

# CHAPTER 3

## Material

### 3.1 Bunge Meat Industries

The animals included in this study were part of the breeding herd of Bunge Meat Industries, Australia (BMI). The main facilities of BMI are located near the town Corowa (36°S,146°34'E), which is located on the western slope of the Great Dividing Range in the southern part of New South Wales, Australia. Altitude for Corowa is 140 m and climate is characterised by an average yearly rainfall of 700 mm, mainly falling in winter and autumn (Bureau of Meteorology, 1994). Further information on climate is available from the weather station in Albury, which is located 50 km east of Corowa (Table 3-1). During summer months (December to February) temperatures are high with average maximum temperatures around 30°C while rainfall is low (40 to 50 mm per month).

Table 3-1 Monthly rainfall and average maximum and minimum temperatures for Albury, NSW (Bureau of Meteorology, 1994).

	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sept	Oct	Nov	Dec
Ø rainfall (mm)	40	44	50	52	64	82	73	72	62	70	50	46
Ø maximum temp. (°C)	29.2	28.4	25.0	23.3	17.8	13.8	13.8	15.0	17.0	22.0	26.3	32.7
Ø minimum temp. (°C)	13.4	13.5	10.2	7.2	4.3	3.6	1.5	0.7	3.1	6.6	11.6	15.5

The facilities on the site in Corowa include the main office, 5 production units (modules), each including a mating centre, dry sow sheds and farrowing sheds housing 23000 sows in total. In addition, each module has weaning, growing and finishing sheds for fattening pigs. On site is a specialised pig abattoir slaughtering about 9000 pigs per week (PRDC/APC, 1995). The main

research facilities are located in module one which accommodates 2900 nucleus sows and includes a boar test station with 240 single pens where individual feed intake is recorded.

The distance from module one to the abattoir is approximately 2 km. Since June 1993, CO<sub>2</sub> stunning equipment is used, which replaced electrical stunning. Electrical stunning used 300 volts, with 1.6 to 4.0 amps. for 4 seconds. For CO<sub>2</sub> stunning, a gas mixture containing 80% CO<sub>2</sub> is applied for 30 to 60 seconds depending on the operator. Throughput is 300 to 310 pigs per hour, which enter the chiller after 45 minutes. Chilling occurs in two stages, firstly with a temperature of -12°C for 40 minutes and secondly in a temperature of -8°C for 50 minutes. Subsequently carcasses are stored at a temperature of 3 to 4°C in the holding chiller. Most carcasses are marketed as whole carcase, while 20% of carcasses are boned out and further processed in the boning room the day after slaughter.

Module one houses the nucleus lines of BMI with Landrace, Large White and Duroc being the major breeds. The selection program includes the use of animal model BLUP evaluation (PIGBLUP) and selection is based on growth rate, feed efficiency, backfat and number born alive. However, the main selection emphasis has been put on feed efficiency. Gilts are selected at the age of 160 to 180 days after they have been performance tested for growth rate and backfat. Gilts are then moved to the mating centre where they remain until three weeks after service. Since 1993 all sows are artificially inseminated in module one and gilts are served three times in contrast to sows being served twice. Sows are then transferred to the dry shed where they are penned in single stalls. During gestation, sows are on a restricted feeding regime with gilts obtaining 2.3 kg and sows 2.5 kg of feed (13MJ ME; 0.60% Lysine) per day. A week prior to farrowing sows are relocated to farrowing sheds which accommodate 100 sows each. There is no all in all out system and therefore sows are continuously put into farrowing sheds. Within the first three days after farrowing, cross fostering is practised to standardise litter size and individual piglet weights within one litter. On average piglets are weaned at four weeks.

After weaning piglets are placed into the weaning shed where they stay for seven weeks. Feed with 14.5 MJ ME/kg and 1.25% Lysine equivalent to 200 g. crude protein is provided ad libitum. Energy and protein content is slightly reduced in the ratio fed ad libitum in the grower shed (14.0 MJ ME /kg with 1.15% Lysine). This ratio is continued in the boar test station while feed in finisher shed has an energy level of 13.5 MJ ME/kg with a lysine content of 0.82%. Pigs remain in the growing and finishing shed for six to seven weeks which leads to an average slaughter age of 22 weeks.

All sheds in module one are half open sheds where the windows can be opened according to weather conditions. These sheds are not tiled and no sprinkler system is installed to cool animals during summer months.

## 3.2 Production, carcase and meat quality traits

### 3.2.1 Data recording and testing procedure

Data for this study were recorded at BMI from July 1992 to June 1995. The design of the project aimed to have two male piglets randomly chosen from 20 litters per week of Large White, Landrace and Duroc sows. Piglets participating in this project were chosen at 21 days. It was a policy not to take piglets that had been transferred to a foster sow. Since cross fostering is a management practice at BMI it reduced the number of piglets available for this project. In addition, it was not always possible to obtain 20 litters per week and therefore more than two male piglets were chosen per litter whenever they were available. Data characterisation including number of animals that were tagged in each recording year, as well as number of sires, dams and litters per year is given in Table 3-2. In total, 4733 animals were tagged for this project coming from 2045 litters (2.3 pigs per litter) with 185 sires and 1540 dams. The two main breeds are Large White and Landrace with 2335 and 2023 animals, while only 375 Duroc animals were available. However, only 3600 animals have performance traits available which is due to relocation of pigs and loss of earmarks which made the identification of pigs impossible. Another loss of approximately 400 animals resulted in a total of 3200 pigs that have meat quality traits available. This additional loss of animals resulted from a further loss of earmarks during the slaughter procedure especially during the dehairing and descaling procedure in the abattoir.

The testing procedure started with the recording of animal weight at 21 days when project animals were tagged. Animals stayed within their litter until weaning at four weeks. Each weekly batch of tagged animals (30 - 40 pigs) was then kept in one pen within the weaner and growing shed. At an age of 18 weeks, animals entered the boar test station where they were single penned. Pigs were fed ad libitum and feed intake was recorded over a testing period of four weeks. Weight of the animal was recorded at the beginning of the testing period and shortly before slaughter at 22 weeks.

Carcase traits included real time ultrasound measurements and measurements taken in the abattoir. Real time ultrasound measurements were recorded 24 hours before slaughter at the

real time ultrasound station at BMI and included fat depth at P2 site and fat and eye muscle depth between third and fourth last rib. To obtain reliable measurements pigs were restrained and lubricant was put on the skin before measurements were taken. Pigs were then loaded and transported to the abattoir where they stayed in one pen until the next morning. This led to a lairage time of approximately 18 hours.

Table 3-2 Number of animals, sires, dams and litters per year of birth

	<b>Large White</b>	<b>Landrace</b>	<b>Duroc</b>	<b>Total</b>
<b>1992</b>				
animals	511	415	83	1009
sires	17	7	6	30
dams	127	110	31	268
litters	217	188	46	451
<b>1993</b>				
animals	1003	871	117	1991
sires	24	33	13	70
dams	306	266	47	619
litters	424	372	58	854
<b>1994</b>				
animals	821	737	175	1733
sires	29	39	17	85
dams	303	280	70	653
litters	346	312	82	740
<b>Total</b>				
animals	2335	2023	375	4733
sires	70	79	36	185
dams	736	656	148	1540
litters	987	872	186	2045

Project animals were slaughtered each Wednesday as the second group of animals in the abattoir to ensure that the line was working and no stop of the line occurred during slaughter of these animals. Hot carcass weight and fat depth at the P2 site were measured at the grading station in the abattoir with a Hennessy Chong machine. A second Hennessy Chong machine was used to record the fat and muscle depth between the third and fourth last rib. These carcass measurements were done 30 minutes after slaughter while the first meat quality trait, a pH measurement, was taken later in the line at 40 minutes shortly before carcasses entered the chiller. The pH was recorded with a TPSmeter LC80A through the puncture mark between the third and fourth last rib in the *m. longissimus dorsi*.

Meat quality traits were measured on a chop including the loin eye area and the belly, which was taken from the anterior end of the left hand side of the middle. Meat quality traits include pH taken 24 hours after slaughter and colour of the *m. longissimus dorsi* and *m. multifidus dorsi*. Colour measurements were measured with a Minolta Chromamometer CR200b, calibrated on a red and white standard sample. The L-value was recorded as measurement of colour which describes the brightness of meat. The scale ranges from 0 to 100 with higher values representing lighter colour and a paler meat. A sample from the *m. longissimus dorsi* was then cut to record drip loss percentage. This meat sample was suspended in an air filled plastic bag for further 24 hours in the cooling room. The following day, the whole sample was weighed, dried and weighed a second time. The meat sample was frozen and later used to obtain information about the intramuscular fat content.

In addition to these meat quality traits, ham weight was obtained on the day after slaughter as an additional carcass characteristic. To obtain ham weight, the left back leg was derinded, defatted and slash boned, excluding the hock muscles.

Intramuscular fat content was determined from meat samples of *m. longissimus dorsi* with the Soxtec solvent extraction method (Foster and Gonzales, 1992). Since this method is time consuming and only 75 samples could be processed per week, Near Infrared Spectroscopy (NIR) was used to determine intramuscular fat content. Near Infrared Reflectance spectra measurements were performed with a NIR scanning spectrophotometer. This machine was calibrated on 300 samples resulting in a correlation of  $> 0.95$  between the two measurement techniques and was additionally used to allow for a quicker analysis of all samples (150 - 250 samples per week). Samples were allocated randomly to the two measurement techniques resulting in 882 samples for the Soxtec solvent extraction method and 1712 samples for NIR method. No confounding existed with other systematic effects.

From February 1994 onwards, manufacturing properties of 20 slash boned ham and 20 string boned middles were recorded per week, which included pickling, massaging and cooking of these carcass parts. Shortly after boning, hams and middles were pickled with a pickle mixture consisting of 80 litres of water, 11 kg of ice, 13.6 kg of salt, 9kg of Globus Injectamix and 3.2 kg of sugar. The ice in the pickle mixture guaranteed a temperature of the pickle below 4°C. Ham and middles were then injected with this pickle mixture to 120%. Middles were then placed in a tub, covered with pickle solution and left until further processing two days later. Hams were tumbled for six hours, and left overnight at 4°C before processing the next day. Hams and middles were cooked for 6.5 hours and 5 hours, respectively. A description of the cooking procedure is given in Appendix 1.

### 3.2.2 Data characterisation

Although piglets were tagged and weighed at approximately three weeks with a range of 17 to 23 days, performance recording started when pigs entered the boar test station at 18 weeks. The information recorded in the boar test station is listed in more detail in Appendix 2 and was used to obtain the following growth and feed efficiency traits:

- average daily gain from 3 to 18 weeks (ADG1)
- average daily gain from 18 to 22 weeks (test station) (ADG2)
- lifetime average daily gain (ADG3)
- daily feed intake (FDINT)
- feed conversion ratio defined as feed intake per gain (FCR)
- lean meat growth (LEANG)

In some cases pigs did not enter the boar test station at exactly 18 weeks, but a week earlier or a week later. As a consequence, growth period for ADG1 ranges from 17 weeks to 20 weeks. Test period in the boar test station varies between four and five weeks, with the majority of pigs having a test period of four weeks. Differences in these testing periods lead to a variation in slaughter age of 20 to 26 weeks which represents the growth period for ADG3.

Daily feed intake represents the average amount of feed consumed per day during the testing period in the test station. Feed conversion ratio is defined as the ratio of amount of feed consumed per weight gained. From carcass measurements lean meat percentage was predicted, which is described later in this chapter, and the amount of lean meat yield was obtained using this information. Lean growth was then defined as lean gained over lifetime period.

Carcass characteristics were measured on the live animal as well as in the abattoir and boning room (Appendix 2) and include the following traits:

- backfat depth at P2 measured with real time ultrasound (LFDP2)
- backfat depth between 3rd/4th last ribs measured with real time ultrasound (LFD3/4)
- muscle depth between 3rd/4th last ribs measured with real time ultrasound (LMD3/4)
- backfat depth at P2 measured with Hennesy Chong machine (FDP2)
- backfat depth between 3rd/4th last ribs measured with Hennesy Chong machine (FD3/4)
- muscle depth between 3rd/4th last ribs measured with Hennesy Chong machine (MD3/4)
- weight of left back leg (BLW)
- weight of slash boned ham (LMW)
- lean meat percentage based on Hennesy Chong measurements (LEAN)
- lean meat percentage based on real time ultrasound measurements (LEANL)

Lean meat percentage was predicted using equations developed by Ferguson et al. (1994). Lean meat percentage based on Hennesy Chong measurements was predicted as:

$$\text{LEAN} = 64.2704 + 0.1090 \times \text{standardized hot carcass weight} - 1.0231 \times \text{FDP2}$$

Lean meat percentage based on real time ultrasound measurements was predicted through:

$$\text{LEANL} = 64.8473 - 0.4538 \times \text{LFDP2} - 0.5263 \times \text{LFD3/4} + 0.1375 \times \text{LMD3/4}$$

Meat quality characteristics measured on the slaughter day and the day after slaughter include the following traits:

- Colour of *m. longissimus dorsi* (L-value) (CLD)
- Colour of *m. multifidus dorsi* (L-value) (CMD)
- pH measured 45 minutes after slaughter (pH45)
- pH measured 24 hours after slaughter (pH24)
- drip loss percentage (DLP)
- intramuscular fat content (IMF)

Manufacturing traits include:

- yield of ham defined as
  - percentage of ham after processing in relation to green weight (HAM)
  - weight difference of ham after processing in relation to green weight (HAMD)
- yield of middle defined as
  - percentage of middle after processing in relation to green weight (MID)
  - weight difference of middle after processing in relation to green weight (MIDD)

Drip loss percentage was obtained by calculating the difference of the weights before and after drying of the meat sample. This difference was then expressed as a percentage of the initial weight. Measurements of intramuscular fat content were repeated once and the average of these two measurements was taken as intramuscular fat content available for analysis.

Weight of hams and middles were recorded after pickling, tumbling and cooking (see Appendix 2). Yield of ham and yield of middle were then defined as weight of ham and middle after processing in relation to unprocessed weight of ham and middle as well as the weight difference to the initial weight.

Table 3-3 Number of records, means and standard deviations for analysed traits

	Number of records	Mean	Standard deviation	limits imposed	unit
<b>Performance traits</b>					
ADG1	3257	616.0	80.1	100 - 1000	grams
ADG2	3299	946.0	185.8	300 - 1500	grams
ADG3	3271	626.0	68.4	300 - 1000	grams
FDINT	3294	2.62	0.43	0.8 - 5.0	kg
FCR	3294	2.85	0.58	0.5 - 6.6	
LEANG	2349	273.0	35.0	150 - 400	grams
<b>Carcase traits</b>					
LFDP2	3348	13.0	2.59	5 - 35	mm
LFD3/4	3327	13.1	2.61	5 - 35	mm
LMD3/4	3012	37.8	4.56	17 - 70	mm
FDP2	2670	12.9	3.13	3 - 35	mm
FD3/4	1726	13.2	3.00	3 - 35	mm
MD3/4	1745	46.5	9.57	10 - 85	mm
BLW	2960	10.6	1.24	5 - 20	kg
LMW	2962	5.7	0.73	2 - 15	kg
LEAN	2656	59.8	2.94	40 - 70	%
LEANL	3011	57.1	2.53	40 - 70	%
<b>Meat quality traits</b>					
CLD	2867	53.16	4.91	35 - 75	
CMD	2861	45.78	4.10	30 - 75	
pH45	2510	5.36	0.46	4.7 - 8.7	
pH24	2671	5.74	0.26	4.5 - 9.0	
DLP	2996	1.98	1.87	0.0 - 15	%
IMF	2594	1.69	0.67	0.1 - 7	%
<b>Manufacturing traits</b>					
HAM	953	104.6	3.08	70 - 130	%
HAMD	953	0.268	0.194	-1.0 - 1.5	kg
MID	816	105.9	3.64	75 - 125	%
MIDD	811	0.480	0.288	-1.0 - 1.5	kg

Abbreviations for traits:

ADG1	Average daily gain from three to 18 weeks
ADG2	Average daily gain in test station from 18 to 22 weeks
ADG3	Lifetime average daily gain
FDINT	Feed intake recorded in test station from 18 to 22 weeks
FCR	Feed conversion ratio defined as feed intake over growth rate (18 to 22 weeks)
LEANG	Lean meat growth
LFDP2	Backfat depth at P2 measured with real time ultrasound
LFD3/4	Backfat depth between the third and fourth last ribs measured with real time ultrasound
LMD3/4	Muscle depth of <i>m. longissimus dorsi</i> between the third and fourth last ribs on the live animal
FDP2	Backfat depth at P2 measured with Hennesy Chong grading machine
FD3/4	Backfat depth between third and fourth last ribs measured with Hennesy Chong grading machine
MD3/4	Muscle depth between third and fourth last ribs measured with Hennesy Chong grading machine

BLW	Weight of whole left back leg
LMW	Weight of slash boned left back leg
LEAN	Lean meat percentage derived from Hennesy Chong measurements on carcass
LEANL	Lean meat percentage derived from real time ultrasound measurements on live animal
pH45	pH measured 45 minutes after slaughter
pH24	pH measured 24 hours after slaughter
CLD	L-value of Minolta chromamometer of <i>m. longissimus dorsi</i>
CMD	L-value of Minolta chromamometer of <i>m. multifidus dorsi</i>
DLP	Drip loss percentage
IMF	Intramuscular fat content
HAM	Ham yield expressed as percentage of ham weight after processing in relation to green weight
HAMD	Ham yield expressed as difference of ham weight after processing in relation to green weight
MID	Yield of middle expressed as percentage of middle weight after processing in relation to green weight
MIDD	Yield of middle expressed as percentage of middle weight after processing in relation to green weight



Although 4700 animals were tagged for this project at the age of three weeks, only 3600 animals entered the boar test station at 18 weeks. This was mainly due to loss of earmarks during the fattening period. In addition, pigs might have moved to another pen and therefore could not be found to go into the test station. Another loss of stig numbers occurred during the slaughter procedure especially during dehairing and descalding. In some cases it was possible to identify pigs through their earmarks. However, if there was any doubt about the identification of a pig it was excluded from the analysis. Technological traits were only measured on 20 animals per week since February 1994, resulting in a total of 1044 hams and 897 middles until the end of the project.

Table 3-3 presents means and raw standard deviations for all investigated traits of Large White and Landrace pigs. Only 300 Duroc pigs had performance traits available which was not sufficient to estimate heritabilities for this breed separately. In addition, this performance could not be linked to reproductive performance of the sow. It was therefore decided not to include Duroc pigs in the analysis. This decision was further supported by differences in means and standard deviations for this breed in comparison to Large White and Landrace pigs.

Growth rate is substantially higher in the test station (ADG2: 940 g.) than in the growing period from three to 18 weeks before the testing period (614 and 624 g.) Besides this increase in average growth rate the standard deviation is more than double which is higher than the standard deviation presented by van Steenbergen et al. (1990). This drastic increase in variation is unusual and might be caused by the testing procedure.

The average muscle depth is 37.8 mm recorded with real time ultrasound equipment and 46.6 mm when muscle depth is measured with Hennesy Chong machine. Besides this higher mean for the Hennesy Chong measurement, the standard deviation is also increased. These differences between measurement techniques were also found by Gresham et al. (1992).

The intramuscular fat content is 1.69 % for Large White and Landrace pigs. Although this is below the optimum level of 2.5 % proposed by de Vol et al. (1988) it is higher than the mean of 1.33 % presented by de Vries et al. (1994b) for Dutch Yorkshire.

### 3.3 Reproductive performance of the sow

From the herd recording system of BMI a data set was obtained including approximately 48,000 sow litter records. Information included in this data set is listed in Appendix 3 and

consists of general information for each sow and reproductive performance for each parity. Various restrictions were then imposed on this data set which resulted in 13518 litter records for the first three parities from 6050 sows. As a first step, only Large White and Landrace sows which farrowed between 1991 and March 1995 were included in the data set. The number of sows and number of sires and dams are presented in Table 3-4 for the two breeds and for each farrowing year. The data set included 3776 Large White sows and 2274 Landrace sows, with 252 sires and 1999 dams.

Table 3-4 Number of sows with records per year of farrowing with number of sires and dams

	Large White	Landrace	Total
<b>1991</b>			
sows with records	732	67	799
sires	44	7	51
dams	264	10	274
<b>1992</b>			
sows with records	938	461	1399
sires	50	40	90
dams	379	117	496
<b>1993</b>			
sows with records	1036	821	1857
sires	34	31	65
dams	288	277	565
<b>1994</b>			
sows with records	956	775	1731
sires	19	19	38
dams	319	265	584
<b>1995</b>			
sows with records	114	150	264
sires	3	5	8
dams	34	46	80
<b>Total</b>			
sows with records	3776	2274	6050
sires	150	102	252
dams	1284	715	1999

Production unit one accommodates all purebred sows and pigs were therefore raised in module one. Farrowing occurred in either module one or unit two, which is the multiplier unit. As another restriction, only litters from Large White (LW) or Landrace (LR) sows or crossbred litters from Large White sows and Landrace service sires (LW\*LR) or Landrace sows and Large White service sires (LR\*LW) were included in the data set. The percentages of crossbred litters for the first three parities were 60.3, 64.4 and 74.2 for Large White and 52.0,

56.2 and 69.1 for Landrace. The proportion of sows located in module two increases from 67.1 %, 78.7 % to 88.0 % from the first to third parity. Each litter originated from the first mating only and the proportion of litters from artificial insemination was 18.3, 23.0 and 24.8 % for the first to third parity.

The following traits of the sow were available for analysis:

- number born alive in the first to third parity ( $NBA_{1,2,3}$ )
- litter birth weight in the first to third parity ( $LBW_{1,2,3}$ )
- average piglet weight at birth in the first to third parity ( $ABW_{1,2,3}$ )
- litter weight at 21 days in the first and second parity ( $LW21_{1,2}$ )

The farrowing age for the first litter was restricted to 270 to 500 days. Age of litter when 21 day litter weight was recorded ranges from 10 to 28 days with a mean of 19 days. Number of records, mean values and standard deviations are presented for analysed traits of the sow in Table 3-5. All reproductive traits of the sow increase with higher parity numbers. In particular 21 day litter weight shows a high increase from the first to second parity which could be caused by different cross fostering practices. It is a general custom to place the smallest piglets to gilts and move bigger piglets to older sows. No culling was performed on performance criteria. Reasons for culling between parities were based on returning to mating more than once in a lifetime and abortions.

Table 3-5 Number of records, means and raw standard deviations for reproductive traits of the sow

	N	Mean	Standard deviations	Limits imposed	Unit
<b>NBA<sub>1</sub></b>	5986	9.61	2.44	2 - 20	
<b>NBA<sub>2</sub></b>	4317	10.04	2.47	2 - 20	
<b>NBA<sub>3</sub></b>	3114	10.78	2.48	2 - 20	
<b>LBW<sub>1</sub></b>	4506	12.47	3.60	2 - 25	kg
<b>LBW<sub>2</sub></b>	2670	13.54	4.08	2 - 25	kg
<b>LBW<sub>3</sub></b>	1538	14.71	4.22	2 - 25	kg
<b>ABW<sub>1</sub></b>	4403	1333	418	300 - 3000	grams
<b>ABW<sub>2</sub></b>	2636	1407	455	300 - 3000	grams
<b>ABW<sub>3</sub></b>	1528	1427	394	300 - 3000	grams
<b>LW21<sub>1</sub></b>	1418	42.95	11.17	20 - 90	kg
<b>LW21<sub>2</sub></b>	810	49.25	11.19	20 - 90	kg

- NBA<sub>1,2,3</sub> - number born alive in the first to third parity
- LBW<sub>1,2,3</sub> - litter birth weight in the first to third parity
- ABW<sub>1,2,3</sub> - average piglet weight at birth in the first to third parity
- LW21<sub>1,2</sub> - litter weight at 21 days in the first and second parity

# CHAPTER 4

## Method and models

### 4.1 Theoretical background on variance component estimation

#### 4.1.1 Historical overview

The terms “variance “ and “analysis of variance” were first used by Fisher (1918) who developed the use of variance component models to describe fractions of the variation due to constituent causes as percentages of total variance in a trait. In animal breeding applications, sources of variation are due to additive genetic effects, dominance, epistasis, and permanent and temporary environmental effects (Falconer, 1989) which describe genetic and environmental properties of a trait. Genetic variance components can be estimated from the resemblance of relatives using linear models which has been common since 1939 (Jackson, 1939). Eisenhart (1947) described properties of fixed and random models and used the term “mixed analysis of variance”. In the context of mixed models, the landmark paper of Henderson (1953) made a substantial contribution to the estimation of variance components. In that paper, the ANOVA method of estimation was extended for unbalanced data to equate a wide variety of quadratic forms to their expected values. After limitations due to computational requirements had been removed, this method has been widely applied in animal breeding with the availability of a computer program (LSML76) using general least squares (Harvey, 1977).

Interest in Maximum Likelihood (ML) procedures for variance component estimation originates from useful properties of its estimators, which are consistent, efficient and asymptotically normal (Miller, 1973). Although ML had already been introduced by Fisher (1922, 1925) complexity of computational problems caused a time delay until Hartley and Rao (1967) renewed the interest in the method of ML by showing its use for the estimation of variance components under general mixed linear models.

In animal breeding applications, data originate from selection experiments or from performance records where animals have been culled on the basis of their performance. In contrast to ANOVA estimators, which assume that data are randomly sampled, ML estimators do account for selection under certain conditions. This was shown by Meyer and Thompson (1984) and Sorensen and Kennedy (1984) who studied the effect of selection on ML and ANOVA estimators.

Ignoring the loss in degrees of freedom due to fixed effects in the model of analysis is a major drawback of ML estimators (Harville, 1977). This disadvantage of ML estimation is overcome by Restricted Maximum Likelihood (REML), first developed by Anderson and Brancroft (1952) and by W.A. Thompson (1962) for balanced data in general. Patterson and R. Thompson (1971) described REML for the general mixed model by maximizing only that part of the likelihood which is independent of fixed effects.

The maximum of a likelihood function is at the point where the first derivative is zero and the second derivative is less than zero. To locate the point of the maximum likelihood function for parameters to be estimated, algorithms using first and second derivatives of the likelihood function have been applied. The Newton-Raphson algorithm, described by Jennrich and Sampson (1976) for ML estimation of variance components in mixed model analyses, uses the first and second partial derivatives of the likelihood function to estimate variance components. The vector of first moments, also called the gradient vector, is used to find the direction of the steepest ascent whereas the matrix of second moments, the Hessian matrix defines the step size in that direction.

The advantages of the Newton-Raphson algorithm were summarised by Gill and Murray (1974). The algorithm is effective on highly nonlinear problems requiring only a few iterations for convergence. When a large number of elements of the Hessian matrix are constant the Newton-Raphson algorithm is most effective. On the other hand, when poor starting points are used, it may converge to a stationary point which is not a local or global maximum or it might not converge at all (Redner and Walker, 1984). Furthermore the Newton-Raphson algorithm requires at each iteration the computation of the Hessian matrix and the solution of a system of linear equations having the Hessian matrix as the coefficient matrix.

Replacing second derivatives of the likelihood function by their expectations yields Fisher's Method of Scoring which was used in the original REML paper by Patterson and Thompson (1971). In comparison to the Newton-Raphson algorithm, the Method of Scoring is less computationally demanding (Harville, 1977) and performs better in the case of poor starting

values. However, it might be slower to converge, since the Method of Scoring converges only linearly in comparison to the Newton-Raphson converging quadratically (Redner and Walker, 1984).

Wide use of REML estimation of variance components in animal breeding applications was assisted through the development of a derivative free algorithm by Graser et al. (1987). Fitting a quadratic approximation, the log likelihood is maximized with respect to only one parameter, the ratio of error and additive genetic variances. The residual sums of squares and the log determinant of the coefficient matrix in the mixed model equations are derived through a Gaussian elimination, absorbing one row at a time which does not need inversion, as described by Smith and Graser (1986). The error variance can then be calculated directly from the residual sums of squares at convergence. This approach has been extended to models including additional random effects by Meyer (1989) and to multivariate analyses by Meyer (1991).

With the availability of ready to use REML packages and more computational power, larger data sets have been analysed with more sophisticated models with simultaneous analysis of more traits. Since derivative free approaches are slow to converge for this scenario (Miszta et al., 1994), new interest has risen in algorithms using derivatives. An approach presented by Johnson and Thompson (1994) for the univariate case and by Madsen et al. (1994) for the multivariate case, approximates the second derivative of the likelihood function by taking an average of observed information (Newton-Raphson) and expected information (Fisher's Method of Scoring). This method is computationally highly advantageous while it converges almost as quickly as algorithms evaluating second derivatives of the log likelihood explicitly (Meyer and Smith, 1996).

### 4.1.2 Model of analysis

Consider the multivariate linear model for analysis of  $t$  traits:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e} \quad (1)$$

with  $\mathbf{y}$  being the vector of  $N$  observations for all traits,  $\mathbf{b}$  the vector of  $N_f$  fixed effects including covariables,  $\mathbf{X}$  the  $N \times N_f$  incidence matrix of fixed effects,  $\mathbf{u}$  the vector of  $N_u$  random effects,  $\mathbf{Z}$  the  $N \times N_u$  incidence matrix of random effects, and  $\mathbf{e}$  the vector of  $N$  random residual errors.

The covariance structure is assumed to be  $V(\mathbf{u}) = \mathbf{G}$ ;  $V(\mathbf{e}) = \mathbf{R}$ ;  $\text{COV}(\mathbf{u}, \mathbf{e}') = 0$ ; and  $V(\mathbf{y}) = \mathbf{V} = \mathbf{Z}\mathbf{G}\mathbf{Z}' + \mathbf{R}$ .  $\mathbf{X}$  is assumed to be  $\sigma^2$  full rank  $r(\mathbf{X}) = N_f$ .

The mixed model equations (MME) pertaining to (1) are then (Henderson, 1973):

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix} \quad (2)$$

where  $\mathbf{G}$  is the covariance of  $\mathbf{u}$ , and  $\mathbf{R}$  is a covariance matrix of residuals.

For an animal model  $\mathbf{u}$  always includes the vector of animals' additive genetic effects ( $\mathbf{a}$ ). In addition, other random effects such as common environmental effects ( $\mathbf{c}$ ) including litter effects or the animals' maternal genetic effect ( $\mathbf{m}$ ) could also be fitted.

Let  $\mathbf{A}$  be the numerator relationship matrix and  $\mathbf{I}$  the identity matrix and ' $\otimes$ ' be the direct matrix product. Consider  $\sum_A = \{\sigma_{A_{ij}}\}$  as the  $t$  by  $t$  matrix of direct additive genetic effects,  $\sum_M = \{\sigma_{M_{ij}}\}$  as the  $t$  by  $t$  matrix of maternal additive genetic effects with  $\sum_{AM} = \{\sigma_{AM_{ij}}\}$  as the  $t$  by  $t$  matrix of direct and maternal additive genetic covariances and  $\sum_C = \{\sigma_{C_{ij}}\}$  as the  $t$  by  $t$  matrix of common environmental effects. The (co)variance structure for the analysis can then be described as:

$$\mathbf{V}(\mathbf{a}) = \sum_A \otimes \mathbf{A}; \quad \mathbf{V}(\mathbf{m}) = \sum_M \otimes \mathbf{A}; \quad \mathbf{V}(\mathbf{c}) = \sum_C \otimes \mathbf{I}; \quad \text{COV}(\mathbf{a} \mathbf{m}') = \sum_{AM} \otimes \mathbf{A}; \\ \text{COV}(\mathbf{a} \mathbf{c}') = 0; \quad \text{and} \quad \text{COV}(\mathbf{m} \mathbf{c}') = 0.$$

In the situation of uncorrelated random effects  $\mathbf{G}$  is block-diagonal while in the case of correlations amongst random effects,  $\mathbf{G}$  is the direct product of a matrix of parameters and a matrix of correlations between levels of random effects. Assuming that traits are ordered within animals and error covariances are zero for traits measured on different animals,

$$\mathbf{R} = \sum_{i=1}^N {}^+ \mathbf{R}_i$$

where  $N$  is the number of animals with records, and  $\sum^+$  denotes the direct matrix sum. Only a brief description of models has been presented in this chapter, and further details on various models are given in Meyer (1991).

### 4.1.3 The likelihood

REML estimation of variance components utilizes linear combinations of the data vector  $\mathbf{y}$  instead of using the data vector itself. These linear combinations of  $\mathbf{y}$  have expectations of zero and are independent of fixed effects.

The log likelihood is then (Harville, 1977):

$$\log L = \frac{1}{2} \left[ \text{const} + \log |\mathbf{V}| + \log |\mathbf{X}' \mathbf{V}^{-1} \mathbf{X}| + (\mathbf{y} - \mathbf{X}\hat{\mathbf{b}})' \mathbf{V}^{-1} (\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}) \right] \quad (3)$$

This likelihood can be rewritten as (Searle et al., 1992):

$$-2 \log L = \text{const} + \log |\mathbf{R}| + \log |\mathbf{G}| + \log |\mathbf{C}| + \mathbf{y}' \mathbf{P} \mathbf{y} \quad (4)$$

where  $\mathbf{C}$  denotes the coefficient matrix in MME (2), and  $\mathbf{P}$  is a matrix:

$$\mathbf{P} = \mathbf{V}^{-1} - \mathbf{V}^{-1} \mathbf{X} (\mathbf{X}' \mathbf{V}^{-1} \mathbf{X})^{-1} \mathbf{X}' \mathbf{V}^{-1} \quad (5)$$

The first two components of  $\log L$  can be evaluated indirectly, requiring only the log determinant of the  $t$  by  $t$  matrix of random effect while calculation of  $\log |\mathbf{C}|$  and  $\mathbf{y}' \mathbf{P} \mathbf{y}$  is computationally more demanding and requires factorisation of the coefficient matrix of MME (2) (Meyer, 1991).

#### 4.1.4 Gaussian elimination

For given values of other variance components, the error variance can be obtained from the residual sums of squares (Graser et al., 1987):

$$\hat{\sigma}_e^2 = \frac{\mathbf{y}' \mathbf{P} \mathbf{y}}{N - N_f} \quad (6)$$

where  $\mathbf{y}' \mathbf{P} \mathbf{y}$  can be computed directly through absorption with backward substitution.

Consider the following array:

$$\mathbf{M} = \begin{bmatrix} \mathbf{y}' \mathbf{R}^{-1} \mathbf{y} & \mathbf{y}' \mathbf{R}^{-1} \mathbf{X} & \mathbf{y}' \mathbf{R}^{-1} \mathbf{Z} \\ \mathbf{X}' \mathbf{R}^{-1} \mathbf{y} & \mathbf{X}' \mathbf{R}^{-1} \mathbf{X} & \mathbf{X}' \mathbf{R}^{-1} \mathbf{Z} \\ \mathbf{Z}' \mathbf{R}^{-1} \mathbf{y} & \mathbf{Z}' \mathbf{R}^{-1} \mathbf{X} & \mathbf{Z}' \mathbf{R}^{-1} \mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix} \quad (7)$$

Absorption of rows and columns pertaining to random effects into the rest of the equations leads to:

$$\begin{bmatrix} \mathbf{y}' \mathbf{V}^{-1} \mathbf{y} & \mathbf{y}' \mathbf{V}^{-1} \mathbf{X} \\ \mathbf{X}' \mathbf{V}^{-1} \mathbf{y} & \mathbf{X}' \mathbf{V}^{-1} \mathbf{X} \end{bmatrix} \quad (8)$$

and further absorption of rows and columns pertaining to fixed effects, leads to  $\mathbf{y}' \mathbf{P} \mathbf{y}$ . Absorption is carried out using Gaussian elimination as described by Smith and Graser (1986).



This also allows calculation of  $\log|C|$  which is the sum of the log of pivots obtained during Gaussian elimination (Graser et al, 1987).

Since  $\hat{\sigma}_e^2$  is obtained for a fixed  $r = \hat{\sigma}_a^2 / \hat{\sigma}_e^2$ , the log likelihood can be obtained and knowing  $\hat{\sigma}_e^2$  and  $\hat{r}$ ,  $\hat{\sigma}_a^2$  is obtained through:  $\hat{\sigma}_a^2 = \hat{r} * \hat{\sigma}_e^2$ .

In practical applications, rather than calculating  $r$  for the whole parameter space, Graser et al. (1987) suggested fitting three initial values of  $r$  to evaluate the likelihood function for each chosen  $r$  and then to fit a quadratic approximation through these three values of  $r$  to predict a new value for  $r$ . While quadratic approximation performed best for one-dimensional search, it appeared to be unsuitable as a general search procedure in the situation of multiple parameters (Meyer, 1989). When the likelihood is maximized with respect to multiple parameters, Meyer (1989) suggested using other search procedures and possibilities are the Simplex method due to Nelder and Mead (1965) and Powell's Method of Conjugate directions (Powell, 1965).

#### 4.1.5 Average information

Johnson and Thompson (1994) showed that by averaging the observed and expected second derivatives, the trace term is cancelled out which simplifies computation.

The first derivative of (3) is (Harville, 1977):

$$\frac{\delta \log L}{\delta \theta_i} = tr\left(\frac{\delta V}{\delta \theta_i} \mathbf{P}\right) - \mathbf{y}' \mathbf{P} \frac{\delta V}{\delta \theta_i} \mathbf{P} \mathbf{y} \quad (9)$$

with  $\theta_i$  being the vector of parameters.

The second derivatives are derived as (Harville, 1977):

$$\frac{\delta^2 \log L}{\delta \theta_i \delta \theta_j} = -\frac{1}{2} tr\left[\mathbf{P} \frac{\delta^2 \mathbf{V}}{\delta \theta_i \delta \theta_j} - \mathbf{P} \frac{\delta \mathbf{V}}{\delta \theta_i} \mathbf{P} \frac{\delta \mathbf{V}}{\delta \theta_j}\right] + \frac{1}{2} \mathbf{y}' \mathbf{P} \left[\frac{\delta^2 \mathbf{V}}{\delta \theta_i \delta \theta_j} - 2 \frac{\delta \mathbf{V}}{\delta \theta_i} \mathbf{P} \frac{\delta \mathbf{V}}{\delta \theta_j}\right] \mathbf{P} \mathbf{y} \quad (10)$$

The expected value of the second derivative is then (Harville, 1977):

$$E\left[\frac{\delta^2 \log L}{\delta \theta_i \delta \theta_j}\right] = -\frac{1}{2} tr\left(\mathbf{P} \frac{\delta \mathbf{V}}{\delta \theta_i} \mathbf{P} \frac{\delta \mathbf{V}}{\delta \theta_j}\right) \quad (11)$$

For  $\mathbf{V}$  being a linear function of  $\theta_i$ , the average of observed (10) and expected (11) is then (Johnson and Thompson, 1994):

$$\frac{1}{2} \left( \frac{\delta^2 \log L}{\delta \theta_i \delta \theta_j} + E \left[ \frac{\delta^2 \log L}{\delta \theta_i \delta \theta_j} \right] \right) = \frac{1}{2} \mathbf{y}' \mathbf{P} \frac{\delta \mathbf{V}}{\delta \theta_i} \mathbf{P} \frac{\delta \mathbf{V}}{\delta \theta_j} \mathbf{P} \mathbf{y} \quad (12)$$

By applying a sparse inversion method of Takahashi et al. (1973), Johnson and Thompson (1994) for the univariate case and Madsen et al. (1994) for the multivariate case, expressions of first derivatives of (3) as outlined in (9) require selected elements of  $\mathbf{C}^{-1}$ . In contrast, Meyer (1996) used first derivatives of (4), which are derived as:

$$\frac{\delta \log L}{\delta \theta_i} = -\frac{1}{2} \left[ \frac{\delta \log |\mathbf{R}|}{\delta \theta_i} + \frac{\delta \log |\mathbf{G}|}{\delta \theta_i} + \frac{\delta \log |\mathbf{C}|}{\delta \theta_i} + \frac{\delta \mathbf{y}' \mathbf{P} \mathbf{y}}{\delta \theta_i} \right] \quad (13)$$

Calculation of  $\frac{\delta \log |\mathbf{R}|}{\delta \theta_i}$  and  $\frac{\delta \log |\mathbf{G}|}{\delta \theta_i}$  is not computationally demanding and can be determined indirectly (Meyer, 1996), while first derivatives of  $\log |\mathbf{C}|$  and  $\mathbf{y}' \mathbf{P} \mathbf{y}$  are obtained implementing Cholesky factorisation as initially outlined by Smith (1995) and further extended to the Cholesky factorisation of  $\mathbf{M}$  (7) by Meyer and Smith (1996).

#### 4.1.6 Sampling variances

The inverse of the information matrix is an approximate matrix of sample covariances among estimated variance components. Furthermore this matrix can be approximated through the inverse of the Hessian matrix, the matrix of second derivatives with respect to the parameters to be estimated. This approximation of the Hessian matrix is provided through quadratic approximation as proposed by Graser et al. (1987).

Consider the quadratic equation:

$$\mathbf{L}(\mathbf{t}) = \mathbf{q}_0 + \mathbf{q}_1' \mathbf{t} + \mathbf{t}' \mathbf{Q} \mathbf{t} \quad (14)$$

with  $\mathbf{t}$  denoting the vector of parameters with respect to which  $\mathbf{L}$  is to be maximised and  $\mathbf{Q}$  is a symmetric matrix with  $\mathbf{q}_0$ ,  $\mathbf{q}_1$  and  $\mathbf{Q}$  unknown. In the situation of a model including the animal genetic effect and the residual as the only random effects,  $\mathbf{Q}$  was obtained through quadratic approximation as outlined in Graser et al. (1987) while models with more than two random effects require the use of the Simplex method to obtain  $\mathbf{Q}$  (Meyer, 1989). This provides an approximate (co)variance matrix for REML estimates of  $\mathbf{t}$  through the inverse of  $(-\mathbf{2Q})$ .

In the derivative free REML package approximate standard errors of heritabilities are provided while in the average information REML sampling variances of variance components are given which are derived from an approximation of the inverse of the Hessian matrix. Genetic

parameters are functions of variance components and by deriving sampling variances for these functions, approximate standard errors of genetic parameters are obtained.

Given parameter estimate  $\hat{\theta}$  with dispersion matrix  $\mathbf{V}$ , then the variance of a linear function of  $\hat{\theta}$ ,  $\mathbf{a}'\hat{\theta}$  is  $\mathbf{a}'\mathbf{V}\mathbf{a}$  and the covariance of  $\mathbf{a}'\hat{\theta}$  and  $\mathbf{b}'\hat{\theta}$  is  $\mathbf{a}'\mathbf{V}\mathbf{b}$ . For non-linear functions  $g(\hat{\theta})$  the vector  $\mathbf{a}$  is the vector of first partial derivatives  $\mathbf{g}'_j(\hat{\theta})$  (Ross, 1990).

Applying this to a function with two variables e.g. heritability gives:

$$V(f(x,y)) = V(x)\left(\frac{\delta f}{\delta x}\right)^2 + V(y)\left(\frac{\delta f}{\delta y}\right)^2 + 2 \text{COV}(xy)\left(\frac{\delta f}{\delta x} \frac{\delta f}{\delta y}\right) \quad (15)$$

In the situation of a function with three variables (e.g. a correlation), this equation is extended correspondingly.

Heritability is estimated through:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2} \quad (16)$$

Partial first derivatives of (16) are then:

$$\frac{\delta(h^2)}{\delta \sigma_a^2} = \frac{\sigma_e^2}{(\sigma_a^2 + \sigma_e^2)^2} \quad (17)$$

$$\frac{\delta(h^2)}{\delta \sigma_e^2} = \frac{-\sigma_a^2}{(\sigma_a^2 + \sigma_e^2)^2} \quad (18)$$

Using (15), sampling variance of heritability is then estimated through:

$$V(h^2) = V(\sigma_a^2)(\sigma_e^2)^2 + V(\sigma_e^2)(\sigma_a^2)^2 - 2\text{COV}(\sigma_a^2\sigma_e^2)\sigma_a^2\sigma_e^2 \quad (19)$$

with  $V(\sigma_a^2)$  and  $V(\sigma_e^2)$  and  $\text{COV}(\sigma_a^2\sigma_e^2)$  being sampling (co)variances of variance components.

A correlation is defined as:

$$r = \frac{\sigma_{12}^2}{\sqrt{\sigma_1^2\sigma_2^2}} \quad (20)$$

Partial derivatives of a correlation are:

$$\frac{\delta(r)}{\delta\sigma_{12}^2} = \frac{1}{\sqrt{\sigma_1^2 \sigma_2^2}} \quad (21)$$

$$\frac{\delta(r)}{\delta\sigma_1^2} = -\frac{1}{2} \frac{\sigma_{12}^2}{\sqrt{\sigma_1^2 \sigma_2^2} * \sigma_1^2} \quad (22)$$

$$\frac{\delta(r)}{\delta\sigma_2^2} = -\frac{1}{2} \frac{\sigma_{12}^2}{\sqrt{\sigma_1^2 \sigma_2^2} * \sigma_2^2} \quad (23)$$

Sampling variance of correlations is then estimated by:

$$\begin{aligned} V(r) = & [4(V(\sigma_{12}^2))(\sigma_1^2)^2(\sigma_2^2)^2 + (V(\sigma_1^2))(\sigma_{12}^2)^2(\sigma_2^2)^2 + (V(\sigma_2^2))(\sigma_{12}^2)^2(\sigma_1^2)^2 \\ & - 4(COV(\sigma_{12}^2 \sigma_1^2))(\sigma_{12}^2)(\sigma_1^2)(\sigma_2^2)^2 - 4(COV(\sigma_{12}^2 \sigma_2^2))(\sigma_{12}^2)(\sigma_1^2)^2(\sigma_2^2) \\ & - 4(COV(\sigma_1^2 \sigma_2^2))(\sigma_{12}^2)^2(\sigma_1^2)(\sigma_2^2)] / 4((\sigma_1^2)(\sigma_2^2))^3 \end{aligned} \quad (24)$$

with  $V(\sigma_i^2)$  denoting sampling variance of variance components.

#### 4.1.7 Conclusions

A brief overview of the historical development of variance component estimation has been presented. Estimation is based on mixed models including fixed and random effects which were described for a multitrait animal model. REML procedures are applied in this study to estimate heritabilities and genetic correlations which were described in this chapter. The main emphasis has been put on a derivative free algorithm and a newly developed average information REML which offers the possibility of obtaining standard errors for variance components. This allows the calculation of standard errors for genetic correlations. In order to automate the preparation of input files into the REML package, a front end program developed by Swan (1994) was used.

## 4.2 Models for analyses

### 4.2.1 Fixed effects

Analyses of traits are based on mixed models including random and fixed effects, which were described in Chapter 4.1.2. The fixed effect part of the model was derived using the SAS procedure PROC GLM (SAS, 1991) and relevant fixed effects for production traits as well as the corresponding proportion of variation explained by these effects ( $R^2$ ) are presented in Table 4-1. Fixed effects include week of performance recording, breed of the animal and parity number of the litter the animal was born in. It is common to define management groups in two to three month time periods while in this analysis week of recording was used to define management group. All project animals stayed in one pen before entering the test station and were then put into one group of pens within the test station, which were the same for each week. No information was available on the pen number within the weaning and growing shed and group of pens was only recorded for the second part of the project and was therefore not available for all animals. However, by including week in the model in contrast to year-season classes these effects and their interactions were taken into account and they contribute to the percentage of variation explained by this effect. Since Duroc pigs were not included in the analysis, breed included only Large White and Landrace pigs. Breed was only significant for average daily gain recorded before pigs entered the test station (ADG1) and lifetime average daily gain (ADG3). In addition, strain within breed was analysed but was not significant for any trait. Parity number of the litter the animal originated from was significant for all three growth traits.

Weight at test entry was fitted as a linear covariable for feed intake (FDINT) and feed efficiency (FCR), explaining 18 % of the total variation for feed intake. Animals entered the test station between 18 to 20 weeks of age. The resulting range in weight at test entry was limited to three standard deviations below and above the mean (45 to 110 kg). This leads to the question whether weight of the animal at beginning of test should be fitted for average daily gain recorded in the test station (ADG2). It shows a significant effect on growth rate in the test station and some studies do fit it as a covariable for growth rate in test stations (Savoie and Minvielle, 1988). However, a fixed effect included in the model should explain environmental variation but should not account for additive genetic variation. Since animal weight and average daily gain in the test station (ADG2) are similar traits, including animal weight at test entry would lead to a reduction in additive genetic variance for growth rate from 18 to 22 weeks and weight of the animal at test entry was therefore not included in the model. This

close relationship is not existent between feed intake (FDINT) and feed conversion ratio (FCR) and the animal weight at test entry and therefore this effect was fitted as a linear covariable for these two traits.

Table 4-1 Fixed effects for production traits and total variation explained by these fixed effects ( $R^2$ ).

Trait	$R^2$	week	breed	parity	weight at test entry
ADG1	0.17	***	***	***	
ADG2	0.18	***		***	
ADG3	0.15	***	**	***	
FDINT	0.39	***			***
FCR	0.22	***			***
LEANG	0.21	***			

\*\*\*  $P < 0.1\%$ ; \*\*  $P < 1\%$ ; \*  $P < 5\%$ ;

Table 4-2 shows fixed effects for carcass traits along with percentage of variation explained by these effects. Week of performance recording and breed were fitted as fixed effects for all traits with the exception of muscle depths recorded with the Hennesy Chong machine (MD3/4). Breed was not significant for this trait. Live weight at slaughter and hot carcass weight were included as linear covariables for realtime ultrasound measurement (LFDP2, LFD3/4, LMD3/4) on the live animal and Hennesy Chong measurements in the abattoir (FDP2, FD3/4, MD3/4). These traits are mainly influenced by week of performance recording and weight of the animal, which leads to the high proportion of variation explained by the model ranging from 30 to 37 %. Live animal weight and hot carcass weight were also fitted as linear covariables for lean meat percentage predicted from measurements taken on the live animal (LEANL) and lean meat percentage based on measurements taken in the abattoir (LEAN). A further fixed effect available in the data set was parity of the sow which was fitted for weight of back leg (BLW) and ham weight (LMW). Although animals were mostly slaughtered at 22 weeks some variation remained in age at slaughter which was also fitted as a linear covariable for weight of the back leg (BLW) and ham weight (LMW). None of these covariables were significant as a quadratic covariable.

The main fixed effect influencing meat quality characteristics is date of slaughter which is equivalent to recording week since all animals were slaughtered on the same day each week (Table 4-3). This effect explains 38 and 45 % of the total variation for pH recorded 45 minutes

(pH45) and 24 hours after slaughter (pH24). It is of less importance for colour measurements (CLD, CMD), drip loss percentage (DLP) and intramuscular fat content (IMF) explaining 14 to 20 % of the phenotypic variation. Fitting this effect is an attempt to take into account differences in handling of the animals, transport, slaughter procedures and random environmental influences due to measurement equipment and operator. Although these factors were standardized as much as possible some variation remains. This includes different handling of animals by different staff. Since animals were always directly transported from the test station to the abattoir after real time ultrasound measurements had been taken, no variation in transport distance or transport time occurred. In June 1993, CO<sub>2</sub> stunning was implemented which replaced electrical stunning. In comparison to electrical stunning CO<sub>2</sub> stunning decreased the incidence of bruising but showed no effect on meat quality characteristics. Additionally, this effect is totally nested within slaughter weeks and was therefore not fitted. Meat quality traits which are taken 24 hours after slaughter are also influenced by different chilling rates which could explain the higher R<sup>2</sup> for pH24 than pH45. Finally, accuracy of equipment and operator contributes to variation between slaughter dates. pH measurements are temperature dependent and have to be calibrated each week which might explain the higher R<sup>2</sup> of slaughter date for these measurements.

Table 4-2 Fixed effects for carcass traits and total variation explained by these effects (R<sup>2</sup>)

	R <sup>2</sup>	week	breed	live animal weight	hot carcass weight	age	parity
<b>LFDP2</b>	0.35	***	***	***			
<b>LFD3/4</b>	0.37	***	**	***			
<b>LMD3/4</b>	0.31	***	***	***			
<b>FDP2</b>	0.30	***	***		***		
<b>FD3/4</b>	0.34	***	***		***		
<b>MD3/4</b>	0.37	***			***		
<b>BLW</b>	0.15	***	***			***	***
<b>LMW</b>	0.19	***	***			***	***
<b>LEAN</b>	0.22	***	***		***		
<b>LEANL</b>	0.32	***	***	***			

\*\*\* P < 0.1% ; \*\* P < 1% ; \* P < 5%

In addition to slaughter date, breed was significant for colour of *m. longissimus dorsi* (CLD), drip loss percentage (DLP) and intramuscular fat content (IMF). Intramuscular fat content was obtained through ether extraction and Near Infrared Spectroscopy and therefore method of

measurement was fitted for this trait. Weight of meat sample and hot carcass weight were fitted as linear covariables for drip loss percentage and intramuscular fat content.

Special emphasis has been put on the analysis of meat quality traits and therefore these characteristics were analysed separately for Large White and Landrace pigs. The number of animals per slaughter day for each breed was not sufficient to give a reliable estimate of the slaughter day effect. It was therefore decided to estimate this effect from a combined analysis of Large White and Landrace pigs. The solutions for the slaughter day obtained from this analysis were then used to pre-adjust meat quality traits. The pre-adjusted meat quality traits were then analysed for Large White and Landrace pigs separately.

Table 4-3 Fixed effects for meat quality traits and total variation explained by these effects ( $R^2$ )

	$R^2$	week	line	method of measurement	weight of meat sample	hot carcass weight	weight of ham
<b>Meat quality traits</b>							
<b>pH45</b>	0.38	***	*				
<b>pH24</b>	0.45	***					
<b>CLD</b>	0.18	***	***				
<b>CMD</b>	0.14	***					
<b>DLP</b>	0.18	***	***		*		
<b>IMF</b>	0.20	***	***	***		***	
<b>Manufacturing traits</b>							
<b>HAM</b>	0.33	***					
<b>HAMD</b>	0.35	***					***
<b>MID</b>	0.27	***					
<b>MIDD</b>	0.42	***	*				***

\*\*\*  $P < 0.1\%$ ; \*\*  $P < 1\%$ ; \*  $P < 5\%$

The fixed effect part of the model explained 27 to 42 % of the total variation for manufacturing traits (Table 4-3) which is mainly due to week of slaughter and processing. Differences between weeks are not so much due to different slaughter procedures but to differences in manufacturing procedure. This could include variation in pickling procedure and different amount of pickle uptaken by the ham and middle. Additionally, differences might have been introduced in tumbling time and cooking procedure, although manufacturing procedures were standardized as much as possible.



Fixed effects included in the models to analyse reproductive traits of the sow were farrowing season which was defined in three month periods, breed of the sow, farrowing unit and whether the sow was artificially inseminated or naturally mated (Table 4-4). The age at farrowing was included in the model as a linear covariable for litter size in the first and second parity while number of piglets born alive and number of pigs weaned were included as linear and quadratic covariables for litter weight at birth (LBW) and litter weight at 21 days (LW21).

Table 4-4 Fixed effects for reproductive traits of the sow and total variation explained by these effects ( $R^2$ )

	$R^2$	FS	breed	AI	FU	FA	N	Period
<b>NBA<sub>1</sub>*</b>	0.02	*	***	*	*	***		
<b>NBA<sub>2</sub></b>	0.03	***		*	***	***		
<b>NBA<sub>3</sub></b>	0.01	***			***			
<b>LBW<sub>1</sub></b>	0.43	***	***			***		
<b>LBW<sub>2</sub></b>	0.51	***	***	*		*		
<b>LBW<sub>3</sub></b>	0.44	***	***		**			
<b>ABW<sub>1</sub></b>	0.30	***		***				
<b>ABW<sub>2</sub></b>	0.45	***	***	***				
<b>ABW<sub>3</sub></b>	0.48	***	***					
<b>LW21<sub>1</sub></b>	0.26	***				***	***	***
<b>LW21<sub>2</sub></b>	0.27	***					***	***

\* Abbreviations:

NBA <sub>1,2,3</sub> :	Litter size in the first to third parity
LBW <sub>1,2,3</sub> :	Litter weight in the first to third parity
ABW <sub>1,2,3</sub> :	Average piglet weight in the first to third parity
LW21 <sub>1,2</sub> :	Litter weight at 21 days in the first and second parity
FS:	Farrowing season
AI :	Artificial insemination
FU:	Farrowing unit
N:	Number of weighed piglets for LW21 <sub>1,2</sub> (linear and quadratic covariable)
Period:	Period of time between farrowing date and weighing date of litter (linear covariable)

Only a small proportion (1 to 3 %) of the total variation could be explained by the fixed effect model for number of piglets born alive (NBA). In contrast, the fixed effect model explains 53 to 63 % of the total variation for litter birth weight (LBW) and 3 to 48 % for average piglet weight at birth (ABW). These high  $R^2$  values for these traits are mainly due to farrowing season and are caused by a change in performance recording of litter birth weight. Since October 1993, litter birth weight has been recorded three days after farrowing and therefore includes piglets that are crossfostered. Additionally, comparing least squares means of

farrowing seasons showed that litter birth weight increased by 3 kg from March 1992, but no explanation could be given for this increase which was probably caused by a change in recording procedure. These changes in recording procedure could help explain the high  $R^2$  values for these traits.

Fixed effects for 21-day litter weight (LW21) include farrowing season and farrowing unit. Number of piglets weighed was included as a linear and quadratic covariable and includes the sow's own piglets as well as piglets that were crossfostered from other sows. Additionally, time period from farrowing to weighing was fitted as a linear covariable. 21 day litter weight was recorded between 17 and 23 days after farrowing with a mean of 19.3 days.

Further information that was available for each litter was breed of service sire. However, this factor as well as interaction of breed of service sire and breed of sow was not significant and therefore not included in the model. Additionally, litter size the sow was born and weaned in was analysed finding a significant effect of litter size the sow was weaned in on reproductive performance of the sow. However, this information was only available for a proportion of sows and was therefore not included in the model in order not to lose too many records.

#### 4.2.2 Random effects

Possible random effects that could be included in the model comprise the additive genetic effects, litter effects and maternal effects. Different models are summarized in Table 4-5 along with a description of the covariance structure. The significance of these effects can be tested with a likelihood ratio test. Minus twice the difference in the two log likelihoods has to be compared with a Chi-Square distribution with degrees of freedom equal to the number of parameters tested. Higher values of the log likelihood represent a model of higher complexity. In the situation of only fitting one additional parameter at a time, minus twice the difference in log likelihood values has to be compared with tabulated Chi-Square values of 3.84 for  $P < 0.05$ , 6.63 for  $P < 0.01$  and 10.84 for  $P < 0.001$ .

The log likelihood values for model one and minus twice the deviation in log likelihoods for different models are presented in Table 4-6 for production traits. Large White (LW) and Landrace (LR) showed different significance in random effects for production traits and therefore results from the log likelihood ratio test are shown for the two breeds separately as well as for the pooled data set. Litter effects are significant for average daily gain before pigs entered the test station (ADG1), lifetime average daily gain (ADG3) and lean tissue growth

rate (LEANG) for Large White while no significant effect of litter was found for Landrace pigs. During the growth period before the test station, pigs from each litter remained in the same pen while pigs were single penned in the boar test station, which could explain the non significant influence of litter effects on average daily gain recorded during test station period for the two individual breeds. However, litter effects are significant for all three growth rates for the pooled data set.

Table 4-5 Description of random part of model and covariance structures for models tested

Model	Random effects (apart from residuals)	(Co)variance structure <sup>1</sup>
1	additive genetic effect,	$\sum_A \otimes \mathbf{A}$
2	additive genetic effect, litter effect	$\sum_A \otimes \mathbf{A}, \sum_C \otimes \mathbf{I}$
3	additive genetic effect, maternal genetic effect	$\sum_A \otimes \mathbf{A}, \sum_M \otimes \mathbf{A}$
4	additive genetic effect, litter effect, maternal genetic effect	$\sum_A \otimes \mathbf{A}, \sum_C \otimes \mathbf{I}, \sum_M \otimes \mathbf{A}$

<sup>1</sup>Explanation of symbols:

- $\sum_A$  additive genetic (co)variance matrix
- $\sum_C$  litter effect (co)variance matrix
- $\sum_M$  maternal genetic (co)variance matrix
- $\otimes$  "Kronecker" product
- $\mathbf{I}$  Identity matrix
- $\mathbf{A}$  Numerator relationship matrix

The analysis of maternal effects for growth characteristics indicated a significant influence of maternal genetic effects for average daily gain before pigs entered the test station and lifetime average daily gain for Large White pigs and for the pooled data set. However, the increase in log likelihood values is smaller for fitting maternal effects than for including litter effects as an additional random effect. In addition, fitting both litter and maternal genetic effects does not lead to a significant increase in the log likelihood value in comparison to fitting litter effect alone. This is also reflected through estimates of maternal genetic effects which were not significantly different from zero when both random effects, litter and maternal genetic effects, were fitted at the same time. Therefore, model two including additive genetic effects and litter effects was fitted for growth traits and lean meat growth.

No significant influence of litter effects or maternal genetic effects was found for daily feed intake (FDINT) for Large White and Landrace pigs and subsequently for the pooled data set. Therefore model one, including only additive genetic effects was fitted for this trait for all data sets.

Table 4-6 Log likelihood (Log L) for model one and twice the deviation in log likelihood ( $-2 \Delta L$ ) for model two, model three and model four for production traits.

Trait/ Breed	Log L model 1	$-2 \Delta L$ (model 2)	P	$-2 \Delta L$ (model 3)	P	$-2 \Delta L$ (model 4)	P
<b>ADG1</b>							
LW	-7662.7	25.6	< 0.001	9.6	< 0.01	25.6	< 0.001
LR	-6401.8	3.6	> 0.05	0.8	> 0.05	3.6	> 0.05
pooled	-14558.0	29.6	< 0.001	8.2	< 0.01	29.8	< 0.001
<b>ADG2</b>							
LW	-9392.2	3.6	> 0.05	1.4	> 0.05	3.6	> 0.05
LR	-7839.4	2.1	> 0.05	0.5	> 0.05	2.1	> 0.05
pooled	-17835.1	9.2	< 0.01	2.8	> 0.05	9.2	< 0.01
<b>ADG3</b>							
LW	-7766.5	21.4	< 0.001	7.2	< 0.01	21.4	< 0.001
LR	-6513.3	1.2	> 0.05	1.1	> 0.05	1.2	> 0.05
pooled	-14770.6	23.0	< 0.001	12.6	< 0.001	23.6	< 0.001
<b>FDINT</b>							
LW	612.6	0.2	> 0.05	0.0	> 0.05	0.2	> 0.05
LR	598.1	1.0	> 0.05	0.0	> 0.05	1.0	> 0.05
pooled	1364.2	1.4	> 0.05	0.06	> 0.05	1.4	> 0.05
<b>FCR</b>							
LW	135.6	14.4	< 0.001	14.6	< 0.001	14.6	< 0.001
LR	123.9	0.0	> 0.05	0.2	> 0.05	0.2	> 0.05
pooled	285.2	13.2	< 0.001	8.2	< 0.001	13.2	< 0.001
<b>LEANG</b>							
LW	-4549.0	10.6	> 0.001	1.0	> 0.05	10.6	< 0.001
LR	-3955.0	0.2	< 0.05	1.6	> 0.05	1.6	> 0.05
pooled	-8877.0	13.0	< 0.001	0.8	> 0.05	12.8	< 0.001

The influence of additional random effects on feed conversion ratio (FCR) was quite different for the two breeds. While no influence of litter and maternal genetic effects on feed efficiency was found for Landrace pigs, Large White pigs showed a significant influence of litter and maternal genetic effects on feed efficiency, which was also reflected in the pooled data set. This influence of litter effects and maternal genetic effects on feed efficiency for Large White pigs is somewhat unexpected since both components of these trait, average daily gain in the boar test station and feed intake, are not significantly influenced by these random effects in

Large White. Further possible explanations for this phenomenon will be discussed in Chapter 5.1 when estimates of heritabilities and variance components are presented. Considering this, it was decided to fit model one for the pooled data set.

The analysis of random effects for carcass traits showed that litter effects and maternal genetic effects are not significant for fat depth and muscle depth measurements taken by realtime ultrasound or Hennesy Chong equipment (LFDP2, LFD3/4, LMD3/4, FDP2, FD3/4, MD3/4) (Table 4-7). Since muscle depth recorded with the Hennesy Chong machine (MD3/4) showed a low heritability (see Chapter 5.1), variation due to additive genetic effects and litter effects could not be distinguished for muscle depth recorded with the Hennesy Chong machine and therefore model one was used to analyse this trait. Analyses of random effects for carcass traits showed no significant difference for the two breeds and are therefore not separately presented for each breed.

Table 4-7 Log likelihood (Log L) for model one and twice the deviation in log likelihood ( $-2 \Delta L$ ) for model two and model three for carcass traits

Trait	Log L model 1	$-2 \Delta L$ for model 2	P	$-2 \Delta L$ for model 3	P
<b>LFDP2</b>	-3828.4	1.2	> 0.05	0.00	> 0.05
<b>LFD3/4</b>	-3787.6	1.6	> 0.05	0.2	> 0.05
<b>LMD3/4</b>	-5302.8	2.4	> 0.05	0.12	> 0.05
<b>FDP2</b>	-3312.6	-2.0	> 0.05	0.00	> 0.05
<b>FD3/4</b>	-1913.3	0.0	> 0.05	0.00	> 0.05
<b>MD3/4</b>	-3425.2	6.2	< 0.01	4.6	< 0.01
<b>BLW</b>	-1685.1	19.0	< 0.001	10.4	< 0.001
<b>LMW</b>	-312.7	16.0	< 0.001	2.48	> 0.05
<b>LEAN</b>	-3362.5	0.0	> 0.05	0.00	> 0.05
<b>LEANL</b>	-3460.8	1.4	> 0.05	0.00	> 0.05

Weight measurements of the whole back leg and the slash boned ham are positively related to a high growth rate and the significant litter effect is therefore expected and was fitted in the model to analyse these traits. Fitting a maternal genetic effect was of lower importance and fitting both maternal and litter effects did not significantly increase the log likelihood value.

The log likelihood for model one and twice the difference in log likelihood due to including additional random effects are presented for meat quality and manufacturing characteristics in

Table 4-8. Both the litter effect and maternal genetic effects are not significant for meat quality and manufacturing characteristics and were therefore not included in the model. Separate analyses of random effects for Large White and Landrace pigs showed similar results and were therefore not listed in Table 4-1.

Table 4-8 Log likelihood (Log L) for model one and twice the deviation in log likelihood ( $-2 \Delta L$ ) for model two and model three for meat quality and manufacturing traits.

Trait	Log L model 1	$-2 \Delta L$ (model 2)	P	$-2 \Delta L$ (model 3)	P
<b>Meat quality traits</b>					
<b>pH45</b>	916.3	0.0	> 0.05	1.2	> 0.05
<b>pH24</b>	2466.5	0.4	> 0.05	2.6	> 0.05
<b>CLD</b>	-4949.1	0.4	> 0.05	1.8	> 0.05
<b>CMD</b>	-4483.0	0.8	> 0.05	0.2	> 0.05
<b>DLP</b>	-2820.7	2.8	> 0.05	3.6	> 0.05
<b>IMF</b>	-19.3	0.2	> 0.05	0.4	> 0.05
<b>Manufacturing traits</b>					
<b>HAM</b>	-1014.59	0.02	> 0.05	1.36	> 0.05
<b>HAMD</b>	859.57	0.34	> 0.05	1.30	> 0.05
<b>MID</b>	-1041.50	0.02	> 0.05	0.00	> 0.05
<b>MIDD</b>	492.15	0.04	> 0.05	0.04	> 0.05

Since only 19 % of all sows with records had at least one full sister available in the data set, no litter effect was fitted and therefore only maternal effects were analysed as an additional random effect for reproductive traits of the sow (Table 4-9). Generally, maternal effects were not significant for reproductive traits of the sow and were therefore not fitted in the model. However, differences in log likelihood values are higher for reproductive traits of the first and second parity indicating that maternal effects are of higher importance for these parities than for later parities. This is in agreement with Southwood and Kennedy (1990) who found a significant effect of maternal genetic effects on number born alive in the first parity. This was obtained from a data set including 20000 litters and the current data set might not allow reliable simultaneous estimation of additive genetic and maternal genetic effects.

Table 4-9 Log likelihood (Log L) for model one and twice the deviation in log likelihood ( $-2 \Delta L$ ) for model three for reproductive traits of the sow

Trait	Log L for model 1	$-2 \Delta L$ for model 3	P
NBA <sub>1</sub> *	-8039.3	3.4	> 0.05
NBA <sub>2</sub>	-5498.6	1.6	> 0.05
NBA <sub>3</sub>	-3934.7	0.2	> 0.05
LBW <sub>1</sub>	-3435.5	0.0	> 0.05
LBW <sub>2</sub>	-3254.5	3.8	> 0.05
LBW <sub>3</sub>	-2066.8	0.6	> 0.05
ABW <sub>1</sub>	-26647.1	1.4	> 0.05
ABW <sub>2</sub>	-12605.2	3.2	> 0.05
ABW <sub>3</sub>	-7400.3	0.0	> 0.05
LW21 <sub>1</sub>	-3030.2	0.0	> 0.05
LW21 <sub>2</sub>	-1672.1	0.0	> 0.05

### 4.2.3 Conclusions

This chapter presents relevant fixed and random effects fitted for all traits included in the analysis. Fixed effects included recording week equivalent to slaughter day for meat quality traits, breed, parity as well as method of measurement for intramuscular fat content. Weight at test entry, live animal weight before slaughter and hot carcass weight were fitted as linear covariables for some production and carcass traits. Age of the animal was included in the model for the carcass traits back leg weight and ham weight.

Fixed effects for reproductive traits of the sow included farrowing season, breed, artificial insemination and farrowing unit. The model for 21 day litter weight also included period of time between farrowing and weighing as a linear covariable, and number of weighed piglets as a linear and quadratic covariable.

Random effects were tested with a log likelihood ratio test. In addition to additive genetic effects, litter effects were fitted for growth rate traits, lean meat growth and the two carcass traits weight of the back leg and ham weight.