Phenotypic variance
Data not harvested			
1.1 LWT = mean + animal + residual	0.441 (0.056)	602.66 (86.07)	1364.53 (32.82)
1.2 LWT = mean + age + animal + residual	0.480 (0.059)	601.73 (84.20)	1250.17 (31.27)
Data randomly harvested			
2.1 LWT = mean + age + animal + residual	0.475 (0.059)	597.10 (84.26)	1254.99 (31.39)
2.2 LWT = mean + harvest day + age + animal + residual	0.475 (0.059)	597.21 (84.31)	1255.07 (31.35)

Variability of EBVs

The additive variance matches the relatively large spread of EBVs for sires and progeny shown in Table 3.5, with the average standard deviation of sire EBVs at 22.33 kg (1.87) and 22.49 kg (1.82) for Analyses 1.1 and 1.2.

Table 3.5 Summary EBV statistics for univariate analyses fitted to data not harvested (all progeny slaughtered at an average age of 580 d) and data randomly harvested (standard deviation of 100 replicates in brackets)

Analyses	Sires			Progeny		
	SD	Min*	Max*	SD	Min*	Max*
Data not harvested						
1.1 LWT = mean + animal + residual	22.33 (1.87)	-90.60	102.70	17.53 (2.02)	-82.60	99.00
1.2 LWT = mean + age + animal + residual	22.49 (1.82)	-89.19	101.50	18.05 (2.05)	-84.60	101.70
Data randomly harvested						
2.1 LWT = mean + age + animal + residual	22.38 (1.83)	-91.58	104.20	17.91 (2.05)	-91.27	110.90
2.2 LWT = mean + harvest day + age + animal + residual	22.38 (1.83)	-91.44	104.10	17.91 (2.05)	-91.15	111.10

* Highest and lowest EBV over 100 replicates

The variance of the EBVs was less than the additive variance for Analyses 1.1 and 1.2. The difference is the prediction error variance (PEV) (Cameron 1997). The square root of the PEV, the standard error of prediction (SEP) for sires was 10.12 (0.64) and 9.70 (0.59) for Analyses 1.1 and 1.2. Corresponding to a PEV of about 100 kg^2, this made up the difference between the EBV variance and the additive variance.

Deterministic calculation of the SEP based on the simulated parameters of accuracy at 0.92 and additive-genetic variance at 612.4 gave 9.64 kg. The SEP for sires under Analysis 1.2 was not significantly different.

Accuracy of EBVs

The accuracy of sire and progeny EBVs resulting from fitting Analyses 1.1 and 1.2 are shown in Table 3.6. Fitting Analysis 1.2 resulted in high accuracy for sire EBVs at 0.92 (0.01). Over all the analyses tested this was the highest accuracy attained, and matches the deterministic calculation of EBV accuracy for a progeny test based on the simulated parameters. Based on the simulated LWT heritability at 580 days of 0.49 and 39.4 effective progeny, the EBV accuracy of sires is expected to be 0.92. The accuracy of sire EBVs under Analysis 1.2 is the standard with which other analyses can be compared.

Table 3.6   Mean accuracy of EBVs for univariate analyses fitted to data not harvested (all progeny slaughtered at an average age of 580 d) and data randomly harvested (standard deviation of 100 replicates in brackets)

Analyses	Sires			Progeny		
	Mean	Min*	Max*	Mean	Min*	Max*
Data not harvested						
1.1 LWT = mean + animal + residual	0.91 (0.01)	0.87	0.94	0.72 (0.01)	0.68	0.74
1.2 LWT = mean + age + animal + residual	0.92 (0.01)	0.89	0.95	0.74 (0.01)	0.71	0.76
Data randomly harvested						
2.1 LWT = mean + age + animal + residual	0.92 (0.01)	0.88	0.95	0.74 (0.01)	0.70	0.76
2.2 LWT = mean + harvest day + age + animal + residual	0.92 (0.01)	0.88	0.95	0.74 (0.01)	0.70	0.76

* Lowest and highest accuracy of 100 replicates

The mean accuracy of sire EBVs under Analysis 1.1 where an age covariate was not fitted was significantly lower than that for Analysis 1.2, but the difference was only 0.01. With 40 progeny per sire randomly born over the season, it is expected that age effects were largely averaged out.

It was expected that the sire EBVs resulting from Analysis 1.2, which accounted for differences in age by fitting an age covariate, would be the most accurate when compared with all univariate analyses fitted to harvested data. This was expected because all the progeny were comparable on a single day with all sires represented by the same number of progeny. Large variation in EBVs reflecting the greater accuracy of estimation was also expected.

The results of these two analyses, particularly the results for Analysis 1.2; and the results of the deterministic calculations based on the simulated parameters, provide points of comparison for other analyses fitted to harvested data.

3.3.2 Random harvesting

Variance partitioning

The variance components that resulted for Analyses 2.1 and 2.2 are given in Table 3.4. The average phenotypic variance was significantly greater than the simulated value for both analyses (P=0.012, two-sided test) by 8 kg^2. This could be largely due to the greater variation in the data expected by harvesting animals across a range of ages, rather than at one average age. The additive variance for these analyses was not significantly different to the additive variance estimated for Analysis 1.2 fitted to non-harvested data of 601.73 kg^2, or to the simulated additive variance of 612.4 kg^2 at 580 days (P>0.07, two-sided test).

Variability of EBVs

The standard deviation of EBVs was the same for both analyses fitted to randomly harvested data at 22.38 kg and 17.91 kg for sires and progeny respectively. The standard deviations of sire EBVs for these analyses were the same as the standard deviations for Analyses 1.1 and 1.2 fitted to non-harvested data, all at 22 kg (Table 3.5).

Accuracy of EBVs

The EBV accuracies resulting from fitting Analyses 2.1 and 2.2 are presented in Table 3.6. The EBV accuracies for both sires and progeny are the same as those obtained when Analysis 1.2 was fitted to non-harvested data.

In these analyses no specific harvest day effects were simulated and the addition of a fixed harvest day effect in Analysis 2.2 made no difference to the accuracy of EBVs (Table 3.6). With 5,000 records, the loss of 3 degrees of freedom has no measurable impact on accuracy.

Fixed effects

The mean estimated linear regression coefficient for age under Analyses 2.1 and 2.2 was 0.63 (0.01) and 0.62 (0.03). Neither were significantly different from the simulated value of 0.627 kg/d (P>0.2, two-sided test). As there was no harvesting over time and no

specific harvest day effects, randomly harvesting the data at three points did not cause a change in the relationship between LWT and age compared to all animals being harvested on the same day. Overall, the results for randomly harvested data were very similar to those under Analysis 1.2 fitted to non-harvested data.

3.3.3 Non-random harvesting

3.3.3.1 Number of progeny per sire across harvests

Each sire was assigned 40 progeny. If these progeny had been equally spread out over the three harvests each sire would have had 13 or 14 progeny in each harvest. However, Table 3.7 shows that there was a wide range in the number of progeny per sire at each harvest.

Table 3.7 Number of progeny per sire across harvest days for 100 simulated populations

	Number of progeny per sire from 100 simulations	
	Minimum range	**Maximum range**
Harvest 1	0-4	25-35
Harvest 2	2-8	19-26
Harvest 3	0-4	24-35

3.3.3.2 Distribution of true breeding values

Table 3.8 shows the TBVs of progeny in each harvest, and the TBVs of progeny and sires over all harvests.

The clear negative trend across harvests in the TBVs of progeny from 17.39 to -0.23 to -18.53 shows that animals with higher genetic value for the selection criteria will be harvested first (Table 3.8).

Table 3.8   Summary statistics of true breeding values (TBVs) (standard deviation of 100 replicates in brackets)

	Number of animals	True breeding values	
		Mean	SD[‡]
Progeny in harvest 1	1689.3 (15.1)	17.39 (1.25)	20.44 (0.43)
Progeny in harvest 2	1683.3 (12.7)	-0.23 (1.27)	18.96 (0.37)
Progeny in harvest 3	1627.4 (20.7)	-18.53 (1.35)	20.32 (0.45)
All progeny	5000.0 (0.0)	-0.23 (1.18)	24.71 (0.42)
All sires	125.0 (0.0)	-0.49 (2.30)	24.80 (1.39)

[‡] Standard deviation

Figure 3.2 and Figure 3.3 show the ages and LWTs at the three harvests averaged over 100 simulated populations for randomly and non-randomly harvested data. Positive linear trends are evident for all except notably the LWTs for non-randomly harvested data which show a negative trend across harvest days.
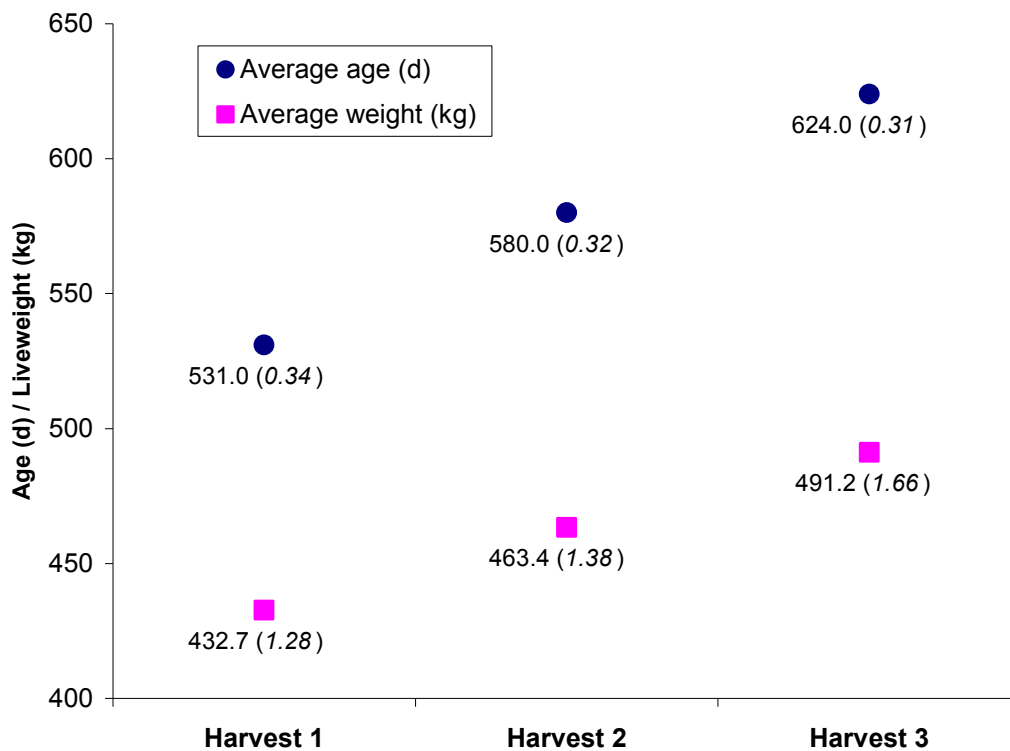

Figure 3.2   Average age and liveweight on the three harvest days for randomly harvested data. (standard deviation over 100 replicate means in brackets).
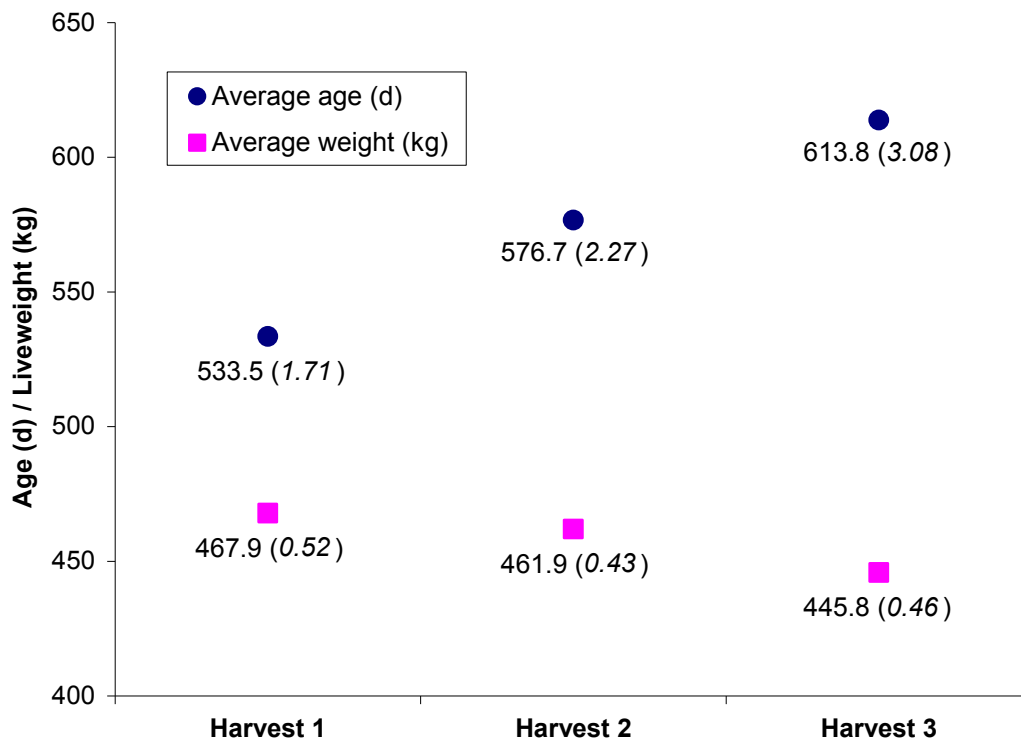
Figure 3.3   Average age and liveweight on the three harvest days for systematically harvested data. (standard deviation over 100 replicate means in brackets).

3.3.3.3 Univariate analyses of harvest liveweight involving data set 3

Variance partitioning

The effect of non-random harvesting was clearly evident in the estimated variance components. There was a large drop in the phenotypic variance from Analysis 1.2 fitted to non-harvested data (1,250.2 kg^2, Table 3.4) to these analyses fitted to harvested data (293.10 to 384.53 kg^2, Table 3.9). Harvesting on LWT resulted in the animals having much more similar LWTs than they had when they were killed on one day or harvested randomly. Non-random harvesting caused both the phenotypic variance and additive variance to drop under Analyses 3.1 to 3.4. These analyses were not able to distinguish between sires with different TBVs as the harvesting caused the progeny of all sires to have similar LWTs. The heritability dropped significantly from 0.44-0.48 for analyses fitted to data not harvested (Table 3.4) to 0.12-0.29 for Analyses 3.1 to 3.4 fitted to harvested data (Table 3.9).

The significant drop in additive variance from Analysis 3.1 to Analyses 3.2 to 3.4 (Table 3.9) suggest that genetic effects were confounded with age and harvest day effects.

Table 3.9 Variance components for univariate analyses fitted to harvested data (standard deviation of 100 replicates in brackets)

Analyses	Heritability	Additive variance	Phenotypic variance
3.1 LWT = mean + animal + residual	0.291 (0.048)	112.02 (20.10)	384.53 (12.88)
3.2 LWT = mean + age + animal + residual	0.136 (0.036)	45.62 (12.64)	334.91 (11.07)
3.3 LWT = mean + harvest day + age + animal + residual	0.120 (0.035)	35.54 (10.72)	294.66 (9.84)
3.4 LWT = mean + harvest day + age(harvest day) + animal + residual	0.120 (0.035)	35.33 (10.69)	293.10 (9.74)
3.5 age-adjusted LWT = mean + animal + residual	0.479 (0.060)	738.36 (103.54)	1538.71 (38.49)
3.6 age-adjusted LWT = mean + harvest day + animal + residual	0.148 (0.034)	60.58 (14.65)	409.46 (9.55)

Table 3.10   Summary EBV statistics for univariate analyses fitted to harvested data where no specific harvest day effect was simulated (standard deviation of 100 replicates in brackets)

Analyses	Sires			Progeny		
	SD	Min*	Max*	SD	Min*	Max*
3.1 LWT = mean + animal + residual	9.17 (1.01)	-49.20	52.11	6.59 (0.92)	-53.48	53.93
3.2 LWT = mean + age + animal + residual	5.10 (0.98)	-35.18	36.87	3.32 (0.73)	-33.91	31.35
3.3 LWT = mean + harvest day + age + animal + residual	4.38 (0.93)	-31.59	35.25	2.82 (0.67)	-30.59	28.92
3.4 LWT = mean + harvest day + age(harvest day) + animal + residual	4.36 (0.93)	-31.95	35.36	2.81 (0.67)	-30.96	28.79
3.5 age-adjusted LWT = mean + animal + residual	24.90 (2.03)	-99.28	109.60	19.98 (2.28)	-93.24	100.00
3.6 age-adjusted LWT = mean + harvest day + animal + residual	6.00 (0.99)	-32.42	42.07	3.93 (0.75)	-31.12	35.62

* Highest and lowest EBV over 100 replicates

Variability and accuracies of EBVs

Reflecting the large drop in estimated additive variance, there was a large significant reduction in the mean standard deviation of sire EBVs from the analyses fitted to data not harvested to Analyses 3.1 to 3.4 which ranged from 4.36 to 9.17 kg (Table 3.10).

The sum of the PEV and variance of the EBVs is not equal to the true simulated additive variance in Analyses 3.1 to 3.4. This shows that the covariance (EBV,EBV-TBV) was not zero.

The drop in accuracy of sire EBVs to between 0.73 and 0.87 for Analyses 3.1 to 3.4 (Table 3.11) reflects the inability of these analyses to partition variance between sires.

Table 3.11 Mean accuracy of EBVs for univariate analyses fitted to harvested data (standard deviation of 100 replicates in brackets)

Analyses	Sires			Progeny		
	Mean	Min*	Max*	Mean	Min*	Max*
3.1 LWT = mean + animal + residual	0.87 (0.02)	0.82	0.91	0.62 (0.02)	0.58	0.66
3.2 LWT = mean + age + animal + residual	0.75 (0.04)	0.66	0.85	0.49 (0.02)	0.43	0.55
3.3 LWT = mean + harvest day + age + animal + residual	0.73 (0.04)	0.64	0.83	0.47 (0.02)	0.41	0.53
3.4 LWT = mean + harvest day + age(harvest day) + animal + residual	0.73 (0.04)	0.64	0.83	0.47 (0.02)	0.41	0.53
3.5 age-adjusted LWT = mean + animal + residual	0.92 (0.01)	0.89	0.95	0.74 (0.01)	0.70	0.76
3.6 age-adjusted LWT = mean + harvest day + animal + residual	0.78 (0.04)	0.69	0.86	0.51 (0.02)	0.45	0.56

* Lowest and highest accuracy of 100 replicates

However, the average accuracy of sire EBVs under Analysis 3.1, where only the fixed effect of the mean and the random effects were fitted, was still high at 0.87 (0.02) (Table 3.11), although significantly different from the mean accuracy of sire EBVs from Analysis 1.2 fitted to non-harvested data at 0.92 (0.01) (Table 3.6). Harvesting on LWT resulted in more progeny of the genetically superior (inferior) sires for LWT being in the earlier (later) harvests. This is indicated by the negative trend in progeny TBVs across harvests as shown in Table 3.8. The EBV of any sire under Analysis 3.1, when only the fixed effect of

the mean was fitted, is expected to be a direct reflection of the number of progeny it had in each harvest. For example, if a sire had more progeny in a harvest with greater phenotypic LWTs, it is expected to have a higher EBV. Figure 3.3 shows that the LWT phenotypes followed a negative trend across harvests. Knowing that genetically superior (inferior) sires were more represented in earlier (later) harvests, the TBVs of sires followed the same negative trend as their EBVs across consecutive harvests, resulting in the high accuracy of their EBVs.

Bias of EBVs

The average simulated TBV for sires over all replicates was -0.49 (2.30) (Table 3.8). Therefore, for all analyses in this study, the mean difference (EBV-TBV) for sires was 0.49 (2.30). Calculation of the mean EBV bias over 100 replicates for the top and bottom third of sires based on EBV was used to examine the possibility of systematic bias occurring between sires. For Analyses 1.1, 1.2, 2.1, and 2.2 fitted to data not harvested or randomly harvested, these values were not significantly different from the expectation with no bias of 0.49 (P>0.06, two-sided test; results not shown).

Table 3.12 EBV bias (EBVs-TBVs) mean and standard deviation [SD (= standard error of prediction)] for univariate analyses fitted to harvested data (standard deviation of 100 replicates in brackets)

Analyses	Sires		Bottom 1/3 sires for EBV		Top 1/3 sires for EBV	
	Mean	SD	Mean	SD	Mean	SD
3.1 LWT = mean + animal + residual	0.49 (2.30)	17.41 (0.92)	13.79 (2.62)	13.30 (1.68)	-13.21 (2.93)	14.10 (1.47)
3.2 LWT = mean + age + animal + residual	0.49 (2.30)	21.19 (1.12)	15.02 (2.98)	17.43 (2.07)	-13.62 (3.30)	18.27 (1.61)
3.3 LWT = mean + harvest day + age + animal + residual	0.49 (2.30)	21.77 (1.13)	15.11 (2.91)	18.29 (2.11)	-13.73 (3.02)	18.88 (1.78)
3.4 LWT = mean + harvest day + age(harvest day) + animal + residual	0.49 (2.30)	21.78 (1.13)	15.07 (2.94)	18.31 (2.06)	-13.82 (3.07)	18.88 (1.83)
3.5 age-adjusted LWT = mean + animal + residual	0.49 (2.30)	9.97 (0.64)	-1.86 (2.36)	9.72 (1.02)	2.72 (3.08)	9.82 (1.04)
3.6 age-adjusted LWT = mean + harvest day + animal + residual	0.49 (2.30)	20.45 (1.06)	14.76 (2.87)	17.01 (2.08)	-13.58 (2.92)	17.27 (1.73)

In contrast, for Analyses 3.1 to 3.4 with harvested data, the EBVs were biased with the EBVs of the bottom third of sires based on EBV significantly biased upwards by 13.3 to 14.6 kg (P~0) and the top third significantly biased downwards 13.7 to 14.3 kg (P~0) (Table 3.12). There was also large variation in individual bias within populations for these bottom and top third of sires, with mean standard deviation over 100 replicates ranging from 13.30 to 18.88 kg (Table 3.12).

Fixed effects

For Analyses 3.1 to 3.4, which are fitted to harvested data, the average age and LWT of progeny at each harvest can be seen in Figure 3.3. These values can be contrasted with corresponding values for randomly harvested data given in Figure 3.2. Harvesting the animals on LWT caused them all to have similar LWTs. Therefore, by including age in Analysis 3.2, the partitioning was affected. The estimated linear effect of age was -0.18 kg/d (0.01), significantly less than the simulated value of 0.627 kg/d. Including this unreal age effect caused the progeny to be even more similar making it more difficult to distinguish between genetically inferior and superior sires, and resulting in a significant drop in sire EBV accuracy compared to Analysis 3.1 (Table 3.11).

Including a harvest day fixed effect to the analysis as in Analyses 3.3 and 3.4 created the tendency for genetically superior (inferior) sires to be compared between themselves resulting in significant reductions in additive variance compared to Analysis 3.1. This suggests that if there were specific harvest day effects, these could not be accounted for by simply fitting a harvest day fixed effect in the analysis.

The estimated linear effect of age under Analysis 3.3 was 0.12 kg/d (0.02), significantly less than the simulated value of 0.627 kg/d. Estimating a separate age covariate within each harvest in Analysis 3.4 did not improve EBV estimation. The estimated linear age effects nested within harvest day were 0.224 kg/d (0.029), 0.034 kg/d (0.015) and 0.125 kg/d (0.031) for harvests 1 to 3.

3.3.3.4 Analyses 3.5 & 3.6: Age-adjusted LWT univariate analyses involving harvested data

Variance partitioning and variability of EBVs

For Analyses 3.5 and 3.6 LWTs were pre-adjusted for age according to [3.2]. Although the phenotypic and additive variances were overestimated under Analysis 3.5 at 1,538.71 and 738.36 kg^2 compared to the simulated values at 580 days of 1,247.0 and 612.4 kg^2, the estimated heritability was not significantly different from the simulated heritability at 580 days of 0.49 (P=0.070) (Table 3.9). The sire EBVs from Analysis 3.5 were significantly more variable than those from Analysis 1.2 fitted to non-harvested data. Under Analysis 3.5, the mean standard deviation of sire EBVs over 100 replicates was 24.90 kg (Table 3.10).

The animals were harvested on LWT, so the expectation was that older (younger), faster-growing (slower-growing) animals would be harvested first (last). The Analysis 3.6 results show that the difference between the harvests for Adj.LWT was about 40 kg, harvest 1 having the highest LWT followed by the second and finally the third (Table 3.13).

Table 3.13 Mean liveweight difference (kg) between harvest day fixed effects under Analysis 3.6 (standard deviation of 100 replicates)

Harvest 1 – harvest 2	Harvest 2 – harvest 3
40.35	40.48
(0.82)	(0.80)

By including a harvest day fixed effect (Analysis 3.6), the large between-harvest differences in LWT that were created originally by pre-adjusting the LWTs for age were removed, and the animals in each group were compared about a common average. As happened under Analyses 3.3 and 3.4 the inclusion of the harvest day effect in Analysis 3.6 created the tendency for genetically superior (inferior) sires to be compared between themselves, causing a large significant reduction in the additive variance and heritability from Analysis 3.5 (Table 3.9).

Accuracy of EBVs

Fitting Analysis 3.5 resulted in a high EBV accuracy for sires of 0.92 (0.01) (Table 3.11). This was the same as that attained from Analysis 1.2 fitted to non-harvested data. This indicates that it is possible to get accurate EBVs for harvested data fitting the assumptions made in this simulation work by treating all animals as one group – making no distinction between progeny harvested at different times, and accounting well for age and growth rate differences. Assumptions included mean linear growth, no existence of specific harvest day effects, and relatively large number of progeny per sire. The sire EBVs under Analysis 3.5 were accurate for an age-dependent trait which was also the criteria for harvesting.

Including a harvest day fixed effect (Analysis 3.6) significantly reduced the accuracy of sire EBVs from 0.92 (0.01) (Analysis 3.5) to 0.78 (0.04) (Table 3.11).

Bias of EBVs

The mean EBV bias over 100 replicates for the bottom and top third of sires based on EBV were -1.86 kg (2.36) and 2.72 kg (3.08) for Analysis 3.5 (Table 3.12). Although these values were relatively small, they were significantly different from the expectation of 0.49 (P~0).

The results to this point suggest ignoring harvest day is appropriate. However, this may not work if there were specific harvest day effects. The next section analyses simulated data with specific harvest day effects added.

3.3.4 Harvested data with the addition of specific harvest day effects

3.3.4.1 Univariate analyses for harvested data with specific harvest day effects added

Specific harvest day effects were simulated with N(0, 16.6 kg). To account for the specific harvest day effects a fixed harvest day effect was included in an analysis for LWT (Analysis 4.3). In previous sections it was shown that fitting a fixed covariate of age is inappropriate for non-randomly harvested data. The addition of specific harvest day effects does not change this.

Variance partitioning

Adding a fixed harvest day effect in Analyses 4.2 and 4.3 to take account of the specific harvest day effects caused the same problems stated earlier, the LWTs of progeny in each harvest group are deviated about a common mean and created the tendency for genetically superior (inferior) sires to be compared between themselves. As a result the phenotypic variance, additive variance and heritability showed large significant reductions from those under Analysis 1.2 fitted to non-harvested data (compare Table 3.4 and Table 3.14).

In contrast to Analyses 4.2 and 4.3, the phenotypic and additive variances, as well as the heritability were far greater for Analysis 4.1 where LWTs were pre-adjusted for age and no harvest day effect was included in the analysis.

Table 3.14 Variance components for univariate analyses fitted to harvested data with specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	Heritability	Additive variance	Phenotypic variance
4.1 age-adjusted LWT = mean + animal + residual	0.441 (0.073)	801.87 (339.59)	1797.06 (665.08)
4.2 age-adjusted LWT = mean + harvest day + animal + residual	0.147 (0.034)	60.55 (14.74)	409.86 (11.91)
4.3 LWT = mean + harvest day + animal + residual	0.105 (0.033)	31.38 (10.20)	298.20 (10.07)

It is of particular interest to compare Analysis 4.1 and Analysis 3.5. These were the same analyses applied to data with or without the addition of specific harvest day effects. The addition of specific harvest day effects to the data caused the average phenotypic and additive variances to increase along with very large increases in the variability of these variances. The average phenotypic and additive variances for Analysis 3.5 were 1,538.71 (38.49) and 738.36 kg (103.54) compared to 1,797.06 (665.08) and 801.87 kg (339.59) for Analysis 4.1. The mean heritability was significantly lower for Analysis 4.1 compared to Analysis 3.5, but the heritability variance was not significantly different between the analyses. Average heritabilities under Analyses 3.5 and 4.1 were 0.479 (0.060) and 0.441 (0.073) (Table 3.9 and Table 3.14).

Variability and accuracy of EBVs

The mean standard deviation of sire EBVs over 100 replicates from Analysis 4.1 was not significantly different from Analysis 3.5, but these standard deviations of the replicates were significantly more variable for Analysis 4.1 than Analysis 3.5. The mean standard deviation for Analyses 3.5 and 4.1 was 24.90 kg (2.03) and 25.23 kg (5.74). The sire EBVs from Analysis 4.1 had a greater range over all replicates than Analysis 3.5. The ranges for Analyses 3.5 and 4.1 were -99.28 to 109.60 kg and -109.20 to 127.20 kg (see Table 3.10 and Table 3.15).

Table 3.15 Summary EBV statistics for univariate analyses fitted to harvested data with specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	Sires			Progeny		
	SD	Min*	Max*	SD	Min*	Max*
4.1 age-adjusted LWT = mean + animal + residual	25.23 (5.74)	-109.20	127.20	19.87 (5.03)	-99.78	109.40
4.2 age-adjusted LWT = mean + harvest day + animal + residual	6.00 (0.99)	-32.48	42.12	3.93 (0.75)	-31.11	35.92
4.3 LWT = mean + harvest day + animal + residual	3.97 (0.94)	-30.41	33.66	2.53 (0.66)	-28.72	27.53

* Highest and lowest EBV over 100 replicates

The mean EBV accuracy of sires under Analyses 4.2 and 4.3 was 0.78 (0.04) and 0.71 (0.04), significantly lower than Analysis 4.1 at 0.91 (0.02), reflecting the lower additive variance and heritability values under Analyses 4.2 and 4.3. The EBV accuracy of sires under Analysis 4.1 was significantly lower than under Analysis 3.5 but with a difference of only 0.01. The variance in sire EBV accuracy for Analysis 4.1 was significantly greater than for Analysis 3.5, but the difference in standard deviation was only 0.01. The range in accuracy for Analysis 3.5 was 0.89 to 0.95 (Table 3.11) compared to a wider range of 0.83 to 0.95 for Analysis 4.1 (Table 3.16).

From the results of Analysis 3.6 it is expected that for Analysis 4.1 the average reduction in age-adjusted LWT from harvest to harvest of 40 kg will still apply. With the simulated specific harvest day effect having a mean of zero and a standard deviation of 16.6 kg, the descending trend in age-adjusted-LWT over consecutive harvest days was not likely

to change direction in any replicate. This helps explain why the EBV accuracy of sires remained high after the addition of specific harvest day effects.

Table 3.16 Mean accuracy of EBVs for univariate analyses fitted to harvested data with specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	Sires			Progeny		
	Mean	Min*	Max*	Mean	Min*	Max*
4.1 age-adjusted LWT = mean + animal + residual	0.91 (0.02)	0.83	0.95	0.72 (0.03)	0.62	0.75
4.2 age-adjusted LWT = mean + harvest day + animal + residual	0.78 (0.04)	0.69	0.86	0.51 (0.02)	0.45	0.56
4.3 LWT = mean + harvest day + animal + residual	0.71 (0.04)	0.61	0.81	0.45 (0.03)	0.39	0.52

* Highest and lowest accuracy of 100 replicates

Bias of EBVs

Fitting Analysis 4.1 resulted in relatively low EBV bias for the bottom and top third of sires based on EBV at -2.40 (5.87) and 3.26 (6.65). These averages were not significantly different from those under Analysis 3.5, but were significantly different from the expectation of 0.49 (P~0). These bias averages from Analysis 4.1 were significantly more variable than those from Analysis 3.5 (Table 3.12 and Table 3.17).

Table 3.17 EBV bias (EBVs-TBVs) mean and standard deviation (SD) for univariate analyses fitted to harvested data with specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	Sires		Bottom 1/3 sires for EBV		Top 1/3 sires for EBV	
	Mean	SD	Mean	SD	Mean	SD
4.1 age-adjusted LWT = mean + animal + residual	0.49 (2.30)	11.67 (1.97)	-2.40 (5.87)	10.42 (1.43)	3.26 (6.65)	10.77 (1.69)
4.2 age-adjusted LWT = mean + harvest day + animal + residual	0.49 (2.30)	20.46 (1.06)	14.78 (2.91)	16.99 (2.08)	-13.57 (2.95)	17.28 (1.76)
4.3 LWT = mean + harvest day + animal + residual	0.49 (2.30)	22.14 (1.17)	14.82 (2.87)	18.88 (2.14)	-13.52 (3.04)	19.47 (1.75)

Results from these analyses fitted to data with specific harvest day effects added suggest, that under similar situations as simulated, the presence of specific harvest day

effects, at the level of variability simulated, can be ignored, with the knowledge that the accuracy of sire EBVs is likely to be slightly reduced and that the sire EBVs are likely to show some bias. For situations similar to that simulated the results suggest that specific harvest day effects would have to be quite large to cause the negative trend in age-adjusted LWT across consecutive harvests to substantially change and therefore reduce the EBV accuracy of sires resulting from Analysis 4.1.

3.3.4.2 Analyses 4.4 & 4.5: Multivariate analyses involving data set 4

For the previous analyses LWT records were only available for animals when they were harvested. If LWTs were available for animals not slaughtered at the time of harvest, multivariate or repeatability models may be used to take account of the history of selection. Analyses 4.4 and 4.5 take into account the history of selection by using LWT records for all animals at harvest 1. However, only the LWT records for animals slaughtered at harvest points 2 and 3 were used.

Table 3.18 Mean accuracy of EBVs for multivariate analyses fitted to harvested data with specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	Trait	Sires			Progeny		
		Mean	Min*	Max*	Mean	Min*	Max*
4.4 h1adlwt h2adlwt h3adlwt = mean + animal + residual[‡]	h1adlwt[‡]	0.92 (0.01)	0.89	0.95	0.74 (0.01)	0.70	0.76
	h2adlwt[‡]	0.92 (0.01)	0.89	0.95	0.74 (0.01)	0.70	0.76
	h3adlwt[‡]	0.92 (0.01)	0.89	0.95	0.74 (0.01)	0.70	0.76
4.5 h1lwt h2lwt h3lwt = mean + age + animal + residual[‡]	h1lwt[‡]	0.92 (0.01)	0.89	0.95	0.74 (0.01)	0.70	0.76
	h2lwt[‡]	0.92 (0.01)	0.89	0.95	0.74 (0.01)	0.70	0.76
	h3lwt[‡]	0.92 (0.01)	0.89	0.95	0.74 (0.01)	0.71	0.76

* Highest and lowest accuracy of 100 replicates
[‡] h1, h2, h3 = harvests 1 to 3; adlwt = liveweight adjusted for age; lwt = liveweight

Accuracy of EBVs

The mean accuracy of sire EBVs resulting from fitting these two analyses for all traits at 0.92 (0.01) was equal to the theoretical accuracy based on the simulated heritability and 39.4 effective progeny. Due to all animals having a record at the first harvest these analyses have been able to take account of the selection and specific harvest day effects occurring over the second and third harvests.

Bias of EBVs

Under Analysis 4.4 for harvest 1 Adj.LWT where all animals had records, the average EBV bias for the top and bottom third of sires based on EBV were not significantly different from the expectation of 0.49 (P>0.75, two-sided test). However, under Analysis 4.5 for harvest 1 LWT where all animals had records the average EBV bias for the top and bottom third of sires based on EBV were significantly different from 0.49 (P~0) (Table 3.19). This difference between analyses may be because the harvest 1 records in Analysis 4.4 were pre-adjusted to 580 days of age, and the harvest 1 records in Analysis 4.5 were measured at an average age of 533.5 days. For both Analyses 4.4 and 4.5, the mean EBV bias for both the bottom and top sires based on EBV were significantly different from 0.49 for harvest 2 weight traits (P~0) but not significantly different for harvest 3 weight traits (P>0.27, two-sided test).

Variance partitioning and variability of EBVs

Table 3.20 and Table 3.21 show the variance partitioning and variability of EBVs resulting under Analyses 4.4 and 4.5. For both Analyses 4.4 and 4.5, both the additive and phenotypic variance for the harvest 2 weight traits were less than those for the harvest 1 and harvest 3 weight traits. This may be explained by the harvesting process where harvest 1 could have extremely heavy LWTs and harvest 3 extremely light LWTs. Evidence for this is presented in Figure 3.3, where harvest 1 LWTs were significantly heavier than harvest 2 LWTs and harvest 3 LWTs significantly lighter than harvest 2 LWTs.

Table 3.19 EBV bias (EBVs-TBVs) mean and standard deviation (SD) for multivariate analyses fitted to harvested data with specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	Trait	Sires		Bottom 1/3 sires for EBV		Top 1/3 sires for EBV	
		Mean	SD	Mean	SD	Mean	SD
4.4 h1adlwt h2adlwt h3adlwt = mean + animal + residual[‡]	h1adlwt[‡]	0.49 (2.30)	9.79 (0.58)	0.51 (2.39)	9.67 (1.00)	0.40 (2.98)	9.84 (1.12)
	h2adlwt[‡]	0.49 (2.30)	10.13 (0.67)	3.28 (2.48)	9.75 (1.02)	-2.38 (3.14)	9.91 (1.08)
	h3adlwt[‡]	0.49 (2.30)	10.08 (0.64)	0.76 (2.48)	10.17 (1.07)	0.41 (2.69)	9.94 (1.02)
4.5 h1lwt h2lwt h3lwt = mean + age + animal + residual[‡]	h1lwt[‡]	0.49 (2.30)	9.99 (0.60)	2.74 (2.33)	9.71 (0.99)	-1.84 (2.99)	9.83 (1.14)
	h2lwt[‡]	0.49 (2.30)	11.31 (0.73)	6.65 (2.33)	10.06 (1.08)	-5.77 (3.09)	10.25 (1.14)
	h3lwt[‡]	0.49 (2.30)	9.90 (0.60)	0.70 (2.47)	10.01 (1.03)	0.33 (2.70)	9.73 (1.00)

[‡] h1, h2, h3 = harvests 1 to 3; adlwt = liveweight adjusted for age; lwt = liveweight

Table 3.20 Variance components for multivariate analyses fitted to harvested data with specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	Trait	Heritability	Additive variance	Phenotypic variance
4.4 h1adlwt h2adlwt h3adlwt = mean + animal + residual[‡]	h1adlwt[‡]	0.48 (0.06)	614.9 (86.4)	1286.2 (33.3)
	h2adlwt[‡]	0.47 (0.06)	485.4 (78.9)	1022.0 (79.9)
	h3adlwt[‡]	0.47 (0.06)	503.5 (77.9)	1062.2 (44.8)
4.5 h1lwt h2lwt h3lwt = mean + age + animal + residual[‡]	h1lwt[‡]	0.48 (0.06)	509.0 (72.0)	1059.3 (28.5)
	h2lwt[‡]	0.47 (0.06)	346.6 (54.9)	730.7 (39.2)
	h3lwt[‡]	0.48 (0.06)	557.7 (90.2)	1168.9 (49.0)

[‡] h1, h2, h3 = harvests 1 to 3; adlwt = liveweight adjusted for age; lwt = liveweight

Table 3.21 Summary EBV statistics for multivariate analyses fitted to harvested data with specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	Trait	Sires			Progeny		
		SD	Min*	Max*	SD	Min*	Max*
4.4 h1adlwt h2adlwt h3adlwt = mean + animal + residual[‡]	h1adlwt[‡]	22.73 (1.85)	-89.91	101.90	18.27 (2.08)	-91.01	94.89
	h2adlwt[‡]	20.19 (1.84)	-84.06	88.76	16.22 (1.98)	-81.90	82.64
	h3adlwt[‡]	20.50 (1.80)	-83.57	94.28	16.45 (1.96)	-86.90	87.96
4.5 h1lwt h2lwt h3lwt = mean + age + animal + residual[‡]	h1lwt[‡]	20.69 (1.69)	-81.48	94.40	16.65 (1.91)	-82.19	87.77
	h2lwt[‡]	17.07 (1.52)	-69.71	79.50	13.74 (1.66)	-71.75	73.91
	h3lwt[‡]	21.58 (1.96)	-89.42	102.80	17.35 (2.13)	-92.39	95.63

* Highest and lowest EBV over 100 replicates
[‡] h1, h2, h3 = harvests 1 to 3; adlwt = liveweight adjusted for age; lwt = liveweight

3.4 Conclusions

Based on these results it is evident that when LWTs were only available for animals as they were harvested and there were no specific harvest day effects, a univariate analysis of LWT pre-adjusted for age fitting only one fixed effect of the mean (Analysis 3.5) was the best. Fitting this analysis resulted in high mean accuracy of sire EBVs equal to theoretical calculation based on the simulation parameters, with little variation between replicates at 0.92 (0.01), as well as low EBV bias evident for sires.

For harvested data affected by specific harvest day effects, when data was only available on animals at their point of slaughter, a univariate analysis of LWT pre-adjusted for age fitting only one fixed effect of the mean (Analysis 4.1) was the best. This analysis was the same as Analysis 3.5 and ignored the addition of specific harvest day effects to the data. As a result, the mean accuracy of sire EBVs over all replicates dropped slightly and the variation between replicates increased slightly (0.91 (0.02) for Analysis 4.1). The addition of specific harvest day effects at the level simulated did not have an extremely negative effect on EBV prediction of sires.

Highly accurate sire EBVs resulted from a univariate analysis when all LWT records were available at the approximate average age of slaughter (0.92 (0.01) for Analysis 1.2), and the addition of a constant to all records as would happen with the addition of a specific harvest day effect would not change the resulting EBVs or their accuracy. The multivariate Analyses 4.4 and 4.5 treated the adjusted or unadjusted LWT at each harvest as separate traits, with LWT records available for all animals at harvest one and then only for the remaining animals as they were harvested thereafter. These analyses accounted for the harvesting and specific harvest day effects, but did not improve the EBV accuracy of sires over a simple univariate analysis fitted to LWT records of all animals taken at the same time.

It must be emphasized that the results are based on specific cases. For practical application, implications of differences in the simulated parameters need to be considered. For the cases studied there were a large number of progeny per sire and only one contemporary group until divided by selective slaughter, with the only difference in fixed effects between progeny being age at slaughter and specific harvest day effects for some simulation runs. It is expected that less progeny per sire, divided between more contemporary groups subject to selective slaughtering, would reduce the accuracy of sire EBVs from those that resulted in this study.

The specific harvest day effect simulated was an effect common to all animals that did not affect the harvesting. There could also be harvest day effects affecting the actual harvesting by causing differences between animals. This study looked at a single trait only and did not take into account the possible usefulness in predicting EBVs of having more than one trait in the analysis. For the analyses involving Adj.LWT, a linear adjustment for age was made when the known underlying mean growth rate was also linear. The adjustment is not likely to work as well if the underlying mean growth rate is not linear.

There are several areas where this work could be extended. Examples are reducing the number of progeny per sire, adding more fixed effects along with different contemporary group definitions, adding other traits including carcase traits, varying the amount of information available before and over the harvest period, adding harvest day effects pre-

harvest, varying the harvesting criteria, and simulating non-linear underlying mean growth curves. Other scenarios could also be examined, for example having an extended period between two harvests, possibly due to unfavourable environmental conditions such as drought.

The following two chapters extend the simulation study of harvested data begun in this chapter. Chapter 4 examines a method that expressly accounts for specific harvest day effects. Chapter 5 examines the estimation of EBVs for a carcase trait genetically correlated to the harvesting criteria LWT, and explores the effects of larger specific harvest day effects and reduction in the number of progeny per sire.

4 ADJUSTING HARVESTED LIVEWEIGHT RECORDS FOR THE DISTRIBUTION

4.1 Introduction

In Chapter 3, no analysis resulted in consistently accurate liveweight (LWT) estimated breeding values (EBVs) for harvested LWT records influenced by specific harvest day effects. Although Analysis 4.1 in Chapter 3 resulted in high mean accuracy of sire EBVs at 0.91, the accuracy was quite variable between replicates with a standard deviation over 100 replicates of 0.02, ranging from 0.83 to 0.95. This is in contrast to the same analysis (Analysis 3.5) applied to harvested data without specific harvest day effects simulated, where the mean accuracy of sires was 0.92 with the standard deviation of accuracy between replicates at 0.01, ranging from 0.89 to 0.95. For Analysis 4.1 the LWTs were pre-adjusted for age, and the effect of harvest day was ignored. Therefore, the adjusted LWTs of progeny used in the EBV analysis were affected up or down depending on the harvest day effect simulated.

This problem cannot be solved in Analysis 4.1 by simply adding harvest day as a classification variable in the fixed effects of the analysis, as benefit gained by adjusting the weights for age would be undone, and genetically superior (inferior) sires would tend to be compared among themselves. This was illustrated by Analysis 4.2 where the mean EBV accuracy was only 0.78 for sires with large variation in accuracy between replicates. Previous analyses have not adequately been able to remove confounding between genetic, age and harvest day effects.

This study proposes a different method of pre-adjusting LWTs affected by specific harvest day effects to enable a univariate analysis of LWTs from harvested data to provide consistently accurate EBVs regardless of the size of the specific harvest day effects.

4.2 Materials and methods

In this case, three harvest days were considered, the number that were simulated, but the method could be applied to any number of harvest days. Based on LWTs measured at the first harvest a normal distribution was created. It was assumed that all second harvest LWTs would have been in the middle third of the distribution at harvest 1 and

that all third harvest LWTs would have been in the left third of the distribution at harvest 1 (see Figure 4.1).
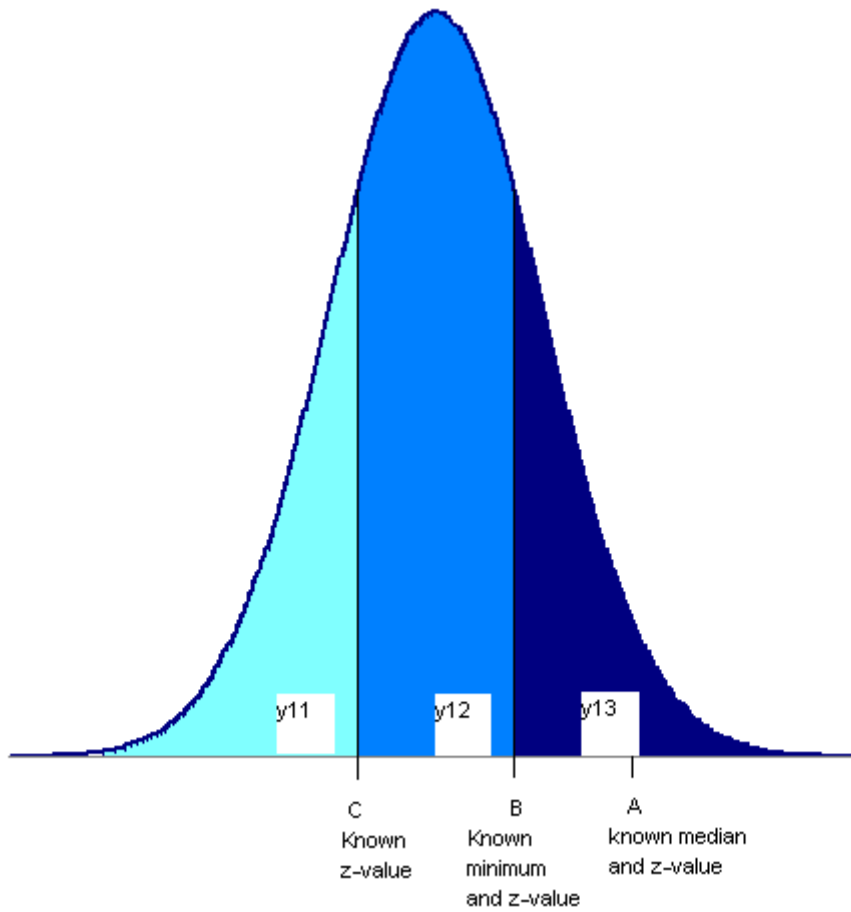
Figure 4.1   Estimated normal distribution of weights at harvest 1 time defined by weights of animals slaughtered at harvest 1 (dark shading on right). The middle area is the assumed distribution of the weights of animals slaughtered at harvest 2 at harvest 1, and the left area is assumed to be the distribution of the weights of animals slaughtered at harvest 3 at harvest 1.

		Group		
		1	2	3
	1	y_{11}	y_{12}	y_{13}
Harvest	2	y_{21}	y_{22}	
	3	y_{31}		

Figure 4.2 Groups of observations within harvests. Dark-shaded groups are harvested animals for which statistics are calculable. Statistics for light-shaded areas were estimated.

Based on normal distribution theory, harvest LWTs from the second and third harvests can be adjusted downwards to the first harvest so that all animals have a LWT at harvest 1. This is possible by estimating the medians and standard deviations for the animals harvested in the second and third harvests at harvest 1, namely for groups y_{11} and y_{12} in Figure 4.2. To calculate these values parameters of the standard normal curve can be utilised. The proportion of animals slaughtered at each harvest is known, enabling us to define the area equating to the probability of different parts of the curve in Figure 4.1. Based on the animals selected at harvest 1 we know their median (point A in Figure 4.1) and minimum phenotypic LWT (point B in Figure 4.1). Knowing the cumulative probability of the standard normal distribution to the left of points A and B, we also know the z-values [standard deviations for N(0,1)] of the standard normal distribution corresponding to these two points. The estimated standard deviation of the weights of all animals at harvest day one is therefore

$$\hat{\sigma} = \frac{\text{median A} - \text{minimum B}}{\text{z\_value}_A - \text{z\_value}_B} \qquad [4.1]$$

where A and B refer to the points indicated in Figure 4.1. The mean of the estimated full distribution at harvest 1 is then

$$\hat{\mu} = \text{minimum B} - \left(\text{z\_value}_B - 0\right)\hat{\sigma} \qquad [4.2]$$

where 0 is the z-value at the mean of the standard normal distribution. Z-values could be calculated at the median points of y_{11} and y_{12} (see Figure 4.1) through knowledge of the proportion of animals to the left of these points. The median LWTs can be estimated as

$$\hat{\text{median}} = \hat{\mu} + \text{z\_value}_{\hat{\text{median}}} * \hat{\sigma} \qquad [4.3]$$

A program was written to estimate the standard deviations of groups y_{11} and y_{12}. This program drew random numbers from a standard normal distribution, and kept only the resulting values that lay between the known z-value$_C$ and z-value$_B$ for y_{12} and the values below z-value$_C$ for y_{11} (see Figure 4.1). Multiplying $\hat{\sigma}$, the estimated standard deviation of all weights at harvest 1 time, by the standard deviation of the values drawn from the

standard normal distribution for y_{11} and y_{12} gave the estimates of the actual standard deviations for y_{11} and y_{12}.

Harvest 2 weights were adjusted to the normal distribution estimated at harvest 1 by using the following equation (see Figure 4.1 and Figure 4.2 for reference):

$$\hat{y}_{12_i} = \overline{y}_{22} + \left(y_{22_i} - \overline{y}_{22}\right)\frac{\hat{\sigma}_{y_{12}}}{\sigma_{y_{22}}} - \left(\text{median}_{y_{22}} - \hat{\text{median}}_{y_{12}}\right) \tag{4.4}$$

Harvest 3 weights were adjusted in the same way where y_{12} is replaced with y_{11} and y_{22} is replaced with y_{31} in the previous equation.

The ages of animals harvested at the second harvest were corrected downward by the time difference between harvest 1 and harvest 2. The ages of animals harvested at the third harvest were corrected downward by the time difference between harvest 1 and harvest 3.

Adjustment for age was then applied to this new set of LWTs, using the adjustment equation used in Chapter 3, i.e. [3.2], repeated below:

$$\text{Adj.LWT}_i = \frac{\text{harvest LWT}_i - \text{birth LWT}_i}{\text{age}_i} * \text{standard age(580d)}$$

where Adj.LWT$_i$ is the LWT pre-adjusted for age for the ith animal, harvest LWT$_i$ is the harvest LWT for the ith animal and age$_i$ is the age at slaughter for the ith animal. Birth LWT was set at 35 kg.

The statistics software ASReml (Gilmour et al. 2002) was used to fit the same univariate animal model as Analysis 4.1 in Chapter 3, specifically:

$$\text{Adj.LWT}_i = \mu + a_i + e_i \qquad\qquad \text{Analysis 1.1}$$

where Adj.LWT$_i$ is the LWT pre-adjusted for age for the ith animal, μ is the overall fixed effect of the mean, and a$_i$ and e$_i$ are additive genetic and residual random effects of the ith animal.

4.3 Results and discussion

Analysis 1.1 was fitted to two of the simulated data sets used in Chapter 3 that had specific harvest day effects added post-harvest. The first data set had specific harvest day effects of 5.507, -11.921 and 11.360; and the second data set had specific harvest day effects of 6.919, -54.447 and 15.221. For the second data set chosen, Analysis 4.1 in Chapter 3 resulted in a relatively low EBV accuracy of 0.880 for sires (Table 4.1). The greater bias that will have resulted in the adjusted LWTs used in modelling the second data set explains the poorer EBV accuracy.

Fitting the analysis with the new method of record adjustment improved the accuracy of EBVs for both data sets, as measured by the Pearson correlation between true and estimated breeding values (see Table 4.1). Specifically, in analysis of the second data set where the accuracy for sires and progeny was found to be relatively low at 0.880 and 0.626 respectively (data set 2 in Table 4.1), the EBV accuracy increased by 0.052 and 0.118. This proposed adjustment will have effectively taken into account the difference in means between harvest days due to the specific harvest day effects. With more extreme specific harvest day effects in data set 2 than data set 1 the improvement in EBV accuracy will have been more pronounced.

Table 4.1 EBV accuracy resulting from fitting the same univariate analysis but having used two different methods of pre-adjusting harvest liveweight (LWT)

| Adjustment to harvest LWT dependent variable | EBV accuracy | | | |
| | Data set 1 | | Data set 2 | |
	Sires	Progeny	Sires	Progeny
Adjusted for age	0.912	0.714	0.880	0.626
Fitted to normal distribution at harvest 1 and then adjusted for age	0.921	0.727	0.932	0.744

4.4 Conclusions

These results provide evidence that the proposed method has potential to account for harvesting over time. If both LWT and carcase trait records are only available for the animals when they are harvested, it could be possible to adjust the LWTs to the estimated normal distribution of LWTs at harvest one, and then use a bivariate or multivariate analysis using these adjusted LWT values to estimate more accurate breeding values for both LWT and carcase traits.

This method accounts for change in mean and variance from the first harvest to each subsequent harvest. However, it implies that beyond the first harvest the ranking and relativity of animals does not change and that there is linear growth between the first harvest and the consecutive harvests. If there is a large time gap between the first harvest and any of the consecutive harvests or large environmental changes after the first harvest, it may be unrealistic to expect the ranking and relativity of animals to remain constant beyond the first harvest. In this work there was 50 days between the first and second harvests and 92 days between the first and third harvests for data set 1. For data set 2 these values were 48 and 94 days, respectively.

As with Analysis 4.1 in Chapter 3, this proposed method adjusts the LWTs (in this case fitted to the estimated normal distribution at harvest 1) by weight for age assuming linear growth. However, it can be seen that in this case the method has still been able to give quite accurate EBVs. Although the underlying mean growth curve was fitted as linear, the random additive-genetic and permanent-environmental effects fitted mean that the growth curves of individual animals were not linear.

The adjustments made to the LWTs to fit them to a common distribution at harvest 1 assume normality throughout. This has not been a valid assumption but the resulting accuracies of EBVs indicate that it is a valid approximation.

Other considerations are that this work assumed animals were harvested based on their actual LWTs and that only the heaviest animals were harvested. In reality if animals are harvested by eye, some of the heaviest animals may not be chosen for harvest. Also, in reality, animals are likely to be harvested both on LWT and fatness.

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When there are only pre-slaughter LWT records available for animals harvested, within certain constraints, this proposed method is able to account for the harvesting, including when there are specific harvest day effects.

Further work could investigate the different issues brought up in this discussion, including assessing the effect on EBV accuracy of increasing the time between the first and subsequent harvests.

5 ACCOUNTING FOR HARVESTING WHEN ESTIMATING BREEDING VALUES FOR CARCASE TRAITS – A TWO-TRAIT SIMULATION STUDY

5.1 Introduction

In Chapters 3 and 4, different models and trait definitions were used in the estimation of breeding values for a single trait, liveweight (LWT), which was the criterion for harvesting. In Chapter 3, when LWT records were only available for animals at slaughter, it was found that accounting for both age and specific harvest day effects resulted in confounding between genetic and specific harvest day effects. However, ignoring the specific harvest day effects in the analysis resulted in slightly reduced accuracy of sires and increased variation in accuracy between replicates. However, using normal distribution theory, it was shown in Chapter 4 that when the trait of interest was the trait harvested on, the records from selected animals taken at the different harvest times could be adjusted to line up with the mean and variance of the distribution at the first harvest. With all animal records pre-adjusted for age, a more accurate estimation of breeding values was possible, accounting for both age and harvest day effects.

When all progeny have records on the same day, there is no need to consider specific harvest day effects in the prediction of estimated breeding values (EBVs). Any effect would only shift the phenotypic mean. When such records are available for the harvesting criteria, for example, LWT or ultrasound measures taken on all animals at a common point, these records can be used in a multi-trait analysis to estimate breeding values of genetically correlated carcase traits where the carcase trait records are only available from harvested animals when they are slaughtered. These carcase traits may be affected by both age and harvest day effects. If records of the harvesting criteria are not available for all progeny on the same day, particular methods may be used to estimate all records for the criteria on one day.

This chapter explores the estimation of breeding values for a second trait, for example, a carcase trait, when harvesting is based on LWT. The carcase trait is analysed with univariate analyses and bivariate analyses utilising LWT records differing in availability. The effects of variation in simulated parameters are examined including variation in the genetic correlation between LWT and the carcase trait, the size of specific harvest day effects and the number of progeny per sire.

5.2 Materials and methods

Replicates were based on a half-sib design with the same pedigree and age structure as used in Chapter 3. Two traits of variable genetic correlation between them were simulated with underlying parameters similar to those of LWT and eye muscle area (EMA).

5.2.1 Simulating liveweight and eye muscle area phenotypes

The mean growth curve for LWT was the same as that used in the simulations in Chapter 3, i.e. [3.1], repeated below

$$liveweight(kg) = 100.2610 + 0.6266 * age(days)$$

The mean growth curve for EMA was simulated as

$$EMA(cm^2) = 9.06 + 0.17 * age(days)$$

and was approximated from Figure 1 in Hassen et al. (2004).

In simulating EMA, random additive-genetic and permanent-environmental effects were fitted as functions of age using Legendre polynomials. The (co)variances between random regression coefficients for both these random effects were taken from Hassen et al. (2004), where estimates were based on ultrasound longissimus muscle area measurements from Angus cattle. The estimates were based on a linear polynomial fitted for the additive-genetic random effect and a quadratic polynomial fitted for the permanent-environmental effect (see Table 5.1 and Table 5.2).

5.2.2 Correlating liveweight and eye muscle area

To simulate LWT and EMA, the RRGibbs program was used to produce random regression coefficients for the additive-genetic effect and permanent-environmental effect, for both traits (Meyer 2002). RRGibbs was run once for each replicate, specifying 5x5 and 6x6 covariance matrices for the (co)variances between random regression coefficients for the genetic and permanent-environmental effects respectively (see Table

5.1 and Table 5.2). The top left corner of these matrices gave the (co)variance matrices for LWT as specified in Chapter 3.

Table 5.1 (Co)variances between random regression coefficients for liveweight (lwt) and eye muscle area (ema) random additive-genetic effects

	lwtβ0	lwtβ1	lwtβ2	emaβ0	emaβ1
lwtβ0	748.93	340.63	-41.65	0.0	0.0
lwtβ1	340.63	186.74	2.76	0.0	0.0
lwtβ2	-41.65	2.76	18.37	0.0	0.0
emaβ0	0.0	0.0	0.0	27.56	3.91
emaβ1	0.0	0.0	0.0	3.91	1.02

Table 5.2 (Co)variances between random regression coefficients for liveweight (lwt) and eye muscle area (ema) random permanent-environmental effects

	lwtβ0	lwtβ1	lwtβ2	emaβ0	emaβ1	emaβ2
lwtβ0	737.48	371.41	-29.42	0.0	0.0	0.0
lwtβ1	371.41	311.18	75.91	0.0	0.0	0.0
lwtβ2	-29.42	75.91	70.83	0.0	0.0	0.0
emaβ0	0.0	0.0	0.0	25.29	0.58	-2.63
emaβ1	0.0	0.0	0.0	0.58	5.96	1.02
emaβ2	0.0	0.0	0.0	-2.63	1.02	1.17

The resulting random regression coefficients took into account the pedigree and the relationships between regression coefficients within traits, but did not account for any correlation between traits. The correlation between the two traits was achieved in the following step.

For the additive-genetic and permanent-environmental random effects simulated based on random regression, the uncorrelated effects for each trait were calculated as:

$$A_{ijk} = K'_{ik} \Phi_j$$

where A_{ijk} is the kth random effect for the jth age for the ith animal, K_{ik} are the specific regression coefficients resulting from running the RRGibbs program for the kth random

effect and the ith animal, and Φ_j are the coefficients for the Legendre polynomial evaluated for the jth age.

These effects were used to correlate the second trait with the first.

$$A_{1ijk}^{new} = A_{1ijk}$$

$$A_{2ijk}^{new} = \left[\frac{A_{1ijk}}{\sigma_{1jk}} \quad \frac{A_{2ijk}}{\sigma_{2jk}} \right]' [D_{k21} \quad D_{k22}] \sigma_{2jk}$$

where the letter subscripts are the same as for the previous equation, and the subscript numerals represent trait 1 or 2. σ_{1jk} and σ_{2jk} are the standard deviations for the jth age within the kth random effect for traits 1 and 2. The effect for the first trait, A_{1ijk}^{new}, remained unchanged. A_{2ijk}^{new} was the new correlated effect for the second trait. Correlation matrices for the kth random effect (additive-genetic and permanent-environmental effects) were decomposed by the Cholesky method, and $[D_{k21} \quad D_{k22}]$ is the second row of the decomposed matrix for the kth random effect.

The permanent-environmental correlation between LWT and EMA was set at 0.8. The additive-genetic correlation between the two traits was varied (0.0, 0.6 and 0.9) to investigate trends in results. The correlation between additive-genetic effects and both permanent-environmental and residual effects was assumed to be zero.

5.2.3 Simulation of residual effects

Step functions were defined for both traits over time to create heterogeneous residual variance for each trait. The step function used for LWT residual variance was the same as that given for LWT in Chapter 3. For EMA, the step function of residual variance over time was estimated based on the additive-genetic and permanent-environmental variances calculated at different ages. The step function for EMA residual variance over time was calculated as

$$\sigma_{ej_1:j_2}^2 = \sigma_{phenj_1:j_2}^2 - \sigma_{aj_1:j_2}^2 - \sigma_{pej_1:j_2}^2$$

where $\sigma^2_{ej_1:j_2}$ is the residual variance between the ages j_1 and j_2 calculated for 20 day increments, and phen, a and pe represent the phenotype, additive-genetic effect and permanent-environmental effect. $\sigma^2_{phenj_1:j_2}$ was calculated as

$$\sigma^2_{phenj_1:j_2} = \frac{\sigma^2_{aj_1:j_2}}{h^2_{j_1:j_2}}$$

where $\sigma^2_{aj_1:j_2}$ is the additive-genetic variance between the ages j1 and j2, and was calculated by averaging the daily variance values over 20 day increments. The additive-genetic (co)variance values between different ages were calculated as

$$G = \Phi K \Phi'$$

where G is the additive-genetic (co)variance matrix between ages, Φ is the matrix of Legendre polynomial coefficients evaluated for each age and K is the matrix of (co)variances between the additive-genetic random regression coefficients. $\sigma^2_{pej_1:j_2}$ was calculated in the same way:

$$PE = \Phi K \Phi'$$

where PE is the permanent-environmental (co)variance matrix between ages and K is the matrix of (co)variances between the permanent-environmental random regression coefficients.

$h^2_{j_1:j_2}$ is the heritability for age range j_1 to j_2 and was taken from Figure 4 in Hassen et al. (2004) for ages 183 to 434 days resulting from the model fitting linear and quadratic polynomials for additive-genetic and permanent-environmental effects, respectively. For ages below and above this range, h^2 was given equivalent to that for the lowest and highest available age range from this paper, respectively. See Table 5.3 for the specific h^2 step function.

Table 5.3 Heritability step function over time (days) for eye muscle area

Age range		Heritability
Minimum	Maximum	
141	182	0.33
183	210	0.33
211	238	0.35
239	266	0.36
267	294	0.37
295	322	0.38
323	350	0.40
351	378	0.42
379	406	0.43
407	434	0.42
435	819	0.42

The residual correlation between LWT and EMA was assumed to be zero, implying that temporary effects affecting the LWT residuals do not have correlated affects on EMA residuals and vice versa.

5.2.4 Data sets

Data set 1: Data not harvested

All animals were measured for both traits on the same day at an average age of 580 days.

Data set 2: Harvested data

No specific harvest day effects were simulated and animals harvested as described in Chapter 3.

Data set 3: Harvested data with smaller specific harvest day effects

Specific harvest day effects were simulated in the same way as given in Chapter 3 for both LWT and EMA, where if treated as random effects would account for 20% of the phenotypic variation. For EMA, for each replicate, one specific effect was simulated for

each harvest day, from N(0, 3.06 cm^2). It was assumed that LWT and EMA specific harvest day effects were not correlated.

Data set 4: Harvested data

Each animal had one LWT and one EMA record taken at harvest time. No specific harvest day effects were simulated for LWT, but were simulated for EMA as detailed above.

Data set 5: Harvested data

Each animal had one LWT and one EMA record taken at harvest time. Specific harvest day effects were simulated for both LWT and EMA as detailed above.

Data set 6: Harvested data with LWT records for all animals at harvest 1

Each animal had a LWT record at harvest one and one EMA record taken at harvest time. Specific harvest day effects were simulated for EMA as detailed above.

Data sets 7-10: Large specific harvest day effects

Data sets 7 to 10 were equivalent to data sets 3 to 6 apart from the size of the specific harvest day effects. The standard deviation of specific harvest day effects affecting EMA was increased to 6.13 cm^2, equivalent to 50 % of the phenotypic variation.

Data sets 11-14: Harvested data with number of progeny per sire reduced

Data sets 11 to 14 were the same as data sets 3 to 6 with the number of progeny per sire reduced from forty to fifteen. The number of sires was not increased.

5.2.5 Statistical analyses

As in Chapter 3 the statistical package ASReml was used to fit animal models to the simulated data. In this chapter, LWT and EMA were analysed separately by univariate analyses and together in bivariate analyses.

Traits analysed were EMA, LWT, and EMA and LWT pre-adjusted for age (Adj.EMA and Adj.LWT) according to the following equations for the ith animal:

$$\text{Adj.EMA}_i = \frac{\text{harvest EMA}_i - \text{birth EMA}_i}{\text{age at harvest}_i} * \text{standard age (580d)}$$

where the EMA at birth was 9.06 cm^2. LWT was adjusted for age with the same equation used in Chapter 3, i.e. [3.2], repeated here:

$$\text{Adj.LWT}_i = \frac{\text{harvest LWT}_i - \text{birth LWT}_i}{\text{age}_i} * \text{standard age (580d)}$$

where LWT at birth was 35 kg.

The univariate animal models fitted followed the general form:

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

where **y** is the vector of observations, **X** is the incidence matrix for fixed effects, **b** is the vector of fixed effects, **Z** is the incidence matrix for random effects, **u** is the vector of random effects, and **e** is the vector of random residual effects. An overall mean fixed effect and random additive-genetic and residual effects were fitted in all univariate analyses.

In general the bivariate analyses fitted for traits 1 and 2 can be represented in the following matrix form:

$$\begin{bmatrix} \mathbf{y_1} \\ \mathbf{y_2} \end{bmatrix} = \begin{bmatrix} \mathbf{X_1} & \mathbf{0} \\ \mathbf{0} & \mathbf{X_2} \end{bmatrix} \begin{bmatrix} \mathbf{b_1} \\ \mathbf{b_2} \end{bmatrix} + \begin{bmatrix} \mathbf{Z_1} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z_2} \end{bmatrix} \begin{bmatrix} \mathbf{u_1} \\ \mathbf{u_2} \end{bmatrix} + \begin{bmatrix} \mathbf{e_1} \\ \mathbf{e_2} \end{bmatrix}$$

where $\mathbf{y}_k$ are the records for the kth trait, $\mathbf{b}_k$ are the fixed effects relevant to the kth trait, $\mathbf{u}_k$ are the random animal effects relevant to the kth trait, $\mathbf{X}_k$ and $\mathbf{Z}_k$ are incidence matrices mapping observations to their fixed and random effects, respectively, and $\mathbf{e}_k$ are the random residual effects for the kth trait;

with variances

$$\text{var}\begin{bmatrix} u_1 \\ u_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} G_{11}A & G_{12}A & 0 & 0 \\ G_{21}A & G_{22}A & 0 & 0 \\ 0 & 0 & R_{11} & R_{12} \\ 0 & 0 & R_{21} & R_{22} \end{bmatrix}$$

where **G** is the matrix of additive-genetic (co)variances between traits, **R** is the matrix of residual (co)variances between traits, and **A** is the Numerator Relationship Matrix (NRM).

Bivariate analysis fitted to data set 1

A bivariate model was fitted, represented here as two component equations:

$LWT_i = \mu + age_i + a_i + e_i$

$EMA_i = \mu + age_i + a_i + e_i$ Analysis 1.1

where μ represents the overall mean for the trait, age_i is the linear age effect for the animal, a_i is the random animal effect (the breeding value) for the ith animal, and e_i is the random residual for the ith animal.

LWT and EMA univariate analyses involving data set 2

$LWT_i = \mu + a_i + e_i$ Analysis 2.1

$Adj.LWT_i = \mu + a_i + e_i$ Analysis 2.2

$EMA_i = \mu + a_i + e_i$ Analysis 2.3

$EMA_i = \mu + age_i + a_i + e_i$ Analysis 2.4

$Adj.EMA_i = \mu + a_i + e_i$ Analysis 2.5

where the effects are as described for Analysis 1.1.

EMA univariate analyses involving data set 3

$EMA_i = \mu + a_i + e_i$ Analysis 3.1

$EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 3.2

$EMA_i = \mu + age_i + a_i + e_i$ Analysis 3.3

$Adj.EMA_i = \mu + a_i + e_i$ Analysis 3.4

Adj.EMA$_{ij}$ = μ + harvest day$_j$ + a$_i$ + e$_{ij}$ 　　　　　　　　　　　　　　Analysis 3.5

where the effects are as described for Analysis 1.1 with the addition of harvest day$_j$.

Bivariate analyses involving data set 4

LWT$_i$ = μ + a$_i$ + e$_i$
EMA$_i$ = μ + a$_i$ + e$_i$ 　　　　　　　　　　　　　　　　　　　　　　Analysis 4.1

Adj.LWT$_i$ = μ + a$_i$ + e$_i$
EMA$_{ij}$ = μ + harvest day$_j$ + a$_i$ + e$_{ij}$ 　　　　　　　　　　　　　　Analysis 4.2

 where the effects are as above.

Bivariate analyses involving data set 5

LWT$_i$ = μ + a$_i$ + e$_i$
EMA$_i$ = μ + a$_i$ + e$_i$ 　　　　　　　　　　　　　　　　　　　　　　Analysis 5.1

Adj.LWT$_i$ = μ + a$_i$ + e$_i$
EMA$_{ij}$ = μ + harvest day$_j$ + a$_i$ + e$_{ij}$ 　　　　　　　　　　　　　　Analysis 5.2

where the effects are as above.

Bivariate analyses involving data set 6

LWT$_i$ = μ + a$_i$ + e$_i$
EMA$_i$ = μ + a$_i$ + e$_i$ 　　　　　　　　　　　　　　　　　　　　　　Analysis 6.1

LWT$_i$ = μ + a$_i$ + e$_i$
EMA$_{ij}$ = μ + harvest day$_j$ + a$_i$ + e$_{ij}$ 　　　　　　　　　　　　　　Analysis 6.2

where effects are as above.

Analyses for when larger specific harvest day effects affected EMA involving data sets 7 to 10

$Adj.EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 7.1

$Adj.LWT_i = \mu + a_i + e_i$
$EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 8.1

$Adj.LWT_i = \mu + a_i + e_i$
$EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 9.1

$LWT_i = \mu + a_i + e_i$
$EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 10.1

where effects are as above.

Analyses for when number of progeny per sire reduced from forty to fifteen

$Adj.EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 11.1

$Adj.LWT_i = \mu + a_i + e_i$
$EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 12.1

$Adj.LWT_i = \mu + a_i + e_i$
$Adj.EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 12.2

$Adj.LWT_i = \mu + a_i + e_i$
$EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 13.1

$Adj.LWT_i = \mu + a_i + e_i$
$Adj.EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 13.2

$LWT_i = \mu + age_i + a_i + e_i$

$EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 14.1

$LWT_i = \mu + age_i + a_i + e_i$

$Adj.EMA_{ij} = \mu + harvest\ day_j + a_i + e_{ij}$ Analysis 14.2

where the effects are as above.

5.2.5.1 Analysis comparison

These analyses were fitted to the corresponding data sets and results presented for 100 replicates. As described in Chapter 3, variance components, and the bias, accuracy and variation of estimated breeding values (EBVs) were calculated. Unless stated, statistics are for the correlated trait, i.e. EMA. Based on the BLUP methodology used, the mean of EBVs for all models fitted was by definition equal to zero. Significance testing was also based on the methods outlined in Chapter 3.

The significance of EMA EBV bias for the top and bottom third of sires based on EBV, was based on an expectation of 0.03 for all levels of r_g(LWT,EMA). This expectation should actually have ranged from 0.00 to 0.04 for levels of r_g(LWT,EMA) ranging from 0.0 to 0.9 according to the mean sire TBVs given in Table 5.9. However the differences from 0.03 were small.

5.3   Results and discussion

5.3.1   Data not harvested

5.3.1.1 Analysis 1.1: Bivariate analysis of LWT and EMA when data was not harvested (genetic correlation between traits = 0.6)

This analysis serves as a control with which comparisons can be made with other analyses fitted. Because the two traits LWT and EMA were recorded on the same day at an average age of 580 days animals were directly comparable. All progeny were in one harvest group, and therefore each sire was equally represented.

Variance partitioning

The phenotypic variances for LWT and EMA at 1,252.17 kg^2 and 37.49 cm^4 (Table 5.4) were not significantly different from the simulated values of 1,246.97 kg^2 (P = 0.11, two-sided test) and 37.55 cm^4 (P = 0.50, two-sided test). Also, the heritabilities for LWT and EMA at 0.495 (0.065) and 0.421 (0.055) were not significantly different from the simulated values of 0.49 and 0.42.

Table 5.4 Variance components for a bivariate analysis fitted to data not harvested (standard deviation of 100 replicates in brackets)

Analysis	Trait	Heritability	Phenotypic variance	Genetic Correlation (LWT,EMA)
1.1 LWT = mean + age + animal + residual EMA = mean + age + animal + residual‡	LWT‡	0.495 (0.065)	1252.17 (32.08)	0.598 (0.061)
	EMA‡	0.421 (0.055)	37.49 (0.88)	

‡ LWT = liveweight, EMA = eye muscle area

Variance of EBVs

The mean standard deviation of sire EBVs over 100 replicates was 3.60 cm^2 (0.30), and the sire EBVs ranged from -13.68 to 12.26 cm^2 over all the replicates (Table 5.5).

Table 5.5 Summary EBV statistics for a bivariate analysis fitted to data not harvested (standard deviation of 100 replicates in brackets)

Analysis	Trait	Sires				Progeny			
		Mean	SD	Min*	Max*	Mean	SD	Min*	Max*
1.1 LWT = mean + age + animal + residual EMA = mean + age + animal + residual‡	EMA‡	0.00 (0.00)	3.60 (0.30)	-13.68	12.26	0.00 (0.00)	2.80 (0.32)	-12.99	14.81

‡ LWT = liveweight, EMA = eye muscle area
* Highest and lowest EBV over 100 replicates

Accuracy of EBVs

The accuracy of sire and progeny EBVs for EMA was 0.91 (0.02) and 0.70 (0.01) (Table 5.6). The EBV accuracy for sires was equal to the deterministic calculation of EBV accuracy at 0.91 for a progeny test based on the simulated parameters, heritability at 0.42 and 39.4 effective progeny.

Table 5.6 Mean accuracy of EMA EBVs for a bivariate analysis fitted to data not harvested (standard deviation of 100 replicates in brackets)

Analysis	Sires			Progeny		
	Mean	Min*	Max*	Mean	Min*	Max*
1.1 LWT = mean + age + animal + residual EMA = mean + age + animal + residual‡	0.91 (0.02)	0.87	0.94	0.70 (0.01)	0.67	0.73

‡ LWT = liveweight, EMA = eye muscle area
* Lowest and highest accuracy of 100 replicates

Bias of EBVs

The average TBV for sires and progeny over all replicates for a genetic correlation between LWT and EMA [r_g(LWT,EMA)] of 0.6 were -0.03 (0.37) and -0.01 (0.18) (Table 5.9). Therefore the calculated EBV bias over all sires and progeny of 0.03 (0.37) and 0.01 (0.18) were equal to expectation, showing no EBV bias (Table 3.12). The calculated EBV bias for the bottom and top third of sires based on EBV at 0.01 (0.43) and 0.05 (0.40) were also not significantly different from the expectation of 0.03 ($P > 0.6$, two-sided test), showing no bias.

Table 5.7 EMA EBV bias (EBVs-TBVs) mean and standard deviation [SD (= standard error of prediction)] for a bivariate analysis fitted to data not harvested (standard deviation of 100 replicates in brackets)

Analysis	Progeny		Sires		Bottom 1/3 sires for EBV		Top 1/3 sires for EBV	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1.1 LWT = mean + age + animal + residual EMA = mean + age + animal + residual‡	0.01 (0.18)	2.85 (0.04)	0.03 (0.37)	1.66 (0.11)	0.01 (0.43)	1.67 (0.18)	0.05 (0.40)	1.67 (0.20)

‡ LWT = liveweight, EMA = eye muscle area

5.3.2 Data harvested

Harvesting on LWT was associated with increasing average age across harvest days as shown in Figure 5.1, with an increase of approximately 40 days occurring between consecutive harvest days. Average LWT however, showed a decline between harvest days, with similar LWT between harvests 1 and 2, but a sharper drop from the 2nd to 3rd harvests (see Figure 5.1). Conversely, average EMA showed an increasing trend over consecutive harvest days, even when LWT and EMA were highly correlated for both additive-genetic and permanent-environmental effects as illustrated in Figure 5.1. This can be explained by comparing the two linear mean growth curves simulated for EMA

and LWT. The increase in EMA between consecutive harvests was proportionally greater than for LWT.
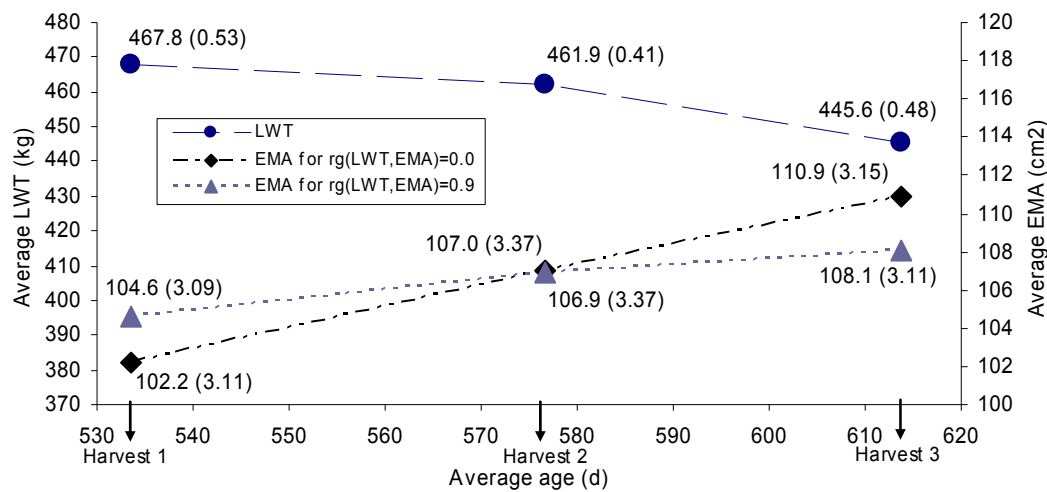
Figure 5.1 Mean age, liveweight (LWT) and eye muscle area (EMA) (for two levels of genetic correlation) at consecutive harvests over 100 replicates (standard deviations).

Harvesting on LWT resulted in unequal distribution of each sire's progeny across harvests. There was a large range in progeny per sire for every harvest (Table 5.8). For 40 progeny simulated per sire and three harvests, the effective number of progeny for sires could range from 39.04 to 39.66, corresponding to the possible extremes in progeny distribution over harvests from a sire having all progeny in one harvest to having progeny equally spread over the three harvests. Based on these effective progeny numbers and simulated heritability of 0.42, sires could vary in EBV accuracy for EMA between 0.9060 and 0.9072. Similarly, for 15 progeny simulated per sire the effective number of progeny could range from 14.64 to 14.88, corresponding to a range in EBV accuracy of 0.795 to 0.797.

Table 5.8 Distribution of sire progeny across harvest days for 100 simulated populations

	Progeny per sire from 100 replicates	
	Minimum range	**Maximum range**
Harvest 1	0-5	24-36
Harvest 2	3-8	19-25
Harvest 3	0-4	24-33

Table 5.9 shows the variability of LWT and EMA TBVs that resulted for sires and progeny with varying levels of genetic correlation between the two traits. The mean standard deviation of TBVs over 100 replicates for LWT and EMA was approximately 25 kg and 4 cm^2.

Table 5.9 Summary TBV statistics for two-trait simulations for varying levels of genetic correlation between liveweight and eye muscle area [R_g(LWT,EMA)] (standard deviation of 100 replicates in brackets)

Trait	R_g (LWT, EMA)	Sires		Progeny	
		Mean	Standard deviation	Mean	Standard deviation
LWT	All	-0.29 (2.27)	24.60 (1.57)	-0.18 (1.08)	24.76 (0.49)
EMA	0.0	0.00 (0.38)	4.00 (0.25)	0.01 (0.19)	3.99 (0.07)
	0.6	-0.03 (0.37)	3.95 (0.24)	-0.01 (0.18)	3.98 (0.07)
	0.9	-0.04 (0.36)	3.95 (0.24)	-0.02 (0.17)	3.99 (0.07)

5.3.2.1 Analyses 2.1-2.5: LWT and EMA univariate analyses of harvested data with no specific harvest day effects simulated

Variance partitioning

Analysing LWT (Analysis 2.1) resulted in significantly lower heritability and phenotypic variance than the simulated values of 0.49 and 1,247.0 kg^2 (Table 5.10). However, although analysing Adj.LWT (Analysis 2.2) resulted in significantly higher phenotypic variance than the simulated value, the mean heritability was equal to the simulated value of 0.49. These results were similar to those of the equivalent analyses in Chapter 3 (Analyses 3.1 and 3.5).

Table 5.10 Heritability and phenotypic variance for univariate analyses fitted to harvested data without specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g(LWT,EMA)	Heritability	Phenotypic variance
2.1 Liveweight = mean + animal + residual	NA	0.31 (0.04)	386.4 (13.2)
2.2 Age-adjusted weight = mean + animal + residual	NA	0.49 (0.06)	1540.1 (39.86)
2.3 EMA = mean + animal + residual	0.0	0.58 (0.07)	52.65 (1.59)
	0.6	0.36 (0.05)	34.57 (0.86)
	0.9	0.13 (0.03)	25.53 (0.62)
2.4 EMA = mean + age + animal + residual	0.0	0.51 (0.07)	34.03 (0.86)
	0.6	0.39 (0.06)	26.32 (0.64)
	0.9	0.21 (0.04)	20.94 (0.50)
2.5 Age adjusted EMA = mean + animal + residual	0.0	0.42 (0.06)	38.69 (0.98)
	0.6	0.42 (0.05)	38.68 (1.04)
	0.9	0.42 (0.05)	38.72 (1.03)

Similar to Analysis 2.2 for Adj.LWT, Analysis 2.5 for Adj.EMA resulted in heritability values equal to the simulated value of 0.42 for r_g(LWT,EMA) ranging from 0.0 to 0.9. The phenotypic variances under Analysis 2.5 for all levels of r_g(LWT,EMA) were significantly larger than the simulated value of 37.55 cm^4, but by less than 2 cm^4. Pre-adjusting an age-dependent trait correlated to the harvesting criteria, i.e. EMA, for age was able to account for the true effect of age and resulted in the correct partitioning of variance regardless of the level of r_g(LWT,EMA).

For EMA under Analyses 2.3 and 2.4 the phenotypic variance and heritability values showed negative trends as the r_g(LWT,EMA) increased.

Accuracy and variability of EBVs

The mean accuracy of sire EBVs under Analyses 2.1 and 2.2 analysing LWT were equal to those for the same analyses in Chapter 3 (Analyses 3.1 and 3.5) when only LWT was simulated. The mean accuracy of sire EBVs for Analysis 2.2 analysing LWT pre-adjusted for age at 0.92 (0.01) was equal to the expected value based on the parameters simulated.

Similarly, Analysis 2.5 that analysed Adj.EMA, resulted in mean accuracies of sire EBVs for all levels of r_g(LWT,EMA) of 0.91 (0.02), equal to the deterministically calculated expectation of 0.91.

Analysing EMA with Analysis 2.3, which was the same basic analysis as that used for LWT in Analysis 2.1, it is noticeable that even when the two traits have high permanent-environmental and genetic correlations (0.8 and 0.9), the accuracy of sire EMA EBVs was significantly lower at 0.25 (0.09) than the accuracy of sire LWT EBVs resulting from Analysis 2.1 at 0.87 (0.02) (Table 5.11).

Consideration of the TBVs and EBVs separately can explain the results. Considering TBVs, when harvesting is on LWT it is expected that progeny of sires with higher LWT TBVs would be harvested first, and therefore sires represented more in earlier harvests would have greater LWT TBVs than those in later harvests. The magnitude of sire LWT and EMA TBVs at each harvest can be gauged from the corresponding magnitude of average progeny TBVs, given in Table 5.12. When r_g(EMA,LWT) = 0, the EMA TBVs of sires are expected to show no association with harvest days, but as r_g(EMA,LWT) increases, the expectation is a strengthening trend for sires more represented in earlier harvests to have greater EMA TBVs, increasingly approaching the trend seen for LWT TBVs.

CHAPTER 5. TWO-TRAIT SIMULATION STUDY

Table 5.11 Mean accuracy and standard deviation of EBVs for univariate analyses fitted to harvested data without specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g (LWT, EMA)	EBV accuracy of Sires			EBVs of Sires		
		Mean	Min*	Max*	SD	Min^	Max^
2.1 Liveweight = mean + animal + residual	NA	0.87 (0.02)	0.82	0.92	9.48 (0.94)	-49.42	40.56
2.2 Age-adjusted weight = mean + animal + residual	NA	0.92 (0.01)	0.89	0.95	25.30 (2.15)	-95.99	108.20
2.3 EMA = mean + animal + residual	0.0	0.68 (0.05)	0.58	0.79	5.15 (0.40)	-20.31	21.61
	0.6	0.44 (0.08)	0.27	0.64	3.12 (0.28)	-12.63	14.15
	0.9	0.25 (0.09)	0.06	0.44	1.33 (0.20)	-5.64	6.17
2.4 EMA = mean + age + animal + residual	0.0	0.88 (0.02)	0.81	0.94	3.86 (0.32)	-16.04	16.64
	0.6	0.78 (0.03)	0.70	0.87	2.89 (0.26)	-12.17	11.01
	0.9	0.72 (0.04)	0.59	0.80	1.76 (0.20)	-6.78	6.57
2.5 Age adjusted EMA = mean + animal + residual	0.0	0.91 (0.02)	0.85	0.95	3.63 (0.33)	-15.78	14.14
	0.6	0.91 (0.02)	0.86	0.94	3.63 (0.30)	-14.14	12.14
	0.9	0.91 (0.02)	0.86	0.94	3.65 (0.29)	-13.67	14.25

* Lowest and highest accuracy of 100 replicates
^ Highest and lowest EBV over 100 replicates

Table 5.12 Progeny liveweight (LWT) TBVs and eye muscle area (EMA) TBVs, for varying levels of genetic correlation, for consecutive harvests (standard deviation of 100 replicates in brackets)

	Average LWT TBV	Average EMA TBV		
		Genetic correlation (EMA, LWT)		
		0.0	0.6	0.9
Harvest 1	17.48 (1.28)	-0.01 (0.20)	1.68 (0.21)	2.53 (0.21)
Harvest 2	-0.12 (1.20)	0.01 (0.21)	0.00 (0.20)	-0.01 (0.20)
Harvest 3	-18.58 (1.18)	0.02 (0.21)	-1.78 (0.19)	-2.69 (0.18)

Considering EBVs, under Analyses 2.1 and 2.3, where neither age nor harvest day was fitted, the trait EBV of an individual sire is expected to simply match the phenotypic ranges of harvests in proportion to the number of progeny it has in each one. LWT showed a negative phenotypic trend across consecutive harvests, but EMA showed a positive trend regardless of r_g(EMA,LWT), as explained earlier (Figure 5.1). Therefore, the LWT EBVs of sires followed the same trend as their TBVs across harvests leading to a high EBV accuracy under Analysis 2.1. The EMA EBVs of sires followed the opposite trend to their TBVs across harvests when r_g(EMA,LWT) = 0.6 or 0.9, resulting in low EBV accuracy under Analysis 2.3. When r_g(EMA,LWT) = 0, EMA TBVs of sires were not related to harvest days, but the EBVs of random sires resulting from fitting Analysis 2.3 followed the positive phenotypic trend in EMA across consecutive harvests leading to a low EBV accuracy.

In contrast, for r_g(EMA,LWT) = 0, the addition of an age covariate in Analysis 2.4 resulted in a significant increase in the mean accuracy of sire EBVs (Table 5.11). Like Analysis 2.3, sires were unequally represented across harvests and their TBVs were random. Fitting an age covariate was able to account for the phenotypic increase across harvests due to age. As the r_g(EMA,LWT) increased the age covariate was less able to account for the true effect of age and the accuracy of sire EBVs reduced.

Bias of EBVs

For Analysis 2.5, the mean EBV bias of the bottom and top third of sires based on EBV were not significantly different from the expectation of 0.03 for all levels of r_g(EMA,LWT) (P > 0.08, two-sided test), apart from the EBV bias of the top third of sires when the r_g(EMA,LWT) was 0.9 (P = 0.0166, two-sided test), with an EBV bias of 0.13 (0.41) (Table 5.13).

Table 5.13 EBV bias (EBVs-TBVs) mean and standard deviation (SD) for univariate analyses fitted to harvested data without specific harvest day effects simulated for varying levels of genetic correlation between liveweight and eye muscle area [R_g(LWT,EMA)] (standard deviation of 100 replicates in brackets)

Analyses	R_g (LWT, EMA)	Sires		Bottom 1/3 sires for EBV		Top 1/3 sires for EBV	
		Mean	SD	Mean	SD	Mean	SD
2.1 Liveweight = mean + animal + residual	NA	0.29 (2.27)	16.97 (1.01)	13.27 (2.57)	13.15 (1.34)	-12.70 (2.97)	13.85 (1.53)
2.2 Age-adjusted weight = mean + animal + residual	NA	0.29 (2.27)	9.91 (0.60)	-2.62 (2.83)	9.57 (1.10)	3.14 (2.61)	9.71 (0.93)
2.3 EMA = mean + animal + residual	0.0	0.00 (0.38)	3.79 (0.29)	-2.62 (0.65)	3.12 (0.35)	2.64 (0.58)	3.15 (0.39)
	0.6	0.03 (0.37)	3.79 (0.25)	-1.46 (0.63)	3.57 (0.37)	1.49 (0.64)	3.58 (0.39)
	0.9	0.04 (0.36)	3.83 (0.25)	-0.37 (0.58)	3.83 (0.41)	0.40 (0.61)	3.77 (0.43)
2.4 EMA = mean + age + animal + residual	0.0	0.00 (0.38)	1.91 (0.12)	-0.35 (0.49)	1.90 (0.23)	0.36 (0.45)	1.91 (0.21)
	0.6	0.03 (0.37)	2.48 (0.16)	0.27 (0.45)	2.47 (0.29)	-0.17 (0.50)	2.48 (0.25)
	0.9	0.04 (0.36)	2.95 (0.19)	1.23 (0.43)	2.78 (0.28)	-1.09 (0.55)	2.80 (0.28)
2.5 Age adjusted EMA = mean + animal + residual	0.0	0.00 (0.38)	1.69 (0.11)	0.02 (0.47)	1.68 (0.19)	0.01 (0.40)	1.67 (0.21)
	0.6	0.03 (0.37)	1.67 (0.10)	-0.02 (0.43)	1.67 (0.19)	0.10 (0.40)	1.67 (0.19)
	0.9	0.04 (0.36)	1.66 (0.10)	-0.02 (0.41)	1.64 (0.19)	0.13 (0.41)	1.65 (0.17)

5.3.2.2 Analyses 3.1 – 3.5: EMA univariate analyses involving harvested data with smaller specific harvest day effects (data set 3)

Variance partitioning

In general, Analyses 3.1, 3.3 and 3.4 (Table 5.14) showed the same trends in variance components with increase in the level of r_g(LWT,EMA) but with greater variability compared to the equivalent analyses fitted to harvested data without specific harvest day effects added (Analyses 2.3, 2.4 and 2.5). Under Analyses 3.1 to 3.3 analysing EMA with

non-zero r_g(LWT,EMA), heritability values were all significantly below the simulated value of 0.42 (P ~ 0). These analyses were not able to differentiate between animals.

Pre-adjusting EMA for age but ignoring the specific harvest day effects as in Analysis 3.4 resulted in significantly lower heritability than that simulated for all levels of r_g(LWT,EMA), but these values ranging from 0.37 to 0.38 were not significantly different from one another. These results suggest that the EBVs were more accurately estimated than under Analyses 3.1 to 3.3. Compared to the equivalent analysis applied to harvested data without specific harvest day effects, Analysis 2.5, heritability values were significantly lower for all levels of r_g(LWT,EMA) and were significantly more variable for r_g(LWT,EMA) of 0.0 and 0.9.

Attempting to account for specific harvest day effects by adding harvest day as a fixed effect in Analysis 3.5 resulted in reduced additive variance and heritability as r_g(LWT,EMA) increased. This was the result of a tendency for superior (inferior) sires to be compared between themselves as r_g(LWT,EMA) increased.

Table 5.14 Heritability and phenotypic variance for univariate analyses fitted to harvested data with EMA specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g(LWT,EMA)	Heritability	Phenotypic variance
3.1 EMA = mean + animal + residual	0.0	0.53 (0.08)	58.67 (13.53)
	0.6	0.32 (0.05)	40.92 (9.57)
	0.9	0.13 (0.04)	32.05 (7.96)
3.2 EMA = mean + harvest _group + animal + residual	0.0	0.49 (0.06)	39.09 (0.96)
	0.6	0.35 (0.05)	29.37 (0.67)
	0.9	0.16 (0.03)	23.04 (0.52)
3.3 EMA = mean + age + animal + residual	0.0	0.46 (0.07)	38.74 (5.28)
	0.6	0.34 (0.06)	31.04 (5.38)
	0.9	0.18 (0.04)	25.66 (5.41)
3.4 Age adjusted EMA = mean + animal + residual	0.0	0.38 (0.08)	46.38 (10.04)
	0.6	0.37 (0.06)	46.72 (14.01)
	0.9	0.37 (0.08)	46.93 (16.14)
3.5 Age adjusted EMA = mean + harvest day + animal + residual	0.0	0.51 (0.07)	35.06 (0.89)
	0.6	0.39 (0.06)	27.45 (0.69)
	0.9	0.22 (0.04)	22.13 (0.55)

Accuracy and variability of EBVs

Analysis 3.1 ignored the specific harvest day effects. For increasing r_g(LWT,EMA), the accuracy of sire EBVs followed the same trend as the same analysis applied to data without specific harvest day effects (Analysis 2.3). At all levels of r_g(LWT,EMA), the mean accuracies of sire EBVs were not significantly different between these two analyses, but the accuracies of Analysis 3.1 were significantly more variable. For r_g(LWT,EMA) of 0.0, 0.6 and 0.9 the mean accuracies of sire EBVs under Analysis 3.1 were 0.69 (0.09), 0.45 (0.20) and 0.26 (0.32) (Table 5.15).

For r_g(LWT,EMA) of 0.0, adding a harvest day fixed effect (Analysis 3.2) resulted in a large significant increase in the mean accuracy of sire EBVs over Analysis 3.1 and a significant reduction in the variability of accuracy between replicates. For r_g(LWT,EMA) of 0.0, sires were unequally represented across harvests due to harvesting on LWT, but their EMA TBVs were random. The genetically superior (inferior) sires were expected to have progeny with the top (poor) phenotypes in each harvest regardless of the size of the specific harvest day effect, so although the comparisons between sires were limited by the division into harvest days, on average the expectation is equal representation of sires with lower and higher EMA TBVs within each harvest. This explains the relatively high mean accuracy of sire EBVs at 0.85 (0.02) with relatively low variation between replicates. This accuracy was however significantly lower than the expected value of 0.91 based on the simulated parameters (P ~ 0).

For Analysis 3.3, an age covariate was added to Analysis 3.1 rather than a harvest day fixed effect. For r_g(LWT,EMA) of 0.0, the mean accuracy of sire EBVs for Analysis 3.3 at 0.87 (0.02) was significantly greater than that for Analysis 3.2. Under Analysis 3.3 the estimated linear effect of age was 0.110 cm^2/day (0.04) ranging from 0.008 to 0.212 cm^2/day. This mean effect was significantly less than the simulated value of 0.17 cm^2/day (P ~ 0) but always positive. This high accuracy suggests that the trend for EMA to increase with age as shown in Figure 5.1 was not substantially changed by the addition of this level of specific harvest day effects. The age covariate enabled the records for the three harvests to be adequately adjusted for age and identified the genetically best and worst sires.

Table 5.15 Mean accuracy and standard deviation of EBVs for univariate analyses fitted to harvested data with EMA specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g (LWT, EMA)	Accuracy of Sires			EBVs of Sires		
		Mean	Min*	Max*	SD	Min^	Max^
3.1 EMA = mean + animal + residual	0.0	0.69 (0.09)	0.47	0.86	5.13 (0.77)	-21.60	22.17
	0.6	0.45 (0.20)	-0.02	0.83	3.18 (0.48)	-13.67	14.47
	0.9	0.26 (0.32)	-0.45	0.80	1.53 (0.37)	-10.16	7.11
3.2 EMA = mean + harvest day + animal + residual	0.0	0.85 (0.02)	0.77	0.91	4.00 (0.32)	-16.29	17.15
	0.6	0.70 (0.04)	0.61	0.82	2.84 (0.27)	-11.38	11.46
	0.9	0.60 (0.05)	0.46	0.70	1.51 (0.21)	-6.03	5.88
3.3 EMA = mean + age + animal + residual	0.0	0.87 (0.02)	0.81	0.93	3.82 (0.31)	-15.68	16.62
	0.6	0.76 (0.04)	0.63	0.85	2.84 (0.26)	-11.13	10.98
	0.9	0.69 (0.05)	0.50	0.79	1.71 (0.22)	-8.04	6.21
3.4 Age adjusted EMA = mean + animal + residual	0.0	0.87 (0.04)	0.74	0.94	3.71 (0.36)	-15.52	13.79
	0.6	0.87 (0.05)	0.66	0.93	3.70 (0.62)	-19.16	13.27
	0.9	0.88 (0.05)	0.68	0.94	3.68 (0.90)	-20.23	16.44
3.5 Age adjusted EMA = mean + harvest day + animal + residual	0.0	0.88 (0.02)	0.81	0.94	3.89 (0.33)	-17.16	16.53
	0.6	0.79 (0.03)	0.71	0.88	2.93 (0.27)	-12.27	11.10
	0.9	0.74 (0.04)	0.59	0.82	1.82 (0.20)	-6.54	7.09

* Lowest and highest accuracy of 100 replicates
^ Highest and lowest EBV over 100 replicates

For r_g(LWT,EMA) greater than 0.0, neither Analysis 3.2 or 3.3 were able to accurately estimate sire EBVs, following the same trend as Analysis 3.1 with greater r_g(LWT,EMA)

leading to lower accuracies. However the accuracies under these two analyses were significantly larger than those under Analysis 3.1 with a significant reduction in variability between replicates. Fixed effects were better accounted for by adding an age covariate or a harvest day effect to Analysis 3.1. Analysis 3.3 fitted an age covariate and was equivalent to Analysis 2.4 fitted to data without the addition of specific harvest day effects. The addition of specific harvest day effects significantly reduced the mean accuracy of sire EBVs and for non-zero r_g(LWT,EMA) significantly increased the variability between replicates. For r_g(LWT,EMA) of 0.6 and 0.9, Analysis 3.3 resulted in accuracies of 0.76 (0.04) and 0.69 (0.05) (Table 5.15), which were less accurate than Analysis 2.4 at 0.78 (0.03) and 0.72 (0.04) (Table 5.11).

For Analysis 3.4 analysing Adj.EMA fitting only the fixed effect of the mean, the mean accuracies for sire EBVs for all the levels of r_g(LWT,EMA) were not significantly different from one another ranging from 0.87 to 0.88, but were significantly lower than the accuracies for the equivalent analysis fitted to data without specific harvest day effects (Analysis 2.5). The accuracies of sire EBVs were also significantly more variable between replicates than Analysis 2.5 for all levels of r_g(LWT,EMA).

Adding a fixed harvest day effect to the analysis for Adj.EMA (Analysis 3.5) did not improve the accuracy of sire EBVs significantly, but significantly reduced the variability between replicates for r_g(LWT,EMA) of 0.0 at 0.88 (0.02). However, there was a large significant reduction in accuracy when the r_g(LWT,EMA) was greater than 0.0, but there was significantly less variability between replicates (Table 5.15).

Bias of EBVs

Under Analysis 3.4 the bottom and top third of sires based on EBV had significantly biased EBVs (P < 0.0083, two-sided tests) except for the bottom third of sires at a r_g(LWT,EMA) of 0.9 (P = 0.0828). For Analysis 3.4, with r_g(LWT,EMA) of 0.6 and 0.9, the bias values for bottom sires based on EBV were -0.24 (0.74) and -0.14 (0.97) and for top sires were 0.30 (0.66) and 0.27 (0.89) (Table 5.16). Comparison with the results of Analysis 2.5 shows that the presence of specific harvest day effects caused EBV bias.

Table 5.16 EBV bias (EBVs-TBVs) mean and standard deviation (SD) for univariate analyses fitted to harvested data with EMA specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g (LWT, EMA)	Sires		Bottom 1/3 sires for EBV		Top 1/3 sires for EBV	
		Mean	SD	Mean	SD	Mean	SD
3.1 EMA = mean + animal + residual	0.0	0.00 (0.38)	3.77 (0.89)	-2.55 (1.16)	3.10 (0.58)	2.61 (1.28)	3.14 (0.65)
	0.6	0.03 (0.37)	3.79 (0.81)	-1.49 (1.29)	3.48 (0.61)	1.53 (1.41)	3.50 (0.65)
	0.9	0.04 (0.36)	3.82 (0.67)	-0.49 (1.52)	3.63 (0.64)	0.60 (1.61)	3.66 (0.63)
3.2 EMA = mean + harvest _group + animal + residual	0.0	0.00 (0.38)	2.22 (0.13)	-0.67 (0.50)	2.15 (0.24)	0.69 (0.45)	2.15 (0.25)
	0.6	0.03 (0.37)	2.81 (0.17)	-0.02 (0.49)	2.80 (0.30)	0.06 (0.54)	2.80 (0.30)
	0.9	0.04 (0.36)	3.27 (0.21)	0.96 (0.51)	3.20 (0.31)	-0.83 (0.60)	3.16 (0.30)
3.3 EMA = mean + age + animal + residual	0.0	0.00 (0.38)	1.99 (0.16)	-0.33 (0.48)	1.96 (0.24)	0.36 (0.48)	1.99 (0.26)
	0.6	0.03 (0.37)	2.55 (0.19)	0.24 (0.44)	2.51 (0.33)	-0.14 (0.51)	2.56 (0.28)
	0.9	0.04 (0.36)	3.02 (0.22)	1.17 (0.50)	2.88 (0.32)	-1.03 (0.55)	2.89 (0.31)
3.4 Age adjusted EMA = mean + animal + residual	0.0	0.00 (0.38)	1.98 (0.33)	-0.22 (0.53)	1.96 (0.35)	0.24 (0.56)	1.95 (0.35)
	0.6	0.03 (0.37)	1.96 (0.32)	-0.24 (0.74)	1.89 (0.32)	0.30 (0.66)	1.89 (0.33)
	0.9	0.04 (0.36)	1.97 (0.35)	-0.14 (0.97)	1.86 (0.36)	0.27 (0.89)	1.86 (0.32)
3.5 Age adjusted EMA = mean + harvest day + animal + residual	0.0	0.00 (0.38)	1.90 (0.13)	-0.38 (0.48)	1.91 (0.23)	0.36 (0.45)	1.86 (0.21)
	0.6	0.03 (0.37)	2.42 (0.16)	0.28 (0.46)	2.44 (0.29)	-0.20 (0.51)	2.39 (0.25)
	0.9	0.04 (0.36)	2.88 (0.19)	1.22 (0.44)	2.78 (0.28)	-1.13 (0.54)	2.72 (0.29)

No univariate analysis was found suitable to estimate breeding values for the age-dependent carcase trait of interest (EMA) when it was genetically correlated to the harvesting criteria LWT and also affected by specific harvest day effects. The best analysis, which analysed Adj.EMA (Analysis 3.4), resulted in mean EBV accuracy for

sires significantly less than the expected accuracy of 0.91. Although the differences were only 0.04 and 0.03 for r_g(LWT,EMA) of 0.6 and 0.9, the standard deviation of accuracy between replicates was 0.05 (Table 5.15). Adding LWT to the models increases the amount of information available to estimate EMA breeding values. The next sections therefore examine the potential of bivariate analyses of LWT and EMA, with varying amounts of information, to predict EBVs.

5.3.2.3 Analyses 4.1 & 5.1 Bivariate analyses involving data sets 4 and 5

Variance component estimation problem

To better understand the results of Analyses 4.1 and 5.1 a problem in the analysis is explained here. A univariate analysis of LWT including the fixed effect of the overall mean, and random animal and residual effects was fitted to harvested LWT data with and without the addition of specific harvest day effects to the LWTs (as applied for LWT in the bivariate Analyses 5.1 and 4.1). Figure 5.2 and Figure 5.3 present the resulting estimated additive variances over 100 replicates. These figures show that the addition of specific harvest day effects caused the estimated additive variance to fluctuate greatly. Without specific harvest day effects added, Figure 5.3 shows the estimated additive variance to be relatively constant over all replicates, centred on approximately 130 kg. Although not noticeable from Figure 5.2, when specific harvest day effects had been added to LWTs, two additive variance values were close to zero at 0.211 and 0.434 kg^2. These two very low values appear reasonable considering the large variability in variance values, but when Analysis 5.1, the bivariate analysis, was run, the analysis did not converge within the parameter space for these two replicates. The estimated additive variances of close to zero found in the univariate analyses explain the analysis not converging. To calculate statistics over 100 replicates, the additive-genetic variance for LWT as well as the r_g(LWT,EMA) were set to zero for these two particular replicates. This is important to note when considering the resulting statistics for Analysis 5.1.
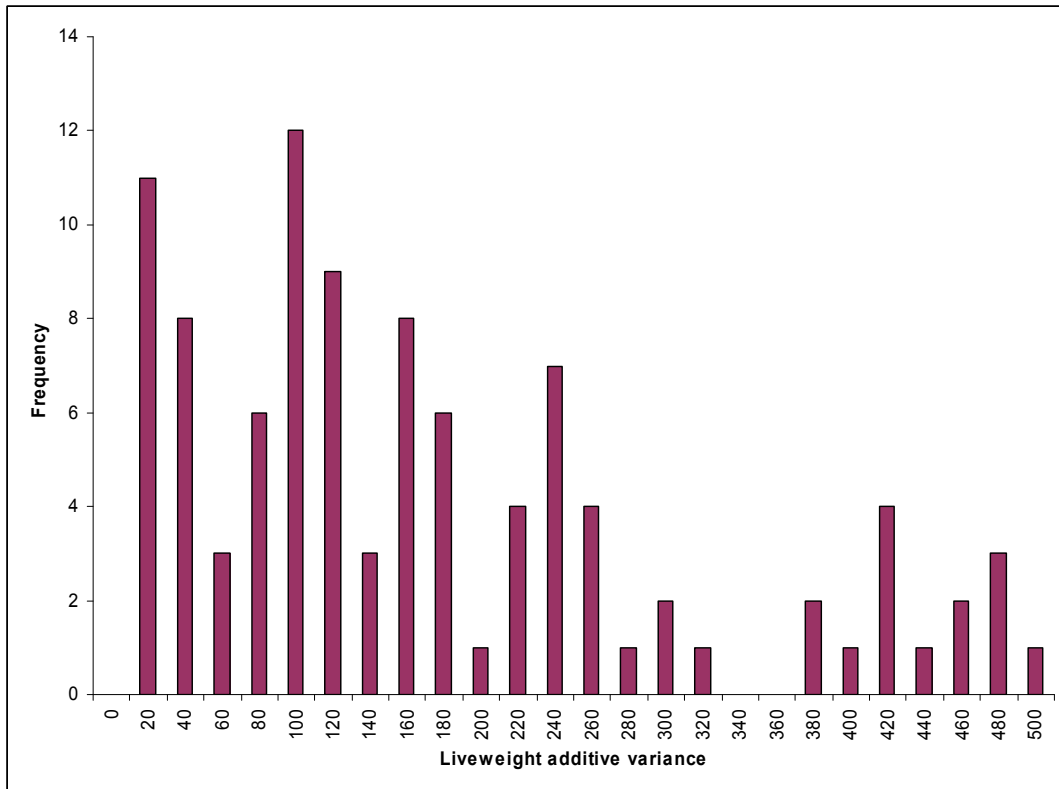
Figure 5.2   Spread of estimated additive variance values resulting from 100 univariate analyses of harvested liveweight influenced by specific harvest day effects
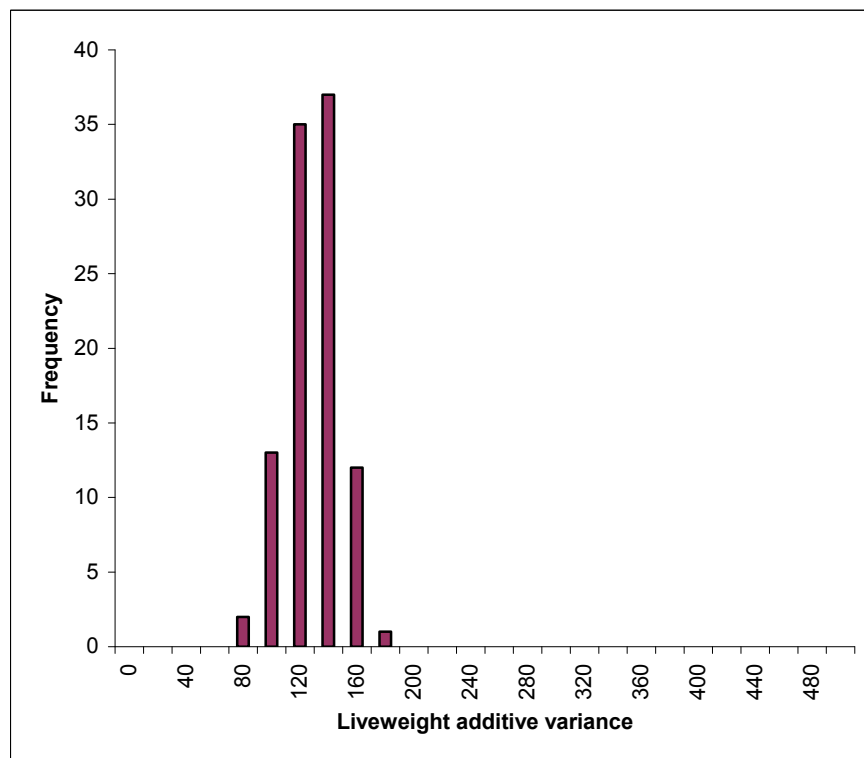

Figure 5.3   Spread of estimated additive variance values resulting from 100 univariate analyses of harvested liveweight not influenced by specific harvest day effects

Variance partitioning

The large variation in additive variance shown in Figure 5.2, when specific harvest day effects were added to the harvested LWT, compared to the variance in Figure 5.3 when these effects were not added, illustrates how great an effect specific harvest day effects can potentially have on EBVs.

Table 5.17 EMA heritability and phenotypic variance for bivariate analyses fitted to harvested data with EMA specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g(LWT,EMA)	Heritability	Phenotypic variance
4.1 LWT(noef) = mean + animal + residual	0.0	0.53 (0.08)	58.67 (13.53)
EMA = mean + animal + residual‡	0.6	0.32 (0.05)	40.92 (9.57)
	0.9	0.13 (0.04)	32.05 (7.96)
5.1 LWT(ef) = mean + animal + residual	0.0	0.53 (0.08)	58.68 (13.55)
EMA = mean + animal + residual‡	0.6	0.32 (0.05)	40.93 (9.58)
	0.9	0.13 (0.04)	32.05 (7.96)
4.2 Adj.LWT(noef) = mean + animal + residual	0.0	0.49 (0.06)	39.23 (0.97)
EMA = mean + harvest day + animal + residual‡	0.6	0.35 (0.05)	30.51 (0.82)
	0.9	0.24 (0.04)	26.26 (0.88)
5.2 Adj.LWT(ef) = mean + animal + residual	0.0	0.49 (0.06)	39.23 (0.97)
EMA = mean + harvest day + animal + residual‡	0.6	0.34 (0.05)	30.83 (1.28)
	0.9	0.24 (0.05)	27.00 (2.28)
6.1 LWT = mean + animal + residual	0.0	0.53 (0.08)	58.67 (13.53)
EMA = mean + animal + residual‡	0.6	0.32 (0.05)	40.92 (9.57)
	0.9	0.13 (0.04)	32.05 (7.96)
6.2 LWT = mean + animal + residual	0.0	0.35 (0.05)	45.19 (1.34)
EMA = mean + harvest day + animal + residual‡	0.6	0.34 (0.05)	43.85 (1.49)
	0.9	0.33 (0.05)	43.04 (1.52)

‡ LWT = liveweight, Adj.LWT = liveweight pre-adjusted for age, noef = no specific harvest day effects simulated for trait, ef = specific harvest day effects simulated for trait, EMA = eye muscle area

For all levels of r_g(LWT,EMA), the addition of harvested LWT as a correlated trait in the analysis (whether affected by specific harvest day effects or not) (Analyses 4.1 and 5.1, Table 5.17) compared to the simple univariate analysis of EMA (Analysis 3.1) did not result in change in the phenotypic variance or heritability of EMA.

Accuracy and variability of EBVs

The mean accuracies of sire EBVs under Analyses 4.1 and 5.1 (Table 5.18), where records of LWT were either influenced by specific harvest day effects or not, were either significantly less than [r_g(LWT,EMA)=0.0] or not significantly different from [r_g(LWT,EMA)>0.0] the mean accuracies resulting under the simple univariate analysis of EMA ignoring harvesting of Analysis 3.1. For Analyses 4.1 and 5.1, the accuracies of sire EBVs were also very variable between replicates. Adding the harvested LWTs in a bivariate analysis did not provide information that was able to improve the accuracy of the EMA EBVs.

5.3.2.4 Analyses 4.2 & 5.2 Bivariate analyses involving data sets 4 and 5

Accuracy of EBVs

Analyses 4.2 and 5.2 were used to analyse the effect on EMA EBV prediction of using an alternative measure of the LWTs of the animals in a bivariate analysis, i.e. Adj.LWT, along with a harvest day fixed effect fitted for EMA. The mean accuracies of sires showed large significant increases over Analyses 4.1 and 5.1, and the accuracies were significantly less variable between replicates (Table 5.18). With increasing r_g(LWT,EMA), the effect of the adjustment to LWT became a greater factor in the prediction of EMA EBVs. For r_g(LWT,EMA) of 0.0, 0.6 and 0.9 fitting Analysis 4.2 resulted in accuracies of sire EBVs of 0.82 (0.03), 0.79 (0.04) and 0.86 (0.03). The mean accuracy of sire EBVs were not significantly changed by the addition of specific harvest day effects to LWT (Analysis 5.2).

When r_g(LWT,EMA) was zero, univariate Analyses 3.2, 3.3, 3.4 and 3.5 all resulted in significantly greater mean accuracies of sire EBVs than bivariate Analyses 4.2 and 5.2. For r_g(LWT,EMA) greater than zero univariate Analysis 3.4 resulted in significantly greater mean accuracy of sire EBVs than Analyses 4.2 and 5.2.

Table 5.18 Mean accuracy and standard deviation of EBVs for bivariate analyses fitted to harvested data with EMA specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g (LWT, EMA)	Accuracy of Sires			EBVs for Sires		
		Mean	Min*	Max*	SD	Min^	Max^
4.1 LWT(noef) = mean + animal + residual	0.0	0.64 (0.10)	0.38	0.84			
EMA = mean + animal + residual‡	0.6	0.37 (0.23)	-0.15	0.82			
	0.9	0.16 (0.43)	-0.69	0.83			
5.1 LWT(ef) = mean + animal + residual	0.0	0.65 (0.10)	0.43	0.86	5.16 (0.77)	-21.58	22.94
EMA = mean + animal + residual‡	0.6	0.39 (0.22)	-0.09	0.84	3.21 (0.49)	-13.58	14.09
	0.9	0.18 (0.41)	-0.65	0.84	1.57 (0.39)	-10.18	7.27
4.2 Adj.LWT(noef) = mean + animal + residual	0.0	0.82 (0.03)	0.70	0.91	4.06 (0.33)	-16.50	17.40
EMA = mean + harvest day + animal + residual‡	0.6	0.79 (0.04)	0.69	0.89	2.88 (0.27)	-11.90	10.41
	0.9	0.86 (0.03)	0.77	0.92	2.15 (0.24)	-8.86	8.37
5.2 Adj.LWT(ef) = mean + animal + residual	0.0	0.82 (0.03)	0.71	0.91	4.06 (0.33)	-16.58	17.24
EMA = mean + harvest day + animal + residual‡	0.6	0.79 (0.05)	0.66	0.87	2.88 (0.28)	-11.76	10.80
	0.9	0.85 (0.04)	0.73	0.91	2.17 (0.33)	-9.69	8.66
6.1 LWT = mean + animal + residual	0.0	0.65 (0.10)	0.42	0.85			
EMA = mean + animal + residual‡	0.6	0.40 (0.22)	-0.12	0.82			
	0.9	0.21 (0.44)	-0.70	0.84			
6.2 LWT = mean + animal + residual	0.0	0.89 (0.02)	0.83	0.94	3.54 (0.33)	-14.89	13.48
EMA = mean + harvest day + animal + residual‡	0.6	0.89 (0.02)	0.82	0.93	3.41 (0.32)	-13.44	11.70
	0.9	0.89 (0.02)	0.83	0.93	3.37 (0.30)	-12.99	12.83

* Lowest and highest accuracy of 100 replicates
^ Highest and lowest EBV over 100 replicates
‡ LWT = liveweight, Adj.LWT = liveweight pre-adjusted for age, noef = no specific harvest day effects simulated for trait, ef = specific harvest day effects simulated for trait, EMA = eye muscle area

Having considered all analyses to this point fitted to harvested data with EMA affected by specific harvest day effects, the best accuracy of sire EBVs for r_g(LWT,EMA) equal to zero resulted from univariate Analysis 3.5 analysing Adj.EMA and fitting a harvest day fixed effect. The mean EBV accuracy of sire EBVs was 0.88 (0.02), ranging from 0.81 to

0.94 (Table 5.15). This was not significantly different from the mean accuracy under Analysis 3.4, also fitting Adj.EMA but not fitting the harvest day fixed effect. The mean accuracy of sire EBVs for Analysis 3.3 which ignored the specific harvest day effects but fitted an age covariate was significantly lower than that for Analysis 3.5, but only by 0.01 at 0.87 (0.02) and had the advantage that pre-adjustment of EMA for age was not necessary. For this r_g(LWT,EMA) of zero, these three analyses all resulted in significant bias for the top and bottom third of sires based on EBV (P < 0.0003, two-sided tests) (Table 5.16).

For r_g(LWT,EMA) greater than 0.0, fitting Analysis 3.4 resulted in the highest mean accuracy of sire EBVs, at 0.87 (0.05) and 0.88 (0.05) for r_g(LWT,EMA) of 0.6 and 0.9 respectively. However, considering the spread in accuracy values, Analysis 3.5 resulted in the best EBV accuracy of sires for r_g(LWT,EMA) of 0.6, at 0.79 (0.03) ranging from 0.71 to 0.88. This mean accuracy was significantly lower than that under Analysis 3.4, but significantly less variable between replicates (Table 5.15). Likewise, for the high r_g(LWT,EMA) of 0.9, bivariate Analysis 4.2 resulted in the best accuracy of sire EBVs at 0.86 (0.03), ranging from 0.77 to 0.92 (Table 5.18). For all these analysis and r_g(LWT,EMA) level combinations significant bias resulted for the top and bottom third of sires based on EBV (P < 0.009, two-sided tests) except for the bottom third of sires for Analysis 3.4 and a r_g(LWT,EMA) of 0.9 (P = 0.0828, two-sided test) (Table 5.16 and Table 5.19).

In conclusion when only harvested data was available and specific harvest day effects were added to EMA, no single analysis resulted in the most accurate EBVs, and consideration of the genetic correlation between the two traits in choosing an appropriate analysis is evidently important. The next section examines the situation when more information is available in the form of LWT records for all animals at one point in time.

5.3.2.5 Analyses 6.1 & 6.2: Bivariate analyses involving data set 6

Accuracy of EBVs

When the LWT records were known for all animals at harvest 1 and a bivariate analysis was fitted including fitting a harvest day fixed effect for EMA (Analysis 6.2), the mean EBV accuracy of sires was 0.89 (0.02) for all levels of r_g(LWT,EMA) (Table 5.18). This

was significantly lower than the deterministic expectation of 0.91 (P ~ 0), but with a difference of only 0.02. The variability between replicates was also relatively low with a standard deviation of only 0.02. For r_g(LWT,EMA) greater than zero, harvesting was accounted for in estimating breeding values for the correlated trait EMA through inclusion of LWT for all animals at harvest 1.

When a harvest day fixed effect was not included in the bivariate analysis for EMA (Analysis 6.1), the mean accuracies of sire EBVs for all levels of r_g(LWT,EMA) showed large significant reductions from Analysis 6.2 and large significant increases in accuracy variability between replicates (Table 5.18). Considering Analyses 6.1 and 6.2, fitting the harvest day fixed effect for EMA was critical to attaining accurate sire EBVs, and exemplifies the importance of correctly accounting for fixed effects.

It is interesting to note that even when the r_g(LWT,EMA) was zero, using bivariate Analysis 6.2 significantly increased the mean accuracy of sire EBVs for EMA over Analysis 3.2 which was the univariate analysis of EMA fitting the same effects for EMA as in Analysis 6.2. The mean accuracy of sire EBVs was 0.85 (0.02) for Analysis 3.2 (Table 5.15), and 0.89 (0.02) for Analysis 6.2 (Table 5.18).

Bias of EBVs

For Analysis 6.2 and r_g(LWT,EMA) of zero the top and bottom third of sires based on EBV were not significantly biased (P > 0.11), but for r_g(LWT,EMA) greater than zero they were significantly biased (P < 0.04) (Table 5.19
Table 5.19).

Table 5.19 EMA EBV bias (EBVs-TBVs) mean and standard deviation (SD) for bivariate analyses fitted to harvested data with EMA specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g (LWT, EMA)	Sires		Bottom 1/3 sires for EBV		Top 1/3 sires for EBV	
		Mean	SD	Mean	SD	Mean	SD
4.1 LWT(noef) = mean + animal + residual	0.0	0.00 (0.38)	4.05 (0.91)	-2.79 (1.19)	3.29 (0.59)	2.85 (1.31)	3.39 (0.70)
EMA = mean + animal + residual‡	0.6	0.03 (0.37)	4.06 (0.88)	-1.86 (1.39)	3.64 (0.63)	1.92 (1.54)	3.72 (0.71)
	0.9	0.04 (0.36)	3.98 (0.85)	-0.97 (2.02)	3.58 (0.70)	1.10 (2.11)	3.63 (0.65)
5.1 LWT(ef) = mean + animal + residual	0.0	0.00 (0.38)	3.99 (0.90)	-2.72 (1.19)	3.26 (0.58)	2.80 (1.29)	3.35 (0.66)
EMA = mean + animal + residual‡	0.6	0.03 (0.37)	4.00 (0.87)	-1.79 (1.37)	3.61 (0.63)	1.85 (1.49)	3.67 (0.69)
	0.9	0.04 (0.36)	3.94 (0.82)	-0.88 (1.90)	3.60 (0.68)	1.04 (1.99)	3.62 (0.65)
4.2 Adj.LWT(noef) = mean + animal + residual	0.0	0.00 (0.38)	2.44 (0.17)	-0.85 (0.52)	2.32 (0.24)	0.88 (0.48)	2.34 (0.27)
EMA = mean + harvest day + animal + residual‡	0.6	0.03 (0.37)	2.42 (0.15)	0.34 (0.47)	2.40 (0.24)	-0.24 (0.50)	2.40 (0.26)
	0.9	0.04 (0.36)	2.36 (0.15)	1.40 (0.46)	2.09 (0.21)	-1.31 (0.50)	2.10 (0.22)
5.2 Adj.LWT(ef) = mean + animal + residual	0.0	0.00 (0.38)	2.44 (0.17)	-0.86 (0.52)	2.32 (0.24)	0.88 (0.49)	2.34 (0.27)
EMA = mean + harvest day + animal + residual‡	0.6	0.03 (0.37)	2.43 (0.19)	0.33 (0.47)	2.40 (0.27)	-0.24 (0.52)	2.41 (0.30)
	0.9	0.04 (0.36)	2.38 (0.24)	1.35 (0.48)	2.12 (0.26)	-1.26 (0.50)	2.15 (0.29)
6.1 LWT = mean + animal + residual	0.0	0.00 (0.38)	3.96 (0.88)	-2.72 (1.18)	3.24 (0.55)	2.74 (1.27)	3.30 (0.66)
EMA = mean + animal + residual‡	0.6	0.03 (0.37)	3.95 (0.86)	-1.73 (1.37)	3.57 (0.63)	1.74 (1.50)	3.62 (0.69)
	0.9	0.04 (0.36)	3.88 (0.86)	-0.74 (2.03)	3.52 (0.71)	0.88 (2.13)	3.54 (0.69)
6.2 LWT = mean + animal + residual	0.0	0.00 (0.38)	1.81 (0.11)	0.03 (0.47)	1.83 (0.21)	-0.04 (0.44)	1.80 (0.21)
EMA = mean + harvest day + animal + residual‡	0.6	0.03 (0.37)	1.84 (0.11)	0.14 (0.45)	1.84 (0.19)	-0.06 (0.43)	1.82 (0.19)
	0.9	0.04 (0.36)	1.80 (0.11)	0.21 (0.43)	1.78 (0.21)	-0.14 (0.43)	1.81 (0.20)

‡ LWT = liveweight, Adj.LWT = liveweight pre-adjusted for age, noef = no specific harvest day effects simulated for trait, ef = specific harvest day effects simulated for trait, EMA = eye muscle area

5.3.2.6 Analyses 7.1 – 10.1: Analyses of data with large specific harvest day effects affecting EMA

Variance partitioning

For Analyses 7.1 to 10.1 the mean heritabilities and phenotypic variances (Table 5.20) were either the same or not significantly different from those under the equivalent analyses with smaller specific harvest day effects (Analyses 3.5, 4.2, 5.2 and 6.2 respectively). The variability of these variance components between replicates was also the same or not significantly different for these analysis comparisons. Larger specific harvest day effects did not change how the analyses partitioned variance.

Table 5.20 EMA heritability and phenotypic variance for bivariate analyses fitted to harvested data with EMA specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g(LWT,EMA)	Heritability	Phenotypic variance
7.1 Age adjusted EMA = mean + harvest day + animal + residual	0.0	0.508 (0.068)	35.08 (0.91)
	0.6	0.387 (0.057)	27.47 (0.72)
	0.9	0.217 (0.035)	22.15 (0.60)
8.1 Adj.LWT(noef) = mean + animal + residual	0.0	0.495 (0.062)	39.23 (0.97)
EMA = mean + harvest day + animal + residual‡	0.6	0.345 (0.051)	30.51 (0.82)
	0.9	0.239 (0.039)	26.26 (0.88)
9.1 Adj.LWT(ef) = mean + animal + residual	0.0	0.495 (0.062)	39.23 (0.97)
EMA = mean + harvest day + animal + residual‡	0.6	0.343 (0.051)	30.83 (1.28)
	0.9	0.238 (0.046)	27.00 (2.28)
10.1 LWT = mean + animal + residual	0.0	0.349 (0.052)	45.19 (1.33)
EMA = mean + harvest day + animal + residual‡	0.6	0.339 (0.049)	43.85 (1.49)
	0.9	0.334 (0.046)	43.04 (1.52)

‡ LWT = liveweight, Adj.LWT = liveweight pre-adjusted for age, noef = no specific harvest day effects simulated for trait, ef = specific harvest day effects simulated for trait, EMA = eye muscle area

Accuracy and variability of EBVs

By comparing the equivalent Analyses 3.5, 4.2, 5.2 and 6.2 with Analyses 7.1 to 10.1 in Table 5.21, it is shown that the mean accuracy of EMA sire EBVs or the variability of accuracy between replicates did not change with the large increase in specific harvest day effects affecting EMA. There was no reduction in accuracy for the increase in the specific harvest day effects.

Table 5.21   Mean accuracy and standard deviation of EBVs for analyses fitted to harvested data with large EMA specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g (LWT, EMA)	Accuracy of Sires			EBVs of sires		
		Mean	Min*	Max*	SD	Min^	Max^
7.1 Age adjusted EMA = mean + harvest day + animal + residual	0.0	0.88 (0.02)	0.81	0.94	3.89 (0.33)	-17.14	16.54
	0.6	0.79 (0.03)	0.71	0.88	2.93 (0.27)	-12.26	11.11
	0.9	0.74 (0.04)	0.59	0.82	1.82 (0.20)	-6.53	7.09
8.1 Adj.LWT(noef) = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.82 (0.03)	0.70	0.91	4.06 (0.33)	-16.50	17.40
	0.6	0.79 (0.04)	0.69	0.89	2.88 (0.27)	-11.90	10.41
	0.9	0.86 (0.03)	0.77	0.92	2.15 (0.24)	-8.86	8.37
9.1 Adj.LWT(ef) = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.82 (0.03)	0.71	0.91	4.06 (0.33)	-16.58	17.24
	0.6	0.79 (0.05)	0.66	0.87	2.88 (0.28)	-11.76	10.80
	0.9	0.85 (0.04)	0.73	0.91	2.17 (0.33)	-9.69	8.66
10.1 LWT = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.89 (0.02)	0.83	0.94	3.54 (0.33)	-14.89	13.48
	0.6	0.89 (0.02)	0.82	0.93	3.41 (0.32)	-13.43	11.70
	0.9	0.89 (0.02)	0.83	0.93	3.37 (0.30)	-12.99	12.83

* Lowest and highest accuracy of 100 replicates
^ Highest and lowest EBV over 100 replicates
‡ LWT = liveweight, Adj.LWT = liveweight pre-adjusted for age, noef = no specific harvest day effects simulated for trait, ef = specific harvest day effects simulated for trait, EMA = eye muscle area

Bias of EBVs

By comparing the equivalent Analyses 3.5, 4.2, 5.2 and 6.2 with Analyses 7.1 to 10.1 in Table 5.22, increasing the size of the specific harvest day effects affecting EMA did not result in any difference in the mean EBV bias for the top and bottom third of sires based on EBV.

Table 5.22 EMA EBV bias (EBVs-TBVs) mean and standard deviation (SD) for bivariate analyses fitted to harvested data with EMA specific harvest day effects simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g (LWT, EMA)	Sires		Bottom 1/3 sires for EBV		Top 1/3 sires for EBV	
		Mean	SD	Mean	SD	Mean	SD
7.1 Age adjusted EMA = mean + harvest day + animal + residual	0.0	0.00 (0.38)	1.90 (0.13)	-0.38 (0.49)	1.92 (0.23)	0.36 (0.45)	1.86 (0.21)
	0.6	0.03 (0.37)	2.43 (0.16)	0.28 (0.46)	2.44 (0.29)	-0.20 (0.51)	2.39 (0.26)
	0.9	0.04 (0.36)	2.88 (0.19)	1.22 (0.44)	2.78 (0.28)	-1.14 (0.54)	2.72 (0.29)
8.1 Adj.LWT(noef) = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.00 (0.38)	2.44 (0.17)	-0.85 (0.52)	2.32 (0.24)	0.88 (0.48)	2.34 (0.27)
	0.6	0.03 (0.37)	2.42 (0.15)	0.34 (0.47)	2.40 (0.24)	-0.24 (0.50)	2.40 (0.26)
	0.9	0.04 (0.36)	2.36 (0.15)	1.40 (0.46)	2.09 (0.21)	-1.31 (0.50)	2.10 (0.22)
9.1 Adj.LWT(ef) = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.00 (0.38)	2.44 (0.17)	-0.86 (0.52)	2.32 (0.24)	0.88 (0.49)	2.34 (0.27)
	0.6	0.03 (0.37)	2.42 (0.19)	0.33 (0.47)	2.40 (0.27)	-0.24 (0.52)	2.41 (0.30)
	0.9	0.04 (0.36)	2.38 (0.24)	1.35 (0.48)	2.12 (0.26)	-1.26 (0.50)	2.15 (0.29)
10.1 LWT = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.00 (0.38)	1.81 (0.11)	0.03 (0.47)	1.83 (0.21)	-0.04 (0.44)	1.80 (0.21)
	0.6	0.03 (0.37)	1.84 (0.11)	0.14 (0.44)	1.84 (0.19)	-0.06 (0.43)	1.82 (0.19)
	0.9	0.04 (0.36)	1.80 (0.11)	0.21 (0.43)	1.78 (0.21)	-0.14 (0.43)	1.81 (0.20)

‡ LWT = liveweight, Adj.LWT = liveweight pre-adjusted for age, noef = no specific harvest day effects simulated for trait, ef = specific harvest day effects simulated for trait, EMA = eye muscle area

5.3.2.7 Analyses 11.1 to 14.2: Analyses for when number of progeny per sire reduced from forty to fifteen

Variance partitioning

Table 5.23 presents the heritabilities and phenotypic variances estimated under Analyses 11.1 to 14.2. Reducing the number of progeny per sire from the equivalent Analysis 3.5 to Analysis 11.1 did not result in significant differences in the phenotypic variance or heritability, resulting in the same negative trends as r_g(LWT,EMA) increased. However, the phenotypic variance was significantly more variable between replicates. Heritability was not significantly more variable for r_g(LWT,EMA) of 0.0 and 0.6 but was significantly more variable for r_g(LWT,EMA) of 0.9.

Likewise, reducing the number of progeny per sire from the equivalent Analyses 4.2 and 5.2 to Analyses 12.1 and 13.1 did not significantly change the phenotypic variance or heritability values, following the same negative trends as r_g(LWT,EMA) increased. However, the variability of these variance components between replicates significantly increased apart from the increase in variability of phenotypic variance going from Analysis 5.2 to Analysis 13.1 for r_g(LWT,EMA) of 0.9 which was not significant.

By replacing EMA with Adj.EMA (Analyses 12.2 and 13.2) the heritability and phenotypic variance did not follow the original negative trends with increasing r_g(LWT,EMA), but were not significantly different between all levels of r_g(LWT,EMA) apart from the phenotypic variance between r_g(LWT,EMA) of 0.0 and 0.9 which was significantly different for both analyses. Heritability values were not significantly different from the simulated value of 0.42 at all levels of r_g(LWT,EMA) for Analysis 12.2 (P > 0.24, two-sided tests) and Analysis 13.2 (P > 0.05, two-sided tests).

The reduced heritability with increased r_g(LWT,EMA) under Analyses 12.1 and 13.1 suggests that the tendency for genetically superior (inferior) sires to be compared between themselves as the r_g(LWT,EMA) increases has caused a reduction in additive variance. Use of Adj.LWT in these analyses was not able to remove this effect. However, additionally pre-adjusting EMA for age (Analyses 12.2 and 13.2) evidently removed this effect, and resulted in constant heritability values across all levels of r_g(LWT,EMA) equal to the simulated heritability.

For Analysis 14.1, where LWTs of all animals were recorded at the first harvest, the mean heritabilities were not significantly different from the similar analysis with 40 progeny per sire (Analysis 6.2) for r_g(LWT,EMA) equal to 0.6 and 0.9, but the heritabilities were significantly more variable between replicates. Analysis 14.1 included an age covariate in the fixed effects for LWT but Analysis 6.2 did not. The mean heritability for Analysis 14.1 showed a significant reduction from r_g(LWT,EMA) 0.3 to 0.6, but no significant difference between r_g(LWT,EMA) 0.6 and 0.9. For Analysis 14.1 all mean heritability values were significantly different from the simulated value of 0.42, significantly less for r_g(LWT,EMA) greater than zero.

However, for Analysis 14.2 where EMA was replaced with Adj.EMA, the mean heritability was not significantly different from 0.42 for all levels of r_g(LWT,EMA) (P > 0.31, two-sided tests), suggesting that this analysis was able to correctly partition the variance. However, the heritability values were quite variable between replicates, with standard deviations of 0.08 for the different levels of r_g(LWT,EMA).

Accuracy and variability of EBVs

Based on the simulated parameters, including a reduced number of effective progeny per sire of 14.8, the expected accuracy of sire EBVs is 0.80. This is a reduction of 0.11 in theoretical accuracy from the case of 39.4 effective progeny per sire. Accuracies of EBVs under Analyses 11.1 to 14.2 are presented in Table 5.24.

Fitting Analyses 12.2 and 14.2 resulted in the same accuracies of sire EBVs for all levels of r_g(LWT,EMA). The mean accuracies were equal to the theoretically determined accuracy of 0.80 for r_g(LWT,EMA) of 0.0 and 0.9, but significantly less than 0.80 for r_g(LWT,EMA) of 0.3 and 0.6 (P < 0.015, two-sided tests). These differences however were only 0.01. These results are in agreement with the estimated mean heritabilities under these analyses, all not significantly different from the simulated value of 0.42.

When LWT was influenced by specific harvest day effects (Analysis 13.2) the mean accuracy of sire EBVs reduced from Analysis 12.2 for all levels of r_g(LWT,EMA), but the reduction was only significant for r_g(LWT,EMA) of 0.6.

Table 5.23 EMA heritability and phenotypic variance for analyses fitted to harvested data with fifteen progeny per sire simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g(LWT,EMA)	Heritability	Phenotypic variance
11.1 Adj.EMA = mean + harvest day + animal + residual	0.0	0.508 (0.082)	35.17 (1.21)
	0.3	0.472 (0.079)	31.84 (1.09)
	0.6	0.389 (0.072)	27.49 (0.92)
	0.9	0.219 (0.059)	22.10 (0.74)
12.1 Adj.LWT(noef) = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.490 (0.079)	39.49 (1.44)
	0.3	0.424 (0.073)	35.07 (1.25)
	0.6	0.341 (0.068)	30.68 (1.23)
	0.9	0.236 (0.063)	26.32 (1.34)
12.2 Adj.LWT(noef) = mean + animal + residual Adj.EMA = mean + harvest day + animal + residual‡	0.0	0.416 (0.078)	39.34 (1.78)
	0.3	0.416 (0.079)	39.58 (2.02)
	0.6	0.420 (0.079)	39.87 (2.19)
	0.9	0.429 (0.077)	40.23 (2.26)
13.1 Adj.LWT(ef) = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.489 (0.079)	39.50 (1.43)
	0.3	0.422 (0.074)	35.15 (1.29)
	0.6	0.339 (0.068)	31.00 (1.61)
	0.9	0.235 (0.064)	27.08 (2.54)
13.2 Adj.LWT(ef) = mean + animal + residual Adj.EMA = mean + harvest day + animal + residual‡	0.0	0.407 (0.083)	40.62 (3.76)
	0.3	0.405 (0.080)	41.65 (5.75)
	0.6	0.405 (0.076)	42.91 (8.21)
	0.9	0.407 (0.078)	44.43 (11.12)
14.1 LWT = mean + age + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.473 (0.081)	39.47 (1.45)
	0.3	0.386 (0.075)	37.65 (2.51)
	0.6	0.335 (0.072)	41.30 (3.32)
	0.9	0.333 (0.072)	43.93 (2.76)
14.2 LWT = mean + age + animal + residual Adj.EMA = mean + harvest day + animal + residual‡	0.0	0.428 (0.079)	38.23 (1.56)
	0.3	0.423 (0.079)	37.73 (1.74)
	0.6	0.419 (0.079)	37.08 (1.87)
	0.9	0.417 (0.076)	36.24 (1.96)

‡ LWT = liveweight, Adj.LWT = LWT pre-adjusted for age, noef = no specific harvest day effects simulated for trait, ef = specific harvest day effects simulated for trait, EMA = eye muscle area, Adj.EMA = EMA pre-adjusted for age

For Analysis 14.1 where all animals had a LWT record at harvest one, but EMA was used in the bivariate analysis rather than Adj.EMA, the mean accuracies of sire EBVs were all significantly less than the theoretically determined accuracy of 0.80 for all levels of r_g(LWT,EMA), with differences ranging from 0.03 to 0.08.

For Analysis 11.1 which fitted Adj.EMA the mean accuracy of sire EBVs reduced at an increasing rate with increase in r_g(LWT,EMA). However, when r_g(LWT,EMA) was 0.0 and 0.3 the mean accuracy of sire EBVs was 0.79 and 0.74 (Table 5.24). The mean accuracy of 0.79 (0.04) for r_g(LWT,EMA) of 0.0 was significantly different to the theoretical value of 0.80 (P < 0.01, one-tailed test). The equivalent analysis involving 40 progeny per sire (Analysis 3.5, r_g(LWT,EMA) = 0.0) also resulted in mean EBV accuracy for sires significantly different from but close to the theoretical determination. That analysis resulted in a mean accuracy of 0.88 (0.02), compared to the theoretical value of 0.91. This suggests that for a wide range in the number of progeny per sire, this analysis for a similarly age-dependent carcase trait will result in an accuracy of sire EBVs close to expectation when the carcase trait is not genetically correlated to the selection criteria.

Bias of EBVs

Bias of EBVs for Analyses 11.1 to 14.2 are presented in Table 5.25. Although fitting Analyses 12.2 and 14.2 resulted in the same mean accuracy of sire EBVs for all levels of r_g(LWT,EMA), the top and bottom sires based on EBV were not significantly biased for Analysis 14.2 (P > 0.05, two-sided tests), but for Analysis 12.2 the top and bottom sires were not significantly biased for r_g(LWT,EMA) of 0.0 and 0.3 (P > 0.10, two-sided tests) but significantly biased for r_g(LWT,EMA) of 0.6 and 0.9 (P < 0.011, two-sided tests). For Analysis 12.2 the EBVs of the top sires were biased upwards and the EBVs of the bottom sires biased downwards.

When LWT was affected by specific harvest day effects (Analysis 13.2), the top and bottom third of sires for EBV were not significantly more biased than under Analysis 12.2.

For Analysis 11.1 and r_g(LWT,EMA) of 0.0, the top third of sires for EBV were significantly biased upwards by 0.33 cm^2 (P ~ 0) and the bottom third of sires were significantly biased downwards by 0.38 cm^2 (P ~ 0).

Table 5.24 Mean accuracy and standard deviation of EBVs for analyses fitted to harvested data with fifteen progeny per sire simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g (LWT, EMA)	Accuracy of sires			EBVs of sires		
		Mean	Min*	Max*	SD	Min^	Max^
11.1 Adj.EMA = mean + harvest day + animal + residual	0.0	0.79 (0.04)	0.66	0.86	3.48 (0.41)	-13.82	13.66
	0.3	0.74 (0.05)	0.62	0.85	3.15 (0.39)	-13.20	12.40
	0.6	0.68 (0.05)	0.55	0.80	2.56 (0.35)	-10.94	10.75
	0.9	0.59 (0.06)	0.42	0.72	1.49 (0.32)	-6.71	7.15
12.1 Adj.LWT(noef) = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.71 (0.05)	0.54	0.85	3.64 (0.43)	-13.96	14.95
	0.3	0.67 (0.07)	0.49	0.85	3.09 (0.40)	-12.74	13.20
	0.6	0.67 (0.07)	0.50	0.84	2.46 (0.38)	-11.33	10.36
	0.9	0.76 (0.05)	0.62	0.87	1.84 (0.36)	-9.18	7.66
12.2 Adj.LWT(noef) = mean + animal + residual Adj.EMA = mean + harvest day + animal + residual‡	0.0	0.80 (0.037)	0.68	0.88	3.24 (0.44)	-13.45	13.48
	0.3	0.79 (0.04)	0.64	0.88	3.23 (0.46)	-14.09	13.39
	0.6	0.79 (0.038)	0.66	0.88	3.25 (0.47)	-14.48	13.73
	0.9	0.80 (0.03)	0.70	0.87	3.35 (0.45)	-15.77	13.06
13.1 Adj.LWT(ef) = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.71 (0.05)	0.55	0.85	3.64 (0.43)	-14.31	14.75
	0.3	0.68 (0.06)	0.48	0.85	3.08 (0.40)	-12.81	13.13
	0.6	0.67 (0.07)	0.46	0.84	2.46 (0.38)	-11.47	10.30
	0.9	0.74 (0.05)	0.60	0.86	1.84 (0.39)	-10.53	7.79
13.2 Adj.LWT(ef) = mean + animal + residual Adj.EMA = mean + harvest day + animal + residual‡	0.0	0.79 (0.038)	0.66	0.87	3.24 (0.44)	-13.48	13.37
	0.3	0.78 (0.041)	0.65	0.87	3.24 (0.46)	-14.19	13.86
	0.6	0.77 (0.039)	0.66	0.85	3.27 (0.52)	-17.05	14.39
	0.9	0.79 (0.036)	0.68	0.86	3.37 (0.66)	-18.86	14.68
14.1 LWT = mean + age + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.72 (0.054)	0.56	0.86	3.56 (0.44)	-14.01	14.35
	0.3	0.72 (0.059)	0.59	0.87	2.99 (0.42)	-12.87	13.08
	0.6	0.75 (0.046)	0.60	0.85	2.81 (0.46)	-12.60	12.24
	0.9	0.77 (0.042)	0.67	0.86	2.94 (0.48)	-13.05	12.13
14.2 LWT = mean + age + animal + residual Adj.EMA = mean + harvest day + animal + residual‡	0.0	0.80 (0.037)	0.68	0.88	3.26 (0.43)	-13.35	13.47
	0.3	0.79 (0.040)	0.65	0.88	3.19 (0.45)	-13.88	13.04
	0.6	0.79 (0.038)	0.66	0.87	3.13 (0.44)	-13.43	13.22
	0.9	0.80 (0.033)	0.70	0.86	3.13 (0.42)	-14.27	12.38

* Lowest and highest accuracy of 100 replicates
^ Highest and lowest EBV over 100 replicates
‡ LWT = liveweight, Adj.LWT = LWT pre-adjusted for age, noef = no specific harvest day effects simulated for trait, ef = specific harvest day effects simulated for trait, EMA = eye muscle area, Adj.EMA = EMA pre-adjusted for age

Table 5.25 EMA EBV bias (EBVs-TBVs) mean and standard deviation (SD) for bivariate analyses fitted to harvested data with fifteen progeny per sire simulated (standard deviation of 100 replicates in brackets)

Analyses	R_g (LWT, EMA)	Sires		Bottom 1/3 sires for EBV		Top 1/3 sires for EBV	
		Mean	SD	Mean	SD	Mean	SD
11.1 Adj.EMA = mean + harvest day + animal + residual	0.0	0.00 (0.38)	2.49 (0.17)	-0.35 (0.57)	2.47 (0.29)	0.36 (0.58)	2.44 (0.25)
	0.3	0.01 (0.37)	2.66 (0.18)	-0.18 (0.56)	2.63 (0.30)	0.20 (0.58)	2.64 (0.28)
	0.6	0.03 (0.37)	2.90 (0.19)	0.19 (0.53)	2.91 (0.31)	-0.12 (0.57)	2.89 (0.30)
	0.9	0.04 (0.36)	3.30 (0.22)	0.92 (0.57)	3.24 (0.37)	-0.84 (0.60)	3.21 (0.34)
12.1 Adj.LWT(noef) = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.00 (0.38)	2.94 (0.23)	-0.87 (0.59)	2.82 (0.32)	0.89 (0.63)	2.81 (0.33)
	0.3	0.01 (0.37)	2.95 (0.22)	-0.44 (0.59)	2.88 (0.33)	0.44 (0.63)	2.92 (0.35)
	0.6	0.03 (0.37)	2.94 (0.21)	0.28 (0.54)	2.89 (0.35)	-0.17 (0.61)	2.96 (0.31)
	0.9	0.04 (0.36)	2.83 (0.21)	1.29 (0.53)	2.61 (0.33)	-1.22 (0.57)	2.63 (0.31)
12.2 Adj.LWT(noef) = mean + animal + residual Adj.EMA = mean + harvest day + animal + residual‡	0.0	0.00 (0.38)	2.42 (0.16)	-0.06 (0.62)	2.40 (0.30)	0.08 (0.55)	2.39 (0.25)
	0.3	0.01 (0.37)	2.45 (0.16)	-0.07 (0.62)	2.42 (0.29)	0.11 (0.51)	2.41 (0.27)
	0.6	0.03 (0.37)	2.46 (0.17)	-0.13 (0.57)	2.43 (0.31)	0.17 (0.53)	2.43 (0.26)
	0.9	0.04 (0.36)	2.39 (0.17)	-0.15 (0.52)	2.36 (0.27)	0.26 (0.57)	2.36 (0.27)
13.1 Adj.LWT(ef) = mean + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.00 (0.38)	2.93 (0.23)	-0.86 (0.59)	2.80 (0.32)	0.87 (0.64)	2.81 (0.33)
	0.3	0.01 (0.37)	2.95 (0.22)	-0.43 (0.60)	2.87 (0.33)	0.42 (0.62)	2.92 (0.35)
	0.6	0.03 (0.37)	2.95 (0.22)	0.27 (0.54)	2.92 (0.34)	-0.17 (0.60)	2.97 (0.33)
	0.9	0.04 (0.36)	2.86 (0.24)	1.24 (0.55)	2.62 (0.33)	-1.13 (0.59)	2.70 (0.33)
13.2 Adj.LWT(ef) = mean + animal + residual Adj.EMA = mean + harvest day + animal + residual‡	0.0	0.00 (0.38)	2.45 (0.17)	-0.10 (0.65)	2.43 (0.30)	0.08 (0.51)	2.41 (0.27)
	0.3	0.01 (0.37)	2.50 (0.18)	-0.13 (0.63)	2.46 (0.30)	0.14 (0.51)	2.46 (0.27)
	0.6	0.03 (0.37)	2.53 (0.20)	-0.20 (0.66)	2.49 (0.32)	0.28 (0.60)	2.50 (0.28)
	0.9	0.04 (0.36)	2.51 (0.22)	-0.22 (0.76)	2.43 (0.29)	0.31 (0.80)	2.43 (0.29)
14.1 LWT = mean + age + animal + residual EMA = mean + harvest day + animal + residual‡	0.0	0.00 (0.38)	2.87 (0.23)	-0.73 (0.62)	2.77 (0.32)	0.75 (0.62)	2.76 (0.34)
	0.3	0.01 (0.37)	2.76 (0.22)	-0.13 (0.59)	2.71 (0.33)	0.15 (0.58)	2.75 (0.34)
	0.6	0.03 (0.37)	2.63 (0.19)	0.19 (0.60)	2.58 (0.33)	-0.16 (0.57)	2.61 (0.27)
	0.9	0.04 (0.36)	2.53 (0.19)	0.19 (0.56)	2.49 (0.31)	-0.07 (0.59)	2.51 (0.28)
14.2 LWT = mean + age + animal + residual Adj.EMA = mean + harvest day + animal + residual‡	0.0	0.00 (0.38)	2.42 (0.16)	-0.09 (0.61)	2.40 (0.29)	0.09 (0.54)	2.39 (0.25)
	0.3	0.01 (0.37)	2.45 (0.16)	-0.02 (0.59)	2.42 (0.28)	0.08 (0.52)	2.41 (0.27)
	0.6	0.03 (0.37)	2.45 (0.17)	0.00 (0.56)	2.42 (0.30)	0.04 (0.53)	2.42 (0.26)
	0.9	0.04 (0.36)	2.38 (0.17)	0.10 (0.50)	2.36 (0.28)	0.01 (0.57)	2.36 (0.27)

‡ LWT = liveweight, Adj.LWT = LWT pre-adjusted for age, noef = no specific harvest day effects simulated for trait, ef = specific harvest day effects simulated for trait, EMA = eye muscle area, Adj.EMA = EMA pre-adjusted for age

Accurate unbiased EMA EBVs for sires resulted for all levels of r_g(LWT,EMA) when LWTs were known for all animals at harvest 1 and the age-dependent carcase trait EMA was adjusted for age (Analysis 14.2). Knowing LWTs for all animals at harvest 1 but not adjusting EMA for age (Analysis 14.1) did not result in accurate sire EBVs.

When the criteria used for selection, LWT, was not affected by specific harvest day effects, adjusting both LWT and EMA for age resulted in accurate sire EBVs for all levels of r_g(LWT,EMA), but biased sire EBVs for r_g(LWT,EMA) of 0.6 or greater (Analysis 12.2). If LWT was affected by specific harvest day effects (Analysis 13.2) the EBVs of sires tended to show non-significant reductions in accuracy and non-significant increases in bias for the different levels of r_g(LWT,EMA).

5.4 Conclusions

This study illustrated how harvesting over time can conceal the true effect of age and negatively affect the estimation of carcase trait EBVs in a progeny test. When there were no specific harvest day effects added, under the assumption of linear growth curves, linearly adjusting for age enabled simple univariate analyses to give accurate sire EBVs for both the trait harvesting was based on, LWT, and the carcase trait regardless of its genetic correlation with LWT. In this study the mean accuracy of sire EBVs for EMA and LWT was 0.91 (0.02) and 0.92 (0.01) (Analyses 2.5 and 2.2) with 40 progeny per sire.

When the age-dependent carcase trait is affected by specific harvest day effects, this study showed that under the simulated parameters, accurate and unbiased EBVs resulted from a bivariate analysis of LWT known for all animals at harvest 1, and EMA recorded for each animal at harvest adjusted for age. The mean accuracy of sire EBVs was either equal to that expected based on the simulated parameters or differed by not more than 0.01 for r_g(LWT,EMA) ranging from 0.0 to 0.9 (Analysis 14.2).

When LWTs were not available at harvest 1 for all progeny, but LWT was not affected by specific harvest day effects, a bivariate analysis of LWT and EMA recorded at harvest both adjusted for age resulted in accuracies equal to those of Analysis 14.2, but resulted in significant EBV bias of the top and bottom third of sires for EBV when r_g(LWT,EMA) was 0.6 and 0.9 (Analysis 12.2). When LWTs were affected by specific harvest day effects the same analysis did not result in a significant reduction in the mean EBV

accuracy of sire EBVs apart from when r_g(LWT,EMA) was 0.6 with a reduction of 0.02 (Analysis 13.2). The mean EBV bias for the top and bottom third of sires for EBV was not significantly different from Analysis 12.2.

Therefore, under similar parameters to those simulated, including 15 or more progeny per sire and linear growth rates, to estimate EBVs of an age-dependent carcase trait influenced by specific harvest day effects, it is recommended that, where possible, LWTs for all animals are recorded on the same day at the first harvest (or close to the first harvest) when LWT is the criteria for harvesting.

A constant correlation of 0.8 was applied for the permanent environmental effect between LWT and EMA. This may be reasonable for LWT and EMA, but for LWT and tenderness for example, quite unrealistic. However, for any value that this correlation takes, it is expected that with a large number of progeny per sire, the effect on EBVs would be negligible as on average the permanent environmental effects are equal to zero and they are not related to the additive genetic effects. There is also the possibility that this correlation changes over time.

In reality, cattle are unlikely to be chosen for slaughter solely on LWT with fatness likely to be a significant factor. More complex modelling would be necessary to account for the selection process in predicting the EBVs of carcase traits.

This study provides insight into estimating carcase trait EBVs when the available data is from harvested animals. Issues for further consideration include non-linear mean growth curves, robustness of the analyses to imperfect adjustment for age, differences in harvesting strategy and environments, and sensitivity analyses of other parameters involved.

6   APPROPRIATE ANALYSES CAN IMPROVE ACCURACY OF LIVEWEIGHT ESTIMATED BREEDING VALUES FROM HARVESTED DATA – A STUDY OF ACTUAL DATA

6.1   Introduction

Simulation work detailed in the previous chapters showed that pre-adjustment of harvested liveweights (LWTs) to the normal distribution at harvest 1 or pre-adjustment by regression of LWT on age enabled accurate LWT estimated breeding values (EBVs) to be obtained. This chapter explores the applicability of these methods to field beef cattle data. These data, although not harvested in reality, consideration of their structure suggested a data subset representative of harvested data could be formed.

6.2   Derivation and examination of data

6.2.1   Animals

Data were extracted from the Cooperative Research Centre (CRC) for Cattle and Beef Quality straightbreeding progeny test project (Upton et al. 2001). The subset of data used for this chapter were from 1,045 steers of 4 temperate breeds from 22 herds with 206 sires, born over a five year period from 1993 to 1997. The progeny were feedlot finished in northeast New South Wales to meet target carcase weights for either the Korean market (280 kg, ~520 kg LWT) or Japanese market (340 kg, ~630 kg LWT). Animals were randomly allocated to either Korean or Japanese market groups shortly after weaning. Table 6.1 gives the number of progeny, number of herds and mean herd size by breed. Each herd contained only one breed.

Table 6.1 Number of steer progeny and herds, and mean herd size by breed for all data used in this study

Breed	Number of steer progeny	Number of herds	Mean herd size
Angus	508	11	46.2
Hereford	279	6	46.5
Murray Grey	99	2	49.5
Shorthorn	159	3	53.0
Total	1045	22	

6.2.2 General approach taken to create a harvested data subset

Animals were allocated to the Korean and Japanese markets in this CRC experiment at weaning. However, cohorts (herd/year/season) were managed together up until Korean market animals were slaughtered. Therefore the animals allocated to the Korean and Japanese markets had similar LWTs, ages and progeny distribution at the point the Korean animals were killed. To create a harvested data subset from this non-selected data set, containing data that could represent LWTs of animals harvested over time based on LWT, the data from similar animals in the Korean and Japanese market categories were divided in half based on LWT at the point the Korean animals were killed. This created four groups, the heaviest and lightest Korean market animals (Khi and Klo) and the heaviest and lightest Japanese market animals (Jhi and Jlo). The Khi animals were taken to be the animals selected for the first slaughter (Korean kill), and then assuming the Jlo animals were equivalent to the Klo animals at the Korean kill point, the Jlo animals were taken to be the animals slaughtered in the second harvest (Japanese kill) after they had an additional period of time to gain weight. Figure 6.1 shows schematically the animals present at the Korean and Japanese kill points and highlights the data used to create the harvested data subset.
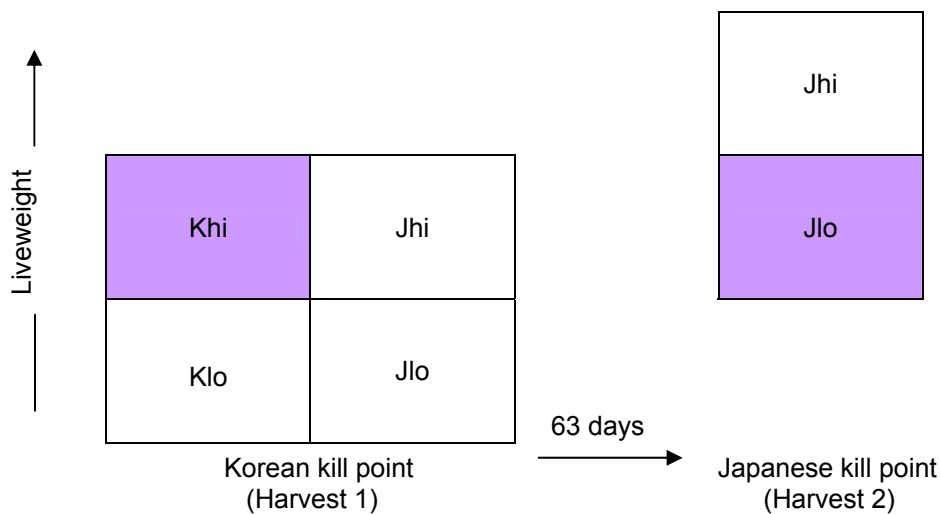

Figure 6.1 Schematic diagram of animals present at the Japanese and Korean kill points with Korean and Japanese market animals divided into the heaviest and lightest halves based on their liveweights at the Korean kill point (Khi, Klo, Jhi and Jlo). The shaded squares represent the data harvested over time based on liveweight.

6.2.3 Validity of method to create the harvested data subset

6.2.3.1 Comparison of animals assigned to Korean and Japanese market groups

The original experiment was designed to balance the progeny of sires across treatments, and Table 6.2 shows that cattle allocated to the Korean and Japanese markets both had nearly the full complement of sires present in all the data with similar variability in progeny per sire.

Table 6.2   Number of progeny per sire for all data, and for Korean and Japanese market animals separately

	Number of sires	Number of progeny per sire		
		Mean	Standard deviation	Range
All data	206	5.1	3.0	1-23
Korean market animals	201	2.7	1.7	1-12
Japanese market animals	198	2.6	1.5	1-11

Animals allocated to the Korean and Japanese markets had similar LWTs and ages at the point the Korean animals were killed (Table 6.3).

Table 6.3 Liveweights (LWTs) and ages for Korean and Japanese market steers at point of Korean kill

	Number of steers	Mean	Standard deviation
LWT of Korean market steers (kg)	536	540.3	52.8
LWT of Japanese market steers (kg)	509	546.0	51.7
Age of Korean market steers (days)	536	615.3	60.1
Age of Japanese market steers (days)	509	612.7	60.3

Comparison of Table 6.3 and Table 6.4 for the Japanese market animals shows that on average approximately 63 days elapsed between the point of measurement at the Korean kill and the point of measurement at the Japanese kill. The Japanese market animals increased in LWT from the Korean kill point to the Japanese kill point by an average of 63.6 kg.

Table 6.4 Liveweights (LWTs) and ages for Japanese market steers at point of Japanese Kill

	Number of steers	Mean	Standard deviation
LWT of Japanese market steers (kg)	509	609.6	55.1
Age of Japanese market steers (days)	509	675.5	60.7

6.2.3.2 Comparison of heavy and light animals within market groups

To create the harvested data subset, animals within market category were divided in half based on LWT at the Korean kill point. Specifically, this was done by splitting each contemporary group in half, where animals with LWTs above or equal to the median were assigned to the heavy half, and animals with LWTs below the median were assigned to the light half. The exception was where there were three animals in a contemporary group. In this case the animal with the middle LWT was assigned to the heavy group if its LWT was above the mean or assigned to the light group if its LWT was below the mean.

Table 6.5 Liveweights (LWTs) and ages of heaviest and lightest halves of animals assigned to the Korean and Japanese market groups (Khi, Klo, Jhi and Jlo) at the points the Korean market and Japanese market animals were killed

		Khi	Klo	Jhi	Jlo
atKlwt* (kg)	**Number of animals**	286	250	280	229
	Mean	569.7	506.7	574.3	511.5
	Standard deviation	42.3	42.6	43.1	38.6
atKage* (days)	**Mean**	618.6	611.5	618.1	606.1
	Standard deviation	58.8	61.6	57.9	62.5
atJlwt* (kg)	**Mean**			638.5	574.2
	Standard deviation			47.6	41.2
atJage* (days)	**Mean**			680.9	669.0
	Standard deviation			58.0	63.2

* atKlwt, LWT at Korean kill point; atKage, age at Korean kill point; atJlwt, LWT at
  Japanese kill point; atJage, age at Japanese kill point

The assumption that the animals in Jlo were representative of the animals in Klo is substantiated in Table 6.5. The mean LWT differences between Jlo and Klo animals and Khi and Jhi animals at the Korean kill point were within 5 kg and not significantly different

(P=0.2). The mean age differences were within 6 days and were also not significantly different (P>0.3). Significance testing between means was based on the pooled t-test assuming equal variances (SAS 1999). The differences in standard deviation for LWT and age were also within 4 units of measurement.

Comparison of the LWTs of Khi animals at the Korean kill point and Jlo animals at the Japanese kill point as given in Table 6.5 supports the assumption that these two groups represent a harvested data set because the difference in LWT was only 4.5 kg.

6.2.3.3 Contemporary group summary for all data and harvested data subset

Liveweight records were from a total of 73 contemporary groups defined as the combination of herd, year of birth and season of birth (1 = January to June, 2 = July to December). Contemporary groups did not separate animals in different market groups and the herd effect accounted for breed. Pre-feedlot nutrition treatments were assigned to all steers but were ignored to increase contemporary group size for this study because it was assumed these treatments were applied randomly within contemporary groups.

For all the data, Table 6.6 shows the distribution of progeny and sires over contemporary groups and Table 6.7 gives the distribution of ages and LWTs at the point the Korean animals were killed averaged over the contemporary groups. There was an average of 3 progeny per sire in the contemporary groups.

Table 6.6 Mean number of progeny and sires per contemporary group (73 total) for all the data

	Mean	Standard deviation	range
Number of progeny	14.3	6.3	2-37
Number of sires	4.8	1.6	2-11

Table 6.7 Mean age and liveweight (LWT) at point of Korean kill per contemporary group (cg) (73 total) for all the data

	Mean of cg means	Standard deviation of cg means
LWT (kg)	544.1	32.0
Age (days)	615.8	56.5

Compared to all the data, taking the subset of Khi+Jlo animals reduced the number of progeny per contemporary group by half from 14.3 to 7.1 and the number of sires per contemporary group by 1 from 4.8 to 3.8 (compare Table 6.6 and Table 6.8). The difference in mean LWT and age at the Korean kill point for the 73 contemporary groups was only 1.3 kg and 0.2 days respectively (compare Table 6.7 and Table 6.9).

Table 6.8 Mean number of progeny and sires per contemporary group (73 total) for Khi+Jlo animals

	Mean	Standard deviation	range
Number of progeny	7.1	3.3	1-19
Number of sires	3.8	1.5	1-10

Table 6.9 Mean age and LWT at point of Korean kill per contemporary group (cg) (73 total) for Khi+Jlo animals

	Mean of cg means	Standard deviation of cg means
LWT (kg)	545.4	32.4
Age (days)	616.0	56.1

6.2.3.4 Comparison of variance components between all data and subsets at Korean kill point

The statistical software ASReml (Gilmour et al. 2006) was used to fit all specific analyses according to the following general univariate animal model:

y = Xb + Zu + e   Model 6

where **y** is a vector of observations, **b** is a vector of fixed effects, **u** is a vector of random animal effects, **X** and **Z** are incidence matrices mapping the fixed and random animal effects to the observations, and **e** is a vector of random residual effects corresponding to the vector of observations.

The variances were assumed to be as follows:

$$\mathrm{Var}\begin{bmatrix} \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

where **A** is the numerator relationship matrix between animals including three generations of pedigree, $\sigma^2 a$ is the additive direct genetic variance, **I** is the identity matrix, and $\sigma^2 e$ is the residual variance.

The following specific analysis was fitted:

$$LWT_{ik} = \mu + cg_i + age_k + a_k + e_{ik}$$ Analysis 6.1

where LWT_{ik} is the unadjusted LWT measurement of animal k, μ is the overall mean, cg_i is the fixed effect of the ith contemporary group, age_k is the linear effect of age, a_k is the random animal effect of animal k and e_{ik} is the residual effect of animal k.

Analysis 6.1 was fitted to LWTs measured at the Korean kill point for all the data and two subsets including Khi plus Jlo, and Klo plus Jhi. These preliminary analyses were done to show the effect the data splitting had on the variance components before harvesting (Table 6.10). Khi and Jlo were those animals considered in the harvested data subset, but Analysis 6.1 was also fitted to the equivalent subset of Klo+Jhi to provide an extra indication of the effect data splitting had on the variance components estimated.

Table 6.10 Estimated additive-genetic variance ($\sigma^2 a$), residual variance ($\sigma^2 e$), heritability (h^2) and linear effect of age (b age) for liveweight measured at the Korean kill point under Analysis 6.1 using all data or subsets of the data

	$\sigma^2 a$	$\sigma^2 e$	h^2 ± standard error	b age ± standard error
All data 73 contemporary groups 1,045 animals	394	1380	0.22 ± 0.12	0.63 ± 0.08
Khi+Jlo data* 73 contemporary groups 515 animals	200	1360	0.13 ± 0.21	0.76 ± 0.11
Klo+Jhi data* 73 contemporary groups 530 animals	374	1726	0.18 ± 0.20	0.62 ± 0.13

* Khi & Klo, Heaviest and lightest half of Korean animals at Korean kill point; Jhi & Jlo, heaviest and lightest half of Japanese animals at Korean kill point

The Khi+Jlo data subset should have been a random sample of the whole data set. However, the additive variance under Analysis 6.1 for the Khi+Jlo data at 200 kg was only half that estimated under the full data set. The heritability (h^2) dropped from 0.22 for all the data to only 0.13 for the Khi+Jlo subset. Although there was a large drop in additive variance and h^2, the similarity between animals in the Khi and Jhi, and the Klo and Jlo groups (see Table 6.5), as well as the large standard errors on the h^2 estimates, suggests that the changes in these variance components when the number of animals was halved to 515 was due to sampling. For comparison, fitting Analysis 6.1 to the Klo+Jhi data resulted in quite different variance components to the Khi+Jlo data with additive variance and h^2 closer to those estimated from the full data set but again with a large standard error on the h^2 estimate. These facts suggest that for the data subsets that should have been random samples of all the data, sampling caused estimated variance components to be different from those based on all the data. Although the Khi+Jlo data subset did not have the same estimated additive variance or h^2 as all the data, this was the only data available and was used to create and evaluate a harvested data set.

6.3 Background analysis for estimating breeding values

6.3.1 Analyses fitted to estimate breeding values

Four specific analyses, including Analysis 6.1 detailed earlier, were fitted to data sets including the Khi+Jlo harvested data subset, to estimate LWT breeding values. These analyses provide evidence of the applicability to actual field data of statistical methodology proposed in the previous simulation chapters. The dependent variable of LWT was considered using the following four definitions:

1.) unadjusted LWT, as in Analysis 6.1.

2.) LWT pre-adjusted for age according to the following equation

$$\text{adj.LWT}_i = \frac{\text{LWT}_i - \text{birth LWT}_i}{\text{age}_i} * \text{standard age} \qquad [6.1]$$

where adj.LWT$_i$ is the ith animal's LWT pre-adjusted for age, LWT$_i$ is the ith animal's LWT at the point of measurement and age$_i$ is the age at measurement of the ith animal. Birth LWT was 35 kg. The standard age was 612.3 days when modelling LWTs measured at the Korean kill point and 640 days when modelling harvested LWTs (The standard age was the approximate average age of measurement.).

3.) LWT pre-adjusted by the approximate lifetime linear effect of age of 0.9 kg/day (Table 6.5) according to the following equation

$$\text{LWTst}_i = \text{LWT}_i - ((\text{age}_i - \text{average\_age})*0.9) \qquad [6.2]$$

where LWTst$_i$ is the ith animal's LWT pre-adjusted by the linear effect of age, LWT$_i$ is the ith animal's LWT at the point of measurement, age$_i$ is the ith animal's age at the point of measurement, and average age is the average age of the animals at the point of measurement.

4.) LWT pre-adjusted to the normal distribution at harvest 1 as detailed in Chapter 4 (referred to as Nadj.LWT). The LWTs of animals recorded at harvest 2 were adjusted to their expected median and variance at harvest 1, where the expectations at harvest 1 were based on normal distribution theory using knowledge of the LWTs of animals slaughtered at harvest 1. Ideally Nadj.LWT should be calculated within contemporary group but for this analysis it was approximated using averages over all contemporary groups. For this study, it was not practical to manually perform the many calculations needed to calculate Nadj.LWT for all the contemporary groups. One exception to this, and the methodology outlined in Chapter 4, was that the LWT standard deviation approximated for the unknown LWTs of the lighter half of animals at harvest 1 was taken to be the same as the known standard deviation for the heavier half of animals at harvest 1.

In addition to Analysis 6.1, the three further analyses were:

$$\text{adj.LWT}_{ik} = \mu + cg_i + a_k + e_{ik} \qquad \text{Analysis 6.2}$$

where adj.LWT$_{ik}$ is the LWT measurement for animal k pre-adjusted for age as shown in [6.1], and the other model terms are as defined for Analysis 6.1;

$$\text{LWTst}_{ik} = \mu + cg_i + a_k + e_{ik}$$
<div align="right">Analysis 6.3</div>

where LWTst$_{ik}$ is the kth animal's LWT pre-adjusted for a set linear effect of age as shown in [6.2], and the other model terms are as defined for Analysis 6.1;

$$\text{Nadj.LWT}_{ik} = \mu + cg_i + \text{Nadj.age}_k + a_k + e_{ik}$$
<div align="right">Analysis 6.4</div>

where Nadj.LWT$_{ik}$ is the LWT of the kth animal adjusted to the normal distribution of harvest 1 (Korean kill) as described above, Nadj.age$_k$ is the linear effect of age of the kth animal at the first harvest, and the other model terms are as defined for Analysis 6.1. This analysis was only applied to harvested data.

6.3.2 Results when variance components estimated from data

This section describes how fitting the specific analyses affected the variance component estimates. Table 6.11 shows the variance components estimated from Analyses 6.2 and 6.3 for non-harvested data, specifically, the LWTs measured at the Korean kill point for all the data and a subset including the Khi and Jlo animals. These results are in addition to those given for Analysis 6.1 in Table 6.10. Compared to Analysis 6.1 fitted to non-harvested data (Table 6.10), the phenotypic variances estimated under Analyses 6.2 and 6.3 were similar for both data sets, but it is not clear why more of the phenotypic variance was partitioned to additive-genetic effects for the Khi+Jlo data subset.

Table 6.11 Estimated additive-genetic variance (σ^2a) and residual variance (σ^2e) for liveweight measured at the Korean kill point using all the data or the Khi+Jlo data subset
Khi, heaviest half of Korean animals at Korean kill point; Jlo, lightest half of Japanese animals at Korean kill point

	All steers at Korean kill point		Khi+Jlo	
	σ^2a	σ^2e	σ^2a	σ^2e
Analysis 6.2	368	1436	274	1267
Analysis 6.3	351	1436	273	1296

Table 6.12 gives estimated variance components and the linear regression coefficient for age under Analyses 6.1 to 6.4 fitted to the harvested data subset. Under Analysis 6.1, harvesting resulted in reduced phenotypic and additive variances, and a much reduced linear effect estimate of age (compare analysis results for Khi+Jlo data in Table 6.10 and Table 6.12). One reason for this is that harvesting on LWT resulted in the LWTs of animals to be much more similar across the range of ages and therefore the linear regression coefficient estimated in Analysis 6.1 was a lot smaller than the true effect of age. Also, because the linear effect of age estimated was not zero, along with the expectation that steers genetically superior for LWT were harvested first, there would also have been some confounding between genetic effects and age. It is suggested that Analysis 6.1 could not take account of the true effect of age and genetic effects were confounded with age.

The much higher variances estimated under Analyses 6.2 and 6.3 using the harvested data compared to Analysis 6.1 suggests that these analyses were able to better account for age and remove confounding between genetic and age effects. Although the phenotypic variance under Analysis 6.4 fitted to harvested data was reduced compared to the expectation indicated in Table 6.10 for the non-harvested Khi+Jlo data, the h^2 at 0.13 was equal to the indicated expectation suggesting Analysis 6.4 was able to correctly partition the variance to genetic and residual effects.

Table 6.12 Estimated additive-genetic variance ($\sigma^2 a$), residual variance ($\sigma^2 e$) and linear effect of age (b age) for liveweights measured at harvest point using harvested data including Khi animals measured at Korean kill point and Jlo animals measured at Japanese kill point
See Table 6.11 headnote for Khi and Jlo definitions

	$\sigma^2 a$	$\sigma^2 e$	b age
Analysis 6.1	160	752	0.10
Analysis 6.2	322	1121	
Analysis 6.3	267	1307	
Analysis 6.4	168	1134	0.51

6.4   Estimation of breeding value accuracy

Analyses 6.1 to 6.4 were fitted to obtain EBVs. EBVs from harvested and non-harvested data were compared to indicate the EBV accuracy resulting under alternative analyses fitted to harvested field data.

6.4.1 Methods

6.4.1.1 Fixed heritability

For non-harvested data, the additive variance estimates from all the data under Analyses 6.1, 6.2 and 6.3 were greater than the additive variance estimates from the Khi+Jlo data (Table 6.10 and Table 6.11). It is proposed that this was due to sampling when only half the data was used. Assuming that using all the data gave better estimates of the true variance components, the h^2 used to compute EBVs from both the harvested data subset and the non-harvested data in all further analyses was fixed at 0.22, [i.e. h^2 estimated under Analysis 6.1 for all the animals measured at the Korean kill point (Table 6.10)].

6.4.1.2 EBV correlations

To assess the EBV accuracy resulting under alternative analyses fitted to harvested data, correlations were calculated between EBVs obtained under Analyses 6.1 to 6.4 fitted to harvested data and EBVs obtained under Analysis 6.1 fitted to non-harvested data. Two data sets were used for the non-harvested data: the LWTs measured at the Korean kill point for all the animals and the LWTs measured at the Korean kill point only for the Khi and Jlo animals in the harvested data subset. This provided comparison of EBVs from harvested data with both EBVs expected to be more accurate because they were based on all the data, and EBVs based on the same animals as used in the harvested data subset.

6.4.1.3 Simulated specific harvest day effects

To examine the influence specific harvest day effects could have on the accuracy of EBVs resulting from analyses fitted to harvested data two further harvested datasets were created. For one dataset a large artificial specific harvest day effect of -100 kg at harvest 2 was created by subtracting 100 kg from all LWT records taken at harvest 2 (Japanese kill). In the same way a second harvested dataset was created but with a specific harvest day effect of +100 kg at harvest 2. As above, correlations were calculated between EBVs estimated under Analyses 6.2 to 6.4 for these altered harvested data subsets and EBVs estimated under Analysis 6.1 for non-harvested data.

6.4.2 Results and discussion

Table 6.13 shows correlations between EBVs of sires and progeny resulting from four alternative analyses fitted to harvested Khi+Jlo data and EBVs resulting from Analysis 6.1 fitted to either all non-harvested data or non-harvested Khi+Jlo data. Fitting Analyses 6.2, 6.3 and 6.4 to the harvested data improved the EBV correlation over Analysis 6.1 fitted to harvested data. This suggests that Analyses 6.2 to 6.4 were able to take account of the true effect of age and remove confounding between genetic effects and age where Analysis 6.1 could not.

When the non-harvested Khi+Jlo data was used in the comparison, the EBV correlations were greater than when all non-harvested data was used. Fitting Analyses 6.2, 6.3 and 6.4 to harvested Khi+Jlo data provided similar information to estimate EBVs as fitting Analysis 6.1 to non-harvested Khi+Jlo data, but this information was less than the information EBVs were based on when Analysis 6.1 was fitted to all the non-harvested data.

Sire EBV correlations greater than 0.93 for Analyses 6.2, 6.3 and 6.4 when non-harvested Khi+Jlo data was used (Table 6.13) suggest that any of these analyses could be used to estimate accurate sire EBVs from harvested LWT data.

Table 6.13 Correlations between EBVs from analyses fitted to harvested data and EBVs from Analysis 6.1 fitted to non-harvested data
See Table 6.11 headnote for Khi and Jlo definitions

	All data		Khi+Jlo data	
	Sires	**Progeny**	**Sires**	**Progeny**
Analysis 6.1	0.411	0.578	0.743	0.669
Analysis 6.2	0.608	0.825	0.934	0.926
Analysis 6.3	0.625	0.837	0.944	0.936
Analysis 6.4	0.634	0.837	0.932	0.922

6.4.2.1 Specific harvest day effect

In the previous analyses of this chapter specific harvest day effects were assumed to be nonexistent. Correlation results above 0.9 between EBVs from particular analyses fitted

to harvested data and EBVs resulting from using non-harvested data gives evidence that specific harvest day effects were not present (Table 6.13).

EBVs from Analyses 6.2 and 6.3 had high correlations with EBVs from non-harvested data in the previous analysis, primarily because harvest day (i.e., Korean vs Japanese kill point) was not fitted in these analyses and specific harvest day effects were not evident. However, if harvest day was fitted in these analyses to account for specific harvest day effects, it is expected that superior (inferior) sires would tend to be compared between themselves resulting in a reduction of additive variance and reduced EBV accuracy. Also, for Analysis 6.2, if there were specific harvest day effects, the age adjustment would be affected by them, also potentially reducing EBV accuracy.

Table 6.14 shows the correlations between EBVs from Analyses 6.2, 6.3 and 6.4 fitted to the harvested data subset with the specific harvest day effect included and the EBVs from Analysis 6.1 fitted to non-harvested data. The addition of either specific harvest day effect caused the EBV correlations for Analyses 6.2 and 6.3 to reduce when the Khi+Jlo non-harvested data was used for comparison, and for effects of -100 kg and +100 kg to increase and decrease when all the non-harvested data was used for comparison. The EBV correlations for Analysis 6.4 did not change with the addition of either specific harvest day effect (compare Table 6.13 and Table 6.14), providing evidence of its usefulness when the effect of harvest day cannot be ignored.

Table 6.14 Correlations between EBVs from analyses fitted to harvested data with specific harvest day effects added and EBVs from Analysis 6.1 fitted to non-harvested data
See Table 6.11 headnote for Khi and Jlo definitions

| | All data | | | | Khi+Jlo data | | | |
| | Sires | | Progeny | | Sires | | Progeny | |
	Ef 1^	Ef 2^	Ef 1^	Ef 2^	Ef 1^	Ef 2^	Ef 1^	Ef 2^
Analysis 6.2	0.769	-0.086	0.843	0.008	0.854	0.326	0.858	0.147
Analysis 6.3	0.768	-0.078	0.847	0.009	0.867	0.323	0.869	0.141
Analysis 6.4	0.634	0.634	0.837	0.837	0.932	0.932	0.922	0.922

^ Ef 1 & Ef 2, Specific harvest day effects of -100 kg or +100 kg added to harvest 2 (Japanese kill point) LWTs, respectively

Under Analyses 6.2 and 6.3, LWT pre-adjusted for age resulted in accurate EBVs for the large negative specific harvest day effect, but poor accuracy for the large positive specific harvest day effect (Table 6.14). Progeny in the second of the two harvest groups were subjected to the specific harvest day effect. For the large positive effect, the progeny in the second harvest expected to be mainly from the genetically poorer sires for growth rate were made much heavier than those in the first harvest explaining the poor accuracy resulting.

6.5 Conclusions

For progeny testing, this study has provided evidence that appropriately pre-adjusting LWT for age, whether it be for a predetermined linear effect of age, or pre-adjustment by weight for age, can take account of the true effect of age and remove the potential confounding of genetic effects with age that can occur by harvesting animals over time based on LWT and give EBVs highly correlated with EBVs from non-harvested data. This is provided that harvest group is not fitted as a fixed effect in the univariate model.

However, if important specific harvest day effects also exist in the harvested data, fitting harvest group as a fixed effect in a univariate model may be considered to account for them. This, however, is expected to create a tendency for superior (and inferior) sires to be compared with each other and reduce EBV accuracy.

Adjusting the LWTs of harvest 2 to the estimated normal distribution at harvest 1 was shown to result in a high EBV correlation with non-harvested data that was robust against the addition of a large specific harvest day effect. For this study, a constant specific harvest day effect was added to all animals at harvest 2. However, there could be many particular specific harvest day effects for different contemporary groups, and it is expected that this method would still be effective if records were adjusted within contemporary group.

7   GENERAL DISCUSSION

Progeny testing can be used to estimate carcase trait breeding values. However, progeny may be sent to feedlots and harvested over time based on live-animal indicators of market requirements for carcase traits. This results in carcase trait records for non-random groups of animals as they are harvested. It was shown that using this harvested data can lead to bias of carcase trait estimated breeding values (EBVs) and accuracies less than expected for data not affected by harvesting.

This study has illustrated how harvesting can conceal the true effect of age and cause confounding between harvest day and genetic effects. Harvesting on liveweight (LWT) causes the LWTs of animals at slaughter to be similar, so that adding a fixed age covariate to the model for LWT in the simulation study could not account for the true effect of age. Harvesting on LWT also tends to cause the progeny of the genetically faster growing sires to be harvested first. This imbalance in progeny across harvests causes confounding between harvest day and genetic effects. Accounting for specific harvest day effects in the model by fitting a harvest day fixed effect can result in additive variance being reduced as harvest day is confounded with genetic effects and genetically superior (inferior) sires tend to be compared between themselves.

These same arguments also apply to an age-dependent carcase trait correlated to the harvesting criteria LWT. However, the results of this study suggest that appropriate statistical methodology including suitable models can result in unbiased and accurate EBVs for this type of harvested data, where the history of selection may not be directly known from the available data.

Recently, Jopson (2007) provided evidence that accurate sire breeding values were possible for the trait progeny were harvested on when records were available for all animals present at each harvest. This work was extended on in the current study to the situation where records for the harvesting criteria were only available as they were harvested. Furthermore, estimating sire breeding values for a second trait genetically correlated to the harvesting criteria has been examined.

CHAPTER 7. GENERAL DISCUSSION

As described in the Literature Review, Pollak et al. (1984) demonstrated how EBV bias could result if only records from selected animals were used in the evaluation and that this was removed by providing the history of selection in the data. The current study shows that when the history of selection is not directly available from the data in the form of all records present at the point of selection, unbiased EBVs are still possible.

It was found that when LWTs were only available for animals as they were harvested and there were no specific harvest day effects, linear pre-adjustment of LWT records by weight for age resulted in accurate sire EBVs, equivalent to deterministic calculation based on the simulated parameters. Sire EBVs also showed small bias.

Similarly, when records were only available for animals when they were harvested for a correlated age-dependent carcase trait, e.g. eye muscle area (EMA), and there were no specific harvest day effects, linear pre-adjustment of EMA for age resulted in accurate EMA sire EBVs. These results were not affected by the magnitude of the assumed genetic correlation between the harvesting criteria and EMA [r_g(LWT,EMA)] (i.e. 0.0 to 0.9). Sire EBVs also showed little or no bias.

The study of actual data provided evidence that in the absence of specific harvest day effects, harvested data pre-adjusted by regression of trait on age or for a predetermined linear effect of age can result in accurate sire EBVs. In this study the EBVs were estimated for an age-dependent trait that was also the criteria for harvesting. However, the simulation work suggests that accurate EBVs can also result for a linearly age-dependent carcase trait correlated to the harvesting criteria.

For the beef industry, these results suggest that simple univariate models of an age-dependent carcase trait linearly pre-adjusted for age result in accurate and unbiased carcase trait EBVs for sires. Pre-adjustment by regression of the trait on age accounted for the effect of age. However, for the simulation study, mean linear growth curves were assumed and there were no specific harvest day effects.

Linear mean growth curves were simulated for both the harvesting criteria and the correlated carcase trait. Pre-adjustments of traits also assumed linear growth. For situations where the underlying growth curves are not linear, pre-adjustments of records

and the models used would have to take this into account. EBV accuracy results for the study of actual data showed that assuming linear growth was appropriate. Linear growth may not be appropriate for some traits or if harvesting occurs over an extended period of time.

When specific harvest day effects influenced the harvesting criteria and records were only available for the harvesting criteria at the point of slaughter, the results showed that the most accurate model did not include harvest day as a fixed effect in the model. This model of LWT pre-adjusted for age resulted in a small drop in mean accuracy of sire EBVs over 100 replicates and an increase in variability of accuracy between replicates compared to the same model applied to data not affected by specific harvest day effects. The mean EBV bias for the top and bottom sires based on EBV were low but significant, and the bias values were more variable between replicates than when no specific harvest day effects were present.

A similar result occurred for an age-dependent correlated carcase trait affected by specific harvest day effects. For levels of genetic correlation greater than zero, the most accurate univariate model was for the carcase trait pre-adjusted for age but not fitting a harvest day fixed effect. This model resulted in mean accuracies not significantly different from one another for the different genetic correlation levels, but significantly lower than the same model fitted to data not affected by specific harvest day effects. The accuracies were also significantly more variable between replicates for all levels of genetic correlation. The bottom and top third of sires based on EBV showed small mean EBV biases but these were quite variable between replicates. Although a univariate model is computationally appealing, results suggest that when there are specific harvest day effects the resulting EBVs are unsatisfactory.

These univariate models have considered age-dependent carcase traits. However some carcase traits may not be age-dependent. If such a carcase trait is not correlated with LWT, it is expected that the only affect of harvesting would be a disproportionate spread of the progeny of individual random sires across harvests. Assuming numbers of progeny for each sire were adequate, a univariate model fitting harvest group if the carcase trait is affected by specific harvest day effects is expected to result in accurate carcase trait EBVs. If the two traits are correlated then a bivariate analysis using LWT adjusted for age, LWT records adjusted to the normal distribution of the first harvest, or LWTs of all

animals recorded on the same day would be expected to help rank the sires correctly for their carcase trait genetic values.

Results showed that adjusting harvested records to their expected values at the first harvest based on normal distribution theory could effectively account for specific harvest day effects and result in accurate EBVs for the trait used as the harvesting criteria in both simulated and actual data. This methodology of adjusting harvested data to the normal distribution of the first harvest may not be directly applicable to an age-dependent carcase trait correlated to the harvesting criteria. However, records for the trait used as harvesting criteria could be adjusted to the first harvest using this methodology when actual records are not available for all animals at the first harvest to provide information on the history of selection for a multivariate analysis to estimate breeding values of genetically correlated carcase traits.

When measurements of the harvesting criteria were available for all animals at the first harvest, accurate and unbiased sire EBVs for a correlated carcase trait affected by specific harvest day effects resulted from a bivariate analysis. Having all records for the harvesting criteria at harvest one provided the history of selection needed to accurately and unbiasedly estimate the sire EBVs of a correlated carcase trait.

When records of all animals for the harvesting criteria LWT were not available for the first harvest, bivariate analyses of both LWT and the correlated carcase trait adjusted for age resulted in heritabilities of the carcase trait not significantly different from the simulated value. This occurred when the carcase trait was affected by specific harvest day effects, for all simulated levels of genetic correlation (0.0 to 0.9), and when there were only 15 progeny per sire. These analyses resulted in accurate mean sire EBVs whether LWT was, or was not, affected by specific harvest day effects. The variability of accuracy between replicates was similar to the most accurate model for the case where all animals had records for the harvesting criteria at harvest one, with the standard deviation ranging from 0.03 to 0.04. Sire EBV bias was small but increased with increasing genetic correlation between the two traits. Although such a bivariate model may be useful to account for harvesting in the beef industry, its use may be inhibited by increased computational demand if an extra trait is required in the genetic evaluation. The

computational demand is likely to be particularly high if the methodology is extended to include more than one harvesting criteria.

More than doubling the magnitude of specific harvest day effects influencing the carcase trait EMA did not result in changes to the EBV accuracy or EBV bias of sires for the models tested. The models tested included bivariate models with the selection criteria LWT and a univariate model of EMA adjusted for age. These results suggest that appropriate models are able to account for large specific harvest day effects affecting age-dependent carcase traits. However, results from the actual data study examining the harvesting criteria LWT showed that using LWT adjusted for age resulted in accurate EBVs for a large artificially induced negative specific harvest day effect, but poor accuracy for a large positive specific harvest day effect. Progeny in the second of two harvest groups were subjected to the specific harvest day effect. For the large positive effect, the progeny in the second harvest expected to be mainly from the genetically poorer sires for growth rate were made much heavier than those in the first harvest explaining the poor accuracy resulting. In that study, adjustment of harvested LWT records to the normal distribution at the first harvest provided consistently high EBV accuracy regardless of the direction of the specific harvest day effect.

Using normal distribution theory to adjust harvested records to their expected values at the first harvest may be useful in practical application to the beef industry, enabling both age and specific harvest day effects to be accounted for. However, the methodology presented assumes that animals were weighed and only the heaviest animals were slaughtered at each harvest. If animals were slaughtered on approximate LWTs, for example, on eye appraisal, this would have to be accounted for. This method also assumes linear growth between the first and subsequent harvests and that the ranking and relativity of animals beyond the first harvest remains the same. These assumptions may not hold if there are large environmental changes after the first harvest or long periods of time between harvests. In practice it is also likely that there is more than one harvesting criteria, which would require extension to the current methodology.

This study has highlighted potential problems that could occur in the beef industry when analysing harvested data from a progeny test. However, the study has given evidence that appropriate models are able to estimate accurate and unbiased sire EBVs for

harvested data affected by specific harvest day effects, including for age-dependent carcase traits varying in level of genetic correlation with the harvesting criteria. For such carcase traits evidence has been given that accurate and unbiased sire EBVs are possible when records of all animals for the harvesting criteria are not available for the first harvest.

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