CHAPTER 5

Results and discussion

5.1 Results from univariate analyses

5.1.1 Introduction

The possibility for genetic improvement in a trait is determined by its heritability. From a breeder's point of view a heritability of one would be optimal, since all differences between animals would be due to genetic causes. However, a heritability of one is not realistic and estimates of heritabilities differ between traits. Generally, carcase traits are highly heritable with estimates around 0.50 while growth traits have heritabilities of approximately 0.30 (see Table 2-19). This has led to annual phenotypic improvements of one percent for growth rate and of two percent for backfat as summarized by de Vries and Kanis (1993) for the last 10 to 20 years. This selection has brought the average backfat depth down to 12 mm (de Vries and Kanis, 1993). Therefore, further reduction might not be beneficial especially when it leads to inferior meat quality. Studies from North America and Europe show average heritabilities of 0.20 for meat quality traits (Table 2-19). For Australia, however, heritability estimates are only available from Klassen (1992) who analysed backfat and growth rate for a number of herds. Heritabilities for meat quality traits and additional production and carcase traits, feed efficiency and lean meat percentage are unknown.

This chapter presents heritabilities and variance components for production, carcase, meat quality and manufacturing traits. Special emphasis has been put on simultaneous estimation of additive genetic effects and litter effects for production traits and differences in heritabilities of these traits between the two breeds, Large White and Landrace. In addition, the influence of the halothane gene on estimates of heritabilities for meat quality traits is discussed.

5.1.2 Growth performance and feed conversion ratio

Results from univariate analyses of growth performance traits, feed intake and feed conversion ratio are presented in Table 5-1. Estimates of heritabilities, litter effects and variance components are presented for Large White and Landrace pigs separately as well as for the combined data set. Estimated heritabilities in the Large White population are low with values of 0.10, 0.11 and 0.10 for average daily gain measurements (ADG1, ADG2, ADG3) while litter effects are of higher magnitude with estimates being 0.20, 0.07 and 0.18 for the three growth traits. In contrast, litter effects are not significant for Landrace while this breed has high heritabilities for average daily gain before the test station (ADG1) and life time average daily gain (ADG3) with values of 0.57 and 0.55 respectively. Average daily gain recorded in the test station (ADG2) has a lower heritability of 0.23. Estimates for the combined data set are intermediate with heritabilities being 0.27 for average daily gain in the test period between three and 18 weeks (ADG1) and lifetime average daily gain (ADG3), and a heritability estimate of 0.12 for average daily gain recorded in the test station (ADG2). Litter effects range from 0.08 to 0.15 for these traits.

The weighted means of heritabilities presented in the literature for growth rates, which originated from either field data or test station data, were 0.23 (Table 2-3) and 0.35 (Table 2-19), while litter effects were 0.26 on average for field and test station data. Heritability estimates obtained for the two breeds are therefore lower for Large White and higher for Landrace in comparison to these means. Estimates of litter effects are higher than the mean literature value for Large White and lower for Landrace. However, both parameters, heritabilities and litter effects, are within the range of parameter estimates found in the literature (Table 2-3).

Differences in heritability estimates for Large White and Landrace

The design of this project guaranteed a similar data structure for both breeds in regard to piglets per litter and management system. This excludes systematic effects as a possible reason for these differences in heritabilities and litter effects. Another explanation for these results might be different levels of inbreeding for the two breeds, since additive genetic variation declines with increasing inbreeding levels (van der Werf and de Boer, 1990). However, inbreeding coefficients based on three generations in the data set are zero for both breeds, giving no explanation for differences in heritabilities. The Landrace strain at Bunge has been established recently in comparison to Large White. The development of this breed started in 1991 with 67 sows farrowing in that year. The number of sows farrowing increased to 461 in 1992 and to 821 in 1993 (see Table 3-4) when the final sow number of this breed was reached.

Large White could be a more homogenous breed than Landrace and non-additive effects might be a possible explanation for the increased heritability in Landrace pigs. Results from Klassen (1992), who analysed life time average daily gain for a number of Australian herds, confirm higher heritabilities for Australian Landrace. Klassen (1992) who did not fit litter effect as an additional random effect, found heritabilities ranging from 0.23 to 0.40 for Large White and from 0.32 to 0.61 for Landrace data sets with considerable variation in heritabilities between herds.

It is also possible that the size or structure of data sets in this study does not allow a reliable simultaneous estimation of additive genetic effects and litter effects. To analyse the effect of size of the data set on estimated parameters, data subsets were used which included data until a certain recording date. These dates were defined in six month steps and heritability and litter effect estimates are presented in Appendix 4 for these data subsets. For both breeds, genetic parameters did not change significantly by adding more data once the data set reached approximately 1000 animals. This was achieved by June 1994 for both breeds indicating that further data collection would lead to a decrease in standard errors for genetic parameters but would not greatly influence the estimates themselves.

The structure of the data set is based on a random choice of two male piglets per litter. However, to obtain enough piglets for the project this policy was changed in the later part of the project when more than two male piglets were randomly chosen per litter. The frequencies of different litter sizes in the data set that have growth performance records available is presented in Table 5-2. The structure of the data set is not different for the two breeds and 14 % of Large White pigs and 16 % of Landrace pigs have no littermates recorded while the majority of pigs have one littermate in this data set (55 % of Large White pigs and 52 % of Landrace pigs). To better separate additive genetic effects and litter effects, pigs with no littermates available were removed and results from this analysis are presented in Table 5-3. Using model one, which does not include litter effects, heritabilities for Large White are 0.39 for average daily gain before the test station (ADG1) and 0.35 for lifetime average daily gain (ADG3) for the reduced data set in comparison to estimates of 0.27 and 0.26 for the complete data set (Table 5-1). Fitting a model including both additive genetic and litter effects (model 2) allows additive genetic variation to be divided into these two random effects. This results in estimates of 0.17 for heritability and 0.16 for litter effects (ADG1) and 0.14 for heritability and 0.16 for litter effects (ADG3) for the reduced data set (Table 5-3). In the full data set heritabilities are 0.10 for both growth characteristics with litter effects being slightly higher ranging from 0.07 to 0.20 (Table 5-1).

Meyer and Hill (1992) stated that parameters are correlated in models with multiple parameters implying that change in one parameter will lead to a corresponding change in the other parameter. Sampling correlations between parameters are therefore often largely negative and in the situation of variance components estimation, a considerable cross-substitution between parameters is possible before a significant change in the log likelihood occurs.

Sampling correlations did not change significantly after the data set reached a size of approximately 1000 animals (June 1994) in both breeds (Appendix 4.). However, for Large White the sampling correlation between heritability and litter effect estimates is -0.43 for the total data set while it increases in magnitude (-0.54) for the reduced data set. The higher sampling correlation implies that cross-substitution between the two parameters is larger in the reduced data set. This helps to explain the change in genetic parameters for the reduced data set in comparison to the full data set. For example, by not fitting litter effect a larger part of the variation due to litter effect is picked up by the additive genetic variance. These results are in agreement with results from a simulation study by Meyer and Hill (1992) who found that the sampling correlation does not appear to be dependent on the number of sire families but is affected by their structure.

Results from this data set were compared with estimates of heritability and litter effects obtained for lifetime average daily gain from the total data set of the Bunge herd recording system used in PIGBLUP (Long et al., 1992). It includes all Large White boars that have been tested since 1990. The data set contains 16,000 records and information from all male littermates is available. Estimates of heritabilities and litter effects for life time average daily gain obtained from this data set are 0.19 and 0.13 respectively. This is closer to the estimates obtained from the reduced data set, indicating that additive genetic effects and litter effects are jointly more accurately estimated in Large White by discarding pigs that have no litter mates available. In Landrace however, litter effects are not significant and estimates of genetic parameters are not significantly influenced by the structure of the data set. This is further emphasized by no significant change in sampling correlations for the two data sets.

Heritability estimates are lower for average daily gain recorded in the test station (ADG2), ranging from 0.11 to 0.23 across data sets and across models. Litter effects have values of 0.06 to 0.08. The raw standard deviation for average daily gain recorded in the test station shown in Table 3-3 is twice as high as values presented in the literature (van Steenbergen et al., 1990; de Vries et al., 1994b). This increase in raw phenotypic variation results in higher estimates of variance components. However, environmental variation has the biggest proportional increase thus leading to a decrease in heritability estimates.

Table 5-1 Heritabilities (h^2), litter effects (c^2) both with standard errors (s.e.) and variance components for production traits from univariate analyses (full data set)

Data set/ (N)	Trait/ model	h^2	s.e. of h^2	c^2	s.e. of c^2	σ^2_a	σ^2_c	σ^2_e	σ^2_p
	ADG1								
LW	model 1	0.27	0.08			1055		2903	3959
(1752)	model 2 *	0.10	0.05	0.20	0.04	403	778	2739	3921
LR	model 1 *	0.57	0.08			2619		1949	4569
(1475)	model 2	0.48	0.09	0.08	0.04	2191	357	2055	4604
combined	model 1	0.43	0.06			1857		2449	4307
(3227)	model 2 *	0.27	0.05	0.15	0.03	1148	616	2445	4210
	ADG2								
LW	model 1 *	0.15	0.05			4352		24925	29277
(1752)	model 2	0.11	0.06	0.07	0.03	3141	1803	24043	28988
LR	model 1 *	0.23	0.07			6487		21959	28446
(1495)	model 2	0.18	0.06	0.05	0.04	5160	1631	21292	28084
combined	model 1	0.18	0.04			5421		23960	29382
(3227)	model 2 *	0.13	0.04	0.08	0.03	3648	2180	23195	29024
	ADG3								
LW	model 1	0.26	0.08			1035		2933	3968
(1770)	model 2 *	0.10	0.05	0.18	0.04	395	679	2805	3880
LR	model 1 *	0.55	0.08			2541		2065	4606
(1495)	model 2	0.49	0.11	0.04	0.04	2246	195	2128	4570
combined	model 1	0.42	0.06			1830		2532	4362
(3265)	model 2 *	0.27	0.06	0.13	0.03	1149	532	2567	4250
	FDINT								
LW	1763 *	0.19	0.05			0.027		0.120	0.147
LR	1489 *	0.32	0.08			0.042		0.089	0.131
combined	3252 *	0.23	0.04			0.030		0.110	0.140
	FCR								
LW	model 1	0.13	0.09			0.033		0.217	0.250
(1739)	model 2 *	0.03	0.04	0.14	0.04	0.008	0.036	0.205	0.249
LR	model 1 *	0.13	0.07			0.031		0.209	0.241
(1482)	model 2	0.13	0.07	0.00	0.05	0.032	0.001	0.211	0.244
combined	model 1	0.15	0.04			0.039		0.225	0.265
(3221)	model 2 *	0.08	0.04	0.11	0.03	0.022	0.028	0.214	0.264
	LEANG								
LW	model 1	0.23	0.07			208		683	891
(1250)	model 2 *	0.15	0.06	0.15	0.05	137	135	634	908
LR	model 1 *	0.68	0.10			807		382	1189
(1083)	model 2	0.64	0.13	0.02	0.05	697	20	371	1089
combined	model 1	0.38	0.06			388		626	1014
(2333)	model 2 *	0.28	0.06	0.12	0.03	274	117	595	988

* significant model according to log likelihood ratio test as described in Chapter 4.

Pigs entered the boar test station at 18 weeks of age. In the test station they were single penned in comparison to group penning before the test period. This change in housing system might influence the results. Roehe et al. (1994) estimated heritabilities for growth rate performance measured every two weeks in a test station. Although Roehe et al. (1994) described testing period as "an extended period of adjustment" and pigs were housed in groups of 15 animals, the heritability estimate was reduced for the first week of performance recording to 0.13. This indicates that pigs need to adjust to their new environment, a process which might take two weeks. However, the whole testing period in this project was only 4 weeks for most of the pigs without allowing pigs to get accustomed to the new environment. Pigs will have adapted to this environment differently, thus the random environmental variation is increased. A longer time period in the test station could overcome this problem.

Feed intake

Feed intake (FDINT) is not influenced by litter effects in all three data sets and heritabilities are 0.19 for Large White, 0.32 for Landrace and 0.23 in the combined data set (Table 5-1). The mean of literature values is 0.36 (Table 2-19) and although estimates in this study are lower they are within the range of estimates (Table 2-4). The testing procedure does not seem to have as strong an influence on this trait as it did on average daily gain recorded in the test station.

Feed conversion ratio

Estimates of heritabilities for feed conversion ratio (FCR) are 0.13 for the two individual breeds and 0.15 for the combined data set using a simple animal model with no additional random effects (Table 5-1). These estimates are lower than the literature mean (0.26) presented in Table 2-19. The testing procedure of feed intake and average daily gain in the test station is the reason for this lower heritability. Another possibility to analyse ratios which might not be normally distributed is to use the logarithm of this ratio. However, heritabilities are the same for the logarithm of feed efficiency than using feed efficiency itself.

The analysis of random effects for feed conversion ratio (FCR) indicated a significant litter effect for Large White pigs. By fitting litter effects, a substantial cross-substitution between additive genetic and litter effects occurs and a proportion of the variation that is explained by additive genetic effects in the less parameterized model is picked up by this additional random effect. For the analysis of the influence of data structure on these estimates, heritabilities and litter effects were obtained for feed conversion ratio using the reduced data set. Results from this analysis are shown in Table 5-3. Generally these results are the same as the estimates

obtained from the full data set (Table 5-1) indicating that estimates of heritabilities and litter effects for feed efficiency are not influenced by data structure.

Table 5-2 Number of pigs (N) originating from a litter size (in data set) of one to six piglets for Large White and Landrace

No. of pigs per litter in data set	Large White		Landrace	
	N	Percentage[1]	N	Percentage[1]
1	243	14	242	16
2	489	55	394	52
3	127	21	111	22
4	41	9	32	9
5 and 6	4	1	4	1

[1] percentage is derived from a within breed basis

Table 5-3 Heritabilities (h^2), litter effects (c^2) both with standard errors (s.e.) and variance components for production traits from univariate analyses (reduced data set)

Data set (N)	Trait/ model	h^2	s.e. of h^2	c^2	s.e. of c^2	σ^2_a	σ^2_c	σ^2_e	σ^2_p
	ADG1								
LW	model 1	0.39	0.10			1525		2381	3906
(1509)	model 2	0.17	0.07	0.16	0.04	670	618	2554	3843
LR	model 1	0.60	0.09			2723		1820	4544
(1233)	model 2	0.48	0.10	0.08	0.05	2173	347	2025	4545
combined	model 1	0.47	0.07			2003		2233	4237
(2687)	model 2	0.27	0.06	0.14	0.03	1039	539	2309	3888
	ADG3								
LW	model 1	0.35	0.09			1405		2621	4027
(1525)	model 2	0.14	0.06	0.16	0.04	533	636	2773	3942
LR	model 1	0.57	0.09			2701		2011	4712
(1248)	model 2	0.51	0.11	0.04	0.05	2337	193	26067	4598
combined	model 1	0.46	0.07			1987		2368	4355
(2718)	model 2	0.28	0.06	0.12	0.03	1182	512	2576	4272
	FCR								
LW	model 1	0.17	0.11			0.043		0.207	0.250
(1222)	model 2	0.04	0.05	0.14	0.04	0.009	0.034	0.203	0.247
LR	model 1	0.10	0.07			0.022		0.200	0.222
(1013)	model 2	0.10	0.08	0.00	0.05	0.022	0.000	0.200	0.222
combined	model 1	0.16	0.06			0.039		0.213	0.252
(2238)	model 2	0.06	0.04	0.11	0.03	0.014	0.026	0.209	0.250

Lean meat growth

A further composite trait is lean meat growth (LEANG) which is derived from the lean meat yield in relation to the age of the animal. Large White pigs have a low heritability of 0.15 for this trait with a litter effect of the same magnitude (model 2, Table 5-1), while heritability is high for Landrace pigs (0.68; model 1 Table 5-1). Since lean meat growth is dependent on growth rate and lean meat percentage, differences in heritabilities and litter effects for lean meat growth are a reflection of differences in growth rate between the two breeds. The literature mean was 0.41 (Table 2-19) in comparison to estimates for individual breeds which are therefore lower for Large White and higher for Landrace. Implementing model two for the combined data set yields estimates of 0.28 for the heritability and of 0.12 for litter effects, which is also lower than the mean literature heritability.

5.1.3 Carcase traits

Heritability and litter effect estimates for carcase traits are presented in Table 5-4. The first three traits included in Table 5-4 are carcase characteristics measured on the live animal with real time ultrasound (LFDP2, LFD3/4). Both backfat measurements are highly heritable with estimates of 0.68 and 0.67 for Large White. Heritabilities are somewhat lower for Landrace with values of 0.54 and 0.56. The combined data set gave intermediate estimates of heritabilities of 0.60 and 0.62 for backfat measured at P2 (LFDP2) and between the third and fourth last ribs (LFD3/4), respectively. These estimates are higher than the mean of literature values for backfat measurements of 0.43 (Table 2-19). However, many studies included litter effects in their analysis which showed an average value of 0.10. Therefore heritability estimates in the literature should be reduced due to the inclusion of this effect in comparison to this study where litter effect is not significant for these carcase traits.

Heritability estimates for the same two backfat measurements, this time recorded on the carcase with the Hennesy Chong machine (FDP2, FD3/4) are lower than estimates obtained on the live animal from real time ultrasound measurements (LFDP2, LFD3/4). Estimates are 0.57 and 0.49 for Large White and 0.34 and 0.36 for Landrace for the two backfat measurements (FDP2, FD3/4). Results from the combined data are intermediate (0.46, 0.45) and in good agreement with literature values (Table 2-19).

Muscle depth

Heritability estimates for backfat measurements are higher for real time ultrasound measurements than for Hennesy Chong recordings. Comparing heritability values of muscle

depth recorded on the live animal with realtime ultrasound equipment (LMD3/4) and muscle depth at the same location recorded via Hennesy Chong equipment on the carcase (MD3/4) confirms these results. Heritabilities range from 0.17 to 0.21 for muscle depth recorded on the live animal (LMD3/4) for the three data sets while heritabilities for muscle depth recorded with the Hennesy Chong machine (MD3/4) are lower with values varying from 0.02 to 0.04.

No estimates of heritabilities for muscle depth were found in the literature, although a few studies analysed loin eye area which will be used as a comparison here. The mean heritability estimate for loin eye was 0.51 (Table 2-19) and is therefore considerably higher than estimates obtained for both muscle depth measurements (LMD3/4, MD3/4). This difference could be due to different measurement techniques used in the listed studies (Lundeheim et al., 1980; Lo et al. 1992; Scholz and Triebler, 1992). However, only Lo et al. (1992) gave information about the measurement technique used including real time ultrasound measurements, which had a heritability of 0.46 for loin eye area (Table 2-5). It is therefore more likely that the differences in heritabilities found for muscle depth in this study and loin eye area presented in other studies are due to differences in the two traits.

Differences in heritabilities for the two muscle depth measurements are due to an increase in environmental variation for muscle depth recorded on the carcase with Hennesy Chong equipment. To explain possible reasons for this increased environmental variation due to Hennesy Chong measurements, the principle of this measurement technique needs to be explained. Measurements of fat and muscle thickness with the Hennesy Chong machine are based on optical properties of the different tissues (Fisher, 1990). A light reflectance probe is used which utilises visible light or light in the near infrared part of the spectrum. This generated light is emitted from the near tip of the probe and reflectance signals are used to determine fat and muscle tissue. The Hennesy Chong grading probe uses light in the green-yellow range (=570nm). In the case of very pale muscle tissue, this could lead to unreliable detection of boundaries between the *m. longissimus dorsi* and the underlying muscles and connective tissues (Ferguson, 1996, pers. comm.). In addition, real time ultrasound measurements were taken from the restrained standing animal while carcases were moving while measurements were taken. Differences in muscle shape of the standing animal (vertical measurement) to the muscle shape of the hanging carcase (horizontal measurements) contribute to differences in these measurements.

Table 5-4 Heritabilities (h^2) with standard errors (s.e.) and variance components for carcase traits from univariate analyses

Trait	No. of rec.s	h^2	s.e. of h^2	σ^2_a	σ^2_e	σ^2_p
	LFDP2					
LW	1756	0.68	0.07	3.27	1.52	4.80
LR	1467	0.54	0.08	2.31	1.99	4.30
pooled	3223	0.60	0.05	2.72	1.79	4.51
	LFD3/4					
LW	1749	0.67	0.07	3.27	1.58	4.85
LR	1454	0.56	0.08	2.33	1.80	4.13
pooled	3203	0.62	0.05	2.76	1.73	4.49
	LMD3/4					
LW	1592	0.17	0.07	2.48	12.19	14.67
LR	1303	0.19	0.06	2.91	12.34	15.25
pooled	2895	0.21	0.04	3.21	11.88	15.10
	FDP2					
LW	1235	0.57	0.09	4.32	3.31	7.63
LR	1068	0.34	0.08	2.31	4.51	6.82
pooled	2303	0.46	0.06	3.33	3.87	7.20
	FD3/4					
LW	730	0.49	0.10	3.48	3.66	7.15
LR	653	0.36	0.12	1.90	3.44	5.35
pooled	1383	0.45	0.07	2.88	3.46	6.34
	MD3/4					
LW	720	0.04	0.08	2.72	59.64	62.36
LR	649	0.03	0.07	1.61	56.81	58.42
pooled	1369	0.02	0.05	1.92	59.68	60.87
	BLW					
LW	1358	0.08[1]	0.05	0.097	0.913	1.199
		0.16	0.04	0.189		
LR	1204	0.46[1]	0.12	0.680	0.695	1.482
		0.07	0.05	0.106		
pooled	2562	0.22[1]	0.05	0.297	0.855	1.340
		0.14	0.03	0.188		
	LMW					
LW	1359	0.27[1]	0.08	0.107	0.244	0.396
		0.11	0.05	0.044		
LR	1204	0.59[1]	0.12	0.310	0.171	0.521
		0.08	0.05	0.041		
pooled	2563	0.38[1]	0.07	0.170	0.230	0.450
		0.13	0.03	0.060		
	LEANL					
LW	1592	0.69	0.07	3.32	1.51	4.83
LR	1303	0.59	0.08	2.61	1.85	4.47
pooled	2895	0.63	0.05	2.89	1.72	4.61
	LEAN					
LW	1235	0.57	0.09	4.52	3.47	7.99
LR	1067	0.34	0.08	2.42	4.73	7.15
pooled	2302	0.46	0.06	3.49	4.05	7.54

[1] second row represents estimate of litter effects with standard errors and estimates of variance components

Weight of the back leg and slash boned ham

Weight of the whole back leg (BLW) and lean meat weight of the back leg (LMW), which is the slash boned ham without the hock muscles, were analysed using a model which included additive genetic effects and litter effects (Table 5-4). Heritabilities for weight of the whole back leg (BLW) are 0.08 for Large White and 0.46 for Landrace with estimates of litter effects of 0.16 and 0.07. Estimates of heritabilities and litter effects are intermediate for the combined data set (h^2=0.22; c^2=0.14). Heritabilities are higher for lean meat of the whole back leg (LMW) with values of 0.27 for Large White, 0.59 for Landrace and 0.38 for the combined data set. The litter effect is of the same magnitude for lean meat weight of the back leg as for the whole back leg (Table 5-4). The mean of heritabilities presented in the literature for ham weight is 0.44 (Table 2-19) which also includes studies that analysed primary cuts of the carcase. The larger differences in heritability estimates compared to the literature mean for back leg weight are expected since this weight measurement also includes skin, bones and fat of the back leg and is therefore a different trait to ham weight which only includes the lean of the back leg.

Lean meat percentage

The prediction equation for lean meat percentage is dominated by backfat measurements and therefore results for lean meat percentage and individual backfat measurements are similar. The prediction equation based on real time ultrasound measurement (LEANL) includes both backfat measurements, muscle depth and animal weight, while lean meat percentage based on Hennesy Chong measurements (LEAN) is based on backfat at P2 and the hot carcase weight. Since backfat at P2 is the major factor in this last prediction equation, heritabilities for lean meat percentage (LEAN) and backfat at P2 measured in the abattoir are identical for these two characteristics (Table 5-4). Lean meat percentage based on real time ultrasound measurement (LEANL) showed only slightly different estimates of heritabilities than the corresponding backfat measurements taken on the live animal, with values of 0.69 for Large White, 0.57 for Landrace and 0.63 for the combined data set. Heritabilities for lean meat percentage derived from Hennesy Chong measurements (LEAN) are 0.57, 0.34 and 0.46 for Large White, Landrace and the combined data set. The mean of literature heritability estimates for lean meat percentage presented in Table 2-19 is 0.70.

5.1.4 Meat quality and manufacturing traits

Table 5-5 summarizes heritabilities and variance components for meat quality characteristics. Estimates of heritabilities are low for pH measured 45 minutes after slaughter (pH45) with

values of 0.11 for Large White, 0.16 for Landrace and 0.15 for the combined data set. These estimates are slightly lower than the mean of recent literature values of 0.20 (Table 2-19) as well as the average estimates of heritabilities as reviewed by Sellier (1988) of 0.18 and by Hovenier et al. (1993) of 0.30 for this trait (Table 2-7).

In contrast to pH45 which is an indication of pale soft and exudative (PSE) meat, pH measured 24 hours post mortem (pH24) represents a measurement of dark firm and dry (DFD) meat. Heritabilities are of the same magnitude for pH24 as for pH45 with heritability estimates of 0.09 for Large White, 0.16 for Landrace and 0.14 for the combined data set. In comparison to literature values (Table 2-19 mean $h^2 = 0.17$) heritabilities in this study are lower for pH24. In addition, genetic variances are a tenth of the magnitude of pH45, which limits the possible genetic progress in this trait.

Colour and drip loss percentage

A substantial difference in heritability estimates for the two breeds analysed was found for colour of the *m. longissimus dorsi* (CLD). Heritabilities are 0.15 for Large White and 0.35 for Landrace. The average of five recent studies shown in Table 2-19 was 0.24. The estimate of the combined data set is in closer agreement to the literature mean with a value of 0.29 than the two individual breeds. The second colour measurement which was taken from the *m. multifidus dorsi* (CMD) is moderately heritable with values of 0.24 for Large White, 0.35 for Landrace and 0.30 for the combined data set. However, variance components are of higher magnitude for colour measurement of the *m. longissimus dorsi* (CLD) than for colour of the *m. multifidus dorsi* (CMD).

Differences in heritability estimates between breeds are also apparent for drip loss percentage (DLP). Heritabilities are moderate to high with values of 0.20 for Large White and 0.47 for Landrace. Both estimates are higher than the literature mean of 0.17 (Table 2-19) and the means presented by Sellier (1988) and by Hovenier et al. (1993) of 0.12 and 0.20, respectively (Table 2-7).

To illustrate these differences in heritabilities for colour of the *m. longissimus dorsi* (CLD) and drip loss percentage (DLP), the distributions of the sire's general least squares means are presented in Figure 5-1 for colour of the *m. longissimus dorsi* and in Figure 5-2 for drip loss percentage. Besides bigger variation in general least squares means for Landrace sires in these two traits, Landrace is also characterized by a few sires with extreme general least squares means for colour and drip loss percentage. The majority of these extreme values are in the PSE

range, with a drip loss percentage higher than 4.0 % and a colour measurement higher than 55. However, Landrace pigs also exhibit a higher frequency of sires having a general least squares mean in the area of DFD meat with drip loss percentage lower than 0.5 and colour lower than 47.

A possible explanation of these differences between breeds might be different frequencies of the halothane gene, which is higher in the Landrace population (Luxford, pers. comm., 1996). Luxford (1995) examined the effect of the halothane gene on meat quality characteristics in these two breeds. The halothane gene did not influence pH45. In addition, Lundström et al. (1989) found no differences in the ultimate pH level between the three genotypes. Since these studies indicate no influence of the halothane gene on pH measurements, similar heritabilities for pH measurements in Large White and Landrace pigs found in this study are therefore as expected.

However, Luxford (1995) found an effect of the halothane gene on colour of the *m. longissimus dorsi* (CLD) and drip loss percentage (DLP). Heterozygotes were found to have a lighter colour and a higher drip loss percentage, both indications for PSE meat, when compared to non-carriers (Table 2-2). These findings are supported by McPhee and Trout (1995) who also found that the unfavourable effect of the halothane gene is of higher magnitude in a line that had been selected for lean meat growth. Since Landrace is the slightly leaner breed and has a higher incidence of the halothane gene, extreme cases of PSE meat are anticipated.

Besides a higher PSE incidence, Landrace also displayed a higher incidence of DFD meat (see Figure 5-1 and Figure 5-2). McPhee and Trout (1995) showed that other genes responsible for leanness lead to a higher degree of DFD in the case of long transport to the abattoir. In addition, their study also included pigs that were reared close to the abattoir. For these pigs, DFD meat occurred only in the line selected for leanness supporting the hypothesis that genes for higher leanness cause a higher incidence of DFD. This could explain the higher incidence of DFD meat for Landrace found in this study, since Landrace is the slightly leaner breed. However, for pigs reared close to the abattoir in the study by McPhee and Trout (1995), the incidence of DFD meat was the same for both genotypes, non-carriers and heterozygotes. Pigs carrying the halothane gene can therefore also develop DFD meat in the situation of short distances to the abattoir and mild slaughter environment. Lundström et al. (1989) stated that this incidence of DFD in halothane positive pigs in a good slaughter environment should be regarded as stress susceptible.

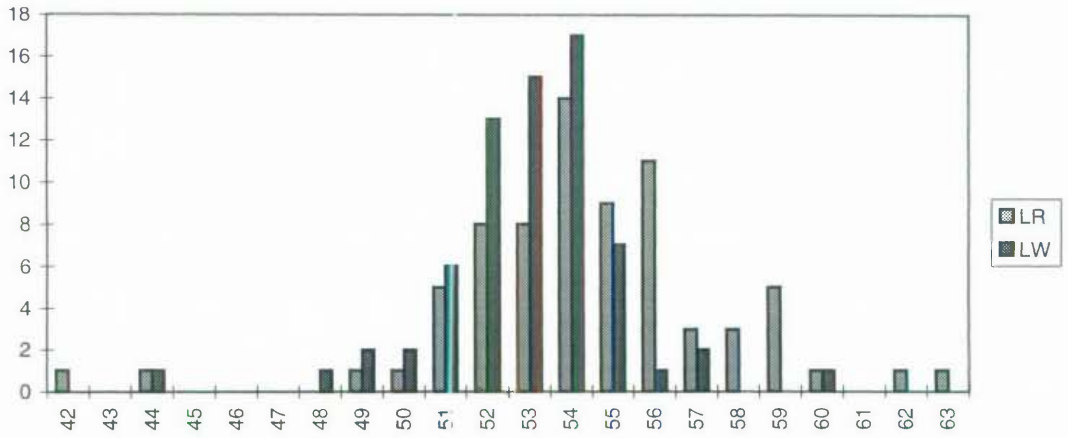

Figure 5-1 Frequencies of general least squares means of colour of the *m. longissimus dorsi* for Large White (LW) and Landrace (LR) sires

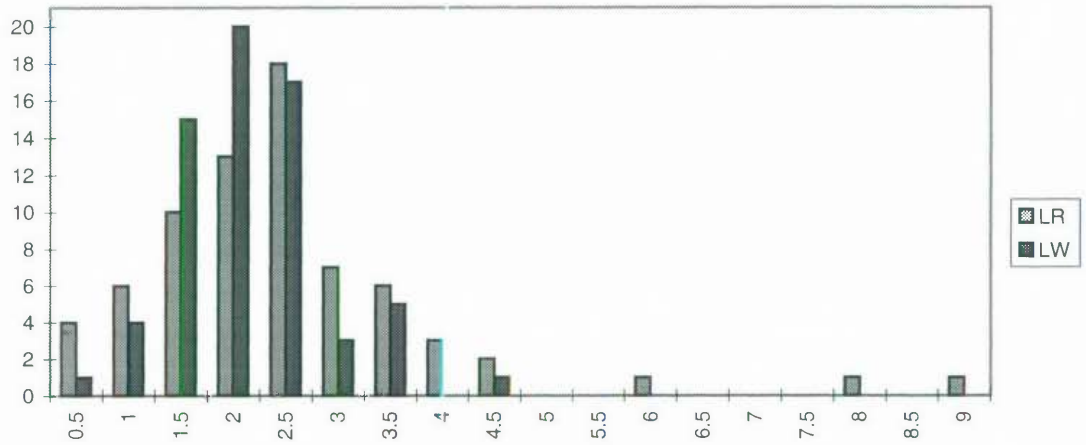

Figure 5-2 Frequencies of general least squares means of drip loss percentage for Large White (LW) and Landrace (LR) sires

Intramuscular fat content

Heritability estimates of intramuscular fat are higher (0.42) for Landrace than for Large White (0.29) while the heritability of the combined data set is intermediate with a value of 0.35. A review of the literature gave a mean heritability of 0.45 for this trait (Table 2-19) and estimates in this study are therefore lower than the literature mean. This low heritability might be due to differences in the two measurement techniques applied in this study. However, no differences are found in coefficient of variation for intramuscular fat content within measurement

techniques and variance components are not significantly different for the two techniques, despite a lower mean for the near infrared measurement of 0.15%.

Table 5-5 Heritabilities (h^2) with standard errors (s.e.) and variance components for meat quality and manufacturing traits from univariate analyses

Data set	Trait No. of rec's	h^2	s.e. of h^2	σ^2_a	σ^2_e	σ^2_p
	pH45					
LW	1188	0.11	0.04	0.02	0.12	0.14
LR	1033	0.16	0.06	0.02	0.10	0.12
pooled	2221	0.15	0.04	0.02	0.11	0.13
	pH24					
LW	1307	0.09	0.04	0.003	0.030	0.033
LR	1172	0.16	0.06	0.006	0.033	0.040
pooled	2479	0.14	0.04	0.005	0.033	0.039
	CLD					
LW	1354	0.15	0.06	2.66	14.69	17.35
LR	1181	0.35	0.08	7.39	13.80	21.19
pooled	2535	0.29	0.06	5.87	14.39	20.25
	CMD					
LW	1375	0.24	0.06	2.91	9.42	12.34
LR	1206	0.35	0.07	5.14	9.58	14.72
pooled	2581	0.30	0.05	4.22	9.63	13.85
	DLP					
LW	1441	0.20	0.07	0.64	2.62	3.26
LR	1264	0.47	0.11	2.00	2.24	4.23
pooled	2705	0.23	0.05	0.71	2.36	3.07
	IMF					
LW	1011	0.29	0.09	0.096	0.238	0.334
LR	870	0.42	0.11	0.144	0.199	0.343
pooled	1881	0.35	0.06	0.120	0.219	0.339
	Manufacturing traits					
pooled	**HAM**	0.11	0.09	0.720	5.714	6.434
pooled	**HAMD**	0.10	0.09	0.002	0.019	0.021
pooled	**MID**	0.06	0.08	0.616	9.639	10.256
pooled	**MIDD**	0.17	0.10	0.009	0.046	0.055

Manufacturing traits

Heritabilities for manufacturing traits were obtained for a subset of animals and are presented in Table 5-5. Estimates of heritabilities are low with values of 0.10 for ham yield after processing expressed as a percentage of the initial weight (HAM) and of 0.11 for ham yield defined as the difference in weight of the ham after processing to the initial weight of the ham (HAMD). Heritabilities vary more strongly between the two definitions of yield of the middle

after processing. Yield of middle after processing expressed as a percentage of weight of the middle after manufacturing to green weight of middle (MID) is lowly heritable with a value of 0.06 while yield of the middle defined as the difference in weights of middles before and after manufacturing (MIDD) has a higher heritability of 0.17. However, both yields defined as the absolute difference to the initial weight of the ham or the middle (HAMD, MIDD) have low genetic variations of 0.002 kg^2 and 0.009 kg^2 which limits genetic improvement in these traits.

No estimates of heritabilities for processed pork were found in the literature and these estimates can only be compared to similar traits. Cooking loss is one similar trait, although it is obtained from a standardized meat sample. The average literature value for cooking loss is 0.15 (Table 2-19) Another similar trait is the "Rendement Technologique Napole" (RTN). This trait is expressed as a percentage of the meat sample after pickling and cooking in relation to the original weight of 150 grams. Naveau (1986) found a heritability of 0.36 for this trait. Since the RTN is also obtained from a standardized meat sample under laboratory conditions this might explain the higher heritabilities in comparison to manufacturing traits in this study which were processed under commercial conditions from the whole ham and middle.

5.1.5 Conclusions

Heritabilities for growth rate are different for Large White and Landrace pigs. Large White pigs have low heritability estimates while litter effects are of higher importance. Heritabilities for growth rate are higher in Landrace and litter effects are not significant for this breed. The structure of the data set might not allow a reliable simultaneous estimation of additive genetic effects and litter effects.

A testing period of four weeks might be too short which is indicated in low heritability estimates for growth rate recorded in the test station and feed efficiency. Estimates of heritabilities are not reduced for feed intake.

Carcase traits are highly heritable with higher estimates for real time ultrasound measurements taken on the live animal than Hennesy Chong measurements recorded on the carcase.

Heritabilities are low for pH measurements and manufacturing traits. Colour of the *m. longissimus dorsi* and drip loss percentage are more highly heritable for Landrace than for Large White which could be due to a higher incidence of the halothane gene in this breed.

5.2 Results from bivariate analyses

5.2.1 Introduction

In the previous chapter heritability estimates were presented for all analysed traits. These heritability estimates represent the proportion of the variance that is due to additive genetic effects. However, different loci can have pleiotropic effects on a number of traits and in the hypothetical situation of infinite number of loci influencing two traits, this association is estimated through the genetic correlation. The evaluation of farm animals is based on multitrait BLUP procedures which require knowledge about genetic correlations for all analysed traits. This information is not yet available for Australian pigs and estimates of genetic correlations might differ between populations due to genetic differences or differences in management practices. Lean meat percentage and meat quality traits for example are unfavourably correlated in populations carrying the halothane gene (Cole et al, 1988) while de Vries et al. (1994b) found no unfavourable relationship between lean meat percentage and meat quality traits in a halothane free population. For Australian pigs only genetic correlation between growth rate and backfat has been estimated by Klassen (1992) for a number of herds but no information is available for further traits which are analysed in this chapter.

This chapter presents estimates of genetic, environmental and phenotypic correlations along with correlations between litter effects for production, carcase and meat quality and manufacturing traits. These results were obtained by bivariate analyses and will be compared with results from multivariate analyses in Chapter 6.3 .

5.2.2 General results

Heritabilities obtained from bivariate analyses are not significantly different from estimates obtained from univariate analyses and are therefore not presented again. Although some production and meat quality traits have different heritabilities for the two breeds only genetic correlations which are obtained from the combined data set are presented and discussed in this chapter since standard errors for genetic correlations obtained for the individual breeds generally exceeded differences in genetic correlations.

Mostly, genetic correlations are of higher magnitude than environmental correlations. Therefore, environmental correlations are not discussed explicitly. Lower environmental correlations in comparison to genetic correlations were also found by Cameron (1990b),

Hovenier et al. (1992) and de Vries et al. (1994b). De Vries et al. (1994b) explained these higher genetic correlations in comparison to environmental correlations with uncorrelated random measurement errors.

5.2.3 Growth, feed intake and feed efficiency traits

The two growth characteristics before and within the testing period (ADG1, ADG2) have a genetic correlation of 0.32 while correlations between litter effects, environmental and phenotypic correlations are not significantly different from zero (Table 5-6). Average daily gain is recorded from three to 18 weeks (ADG1), when animals are group penned, and in the final growth period from 18 to 22 weeks (ADG2) when animals are single penned. Thus, two factors might influence these low genetic and environmental correlations. Firstly, animals have a different age when these growth characteristics are measured and differences in the growth curve might result in a low relationship between these two growth rates. Secondly, animals are kept in two different housing systems which might cause a weak relationship between growth rate before the test station and growth rate recorded in the test station. The genetic relationship between animals kept in these two different housing systems, single penned and group penned, was studied by von Felde (1995). Genetic correlations between growth rate recorded in these two housing systems were 0.55 for average daily gain recorded over the testing period and 0.10 for lifetime average daily gain. These results suggest that the low genetic correlation between the two different growth characteristics before and within the test station (ADG1, ADG2) are in a large part due to different housing systems which might be enhanced in this study since no time of adjustment to the new housing system was given.

Lifetime average daily gain (ADG3) is highly correlated with average daily gain before the test station (ADG1) (r_g=0.95) and moderately correlated with growth rate recorded in the test station (ADG2) (r_g=0.65). The magnitude of these genetic correlations is partly due to the similarity of these traits, since life time average daily gain includes the other two growth rate traits. Lifetime average daily gain is based on a time period of 22 weeks and average daily gain before the test station represents 15 weeks of this time which explains the high relationships between these two traits.

Estimates of genetic correlations are positive between growth rate traits (ADG1, ADG2, ADG3) and feed intake (FDINT) ranging from 0.23 to 0.87 (Table 5-6). These relationships are confirmed by the literature mean of 0.54 for genetic correlations between growth rate and feed intake (Table 2-19). The lower genetic correlation between growth rate before the test

station (ADG1) and daily feed intake recorded in the test station (FDINT) (r_g = 0.23) might be explained by the different time periods when these two traits were recorded.

Feed conversion ratio (FCR) and feed intake (FDINT) have a low genetic correlation (r_g = 0.19). This genetic correlation is confirmed by a literature mean of 0.42 for the genetic correlation between these two traits. The analysis of genetic and environmental correlations between feed conversion ratio and average daily gain before and within the test station (ADG1, ADG2) gave different estimates. Feed conversion ratio is negatively correlated with average daily gain in the test station (r_g = -0.43) with an even stronger environmental correlation of -0.70. This estimate of genetic correlation is equivalent to the literature value which is based on seven recent studies (Table 2-19). In contrast, average daily gain before the test station (ADG1) and feed conversion ratio (FCR) are positively correlated (r_g = 0.27, r_e = 0.24). Various studies analysed the effect of live weight on feed intake and feed conversion ratio. With increasing live weight feed intake increases (Memmert, 1991; Smith et al., 1991). This results in a higher feed conversion ratio since growth rate remains at a constant level or even decreases at the later stage of the growth curve (Memmert, 1991). In this study pigs entered the boar test station at a fixed age rather than a fixed weight. Therefore, animals with a high growth rate before the test station entered the test station with a higher weight. This leads to a higher feed intake but also to a higher requirement in maintenance thus to an inferior and therefore higher feed conversion ratio. By incorporating the animal's weight at test start in the model for feed conversion ratio it was attempted to take this relationship into account but apparently this could not be achieved completely. Estimates of genetic and environmental correlations between lifetime average daily gain and feed efficiency are intermediate in comparison to correlations between the other two growth rates and feed conversion ratio and reflect the dependency of lifetime average daily gain on these two growth rates.

A further composite trait is lean meat growth (LEANG) and its relationships to other production traits are summarized in Table 5-6. No estimate could be obtained for the genetic correlation between lean meat growth and average daily gain before the test station (ADG1) an indication that the estimate is on the boundary of the parameter space (1). However, estimates were obtained for genetic correlations between lean meat growth (LEANG) and growth rate in the test station (ADG2) and life time average daily gain (ADG3) with values of 0.23 and 0.84, respectively. Estimates of genetic correlations found in the literature are strongly positive leading to a mean of 0.87 (Table 2-19). The lower genetic correlation between average daily gain recorded in the test station (ADG2) and lean meat growth can be explained by the short period of 4 weeks.

Table 5-6 Genetic correlations (first row) with standard errors (in brackets), environmental correlations (second row) and phenotypic correlations for production traits

	ADG2		ADG3		FDINT		FCR		LEANG	
ADG1	0.32	(0.23)	0.95	(0.07)	0.23	(0.19)	0.27	(0.24)	*	
	-0.02	(0.26)	0.78	(0.03)	0.11		0.24			
	0.05		0.86		0.13		0.22			
	0.00[1]		0.97[1]							
ADG2			0.60	(0.15)	0.82	(0.11)	-0.48	(0.21)	0.23	(0.24)
			0.56		0.61		-0.70		0.39	(0.54)
			0.52		0.62		-0.67		0.38	
			*[1]						1[1]	
ADG3					0.87	(0.05)	0.14	(0.26)	0.84	(0.06)
					0.74		-0.21		0.80	(0.05)
					0.76		-0.13		0.84	
									1[1]	
FDINT							0.19	(0.27)	0.12	(0.20)
							0.02		0.34	
							0.05		0.26	
FCR									-0.08	(0.27)
									-0.12	
									-0.10	

[1] correlation between litter effects, standard errors (in brackets) on second row where applicable

* estimates not different from one or minus one

The genetic correlation between lean meat growth (LEANG) and feed intake (FDINT) is low with a value of 0.12 (Table 5-6) which is in agreement with the only value found in the literature of 0.16 (Lundeheim et al., 1980). No genetic relationship exists between lean meat growth (LEANG) and feed conversion ratio (FCR). Johannson et al. (1987a) presented a genetic correlation of -0.87 between lean meat growth and feed conversion ratio for Landrace and Large White pigs. In contrast to this study, Johannson et al. (1987a) obtained these estimates iunder restricted feeding which favours pigs with high protein deposition. This leads to a lower, and therefore, improved feed conversion ratio, since protein deposition requires less energy than fat deposition (Webster. 1977). More background information to these relationships will be presented in chapter 5.2.5 when the relationship between growth rate and lean meat content will be discussed.

5.2.4 Carcase traits

The analysis of carcase traits included four backfat measurements, two taken with real time ultrasound on the live animal at the P2 site (LFDP2) and between the third and fourth last ribs

(LFD3/4) and two fat depth measurements taken with Hennesy Chong equipment on the carcase at the same sites (FDP2, FD3/4). Genetic correlations between these characteristics range from 0.93 to 1 (Table 5-7) and are not significantly different from one.

Genetic correlations between backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) and lean meat percentage (LEANL, LEAN) are in the range of -0.94 to -1 (Table 5-7). Literature estimates of this genetic correlation show a mean of -0.84 (Table 2-19) which is slightly lower than the estimates found in this study. However, these estimates of genetic correlations are dependent on how lean meat percentage is derived. Other prediction equations used in the referenced studies did not rely so strongly on backfat measurements as in this study which explains the slightly lower magnitude of estimates.

Although two muscle depth measurements were taken, only relationships between muscle depth taken with real time ultrasound equipment (LMD3/4) and other carcase traits are presented here. Standard errors were greater than one for genetic correlations between the second muscle depth measurement recorded on the carcase with Hennesy Chong equipment and other carcase characteristics. Genetic correlations between muscle depth on the live animal and backfat measurements ranged from -0.16 to 0.01 and were slightly higher for backfat recorded on the live animal (LFDP2, LFD3/4) in comparison to Hennesy Chong measurements (FDP2, FD3/4). This indicates that lower backfat is associated with greater muscle depth. The literature review includes only eye muscle area as a similar trait which showed a genetic correlation of -0.50 (Table 2-19) with backfat. Eye muscle area is therefore more closely related to backfat in comparison to muscle depth which was recorded in this study.

A larger muscle depth is more closely related to back leg weight measurements (r_g = 0.54 for BLW, LMW) than to lean meat percentage of the whole carcase with estimates of genetic correlations of 0.30 and 0.10 for the two lean meat percentage traits (LEANL, LEAN). The higher genetic correlation for lean meat percentage based on real time ultrasound measurements (LEANL) is expected since it is based on real time ultra sound measurements and the prediction equation includes muscle depth. However, these values are lower than the literature value of 0.66 (Lundeheim et al., 1980) for genetic correlation between loin eye area and lean meat percentage again indicating that muscle depth is less closely related to lean meat content than eye muscle area.

Table 5-7 Genetic correlations (first row) with standard errors (in brackets), environmental correlations (second row) and phenotypic correlations for carcase traits

	LFD3/4		LMD3/4		FDP2		FD3/4		BLW		LMW		LEANL		LEAN	
LFDP2	0.99	(0.01)	-0.16	(0.15)	0.93	(0.04)	1	(0.03)	-0.25	(0.15)	-0.63	(0.13)	-0.94	(0.01)	n.p.d.	
	0.73		-0.01		0.36				0.06		-0.33		-0.85			
	0.89		-0.07		0.64				-0.06		-0.47		-0.47			
LFD3/4			-0.14	(0.16)	0.94	(0.03)	1	(0.03)	-0.21	(0.16)	-0.62	(0.13)	-0.98	(0.01)	-0.95	(0.03)
			-0.07		0.34				0.01		-0.35		-0.88		-0.34	
			-0.09		0.65				-0.07		-0.47		-0.94		-0.65	
LMD3/4					-0.10	(0.18)	0.01	(0.21)	0.54	(0.21)	0.54	(0.21)	0.30	(0.15)	0.10	(0.18)
					-0.02		-0.04		0.18		0.24		0.40		0.02	
					-0.04		-0.02		0.25		0.33		0.33		0.04	
FDP2							0.96	(0.04)	-0.23	(0.18)	-0.70	(0.09)	-0.93	(0.04)	-1	(0.01)
							0.48		-0.02		-0.34		-0.35			
							0.69		-0.10		-0.50		-0.66			
FD3/4									-0.25	0.20	-0.70	(0.11)	-1	(0.03)	-0.96	(0.04)
									-0.04		-0.38				-0.48	
									-0.12		-0.51				-0.69	
BLW											0.86	(0.06)	0.25	(0.16)	0.20	(0.18)
											0.87		0.03		0.03	
											0.88		0.13		0.10	
											0.97[1]	(0.03)				
LMW													0.63	(0.12)	0.69	(0.15)
													0.44		0.44	
													0.54		0.54	
LEANL															0.92	(0.04)
															0.35	
															0.66	

[1] correlation between litter effects

Values for genetic correlations range from -0.21 to -0.25 between weight of the back leg (BLW) and fat depth measurements (LFDP2, LFD3/4, FDP2, FD3/4) (Table 5-7). These correlations are of higher magnitude for weight of the slash boned ham (LMW) and backfat measurements varying from -0.62 to -0.70. This stronger relationship for the later weight measurement is expected since it only includes lean meat of the back leg while the whole back leg also includes the skin, fat and connective tissue as well as bones of the whole back leg. The literature value for the genetic correlation between backfat and ham or primary cut weights was -0.58 (Table 2-19) thus confirming results obtained in this study.

Estimates of genetic correlations between the two weight measurements, back leg weight (BLW) and slash boned ham weight (LMW), and lean meat percentage (LEANL, LEAN) are positive with values of 0.25 and 0.20 for back leg weight and 0.63 and 0.69 for ham weight. Again, the literature value for ham weight and lean meat percentage is 0.46 (Table 2-19) which is intermediate to the genetic correlations presented here.

5.2.5 Production and carcase traits

Genetic correlations between production and carcase traits are presented in Table 5-8 along with environmental and phenotypic correlations. Estimates of genetic correlations between average daily gain recorded before the test station period (ADG1) and backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) are negative with values ranging from -0.35 to -0.26. Growth rate in the period between three and 18 weeks is therefore favourably genetically correlated with backfat. Genetic correlations between average daily gain before the test station period (ADG1) and muscle depth measurements are 0.18 and 0.28 for muscle depth recorded on the live animal (LMD3/4) and on the carcase (MD3/4), respectively. Higher growth rate in the time period between three to 18 weeks is genetically related to higher lean meat percentage (rg = 0.34 for LEANL and rg = 0.23 for LEAN).

In contrast, genetic correlations between growth rate recorded in the test station between 18 and 22 weeks (ADG2) and backfat measurements are positive, ranging from 0.29 to 0.48. This unfavourable genetic relationship between average daily gain recorded in the test station and carcase characteristics is also apparent in the genetic relationship with muscle depth measurements (LMD3/4, MD3/4). Genetic correlations between the two muscle depth measurements and growth rate in the time period between 18 and 22 weeks are negative with values of -0.13 and -0.26. Average daily gain in the test station and lean meat percentage are

negatively correlated with similar values of -0.32 and -0.33 for both lean meat percentage characteristics (LEANL, LEAN).

The average genetic correlation between average daily gain and lean meat percentage derived from studies which included ad libitum feeding is -0.18 (Table 2-19). However, in the situation of restricted feeding the mean literature value of genetic correlations was of opposite sign with a value of 0.35 (Table 2-9). The average genetic correlation between growth rate and loin eye area was -0.16 (Table 2-19).

In this study feed intake was not restricted by the feeding regime before or within the test station period. Genetic correlations between average daily gain in the test station (ADG2) and the carcase traits backfat, muscle depth, and lean meat percentage are in good agreement with literature values which are based on ad libitum feeding systems. In contrast, estimates of genetic correlations between average daily gain measured before the test period (ADG1) and these described carcase characteristics are not in agreement with these literature values based on ad libitum feeding systems but correspond to genetic correlations obtained between growth rate and lean meat content under restricted feeding.

In order to explain this difference in estimates of genetic correlations, nutritional factors that might influence these estimates will be investigated. The composition of the diet in testing procedures is dependent on the genetic potential of lean meat growth. Pigs of superior genotype have higher requirements of dietary protein and amino acids to support their higher potential of protein deposition in comparison to pigs with a reduced capacity of lean meat growth (Campbell and Taverner, 1988). The effect of protein content in the diet on selection was studied by Stern (1994) in a selection experiment which included two selection lines based on a high protein and low protein diet. A diet composition evoking fat deposition in an animal with low growth potential could elicit lean deposition in another animal which has a high lean meat growth potential. It was shown that it will be necessary to adapt composition of the diet to higher protein content in order not to limit lean meat growth which has been achieved through selection. Therefore, the genetic potential for lean meat growth was expressed more strongly on the high protein diet than on the low protein diet. Furthermore, both, lean meat percentage and growth rate, improved on the high protein diet, which was due to a favourable genetic correlation of 0.25 between lean meat percentage and growth rate in contrast to an unfavourable genetic correlation of -0.67 between these two traits on the low protein diet.

Besides sufficient protein supply, lean meat growth is also dependent on energy intake. The relationship between energy intake and lean meat growth given a sufficient protein supply can

be described through a linear-plateau relationship as proposed by Whittemore and Fawcett (1976) and experimentally confirmed by Campbell et al. (1985) and Dunkin et al. (1986). This linear-plateau relationship shows that lean meat growth increases with any additional energy intake until the maximum protein deposition (plateau) is reached. Campbell and Taverner (1988) showed that this plateau of protein deposition is higher for pigs with an improved genotype. Comparing two strains of pigs, an intrinsic limitation to protein deposition was not evident for the strain which had been selected for lean meat growth. For pigs from the fatter line, response of protein deposition to energy intake was described by a linear-plateau relationship. For this strain, protein deposition of boars and castrates was compared, with boars having a steeper slope of protein deposition with increasing feed intake and higher plateau of maximum protein deposition.

In this project, pigs were performance tested on a high protein diet with 1.15% lysine content which exceeds the lysine content of 0.96% in the high protein diet in the study by Stern (1994). Therefore, no limitations on lean meat growth were imposed through the diet used in this study. The favourable and unfavourable relationship between growth rate and lean meat percentage is therefore dependent on energy intake. Since younger pigs are limited in feed intake capacity (Campbell et al., 1986) their lean meat growth potential exceeds their appetite and thus might lead to a favourable relationship between average daily gain in the period between 3 to 18 weeks (ADG1) and lean meat content, which is closely related to backfat and muscle depth measurements as well as lean meat percentage. The unfavourable genetic correlation between growth rate in the test station during the later stage of the growing period (ADG2) and lean meat percentage is an indication that pigs at that age have a high feed intake which exceeds their maximum protein deposition. Therefore, the extra energy is deposited as fat tissue. These results are confirmed by Krieter (1986) who found that feed intake at the beginning of the growing period has less unfavourable genetic correlations with lean percentage and more favourable correlation with lean tissue growth rate than feed intake over the entire growing period.

The level of insufficient feed intake of young pigs in relation to their protein deposition is further enhanced with the use of entire boars in this study which have a higher protein deposition potential than castrates (Campbell and Taverner, 1988). This might be another reason for the favourable relationship between growth rate before the test period and lean meat percentage in comparison to literature values which are mainly based on data sets including castrates.

Another difference between the two growth rates (ADG1, ADG2) is manifested in different housing systems. Pigs are group penned before the test station and single penned within the test station. Therefore a higher percentage of energy might be required for maintenance in the group penning due to more movements of pigs and possible fighting. This might specially be the case with boars. However, these two explanations are confounded and can not be distinguished in this project.

Lifetime average daily gain (ADG3) includes both growth periods (ADG1, ADG2) which is also reflected in genetic correlations with carcase characteristics (Table 5-8). Genetic correlations with fat depth recorded with real time ultrasound (LFDP2, LFD3/4) are negative with values being -0.13 and -0.09. In contrast, positive genetic correlations are found between lifetime average daily gain and backfat measurements of the carcase (r_g to FDP2 = 0.11; r_g to FD3/4 = 0.12). The favourable relationship between fat depth measured on the live animal is also reflected in a favourable genetic relationship between lean meat percentage based on real time ultrasound measurements (LEANL) and life time average daily gain. Both muscle depth measurements (LMD3/4, MD3/4) are favourably correlated with life time average daily gain. However, the discrepancy of genetic relationships between fat depth measurements and the magnitude of the standard errors of these genetic correlations suggest that the genetic relationships between carcase traits describing lean meat content of the carcase and life time average daily gain are not significantly different from zero.

Weight of the whole back leg (BLW) and lean meat weight of the back leg (LMW) are positively correlated with average daily gain traits (ADG1, ADG2, ADG3). The magnitude of genetic correlations is higher for weight of the whole back leg in comparison to lean meat weight. This is expected since weight of the whole back leg includes skin, fat and connective tissue as well as lean meat and is therefore more closely related to growth rate than the ham which only includes the lean meat content of the back leg.

Estimates of genetic correlations between growth rate and ham weight are positive in the study of Johansson et al. (1987b) which is based on a restricted feeding regime with values of 0.16 for Landrace and 0.25 for Yorkshire (Table 2-9). Based on ad libitum feeding regimes, estimates of genetic correlations are negative with a mean of -0.19 (Table 2-9; Table 2-19). In this study all genetic correlations between growth rate characteristics and weight measurements of the back leg and lean meat weight are positive. However, genetic correlations are of higher magnitude for average daily gain before the test station (ADG1) than for average daily gain in the test station (ADG2) which supports the hypothesis that these pigs are restricted in their feed intake capacity which leads to this stronger favourable relationship. The

generally higher genetic correlations in this study between growth rate traits (ADG1, ADG2, ADG3) and weight of the whole back leg (BLW) and lean meat weight of the back leg (LMW) in comparison to literature values might be explained by the use of entire boars in this study.

Feed intake and carcase traits

Feed intake (FDINT) is positively correlated with backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) and genetic correlations range from 0.54 to 0.63 (Table 5-8). A reduced feed intake for leaner pigs is also apparent in the genetic correlation of -0.54 with lean meat percentage based on real time ultrasound measurements (LEANL). However, no genetic relationship was found between feed intake and lean meat percentage derived from Hennesy Chong measurements (LEAN). Both muscle depth measurements (LMD3/4, MD3/4) are negatively correlated with feed intake with genetic correlations of -0.13 for muscle depth recorded via real time ultrasound (LMD3/4) and -0.44 for muscle depth recorded in the abattoir (MD3/4). However, this last estimate has a high standard error (s.e. = 0.92). Estimates of genetic correlations are 0.45 between feed intake (FDINT) and weight of the whole back leg (BLW) and -0.11 for the lean meat weight of the whole back leg (LMW).

Generally these genetic correlations are consistent and indicate that a higher feed intake during the growth period between 18 and 22 weeks is associated with a decrease in lean meat content of the carcase. In the context of the linear-plateau relationship between protein deposition and feed intake as was discussed earlier, these genetic correlations show that feed intake capacity in the later growth period exceeds protein deposition potential and thus leads to an unfavourable genetic relationship between feed intake and lean meat content in the carcase.

Genetic correlations presented in this analysis are in good agreement with literature estimates (Table 2-19). The mean literature value of genetic correlations between feed intake and backfat was 0.40. Only one study was available for each genetic correlation between feed intake and lean meat percentage (-0.48, de Vries et al, 1994b) and between feed intake and ham weight (-0.72, Hofer and Schwörer, 1995).

Feed conversion ratio and carcase traits

Feed conversion ratio (FCR) is moderately genetically correlated with backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) with estimates ranging from 0.19 to 0.34 (Table 5-8). Muscle depth recorded with real time ultrasound (LMD3/4) has a low genetic correlation of 0.07 with feed efficiency which is not significantly different from zero. Both lean meat traits (LEANL, LEAN) are negatively correlated with feed efficiency (FCR) (rg=-0.15 for LEANL; rg=-0.63 for LEAN) indicating again that leaner pigs are the more efficient pigs. Webster (1977)

compared the energy required for protein deposition and fat deposition and concluded that the same amount of metabolic energy is deposited in one kg of fat as in about eight kg of fat-free muscle which confirms genetic correlations found in this study between feed efficiency and lean meat content of the carcase.

Feed conversion ratio has a strong genetic relationship with weight of the whole back leg (BLW) (r_g = -0.83) and lean meat weight of the back leg (LMW) (r_g = -0.71). These correlations indicate a strong relationship between highly efficient pigs and pigs with good conformation of the ham. The literature mean of two studies is lower (-0.52, Table 2-19).

Lean meat growth and carcase traits

Lean meat growth (LEANG) was derived from the lean meat content of the carcase estimated from Hennesy Chong measurements. It is therefore closely related to fat depth at P2 recorded in the abattoir (FDP2) and lean meat percentage derived mainly from this measurement (LEAN). This might be the reason for nonconvergence of the analyses since estimates are at the boundary of the parameter space. Further genetic correlations between lean meat growth and carcase characteristics are also of high magnitude ranging from -0.63 to -0.97 for further fat depth measurements (LFDP2, LFD3/4, FD3/4). Lean meat percentage based on real time ultrasound measurements (LEANL) reflects this relationship with a genetic correlation of 0.65. The estimate of genetic correlation between muscle depth (LMD3/4) and lean meat growth (LEANG) is low with a value of 0.24. High genetic correlations were found between lean meat growth and the two carcase weight measurements (r_g = 0.88 for BLW, r_g = 0.95 for LMW) which are not significantly different from one.

Only a few estimates of genetic correlations could be found between lean meat growth and carcase characteristics (Table 2-9). Mrode and Kennedy (1993) reported no relationship between lean meat growth and backfat. Differences to this study might be explained through implementation of different prediction equations to derive lean meat growth. The prediction equation used in this study was mainly based on backfat. Lundeheim et al. (1980) estimated a genetic correlation of 0.47 between lean meat growth and loin eye area which is slightly higher than the estimate obtained in this study for the genetic correlation between lean meat growth and muscle depth. A few studies presented estimates of genetic correlations between lean meat percentage and lean meat growth. However, the mean literature estimate of 0.81 (Table 2-19) is in close agreement with estimates obtained in the present study.

Table 5-8 Genetic correlations (first row) with standard errors (in brackets), environmental correlations (second row) and phenotypic correlations between production and carcase traits

	ADG1		ADG2		ADG3		FDINT		FCR		LEANG	
LFDP2	-0.35	(0.13)	0.31	(0.18)	-0.13	(0.14)	0.56	(0.11)	0.19	(0.19)	-0.63	(0.12)
	0.06		0.00		0.08		0.21		0.17		-0.23	
	-0.11		0.08		0.00		0.33		0.14		-0.37	
LFD3/4	-0.29	(0.14)	0.29	(0.18)	-0.09	(0.15)	0.54	(0.11)	0.23	(0.19)	-0.63	(0.12)
	0.03		0.02		0.09		0.23		0.15		-0.25	
	-0.10		0.09		0.00		0.33		0.15		-0.38	
LMD3/4	0.18	(0.20)	-0.13	(0.25)	0.18	(0.20)	-0.13	(0.20)	0.07	(0.27)	0.24	(0.17)
	0.05		-0.03		0.07		-0.06		-0.02		0.04	
	0.09		-0.05		0.09		-0.08		0.00		0.09	
FDP2	-0.26	(0.16)	0.33	(0.17)	0.11	(0.16)	0.62	(0.12)	0.34	(0.20)	*	
	0.05		0.03		0.28		0.12		0.06			
	-0.06		0.10		0.20		0.28		0.12			
FD3/4	-0.21	(0.19)	0.48	(0.22)	0.12	(0.19)	0.63	(0.14)	0.20	(0.25)	-0.97	(0.09)
	0.13		0.07		0.29		0.18		0.11		-0.84	
	-0.01		0.16		0.21		0.32		0.12		-0.08	
MD3/4	0.28	(0.76)	-0.26	(0.69)	0.21	(0.70)	-0.44	(0.79)	**		**	
	0.01		-0.02		0.02		0.00					
	0.03		-0.03		0.03		-0.03					
BLW	0.83	(0.07)	0.48	**	0.89	**	0.45	(0.24)	-0.83	(0.33)	0.88	***
	0.74	(0.07)	0.43		0.84		0.46		-0.48		0.74	
	0.79		0.40		0.87		0.43		-0.53		0.82	
	0.94[1]		0.04[1]		1[1]						1[1]	
LMW	0.61	(0.12)	0.23	***	0.64	(0.11)	-0.11	(0.18)	-0.71	(0.29)	0.95	***
	0.66	(0.16)	0.37		0.75	(0.08)	0.20		-0.44		0.70	
	0.68		0.29		0.73		0.09		-0.45		0.79	
	0.94[1]		0.09[1]		0.96[1]						1[1]	
LEANL	0.34	(0.14)	-0.32	(0.18)	0.14	(0.17)	-0.54	(0.12)	-0.15	(0.19)	0.65	***
	-0.04		0.00		-0.06		-0.23		-0.18		0.28	
	0.12		-0.09		0.03		-0.33		-0.14		0.40	
LEAN	0.23	(0.16)	-0.33	(0.20)	0.00	(0.18)	0.00	(0.12)	-0.63	(0.20)	*	
	-0.05		-0.03		-0.12		-0.13		-0.12			
	0.05		-0.10		-0.07		-0.07		-0.28			

* estimates of genetic correlations not different from one or minus one
** standard error for genetic correlations above one, *** approximation of s.e. failed
[1] correlation between litter effects, standard errors on second row (in brackets)

5.2.6 Meat quality traits

Genetic correlations were estimated separately for the two individual breeds Large White and Landrace and these estimates are presented in Appendix 5. However, although genetic

correlations were generally of higher magnitude for Landrace than for Large White pigs, differences were not significant and therefore results from the combined analysis will be discussed here (Table 5-9). The two pH measurements (pH45, pH24) are lowly correlated with a genetic correlation of -0.12 and an environmental correlation of 0.12. Therefore pigs with a low pH45, an indication of pale, soft and exudative (PSE) meat, will not develop dark firm and dry (DFD) meat since environmental and phenotypic correlations are slightly positive. However, the estimate of genetic correlation is of low negative magnitude and is in contrast to the literature mean of 0.28 (Table 2-19). Although these estimates are of low magnitude, this difference might be due to the slaughter environment. Lundström et al. (1989) pointed out that the incidence of DFD of halothane positive pigs in a good environment should be regarded as stress susceptible. The distance to the abattoir was only two kilometres and pigs were slaughtered with little pre-slaughter stress. These good conditions might be the reason for this slightly negative genetic correlation between pH45 and pH24. However, the incidence of the halothane gene is low in Large White and a negative genetic correlation between these two pH values was also found in Large White (Appendix 5). This suggests that the statement of Lundström et al. (1989) can be extended to the more general case that the incidence of DFD developed in a good slaughter environment should be regarded as stress susceptible.

Two colour measurements are included in this study, the L-value of the Minolta Chromamometer of the *m. longissimus dorsi* (CLD) and of the *m. multifidus dorsi* (CMD). Colour of the *m. longissimus dorsi* is negatively correlated with pH measurements with estimates of genetic correlations of -0.23 for pH45 and of -0.83 for pH24. A paler colour of the *m. longissimus dorsi* muscle is therefore associated with a reduced pH. Estimates of average genetic correlations from the literature between pH measurements and colour measurements are -0.59 for pH45 and -0.33 for pH24 (Table 2-19).

Colour of the *m. multifidus dorsi* (CMD) is genetically positively correlated with pH measurements (r_g = 0.20 for pH45; r_g = 0.03 for pH24) in contrast to negative environmental and phenotypic correlations with pH measurements. This is an indication that these colour measurements of *m. longissimus dorsi* (CLD) and *m. multifidus dorsi* (CMD) are different traits which is supported by only a moderate genetic correlation of 0.47 between these two traits. In addition, Warner et al. (1993) showed that the *m. longissimus dorsi* is only a reliable indicator of colour and exudate for other muscles in the situation of DFD meat. In the situation of PSE meat the *m. longissimus dorsi* was only a reliable indicator of colour and exudate for the four major ham muscles which are also white muscles in contrast to the *m. multifidus dorsi* analysed in this study.

Table 5-9 Genetic correlations (first row) with standard errors (in brackets), environmental correlations (second row) and phenotypic correlations between meat quality traits

	pH24		CLD		CMD		DLP		IMF	
pH45	-0.12	*	-0.23	(0.24)	0.20	(0.25)	-0.44	(0.23)	0.48	(0.23)
	0.12		-0.17		-0.10		-0.17		-0.01	
	0.08		-0.18		-0.03		-0.21		0.10	
pH24			-0.83	(0.11)	0.03	(0.24)	-0.71	*	-0.20	(0.24)
			-0.47		-0.25		-0.30		-0.09	
			-0.54		-0.19		-0.37		-0.11	
CLD					0.47	(0.16)	0.80	(0.14)	0.26	(0.19)
					0.33		0.47		0.11	
					0.08		0.56		0.15	
CMD							-0.01	*	0.20	(0.19)
							0.12		0.08	
							0.08		0.12	
DLP									-0.06	(0.21)
									0.04	
									0.01	

* approximation of standard error failed to converge

Drip loss percentage (DLP) has moderate to strong genetic correlations with measurements that are also taken from the *m. longissimus dorsi* (CLD, pH) while no genetic relationship exists to colour of the *m. multifidus dorsi* (CMD) (Table 5-9). The estimated genetic correlations are -0.44 for pH45, -0.71 for pH24 and 0.80 for colour of the *m. longissimus dorsi* (CLD). These correlations reflect characteristics of PSE and DFD meat. Meat with a high drip loss percentage has a low pH and a pale colour (PSE) or in the situation of DFD meat, a low drip loss percentage is associated with a high ultimate pH and a dark colour. Generally these relationships are stronger between measurements taken on the same day (24 hours after slaughter) than genetic correlations between pH45 and the other meat quality traits, showing that pH45 is only an indication of ultimate meat quality. Genetic correlations between drip loss percentage and other meat quality characteristics in this study are in agreement with average literature values. These were -0.32, -0.52 and 0.67 for genetic correlations between drip loss percentage and the meat quality traits pH45, pH24 and colour, respectively (Table 2-19).

The merit of a high intramuscular fat content lies in its favourable relationships with eating quality (Cameron, 1990b; Lo et al., 1992). However, to achieve better eating quality de Vol et al. (1988) showed that the intramuscular fat content has to be 2.5% which is above the mean of Large White and Landrace pigs in this study of 1.69%. pH45 has a positive genetic

correlation of 0.48 with intramuscular fat content while pH24 is negatively correlated (-0.20) with intramuscular fat content. Since intramuscular fat content is too low, both relationships are favourable with an increase in intramuscular fat content leading to a lower incidence of PSE and DFD meat. The positive genetic correlations of 0.26 and 0.20 between intramuscular fat content (IMF) and colour measurements (CLD, CMD) indicate that a higher intramuscular fat is associated with a paler colour. This paler colour should not be regarded as an indicator of a higher incidence of PSE. In contrast, the paler colour could be caused by a higher intramuscular fat content in the meat. This relationship indicates a potential problem of using colour as an indicator of PSE meat. Intramuscular fat content and drip loss percentage seem to be genetically uncorrelated (r_g = -0.06).

Favourable genetic correlations between intramuscular fat content, pH45 and drip loss percentage are confirmed through literature means of these estimates of 0.25 and -0.15, respectively (Table 2-19). In regard to genetic associations between intramuscular fat content and ultimate pH (pH24) and colour (CLD, CMD), mean literature estimates are 0.11 and -0.08 (Table 2-19). However, for both relationships literature values have a wide range and estimates found in this study are at the lower boundary of this range (pH24) or within this range (CLD, CMD) (Table 2-8).

5.2.7 Production and meat quality traits

Genetic correlations between growth rate traits (ADG1, ADG2, ADG3) and pH measurements (pH45, pH24) are generally not significantly different from zero (Table 5-10). This finding is confirmed by mean estimates of genetic correlations presented in the literature between average daily gain and pH measurements (r_g = 0.05 for pH45, r_g = -0.01 for pH24, Table 2-19).

Growth rate in the earlier stage of the growing period (ADG1) is negatively correlated with colour measurements (r_g = -0.21 for CLD and -0.31 for CMD). This indicates that a high growth rate between three to 18 weeks would lead to a darker colour and therefore would increase the potential risk of developing DFD meat. As shown earlier, high growth rate in the younger pig is associated with an increase in lean meat content. Since protein contains less energy than fat, glycogen levels might be reduced which cause the higher incidence of DFD meat. Another possibility might be that the intramuscular fat content in the younger pig is lower which also could lead to the darker colour. In contrast, genetic correlations between average daily gain in the test period (ADG2) and colour measurements are positive, with

values of 0.23 for colour of the *m. longissimus dorsi* (CLD) and 0.07 for colour of the *m. multifidus dorsi* (CMD). Higher growth rate in the test station is therefore lowly related to a lighter colour. The mean literature value of genetic correlations was 0.25 (Table 2-19) and is therefore in agreement with genetic correlations found between average daily gain in the test station and colour measurements.

Genetic correlations between drip loss percentage (DLP) and growth rate traits (ADG1, ADG2, ADG3) are not significantly different from zero with values ranging from 0.02 to 0.11. This slightly unfavourable relationship between drip loss percentage and growth rate traits, indicating a higher PSE incidence for higher growth rate, is in agreement with the mean genetic correlation of 0.18 presented in Table 2-19.

Growth rate before the test station (ADG1) and life time average daily gain (ADG3) are genetically uncorrelated with intramuscular fat content (IMF) while average daily gain in the test station (ADG2) is negatively correlated (r_g = -0.21) with intramuscular fat content. No estimate of standard error could be obtained for this relationship using average information REML which might be an indication of a flat likelihood surface causing problems in finding the global maximum. The mean genetic correlation of literature values is 0.10 between growth rate and intramuscular fat content (Table 2-19). However, literature estimates ranged from -0.16 to 0.28 (Table 2-10). Although estimates of this study are lower than the literature mean, they are within, or slightly lower than, the literature range.

Feed intake (FDINT) is moderately correlated with pH45 with a genetic correlation of 0.66. Higher feed intake is therefore associated with lower incidence of PSE, but might lead to higher incidence of DFD meat. However, the genetic correlation between feed intake and the measurement of DFD (pH24) is not significantly different from zero. Therefore no genetic relationship exists between a high feed intake and the incidence of DFD meat. Literature values of mean genetic correlations between feed intake and meat quality traits are only based on two studies. The average genetic correlation between feed intake and pH measurements is -0.02 for pH45 and 0.12 for pH24 (Table 2-19). Finally, estimates of genetic correlations between colour measurements (CLD, CMD) and feed intake are not significantly different from zero which is confirmed by a low literature mean of -0.12 (Table 2-19) for this genetic correlation.

Generally genetic correlations between feed conversion ratio (FCR) and other meat quality traits are of higher magnitude than relationships between other production traits and meat quality traits but also have higher standard errors due to the low heritability of feed conversion ratio. Table 5-10 shows a genetic correlation of 0.40 between feed efficiency and pH45. This is

an unfavourable relationship indicating a higher incidence of PSE for pigs that are more feed efficient. Generally, the more feed efficient pigs are the leaner animals and since a higher lean meat content is associated with a higher incidence of PSE meat (see Table 5-11) this relationship is expected although it is in contrast to the one estimate found in the literature of -0.14 (Hofer and Schwörer, 1995).

The genetic correlation between feed conversion ratio (FCR) and pH24 is -0.16. This estimate is in agreement with the estimate presented by Hofer and Schwörer (1995) of -0.04. Although this relationship indicates that more feed efficient pigs have also a higher incidence of DFD meat, the genetic correlation has a high standard error and is therefore not significantly different from zero.

Table 5-10 Genetic correlations (first row) with standard errors (in brackets), environmental correlations (second row) and phenotypic correlations between production and meat quality traits

	ADG1		ADG2		ADG3		FDINT		FCR		LEANG	
pH45	0.00	(0.25)	0.35	(0.31)	0.20	(0.25)	0.66	(0.19)	0.40	(0.30)	-0.07	(0.26)
	0.22		0.06		0.21		0.02		-0.04		0.15	
	0.15		0.09		0.19		0.14		0.01		0.09	
pH24	0.05	(0.24)	0.07	(0.30)	0.00	(0.24)	-0.04	(0.24)	-0.16	(0.31)	-0.08	(0.25)
	0.06		-0.08		0.04		-0.02		0.07		0.00	
	0.05		-0.05		0.03		-0.02		0.04		-0.02	
CLD	-0.21	(0.20)	0.23	(0.24)	-0.07	(0.20)	-0.10	(0.20)	-0.59	(0.23)	0.25	(0.20)
	-0.09		0.02		-0.09		0.02		0.00		-0.12	
	-0.12		0.06		-0.08		-0.01		-0.09		-0.01	
CMD	-0.31	(0.20)	0.07	(0.23)	-0.21	(0.20)	-0.03	(0.19)	-0.19	(0.25)	0.02	*
	-0.20		-0.09		-0.23		-0.04		0.09		-0.18	
	-0.22		-0.05		-0.21		-0.03		0.04		-0.11	
DLP	0.02	(0.21)	0.10	(0.25)	0.11	(0.21)	-0.15	(0.21)	0.58	(0.23)	0.22	(0.20)
	0.06		0.03		0.05		0.01		0.02		0.01	
	0.04		0.04		0.06		-0.03		-0.08		0.06	
IMF	0.01	(0.18)	-0.21	*	0.00	(0.18)	0.03	(0.20)	0.21	(0.27)	-0.28	(0.20)
	-0.02		0.10		0.04		0.17		0.03		-0.36	
	0.00		0.03		0.02		0.13		0.06		-0.31	

* approximation of standard error failed

Feed conversion ratio (FCR) has negative correlations with colour measurements with values of -0.59 for colour of the *m. longissimus dorsi* (CLD) and -0.19 for colour of the *m. multifidus dorsi* (CMD). Although the latter estimate is not significantly different from zero it indicates that a reduced, and therefore improved, feed efficiency is associated with a lighter colour. This

relationship was also found by the two studies summarized in Table 2-19 resulting in a mean genetic correlation of -0.12 between feed efficiency and colour.

Table 5-10 also shows an unfavourable relationship between feed conversion ratio and drip loss percentage (r_g =-0.58) which is confirmed by the results of de Vries et al. (1994b) who found a genetic correlation of -0.35 between these two traits. The estimate of genetic correlation between feed conversion ratio (FCR) and intramuscular fat content (IMF) is 0.21 Although this estimate is not significantly different from zero it indicates a reduced intramuscular fat content for the more efficient pigs. This estimate is above the literature mean of 0.10 (Table 2-19).

5.2.8 Carcase and meat quality traits

Moderate positive genetic correlations were found between pH45 and backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) ranging from 0.49 to 0.64 (Table 5-11). Selection for reduced backfat will therefore reduce pH45 and thus increase the incidence of PSE meat confirming results from Bidanel et al. (1994a) who found a genetic correlation of 0.26 between these two traits.

As explained earlier both lean meat percentage traits (LEANL, LEAN) are mainly based on backfat measurements and estimates of genetic correlations with pH45 are therefore of the same magnitude but of opposite sign for these two carcase traits (r_g = -0.64 for LEANL, r_g = -0.49 for LEAN). These estimates contradict results from de Vries et al. (1994b) who found a genetic correlation of 0.10 between backfat and pH45 in a halothane free Yorkshire population. Both breeds included in this study carry the halothane gene. This might explain the stronger unfavourable relationship between lean meat percentage and pH45 in comparison to the estimate presented by de Vries et al. (1994b).

An increase in weight of the whole back leg (BLW) is related to a higher pH45 while an increase in the lean meat content of the back leg (LMW) is associated with a decrease in pH45. Both weight measurements are negatively correlated with pH24 (r_g = -0.10 for BLW, r_g = -0.28 for LMW) thus reducing the incidence of DFD with increasing weight of the whole back leg and higher ham weight. No estimates were found in the literature for these trait combinations.

Genetic correlations between backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) and pH24 are close to zero with values ranging from -0.04 to 0.09. In addition, no significant genetic relationship exists between pH24 and lean meat percentage traits (LEANL, LEAN). Mean literature values of genetic correlations between ultimate pH and backfat and lean meat percentage are 0.05 for backfat and -0.05 for lean meat percentage (Table 2-19) confirming that pH24 has no genetic relationship with leanness.

Genetic correlations between colour of *m. longissimus dorsi* (CLD) and the carcase traits backfat and lean meat percentage are low with estimates ranging from -0.13 to -0.05 for backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) and varying from 0.07 to 0.13 for lean meat content traits (LEANL, LEAN) (Table 5-11). Among backfat measurements, colour of the *m. multifidus dorsi* (CMD) has only a significant genetic relationship to fat depth at P2 recorded with Hennesy Chong (FDP2) of -0.20. This is also reflected in an estimated genetic correlation of 0.20 with lean meat content derived from Hennesy Chong measurements (LEAN). Table 2-19 shows genetic correlations of -0.09 between colour and backfat and 0.16 between colour and lean meat percentage thus supporting the low genetic relationship of a paler meat with a reduced backfat and a higher lean meat percentage.

Genetic correlations between drip loss percentage (DLP) and backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) are lowly negative (-0.20 to -0.14). A reduction in backfat is therefore associated with an increased drip loss. This relationship is also apparent in genetic correlations of 0.19 and 0.20 between lean meat percentage measurements (LEANL, LEAN) and drip loss percentage. This is further confirmed by mean literature values of genetic correlations of -0.07 between drip loss percentage and backfat and of 0.17 between drip loss percentage and lean meat percentage (Table 2-19).

Drip loss percentage (DLP) is lowly correlated with weight of the whole back leg (BLW) (r_g = 0.17) and moderately correlated with lean meat weight of the whole back leg (LMW) (r_g = 0.36). The literature provides no comparison for these correlations but they indicate that a high ham weight has a stronger unfavourable genetic correlation with drip loss percentage than carcase characteristics describing lean meat content of the whole carcase. The higher magnitude of this unfavourable relationship might partly be due to a higher incidence of the halothane gene in those pigs that have a high ham weight.

Intramuscular fat content (IMF) is positively genetically correlated with backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) with correlations ranging from 0.19 to 0.34. A decrease in backfat will therefore lead to a reduction in intramuscular fat content. Genetic correlations

between intramuscular fat content and lean meat percentage traits (LEANL, LEAN) are of opposite sign representing the same relationship (rg = -0.24 for LEANL, rg = -0.19 for LEAN). Given the level of intramuscular fat content of 1.69 % which is below the desired level of 2.5 % (de Vol et al., 1988) this relationship is unfavourable. Mean literature values of genetic correlations confirm the reduction of intramuscular fat content with increased leanness with estimates of 0.18 between intramuscular fat content and backfat and -0.06 between intramuscular fat content and lean meat percentage (Table 2-19).

Table 5-11 Genetic correlations (first row) with standard errors (in brackets), environmental correlations (second row) and phenotypic correlations between meat quality and carcase traits

	pH45		pH24		CLD		CMD		DLP		IMF	
LFDP2	0.62	(0.16)	-0.04	(0.19)	-0.08	(0.15)	-0.03	(0.15)	-0.16	(0.16)	0.26	(0.15)
	0.10		0.05		-0.07		-0.04		-0.01		0.09	
	0.24		0.02		-0.07		-0.04		-0.07		0.16	
LFD3/4	0.64	(0.16)	0.00	(0.19)	-0.08	(0.15)	0.00	(0.14)	-0.19	(0.16)	0.27	(0.16)
	0.11		0.05		-0.08		-0.06		0.00		0.10	
	0.25		0.03		-0.08		-0.03		-0.07		0.17	
LMD3/4	0.00	(0.26)	0.13	(0.26)	0.04	(0.21)	-0.17	(0.20)	0.04	(0.22)	0.16	(0.21)
	-0.06		-0.09		0.08		0.06		0.10		-0.13	
	-0.05		-0.05		0.07		0.00		0.09		-0.05	
FDP2	0.49	(0.20)	0.09	(0.21)	-0.13	(0.17)	-0.20	(0.16)	-0.20	(0.18)	0.19	(0.17)
	0.05		0.08		-0.07		0.00		-0.02		0.14	
	0.16		0.08		-0.09		-0.08		-0.08		0.16	
FD3/4	0.59	(0.20)	0.00	(0.24)	-0.05	(0.20)	-0.06	(0.20)	-0.14	(0.22)	0.34	(0.21)
	0.17		0.02		-0.08		0.05		0.00		0.12	
	0.26		0.02		-0.07		0.00		-0.05		0.21	
MD3/4	*		0.21	(0.86)	0.52	(0.76)	0.42	(0.76)	0.25	(0.72)	-0.09	(0.71)
			0.03		-0.02		-0.18		0.06		-0.07	
			0.04		0.03		-0.12		0.06		-0.06	
BLW	0.12	(0.27)	-0.10	(0.27)	0.09	(0.22)	0.01	(0.21)	0.17	(0.23)	0.08	(0.23)
	0.17		0.00		-0.07		-0.23		0.08		0.00	
	0.16		-0.02		0.02		-0.15		0.10		0.02	
LMW	-0.17	(0.25)	-0.28	(0.23)	0.22	(0.19)	0.08	(0.18)	0.36	(0.21)	-0.15	(0.18)
	0.09		0.02		-0.04		-0.02		0.06		-0.20	
	0.00		-0.07		0.06		-0.10		0.16		-0.18	
LEANL	-0.64	(0.17)	0.00	(0.19)	0.07	(0.15)	0.00	(0.15)	0.19	(0.16)	-0.24	(0.16)
	-0.12		-0.07		0.11		0.04		0.04		-0.12	
	-0.25		-0.04		0.09		0.02		0.10		-0.17	
LEAN	-0.49	(0.20)	-0.09	(0.21)	0.13	(0.18)	0.20	(0.16)	0.20	(0.18)	-0.19	(0.18)
	-0.05		-0.08		0.07		0.00		0.02		-0.14	
	-0.16		-0.08		0.09		0.08		0.08		-0.16	

* standard error above one

No significant genetic relationship was found between weight measurements of the back leg (BLW, LMW) and intramuscular fat content (IMF). The genetic correlation is slightly positive between intramuscular fat content and weight of the whole back leg (BLW) (r_g = 0.08) and slightly negative between intramuscular fat content and ham weight (LMW) (r_g = -0.15). No estimates of genetic correlations were found in the literature for this combination of traits.

Genetic correlations between muscle depth recorded with real time ultrasound (LMD3/4) and meat quality traits are low and not significantly different from zero. Although genetic correlations between muscle depth measured with Hennesy Chong machine (MD3/4) have a low to moderate magnitude the high standard errors of 0.71 to 0.86 indicate that these estimates are not very reliable. This is due to the low heritability of this trait and the estimation of covariances with other traits is therefore difficult.

5.2.9 Manufacturing traits

This section summarizes genetic relationships of ham yield and middle yield after processing to meat quality, carcase, and growth and feed efficiency traits. Since only 1000 hams and 800 middles were available estimates of genetic correlations have high standard errors which exceed the magnitude of the genetic correlation in many cases. These results are therefore only a first indication of possible genetic relationships between the manufacturing yield of hams and middles and other economically important traits.

Genetic parameters for cured hams or cured middles are not available in the literature. However, some studies investigated the relationship between PSE meat and processing yield of hams (Kauffman et al., 1978; Honkavaara., 1988; Shand et al., 1995) and middles (Taylor et al., 1973; Smith and Lesser, 1982) while others studied breed and cross breeding effects on yield and quality of dry-cured hams (Gou et al., 1994; Oliver et al., 1994; Gallo et al., 1994). Results of these studies will be used to explain estimates of genetic correlation between manufacturing traits and other traits, mainly meat quality and carcase traits.

Manufacturing traits that were analysed in this study are ham weight after processing expressed as a percentage of the initial weight (HAM), ham weight after processing expressed as a difference from the initial weight (HAMD) and weight of the middle after processing expressed as a percentage of initial weight of the middle (MID), or defined as a difference from initial weight of the middle (MIDD). Both ham measurements and middle measurements are the same trait which is shown through genetic, environmental and phenotypic correlations of

one between each pair of traits. Ham yield and middle yield, both traits expressed as a percentage of the initial weight of the ham (HAM) and the middle (MID) have a genetic correlation of -0.57 with environmental and phenotypic correlation of 0.00 and -0.04 respectively. A high ham yield is therefore genetically associated with a reduced yield of the middle. A possible reason might be that ham weight only includes lean meat whereas the weight of the middle consists of lean meat, fat and skin tissue. In addition, processing of hams and middles was different. While hams were further processed (tumbling and cooking) after pumping, middles were placed in a tub for a further two days until they were cooked. However, this estimate of genetic correlation needs to be confirmed possibly through genetic correlations between ham and middle yield and other meat quality and carcase traits, since the genetic correlation has a standard error of one.

Table 5-12 presents genetic, environmental and phenotypic correlations between manufacturing traits and meat quality traits. Both measurements of ham yield (HAM, HAMD) are moderately correlated with pH45 and pH24 with estimates ranging from 0.38 to 0.53. A higher cooking yield of the ham is therefore achieved in pigs that have a high pH at either 45 minutes after slaughter or 24 hours after slaughter. In regard to PSE and DFD meat, a high pH is related to a paler colour and higher drip loss percentage. An increased ham yield (HAM, HAMD) is related to a darker colour (r_g = -0.28 and r_g = -0.24 for CLD) and a reduced drip loss percentage (r_g = -0.65 for HAM and r_g = -0.70 for HAMD). Ham yield has not been genetically analysed before and these genetic correlations can only be compared to cooking loss and its genetic relationship with other meat quality characteristics. A reduced cooking loss is equivalent to an increased yield and genetic correlations with other meat quality traits are of opposite sign for cooking loss in comparison to ham yield. Genetic correlations presented in Table 2-19 show that an increased cooking loss is associated with a reduced pH45 (r_g =-0.32) and a reduced ultimate pH (r_g = -0.77), as well as a lighter colour (r_g = 0.40) and a higher drip loss percentage (r_g = 0.63). Thus the increased ham yield for pork with better technological meat quality as found in this study is confirmed by these average literature estimates of genetic correlations.

It has to be taken into account that cooking loss was obtained from a standardized meat sample cooked in a water bath which limits a comparison between estimates. It might be beneficial to compare these results with studies that investigated the level of PSE meat and its influence on ham yield after processing. Kauffman et al. (1978) found that additional weight losses of hams after curing and smoking were 5.71% for PSE hams in comparison to normal hams with a weight loss of 3.95% and DFD hams which exhibited a weight loss of 1.64%. A more recent study (Honkavaara, 1988) found technological yields of PSE and non-PSE hams

of 94.0% and 105.%, respectively. In addition, cooked PSE hams had worse organoleptic properties with an inferior appearance, texture and flavour, leading to hams which were described as "crumbly, dry with worst texture". These results were further confirmed by Müller (1991) who found that increased pH leads to higher yield of the cooked ham, while the number of hams with pores and holes as well as the amount of juice exudate declined.

Colour of the *m. multifidus dorsi* (CMD) has genetic correlations of 0.60 and 0.63 with the two ham yield measurements (HAM, HAMD) which indicates an increased ham yield for a lighter colour in this muscle. This is of opposite sign to genetic correlations between ham yield and colour of *m. longissimus dorsi*. However, Warner et al. (1993) showed that quite a substantial difference exists between major muscles from the loin, ham and shoulder in their development of exudate, lightness and ultimate pH in the situation of PSE meat. In addition, this muscle is small which leads to more unreliable colour measurements.

Estimates of genetic correlations between intramuscular fat content and ham yield are 0.14 (HAM) and 0.11 (HAMD) and 0.20 and 0.09 between intramuscular fat content and yield of the middle (MID, MIDD) (Table 5-12). Duroc are known for their higher intramuscular fat content and the influence of Duroc crossbreeds was analysed by Arnau et al. (1992) and Gou et al. (1995). While Arnau et al. (1992) found a significant decrease in weight loss for the Duroc crossbreed, no significant crossbreed effect on cooking yield was found by Gou et al. (1995). However, hams from Duroc-sired pigs had significantly less holes. The beneficial influence of a higher intramuscular fat content might be indirect since fat is water repellent. An increased intramuscular fat content might result in a better structure of the meat which is then better able to retain moisture during processing.

Genetic correlations between middle yield traits (MID, MIDD) and pH45 are 0.07 for middle yield defined as a percentage of the initial weight (MID) and -0.13 for yield of the middle described as a difference to the initial weight (MIDD). Given the standard errors and the low magnitude of these genetic correlations, this indicates that pH45 has no significant relationship with yield of the middle. In contrast, genetic correlations between pH24 and middle yield are negative with values of -0.46 (MID) and -0.51 (MIDD) showing that a low pH24 is related to a high yield of the middle.

Colour of the *m. longissimus dorsi* (CLD) has positive genetic correlations with yield of the middle (MID, MIDD) (r_g = 0.25 for MID; r_g = 0.23 for MIDD). A lighter colour of the *m. longissimus dorsi* is therefore associated with an increased yield of the middle. This corresponds to a genetic correlation of 0.46 and 0.20 between drip loss percentage (DLP) and

the two yield of the middle traits (MID, MIDD). Contrarily to ham yield, yield of the middle is increased for PSE meat.

Table 5-12 Genetic correlations (first row) with standard errors (in brackets), environmental correlations (second row) and phenotypic correlations between meat quality and manufacturing traits

	HAM		HAMD		MID		MIDD	
pH45	0.53	(0.47)	0.52	(0.47)	0.07	(0.33)	-0.13	(0.49)
	0.00		0.01		0.08		0.02	
	0.07		0.08		0.08		0.00	
pH24	0.40	(0.57)	0.38	*	-0.46	(0.63)	-0.51	*
	0.12		0.12		-0.04		-0.04	
	0.15		0.15		-0.08		-0.12	
CLD	-0.28	(0.46)	-0.24	(0.46)	0.25	(0.61)	0.23	(0.38)
	-0.16		-0.16		-0.04		-0.01	
	-0.17		-0.17		0.00		0.04	
CMD	0.60	(0.39)	0.63	(0.42)	0.37	(0.63)	0.39	(0.36)
	-0.26		-0.26		-0.12		-0.08	
	-0.08		-0.08		-0.05		0.03	
DLP	-0.65	(0.46)	-0.70	(0.47)	0.46	(0.64)	0.20	(0.40)
	-0.04		-0.02		-0.05		-0.02	
	-0.13		-0.13		0.00		0.02	
IMF	0.14	(0.46)	0.11	(0.47)	0.20	(0.62)	0.09	(0.39)
	-0.03		-0.03		0.02		0.00	
	0.00		0.00		0.04		0.02	

* approximation of standard error failed

Wismer-Pedersen (1968; cited in Møller et al., 1992) and Taylor et al. (1973) pointed out that PSE meat has a higher uptake of brine due to the looser structure of this meat. However, this also reduces the ability of this meat to retain the absorbed moisture during processing (Taylor et al., 1982) which resulted in a 1.6 % lower bacon yield of PSE meat in comparison to normal meat in the study by Smith and Lesser (1982). Bacon yield was expressed as a proportionate increase of trimmed side weight, in contrast to this study where middles were not trimmed of fat and skin. This might have an influence on the relationship between PSE and bacon yield in this study, since the loss of fluid from meat is reduced when whole sides are cured and muscle membranes are left intact (Wismer-Pedersen, 1968, cited in Møller et al., 1992). In addition, Taylor et al. (1973) compared bacon yield of PSE meat and normal meat for two different maturation times after curing. A longer maturation time reduced the effect of differences in final bacon. The higher yield of middles for PSE meat found in this study is due to a higher

uptake of pickle for PSE meat while the higher loss of moisture of PSE meat is overcome by leaving fat and skin on the middles and by the longer curing time of middles. This is illustrated through least squares means of yield of middles expressed as a percentage of initial weight of middles for PSE, normal and DFD meat in Table 5-13. PSE meat has a 1.36 % higher uptake of pickle after pumping, which reduces to a 0.77 % higher yield after curing and a 0.28 % higher yield after cooking. Thus PSE meat has a higher uptake of pickle but is less able to retain this moisture in further processing after pumping.

Table 5-13 Least squares means of meat quality classes for yield of middles after pumping, tumbling and cooking

Meat quality class	**Yield[1] of middle after:**		
	pumping	**soaking**	**cooking**
PSE	120.00	118.25	106.66
Normal	118.64	117.48	106.38
DFD	118.81	117.52	105.81

[1] expressed as percentage of initial weight

Genetic correlations between both ham yield traits (HAM, HAMD) and fat depth measurements (LFDP2, LFD3/4, FDP2, FD3/4) range from -0.42 to -0.03 (Table 5-14). This relationship is also reflected by mostly positive genetic correlations between ham yield and lean meat percentage characteristics (LEANL, LEAN). However, further carcase characteristics including muscle depth recorded with real time ultrasound measurement (LMD3/4), and weight of the whole back leg (BLW) and weight of the lean meat content of the whole back leg (LMW) are negatively correlated with ham yield measurements. These estimates are of high magnitude with muscle depth measured on the live animals with estimates of -0.77 (HAM) and -0.80 (HAMD). Genetic correlations between ham yield traits and weight of the lean meat content of the back leg are of moderate magnitude with estimates of -0.42 and -0.51 for the two ham yield traits (HAM, HAMD). Weight of the whole back leg shows genetic correlations of lower magnitude in comparison to the lean meat content of the whole back leg with estimates of -0.38 (HAM) and -0.22 (HAMD).

Two different mechanisms might explain these contradictory relationships between carcase traits and ham yield. A higher incidence of PSE reduces ham yield after processing which might be the reason for the reduced ham yield in pigs with a high weight of the back leg (BLW) and lean meat weight of the back leg (LMW). This is because a higher ham weight has the strongest unfavourable relationship to ultimate meat quality (pH24, CLD, DLP, Table 5-11).

Backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) have no significant genetic relationships to ultimate meat quality traits and the slightly favourable genetic correlations might be due to another mechanism as explained by Gou et al. (1995). During processing higher leanness would facilitate crusting in hams which makes the loss of water more difficult thus leading to a higher yield of hams.

Table 5-14 Genetic correlations (first row) , with standard errors (in brackets), environmental (second row) and phenotypic correlations between carcase and manufacturing traits

	HAM		HAMD		MID		MIDD	
LFDP2	-0.15	(0.35)	-0.24	(0.38)	0.33	(0.43)	0.32	(0.27)
	0.05		0.07		0.17		0.10	
	0.00		-0.02		0.17		0.17	
LFD3/4	-0.03	(0.36)	-0.12	(0.38)	0.27	(0.45)	0.27	(0.29)
	0.06		0.09		0.12		0.04	
	0.03		0.02		0.13		0.12	
LMD3/4	-0.77	(0.50)	-0.80	(0.61)	0.11	(0.61)	0.04	(0.40)
	0.04		0.04		0.03		-0.02	
	-0.07		-0.07		0.03		0.00	
FDP2	-0.20	(0.37)	-0.25	(0.39)	0.42	(0.57)	0.29	(0.32)
	0.07		0.08		0.00		0.01	
	0.00		0.00		0.07		0.09	
FD3/4	-0.32	(0.46)	-0.42	(0.50)	0.37	(0.68)	0.28	(0.37)
	0.11		0.09		0.04		0.02	
	0.00		-0.03		0.09		0.10	
BLW	-0.38	(0.42)	-0.22	(0.59)	0.53	*	0.05	*
	0.14		0.19		0.19		0.00	
	0.03		0.12		0.22		0.00	
LMW	-0.42	(0.45)	-0.51	(0.45)	0.46	(0.42)	0.07	*
	0.09		0.03		0.14		-0.01	
	-0.02		-0.08		0.19		0.00	
LEANL	-0.06	(0.38)	0.07	(0.40)	-0.11	(0.49)	-0.19	(0.32)
	-0.04		-0.06		-0.11		-0.05	
	-0.04		-0.02		-0.09		-0.09	
LEAN	0.19	(0.37)	0.25	(0.39)	-0.42	(0.57)	-0.29	(0.32)
	-0.07		-0.07		0.00		-0.01	
	0.00		0.00		-0.07		-0.09	

* approximation of standard error failed

Estimates of genetic correlations from the analysis of backfat characteristics (LFDP2, LFD3/4, FDP2, FD3/4) and yield of the middle (MID, MIDD) range from 0.27 to 0.33. A higher backfat measurement is therefore associated with a higher processing yield of the middle. This

relationship is also apparent in genetic correlations between lean meat percentage traits (LEANL, LEAN) which have genetic correlations of -0.11 to -0.42 with yield of the middle after processing. Higher backfat is related to higher fatness of middles (Fewson et al., 1990; Memmert et al., 1991). As was explained earlier, a higher fatness in middles is beneficial since it increases the amount of moisture retained in the bacon.

Table 5-15 summarizes genetic, environmental and phenotypic correlations between production traits and manufacturing traits. Growth rate traits including growth rate before the test station (ADG1) and life time average daily gain (ADG3) as well as lean meat growth (LEANG) are negatively correlated with ham yield with genetic correlations ranging from -0.52 to -0.34. A high growth rate is therefore associated with a decrease in ham yield while a high feed intake is related to an increase in ham yield. This is indicated through a genetic correlation of 0.17 and 0.26 between feed intake (FDINT) and ham yield (HAM, HAMD). This might be due to a lower protein content in the fat free empty body of pigs with higher lean meat growth (Campbell and Taverner, 1988) which would reduce the moisture uptake of hams during processing.

Table 5-15 Genetic correlations (first row). with standard errors (in brackets), environmental (second row) and phenotypic correlations between production and manufacturing traits

	HAM		HAMD		MID		MIDD	
ADG1	-0.44	(0.39)	-0.52	(0.55)	0.43	(0.59)	-0.08	(0.35)
	0.05		0.11		0.19		0.04	
	-0.04		-0.02		0.20		0.00	
ADG3	-0.41	(0.38)	-0.39	(0.54)	0.33	(0.57)	-0.22	(0.38)
	0.11		0.16		0.25		0.01	
	0.01		0.06		0.24		-0.04	
FDINT	0.17	(0.46)	0.26	(0.50)	0.11	(0.61)	-0.09	(0.40)
	0.08		0.06		0.18		0.09	
	0.10		0.10		0.16		0.06	
FCR	-0.27	(0.55)	0.26	(0.60)	*		-0.28	(0.50)
	0.01		0.01				0.11	
	-0.02		-0.01				0.06	
LEANG	-0.45	(0.45)	-0.34	(0.51)	*		-0.16	(0.39)
	0.14		0.18				-0.04	
	0.03		0.08				-0.07	

* failed to converge

Genetic correlations between yield of the middle and production traits are not consistent for both traits describing yield of the middle. While yield of middle expressed as a percentage of initial weight of the middle is positively correlated with average daily gain within three to 18 weeks (ADG1) (rg = 0.43), life time average daily gain (ADG3) (rg = 0.33) and feed intake (FDINT) (rg = 0.11), negative genetic correlations were found between yield of the middle described as difference between weight of middle after processing in relation to initial weight (MIDD) and production traits. Estimates of genetic correlations ranged from -0.08 to -0.28 for this combination of traits.

5.2.10 Conclusions

Average daily gain from three to 18 weeks is a different trait than average daily gain recorded in the test station between 18 and 22 weeks. Different housing systems and stage of growth, protein accreation phase for ADG1 and fat accretion phase for ADG2, contribute to these differences. A higher average daily gain before the test station period is associated with an increased lean meat percentage, while a higher average daily gain in the later part of the growing period will reduce lean meat percentage. Increasing lean meat percentage reduces feed intake.

Backfat measurements and lean meat percentage have a genetic correlation of one. A reduced backfat is moderately associated with a higher lean meat content in the back leg.

Correlations between meat quality traits reflect characteristics of PSE and DFD meat. The magnitude of genetic correlations between meat quality measured on the second day after slaughter is higher than their relationship to pH measured shortly after slaughter. Increasing intramuscular fat content will improve meat quality characteristics.

Genetic correlations between growth rate and meat quality traits are inconsistent between traits and of low magnitude. A higher feed intake is lowly correlated with a higher incidence of DFD meat.

A reduction in backfat and an increase in lean meat percentage and lean meat weight of the ham is associated with a decrease in pH measured 45 minutes after slaughter. Backfat and lean meat percentage are not significantly genetically related to meat quality traits measured the day after slaughter including pH, colour, and drip loss percentage. A higher lean meat weight of the back leg is somewhat unfavourably associated with meat quality traits measured 24 hours after slaughter. A further reduction in backfat will decrease intramuscular fat content.

A higher ham yield is associated with a reduced yield of the middle. PSE meat has a lower yield of the ham after processing while yield of the middle after processing is increased for PSE meat.

An increased leanness is lowly associated with a decreased ham yield after processing. The yield of middles is higher for fatter pigs. These relationships are dependent on the processing techniques and might be different when other processing techniques are used.

5.3 Genetic analysis of reproductive traits of the sow

5.3.1 Introduction

Sow productivity has been increased phenotypically at the rate of one percent per year in number of piglets weaned per sow per year. This has mainly been achieved by an improvement in the number of litters per sow per year rather than an increase in litter size (de Vries and Kanis, 1993) despite the fact that genetic improvement of reproductive performance of the sow has mainly been focused on number born alive as the selection criterion. It is mostly assumed that litter size is genetically unrelated to growth rate and leanness. However, some selection experiments indicate that selection for growth has a detrimental effect on litter size (e.g. Woltmann 1993, cited in Clutter, 1995) which might be the reason for the lack of genetic improvement in litter size. In addition, improvement of sow productivity might be increased by using additional reproductive traits of the sow. These include litter birth weight and average piglet weight at birth which are favourably related to piglet survival (Rydhmer et al., 1992), and 21 day litter weight, an indirect measurement of the sow's milking and mothering ability.

This chapter presents heritabilities for various reproductive traits of the sow and genetic correlations between these traits. Genetic relationships between these reproductive traits of the sow and traits measured on their offspring including growth and feed efficiency traits, as well as carcase and meat quality traits, will be discussed in the second part of this chapter.

5.3.2 Heritability estimates for reproductive traits of the sow

Heritabilities for reproduction traits of the sow are presented in Table 5-16 along with variance components. Litter size is lowly heritable with estimates of 0.08, 0.09 and 0.08 for the first

three parities ($NBA_{1,2,3}$). These estimates are confirmed by mean heritabilities of 0.09 and 0.07 for litter size as presented by Haley et al. (1988) and Lamberson (1990) and average heritability estimates of recent publications (Table 2-12) of 0.10, 0.11 and 0.11 for number born alive in the first, second and third parity, respectively. Heritability estimates for reproduction traits estimated separately for the two breeds are shown in Appendix 7.

Rydhmer et al. (1992) showed the importance of a high average piglet birth weight for piglet survival. This trait is a ratio of litter birth weight and number born alive. Possible problems in analysing a ratio have been discussed previously (Chapter 5.1.2), and therefore both traits litter birth weight ($LBW_{1,2,3}$) and average piglet weight at birth ($ABW_{1,2,3}$) are analysed. Litter birth weight in the first parity (LBW_1) has a lower heritability (0.08) in comparison to litter birth weights in the second and third parity ($LBW_{2,3}$) with estimates of 0.22 and 0.20. A lower genetic variance rather than an increase in environmental variance is the cause for this reduced heritability for litter birth weight in the first parity. Gilts are farrowing at 337 days on average and their uterine capacity is reduced in comparison to multiparous sows. This might be a restriction on expression of their genetic potential in litter birth weight. Heritabilities are 0.15, 0.16, 0.15 for average piglet birth weight in the first three parities (Table 5-16).

Table 5-16 Heritabilities with standard errors (s.e.) and variance components for reproduction traits of the sow

Trait	N	h^2	s.e. of h^2	σ^2_a	σ^2_e	σ^2_p
NBA_1	5986	0.08	0.02	0.48	5.42	5.90
NBA_2	4113	0.09	0.02	0.55	5.39	5.94
NBA_3	2965	0.08	0.03	0.50	5.60	6.11
LBW_1	4306	0.08	0.02	0.55	6.71	7.26
LBW_2	2084	0.22	0.05	1.88	6.57	8.44
LBW_3	1234	0.20	0.07	2.17	8.42	10.59
ABW_1	4206	0.15	0.03	18425	105703	124129
ABW_2	2032	0.16	0.04	16161	82125	98286
ABW_3	1216	0.15	0.06	11564	67940	79504
$LW21_1$	1111	0.07	0.06	6.02	80.50	86.52

Literature estimates of heritabilities for litter birth weight average 0.20 (Table 2-14). Estimates vary from 0.10 to 0.54 for research data while heritabilities range from 0.11 to 0.16 for field data. Estimates of heritabilities are also lower for average piglet weight at birth derived from field data (h^2 = 0.21, Mercer and Crump, 1990) than from research herds (h^2 = 0.65: Irvin and Swiger, 1990; h^2 = 0.53; Ferguson et al., 1985). Rydhmer et al. (1992) pointed out that litter birth weight is influenced by the milk intake of piglets after birth which is dependent on the

milk performance of the sow. An early weighing of the litter after birth is therefore important and delays in recording litter birth weight in field data might be the reason for lower heritabilities. In practical situations the time span between farrowing and weighing of the litter is dependent on the farrowing time during the day and could be 24 hours or even longer on weekends. In addition, the recording policy for litter birth weight changed in the third quarter of 1993 in this herd, when litter birth weight was recorded 3 days after farrowing and includes cross fostered piglets. This inconsistency in data recording and weighing after cross fostering leads to an increase in environmental variation and therefore reduced heritability (Tholen et al., 1996b).

Litter weight at 21 days recorded in the first parity ($LW21_1$) is lowly heritable (Table 5-16) which is in agreement with mean literature values ranging from 0.07 to 0.14 across parities (Table 2-15). Litter weight at 21 days is mainly influenced by number of piglets weighed and the age of the litter at weighing. Tholen et al. (1996b) compared regression coefficients for number of piglets after weighing. Linear and quadratic regression coefficients varied considerably across parities and herds for these two effects. This shows possible limitations in adjusting environmental variation caused by different policies in cross fostering and weaning. The fixed effect model explained 26% of the total variation for litter weight at 21 days for this herd which was also analysed by Tholen et al. (1996b). In contrast, 72% to 78% was explained by the fixed effect model for this trait in the second herd analysed by Tholen et al. (1996b) which resulted in higher heritabilities of 0.17, 0.12 and 0.28 for the first to third parity.

5.3.3 Estimation of genetic correlations

Reproduction traits are measurements of the sow while performance, carcase and meat quality traits are recorded on offspring of sows. Genetic correlations are therefore estimated for traits that are measured on different animals. This is possible through genetic links in the numerator relationship matrix. However, it is not possible to estimate environmental correlations between this combination of traits and therefore phenotypic correlations will also not be shown.

5.3.3.1 Reproduction traits

Genetic, environmental and phenotypic correlations between reproduction traits of the sow are presented in Table 5-17. Estimates of genetic correlations between litter size in the first to third parity ($NBA_{1,2,3}$) are positive. Number born alive in the first parity is moderately correlated with litter size in the second and third parity (r_g = 0.62 for NBA_2, r_g = 0.61 for NBA_3)

supporting the analysis of number born alive in the first parity as a separate trait to litter size in later parities. Although Haley et al. (1988) suggested analysing litter size as repeated records, results from more recent studies (Table 2-13) confirm that number born alive in the first parity should be regarded as a different trait. The genetic correlation between number born alive in the second and third parity is high (0.95) and these traits should therefore be treated as repeated records in selection programs.

Genetic correlations between litter birth weights ($LBW_{1,2,3}$) in the first to third parity and between average piglet weights ($ABW_{1,2,3}$) in the first to third parity are high ranging from 0.52 to 0.98 (Table 5-17). However, genetic correlations between performance in the first parity and litter birth weight and average piglet weight at birth in the second and third parity are significantly different from one. Litter birth weight and average piglet weight at birth in the first litter should therefore be analysed as a separate trait while performance in later parities should be regarded as repeated records.

Litter birth weight in the first parity (LBW_1) has low negative genetic correlations (-0.15, -0.12, -0.20) with litter size ($NBA_{1,2,3}$) while litter birth weight in later parities ($LBW_{2,3}$) is positively correlated with number born alive with genetic correlations ranging from -0.04 to 0.43. In this study litter birth weight was not corrected for number born alive since number born alive is used as a selection criterion. This is in agreement with reviewed studies (Table 2-16) and a literature mean of genetic correlations of 0.72 (Table 2-20) is therefore expected. The negative genetic correlations between litter birth weight and number born alive could be caused by the recording procedure of litter birth weight. Piglet mortality is higher in larger litters and in litters with a lower average birth weight (Fraser, 1990). Therefore, gilts with large litters are more likely to have a higher mortality rate especially within the first few days after farrowing. With the delay of recording litter birth weight this will reduce the total litter weight. In addition, the cross fostering practice of putting smaller piglets on to gilts and taking their own bigger piglets away to older sows could also lead to this negative genetic correlation.

Genetic correlations between litter size ($NBA_{1,2,3}$) and average piglet weight at birth ($ABW_{1,2,3}$) vary from -0.86 to -0.27 (Table 5-17). Rydhmer et al. (1992) also found an unfavourable relationship between number born alive and average piglet weight at birth (-0.34) while Irvin and Swiger (1984) found no relationship (0.05) between these two traits. Genetic correlations between these traits averaged -0.43 and -0.43 for the two herds analysed by Tholen et al. (1996b).

Table 5-17 Genetic correlations (first row), environmental correlations (second row) with standard errors (in brackets) and phenotypic correlations between reproduction traits

	NBA_2	NBA_3	LBW_1	LBW_2	LBW_3	ABW_1	ABW_2	ABW_3	$LW21_1$
NBA_1	0.62 (0.19)	0.61 (0.30)	-0.15 (0.17)	0.13 (0.22)	-0.04 (0.20)	-0.74 (0.10)	-0.34 (0.25)	-0.27 (0.32)	-0.14 (0.32)[1]
	0.11	0.09	0.42	0.08	0.06	-0.66	-0.05	-0.03	-0.07
	0.16	0.14	0.37	0.08	0.05	-0.66	-0.08	-0.05	-0.08
NBA_2		0.95 (0.04)	-0.12 (0.17)	0.43 (0.18)	0.28 (0.29)	-0.41 (0.21)	-0.69 (0.16)	-0.40 (0.35)	-0.15 (0.30)[1]
		0.12	0.06	0.45	0.04	-0.09	-0.67	-0.09	0.05
		0.21	0.04	0.44	0.08	-0.12	-0.68	-0.12	0.03
NBA_3			-0.20 (0.30)	0.22 (0.27)	0.25 (0.29)	-0.51 (0.24)	-0.86 (0.36)	-0.56 (0.25)	-0.75 (0.17)[1]
			0.10	0.05	0.62	0.00	-0.07	-0.57	0.10
			0.08	0.08	0.57	-0.07	-0.15	-0.56	0.03
LBW_1				0.78 (0.16)	0.52 (0.28)	0.78 (0.13)	0.87 (0.23)	0.55 (0.36)	0.14 (0.32)[1]
				0.10	0.11	0.29	0.07	0.09	0.14
				0.21	0.16	0.35	0.15	0.15	0.14
LBW_2					0.98 (0.34)	0.47 (0.17)	0.29 (0.21)	0.41 (0.32)	-0.10 (0.31)[1]
					0.00	-0.02	0.27	0.05	0.07
					0.20	0.07	0.27	0.11	0.05
LBW_3						0.29 (0.28)	0.48 (0.29)	0.73 (0.27)	0.43 (0.31)[1]
						-0.01	0.03	0.21	0.00
						0.04	0.10	0.30	0.05
ABW_1							0.79 (0.19)	0.58 (0.30)	-0.11 (0.29)[1]
							0.07	0.04	0.28
							0.18	0.12	0.23
ABW_2								0.78 (0.33)	0.42 (0.27)[1]
								0.18	-0.04
								0.26	0.00
ABW_3									0.48 (0.32)[1]
									0.00
									0.05

[1] estimates of standard errors obtained from approximation of Robertson (1959)

Litter birth weight ($LBW_{1,2,3}$) and average piglet weight at birth ($ABW_{1,2,3}$) are moderately correlated (rg: 0.29 to 0.87). A high birth weight is therefore associated with a high average piglet weight at birth which is confirmed by the study of Irvin and Swiger (1984) who found a genetic correlation of 0.76 between these two traits.

Genetic correlations between litter weight at 21 days and other reproduction traits of the sow are generally not different from zero. In contrast, literature means of genetic correlations between 21 day litter weight and other reproductive traits are moderately positively correlated with litter size (r_g = 0.61), litter birth weight (0.79) and average piglet weight at birth (0.40) (Table 2-20). Differing from the studies in the review, litter weight at 21 days was adjusted for number of piglets after cross fostering in this study which is closely related to number of piglets born alive. Therefore, this trait has to be regarded as the average piglet weight at 21 days which explains the lowly negative genetic correlations with number born alive. Tholen et al. (1996b) also adjusted 21 day litter weight for number of piglets after cross fostering, and genetic correlations between number born alive and 21 day litter weight averaged -0.43 across parities while average piglet weight at birth was positively correlated with 21 day litter weight (average rg across parities: 0.32).

5.3.3.2 Reproduction and production traits

Genetic correlations between reproductive traits of the sow and production traits of the offspring are presented in (Table 5-18). Litter size ($NBA_{1,2,3}$) is negatively correlated with growth rate traits (ADG1, ADG2, ADG3). This relationship is stronger between number born alive in the first parity (NBA_1) and growth rate traits (r_g = -0.30, -0.42, - 0.31) in comparison to litter size in the second and third parity ($NBA_{2,3}$). Genetic correlations between these traits and average daily gain traits range from -0.30 to 0.00 while lean meat growth has genetic correlations of -0.21 and -0.20 with litter size in the second and third parity. The literature mean of genetic correlations between litter size and growth rate is -0.02 for litter size in gilts and 0.14 for litter size in later parities (Table 2-21). The tendency of a stronger negative correlation between litter size in gilts and growth rate is also confirmed by Standal (1973b) who found that pigs from gilt litters and especially large gilt litters grew slower than average.

Considering that a high growth rate is associated with a high feed intake, the lowly negative genetic correlations (-0.19, -0.24, -0.05) between litter size ($NBA_{1,2,3}$) and feed intake (FDINT) are therefore in agreement with relationships between litter size and growth rate. The average of genetic correlations between litter size and feed intake presented by Short et al. (1994) is -0.12 (Table 2-21) thus supporting these results.

Genetic correlations between litter size ($NBA_{1,2,3}$) and feed efficiency (FCR) are not significantly different from zero. The averages of genetic correlations presented in the literature between these two traits were -0.12 for gilts and -0.08 for later parities (Table 2-21). However, these means are only based on one study (Morris, 1975) and estimates of genetic correlations vary from -0.46 to 0.49 between data sets.

Table 5-18 Genetic correlations with standard errors (in brackets) between reproduction and production traits

	ADG1		ADG2		ADG3		FDINT		FCR		LEANG	
NBA_1	-0.30	(0.14)[1]	-0.42	(0.16)[1]	-0.31	(0.12)[1]	-0.19	(0.23	0.09	(0.30)	*	
NBA_2	-0.01	(0.14)[1]	-0.30	(0.17)[1]	-0.07	(0.12)[1]	-0.24	(0.25)	0.00	(0.30)	-0.21	(0.15)[1]
NBA_3	-0.26	(0.17)[1]	0.00	(0.20)[1]	-0.20	(0.16)[1]	-0.05	(0.29)	0.08	(0.18)[1]	-0.20	(0.19)[1]
LBW_1	0.39	(0.13)[1]	0.18	(0.20)[1]	0.42	(0.13)[1]	-0.11	(0.22)	-0.53	(0.27)	0.37	(0.14)[1]
LBW_2	0.38	(0.12)[1]	0.08	(0.19)[1]	*		-0.20	(0.22)	-0.60	(0.28)	0.33	(0.14)[1]
LBW_3	0.35	(0.18)[1]	0.12	(0.22)[1]	0.38	(0.13)[1]	-0.22	(0.31)	-0.57	(0.45)	0.38	(0.17)[1]
ABW_1	0.33	(0.12)[1]	0.45	(0.14)[1]	0.42	(0.10)[1]	0.16	(0.20)	-0.38	(0.25)	0.28	(0.13)[1]
ABW_2	0.27	(0.14)[1]	0.35	(0.17)[1]	0.35	(0.12)[1]	0.03	(0.26)	-0.43	(0.33)	0.23	(0.16)[1]
ABW_3	0.33	(0.17)[1]	0.09	(0.25)[1]	0.38	(0.14)[1]	0.10	(0.35)	-0.13	(0.46)	0.21	(0.20)[1]

* estimate is either one or minus one

[1] estimates of standard errors obtained from approximation of Robertson (1959)

Litter birth weight ($LBW_{1,2,3}$) and average piglet weight at birth ($ABW_{1,2,3}$) are positively correlated with growth rate (ADG1 ADG2, ADG3) as well as lean meat growth (LEANG). Estimates of genetic correlations range from 0.08 to 0.42 for litter birth weight and from 0.09 to 0.45 for average piglet weight at birth. These estimates are in agreement with the genetic correlation presented by Young et al. (1978) between average daily gain and litter birth weight and the mean literature value of 0.45 (Table 2-21) for the genetic relationship between average piglet weight and growth rate.

Table 5-18 shows negative genetic correlations of -0.11, -0.20 and -0.22 between litter birth weight in the first to third parity ($LBW_{1,2,3}$) and feed intake (FDINT). In contrast, average piglet weight at birth ($ABW_{1,2,3}$) is positively correlated with feed intake with estimates ranging from 0.03 to 0.16 which is not significantly different from zero. Litter birth weight and average piglet weight at birth are negatively correlated with feed conversion ratio (FCR). This favourable relationship is stronger for litter birth weight ($LBW_{1,2,3}$) with estimates of -0.53, -0.60 and -0.57 for the three parities than for average piglet weight at birth with genetic correlations with feed efficiency of -0.38, -0.43 and -0.13 for the first three parities.

5.3.3.3 Reproduction and carcase traits

Genetic correlations between number born alive ($NBA_{1,2,3}$) and backfat measured with real time ultrasound (LFDP2, LFD3/4) range from -0.07 to 0.17 (Table 5-19). Estimates of genetic correlations between litter size and carcase backfat measurements (FDP2, FD3/4) vary from -0.28 to 0.16. This indicates no genetic relationship between leanness and litter size which is also apparent in genetic correlations of lean meat percentage (LEAN, LEANL) and muscle depth (LMD3/4) with litter size ($NBA_{1,2,3}$). Mean literature estimates of genetic correlations between number born alive in gilts and later parities to backfat are low with estimates of 0.08 and -0.02 (Table 2-21).

Weight of the back leg (BLW) and lean meat weight of the back leg (LMW) are closely related to average daily gain. Negative genetic correlations in the range of -0.45 to -0.08 between these two weight measurements and litter size are therefore in agreement with genetic correlations found between average daily gain traits and litter size (Table 5-18).

In contrast to litter size, litter weight at birth ($LBW_{1,2,3}$) has a favourable genetic relationship to backfat measurements and leanness. Genetic correlations range from -0.54 to -0.08 for backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) and litter birth weight ($LBW_{1,2,3}$) and from 0.08 to 0.47 for lean meat percentage traits (LEANL, LEAN) and litter birth weight. These estimates are of higher magnitude than the genetic correlation of -0.05 presented by Young et al. (1978) for backfat and litter birth weight.

Table 5-19 Genetic correlations with standard errors (in brackets) between reproduction and carcase traits

	NBA_1		NBA_2		NBA_3		LBW_1		LBW_2		LBW_3		ABW_1		ABW_2		ABW_3	
LFDP2	0.10	(0.17)	0.17	(0.19)	-0.07	(0.23)	-0.39	(0.19)	-0.43	(0.21)	-0.30	(0.25)	-0.07	(0.11)	-0.33	(0.09)[1]	-0.14	(0.13)[1]
LFD3/4	0.09	(0.17)	0.16	(0.19)	-0.05	(0.23)	-0.35	(0.09)[1]	*		-0.23	(0.11)	-0.06	(0.09)[1]	*		*	
LMD3/4	-0.13	(0.23)	0.25	(0.25)	0.00	(0.30)	-0.16	(0.24)	0.31	(0.29)	0.15	(0.33)	-0.18	(0.16)	-0.09	(0.15)[1]	0.18	(0.34)
FDP2	-0.15	(0.21)	0.16	(0.23)	-0.07	(0.27)	-0.23	(0.22)	-0.44	(0.25)	-0.08	(0.31)	*		*		0.05	(0.32)
FD3/4	-0.28	(0.23)	-0.02	(0.26)	-0.28	(0.28)	-0.26	(0.25)	-0.54	(0.27)	-0.22	(0.36)	0.12	(0.17)	-0.13	(0.26)	0.13	(0.37)
BLW	-0.45	(0.13)[1]	-0.23	(0.15)[1]	-0.24	(0.19)[1]	0.46	(0.13)[1]	0.42	(0.13)[1]	0.42	(0.16)	0.29	(0.14)[1]	0.27	(0.16)[1]	*	
LMW	-0.31	(0.14)[1]	-0.26	(0.13)[1]	-0.08	(0.18)[1]	0.52	(0.11)[1]	0.55	(0.10)[1]	0.61	(0.11)	0.13	(0.13)[1]	0.32	(0.14)[1]	0.37	(0.17)[1]
LEANL	-0.11	(0.18)	-0.09	(0.20)	0.08	(0.23)	0.30	(0.19)	0.47	(0.21)	0.28	(0.25)	0.04	(0.12)	0.23	(0.09)[1]	0.13	(0.27)
LEAN	0.15	(0.12)[1]	-0.16	(0.12)[1]	0.06	(0.16)[1]	0.23	(0.22)	0.44	(0.25)	0.08	(0.31)	-0.10	(0.14)	0.20	(0.12)[1]	-0.04	(0.32)

* estimate converged to 1 or -1

[1] estimates of standard errors obtained from approximation of Robertson (1959)

Litter birth weight ($LBW_{1,2,3}$) as well as average piglet birth weight ($ABW_{1,2,3}$) are positively correlated with weight of the back leg (BLW) and lean meat weight of the back leg (LMW). Estimates of genetic correlations are in the range of 0.42 to 0.61 for litter birth weight ($LBW_{1,2,3}$) and vary from 0.13 to 0.37 for average piglet weight at birth ($ABW_{1,2,3}$). Average piglet weight at birth is the ratio of litter birth weight to litter size which is negatively correlated with back leg weight and lean meat weight of the back leg. This explains the lower genetic correlations of average piglet weight at birth with these carcase characteristics. However, overall these traits are positively related to growth rate which implies positive genetic correlations among them.

Table 5-19 shows genetic correlations of -0.33 to 0.13 for backfat measurements (LFDP2, LFD3/4, FDP2, FD3/4) and piglet weight at birth ($ABW_{1,2,3}$). and a range of -0.10 to 0.23 for genetic correlations between lean meat content (LEANL, LEAN) and average piglet weight. Average piglet weight at birth is the ratio of litter birth weight and number born alive and non significant correlations between litter size and leanness are reflected in these genetic correlations between average piglet weight and carcase leanness.

5.3.3.4 Reproduction and meat quality

Table 5-20 presents correlations between reproduction and meat quality traits. Genetic correlations between pH45 and litter size ($NBA_{1,2,3}$) range from -0.34 to -0.19 indicating that a higher litter size is associated with a lower pH at 45 minutes. In regard to PSE meat, this is an unfavourable relationship which is also apparent between pH45 and litter birth weight ($LBW_{1,2,3}$) with genetic correlations varying from -0.40 to -0.22. In contrast, average piglet weight at birth ($ABW_{1,2,3}$) is positively correlated with pH45 (0.13, 0.05 and 0.30 for $ABW_{1,2,3}$).

Genetic correlations between ultimate pH (pH24) and reproduction traits (NBA, LBW, ABW) are inconsistent between parities and generally of low magnitude.

Both colour measurements (CLD, CMD) are negatively correlated with litter size ($NBA_{1,2,3}$) and estimates of genetic correlations vary from -0.53 to -0.11. A darker colour is therefore related to a higher litter size. This relationship also exists between colour measurements and litter birth weight ($LBW_{1,2,3}$) with negative genetic correlations of -0.28 to 0.00. An exception is the genetic correlation between litter birth weight in the third parity (LBW_3) and colour of the *m. longissimus dorsi* (CLD) which has a genetic correlation of 0.41.

Genetic correlations range from -0.08 to 0.34 for litter size in the first to third parity ($NBA_{1,2,3}$) and drip loss percentage (DLP). Litter birth weight in the first and second parity ($LBW_{1,2}$) have no genetic relationship to drip loss percentage while litter birth weight in the third parity (LBW_3) is moderately correlated (0.42) with drip loss percentage. Finally average piglet weight at birth in the first to third parity ($ABW_{1,2,3}$) has genetic correlations of -0.23, 0.34 and 0.25 with drip loss percentage. Genetic correlations are therefore inconsistent and of low magnitude.

Table 5-20 Genetic correlations with standard errors* (in brackets) between reproduction and meat quality traits

	pH45		pH24		CLD		CMD		DLP		IMF	
NBA_1	-0.34	(0.16)	-0.26	(0.18)	-0.11	(0.16)	-0.42	(0.12)	0.17	(0.16)	-0.11	(0.14)
NBA_2	-0.19	(0.17)	0.10	(0.18)	-0.53	(0.11)	-0.45	(0.11)	0.34	(0.14)	0.08	(0.14)
NBA_3	-0.26	(0.21)	-0.25	(0.22)	-0.27	(0.18)	-0.34	(0.16)	-0.08	(0.20)	0.11	(0.18)
LBW_1	-0.30	(0.17)	0.08	(0.19)	-0.11	(0.16)	0.00	(0.14)	0.05	(0.16)	-0.37	(0.13)
LBW_2	-0.22	(0.14)	0.17	(0.17)	-0.28	(0.14)	-0.27	(0.13)	0.10	(0.15)	-0.32	(0.12)
LBW_3	-0.40	(0.17)	-0.23	(0.20)	0.41	(0.12)	-0.09	(0.16)	0.42	(0.15)	-0.26	(0.15)
ABW_1	0.13	(0.16)	0.19	(0.16)	0.00	(0.15)	0.21	(0.12)	-0.23	(0.14)	-0.15	(0.13)
ABW_2	0.05	(0.18)	-0.03	(0.19)	0.36	(0.14)	0.00	(0.14)	0.34	(0.14)	-0.19	(0.14)
ABW_3	0.30	(0.21)	0.08	(0.24)	0.31	(0.18)	0.25	(0.19)	0.25	(0.21)	-0.12	(0.18)

* standard errors obtained from approximation of Robertson (1959)

Estimates of genetic correlations between reproduction traits and meat quality traits are not available in the literature. However, both groups of traits are influenced by the halothane gene. The detrimental effect of the halothane gene on meat quality traits is summarized in Table 2-2. Various studies analysed the effect of the halothane gene on reproductive performance of the sow (Willeke et al., 1984; Lampo et al., 1985; Nyström and Andersson, 1993). Willeke et al. (1984) found that halothane negative sows were superior to the halothane positive sows in litter size at birth by 0.17 piglets, and in litter size at the 28th day by 0.32 piglets. Losses until the 28th day were reduced by 0.14 for halothane negative sows in comparison to halothane positive sows. Lampo et al. (1985) found only from the second farrowing an increase in litter size of 0.4 for halothane negative pigs. In a more recent study, Nyström and Anderson (1993) found no differences in litter size between halothane carriers and non-carriers. However, still born rate was lower and litter weights were lower at three, six and nine weeks for halothane carriers.

The influence of the halothane gene on reproductive performance and meat quality traits would suggest that an inferior meat quality in regard to PSE meat is associated with lower reproductive performance. This is only apparent in genetic correlations between colour measurements and the sow performance traits litter size and litter weight at birth. This analysis included two breeds with different levels of the halothane gene. Hermesch et al. (1995) presented genetic correlations between litter size and meat quality traits for Landrace pigs included in this analysis. Genetic correlations between litter size and meat quality ranged from -0.53 to -0.24 for colour of the *m. longissimus dorsi* and from -0.41 to -0.14 for drip loss percentage. The incidence of the halothane gene is higher in Landrace which could explain the higher magnitude of favourable genetic correlations found by Hermesch et al. (1995) between litter size and the meat quality traits colour and drip loss percentage.

Finally, intramuscular fat content (IMF) has no genetic relationship with litter size ($NBA_{1,2,3}$) However, a higher intramuscular fat content is associated with a lower litter birth weight ($LBW_{1,2,3}$) with genetic correlations ranging from -0.37 to -0.26 and a lower average piglet weight at birth ($ABW_{1,2,3}$). Genetic correlations are -0.15, -0.19 and -0.12 for the first three parities. Intramuscular fat content is reduced for leaner pigs. It was shown in the previous chapter that leanness is not genetically related to litter size, while litter birth weight and average piglet weight at birth are favourably related to leanness. These genetic correlations between reproduction traits and intramuscular fat content are therefore in agreement with results between leanness and reproduction traits.

5.3.4 Conclusions

Reproductive performance of the sow is lowly heritable. Litter size and litter birth weight in the first parity have heritability estimates of 0.08 and 0.09. Heritability estimates are higher for litter birth weight in the second and third parity (0.22 and 0.20) while heritability estimates are intermediate for average piglet weight at birth with values of 0.15, 0.16 and 0.15. Management practices of cross fostering and weaning influence litter weight at 21 days. These effects are not always sufficiently adjusted for by the model leading to a reduction in heritability estimate for 21 day litter weight in the first parity to 0.07.

Reproductive performance in the first parity should be regarded as a different trait to reproductive performance in later parities. However, differences in sow performance between first and later parities are smaller for litter birth weight and average piglet weight at birth than for litter size.

Litter size is unfavourably correlated with litter birth weight in the first parity, average piglet weight at birth and 21 day litter weight. A higher litter birth weight is associated with a higher average piglet weight at birth.

Litter size is negatively correlated with growth rate and lean meat growth, while litter birth weight and average piglet weight at birth have positive genetic correlations with these growth performance traits. No significant relationship exists between feed intake and feed efficiency and reproductive traits.

Litter size and leanness of the pig are not genetically correlated. Both carcase weight measurements, weight of the back leg and lean meat weight of the back leg are negatively correlated with litter size. In contrast, litter birth weight traits are favourably correlated with carcase traits. Average piglet weight at birth is positively correlated with carcase weight traits but has no significant relationship to backfat measurement and lean meat percentage.

Genetic correlations between sow reproductive performance and meat quality traits differ between traits and parities. pH at 45 is negatively correlated with litter size and litter birth weight while no significant genetic correlations were found between pH45 and average piglet weight at birth. pH recorded 24 hours after slaughter has no significant relationship with reproductive traits. A darker colour is associated with a higher number of piglets born alive and litter birth weight but at the same time a reduced average piglet weight at birth. Genetic correlations between drip loss percentage and reproduction traits are inconsistent between parities and often of low magnitude.

Intramuscular fat content has no genetic correlation with number born alive. Genetic correlations with litter birth weight and average piglet weight at birth are negative. This corresponds to a higher reproductive performance for leaner pigs which have a lower intramuscular fat content.

CHAPTER 6

General Discussion

6.1 Introduction

The objective of this study was to obtain a complete set of genetic parameters for reproduction, production, carcase and meat quality traits. To achieve this aim a data set was accumulated at Bunge Meat Industries including growth and feed efficiency performance as well as carcase and meat quality traits. This data set was extended in the later stage of the project to processing traits including ham yield and bacon yield. Information about sow productivity was obtained from data of the herd recording system of Bunge Meat Industries.

Important aspects of the project are discussed in this chapter including data recording and testing procedures. Subsequently, estimates from bivariate and multivariate analyses are compared. Finally, individual traits are discussed and strategies of using different traits in a selection index are shown.

6.2 Data recording and testing procedure

Design of project

It was shown in chapter 5.1 that the structure of the data set can affect estimation of different random effects. Performance traits are often influenced by environmental components which are common to litter mates. However, litter mates are also full sibs and in order to estimate additive genetic effects and the litter effects simultaneously a reasonable number of piglets per litter is important. In this data set the number of piglets per litter was low and 15 % of pigs had no records of litter mates available. This led to an over estimation of the litter effect and an underestimation of additive genetic effects in the Large White population. It was concluded that these two random effects are better estimated for Large White by discarding pigs that have no litter mates available.

In this experiment the total number of pigs per week was limited to 40 due to the test station capacity. It was anticipated that these 40 piglets could be obtained from 20 litters with two litter mates per litter. Besides difficulties in the simultaneous estimation of litter effects and additive genetic effects it is questionable whether this design led to the lowest standard errors in genetic parameters. The optimal family size in sib analyses to estimate genetic parameters is $n = 2/h^2$ for a full sib design and $n = 4/h^2$ for a half sib design (Falconer and Mackay, 1996) assuming no variance due to dominance and common environment. Although an animal model was used for the analysis, the statement that the loss of efficiency is much greater if the family size is below the optimum than above the optimum (Falconer and Mackay, 1996) is also true in this situation. The average size of fullsib families is 2.3 and therefore, in theory, the experiment should have been designed to use fewer litters with more piglets per litter. In practice however, this might lead to a pre-selection of large litters and the number of piglets tagged might have been insufficient. This was enhanced by restricting the data to one sex which limits the number of candidates per litter. The practice of tagging as many piglets per litter as there were available, which was done in the last part of the project, is therefore the best practical compromise.

Animal Identification

Animals taken for this project were tagged with yellow eartags at the age of three weeks. These animals were randomly chosen from their litter and kept together in weekly batches after weaning. Although pigs stayed together in one pen from three to 18 weeks and therefore could be identified as pigs for this project they did not receive any special treatment which could have biased these results. Any possible effect of the pen however was taken into account by putting recording week rather than season classes of two to three months into the model.

In total, 4700 animals were tagged at the age of three weeks but only 3600 animals entered the boar test station at 18 weeks. This reduction in numbers is due to the loss of earmarks and relocation of project animals to other pens so that they could not be found at the age of 18 weeks. Animals were tagged at 21 days so they also could be weighed at this age. However, this additional weight measurement is of minor importance and to guarantee the required number of animals in the project, animals could have been tagged at 18 weeks. In addition, tagging animals at 18 weeks could possibly also reduce the loss of earmarks in the abattoir during slaughter since the tag can be placed more precisely at that age and remains in the ear for a shorter period of time. On the other hand, tagging animals at 18 weeks might lead to some bias since animals might be preselected according to their weight. The biggest animals might not be used for the project since they will be used for breeding and operators might be

reluctant to take smaller animals. In addition, animals will come from different pens. Pen number might then become an important effect.

Duroc pigs

The data set included 375 Duroc animals that were tagged resulting in 275 records for Duroc pigs and it was decided not to include these animals in the analysis. The reason for this decision is the occurrence of differences in means and standard deviations for performance traits for this breed in comparison to Large White and Landrace pigs. A separate analysis of Duroc pigs was not possible and Duroc animals could only have been analysed in a pooled data set with Large White and Landrace and the expected reduction in standard errors for genetic parameters is minor.

Test station

Pigs stayed in the test station from 18 to 22 weeks. During this time pigs were single penned and feed intake was recorded manually. This is very labour intensive and the availability of electronic feeders will overcome this problem. In addition, with the use of electronic feeders, pigs could stay in groups and possible genotype by environment interactions due to different housing systems could be overcome.

Recording of meat quality traits

To use meat quality traits in a breeding programme requires the identification of animals within the abattoir. Approximately 15 % of the animals lost their earmarks during the dehairing and descalding process and records could not be collected. In addition, to ensure identification of the animal for meat quality traits, the ear notch of the pig had to be written down on the carcase. In a practical situation this is too labour intensive and other possible identification systems need to be investigated.

One possibility is the use of electronic chips implanted behind the ear (Hilbig et al., 1995). A requirement of using this identification system is the recovery of these chips on the slaughter floor. The detection of these electronic chips in the carcase is difficult under commercial slaughter conditions. Leaving any chip within the carcase is unacceptable and therefore this system of identification can currently not be recommended. Alternatively an electronic ear tag could be used. The price of these electronic ear tags is between A$10 and A$15 and they can be reused 10 times. The total cost of such an identification can be estimated to be between A$2 and A$3 per pig as cleaning costs and the loss of these earmarks have to be taken into account. An alternative would be a tattoo of the animal. Commercial abattoirs use tattoos as an identification system for pigs from different producers at present. A disadvantage is that the

tattoo has to be entered into a computer and the producer has to link the tattoo number with the animal identification. This could lead to errors in the identification of animals.

6.3 Multitrait analyses

Presented genetic correlations were estimated by bivariate analyses. However, genetic evaluation is based on multitrait analyses and variance components should be estimated with the same statistical model. A multitrait analysis of all traits was not feasible and multitrait analyses were therefore only conducted for the most important traits. These include life time average daily gain (ADG3), daily feed intake (FDINT), lean meat percentage (LEANL) and ham weight (LMW). Genetic parameters and variance components are presented in Table 6-1 for these traits. An increase in variance component estimates for feed intake is observed. In comparison to univariate estimates (Table 5-2) the additive genetic variance increases from 0.03 to 0.06 and the environmental variance increases from 0.11 to 0.16, resulting in an increase of the phenotypic variance from 0 14 to 0.22. In addition, correlations of feed intake with lean meat percentage and ham weight (LMW) increase in comparison to estimates obtained from bivariate analyses (Table 5-13).

Additive genetic variances are only expected to increase from univariate analysis to multivariate analysis if selection was applied. Pigs in this data set are a random sample of the whole population and were not selected. In a multivariate analysis a multinormal distribution is assumed which might not be the case especially when parameters are close to the parameter boundary. Hill and Thompson (1978) have shown that the probability of parameters outside the parameter space increases drastically with increased number of traits. However, REML applications will always put parameters back into the parameter space and as a consequence variance components on the diagonal are increased. This was confirmed by Hill and Thompson (1978) who showed that standard deviations of eigenvalues of a sample covariance matrix are generally biased upwards. Among these four traits, feed intake is highly correlated with average daily gain and the estimate of the genetic correlation is close to the boundary of the parameter space. Therefore the assumption of multinormal distribution might have been violated causing this increase in variance components for feed intake. Another explanation might be a non-linear relationship between average daily gain and lean meat percentage since lifetime average daily gain includes two growth rate traits (ADG1, ADG2) which have a positive (ADG1) and negative (ADG2) genetic correlation with lean meat percentage. In a further analysis feed intake was discarded and results from this three trait analysis are presented in Appendix 8. Results are not significantly different between uni- and bivariate analyses. Special emphasis has been put on meat quality traits in this project and the four meat

quality traits pH45, colour of *m. longissimus dorsi*, drip loss percentage and intramuscular fat content were analysed in a four trait analysis as well. However, estimates did not differ significantly from uni- and bivariate analyses and are therefore not presented.

Table 6-1 Variance components and genetic parameters for average daily gain, feed intake, lean meat percentage and ham weight obtained from four trait analysis

	variance components	ADG3	FDINT	LEANL	LMW
ADG3	σ^2_a : 1443	0.34[1]	0.88[2]	0.19	0.69
	σ^2_e : 2588	0.05	0.74	0.09	0.74
	σ^2_c : 197		0.77	0.13	0.72
	σ^2_p : 4228				
FDINT	σ^2_a : 0.06		0.29	-0.11	0.43
	σ^2_e : 0.16			-0.10	0.52
	σ^2_p : 0.22			-0.10	0.46
LEANL	σ^2_a : 2.97			0.63	0.58
	σ^2_e : 1.74				0.30
	σ^2_p : 4.70				0.43
LMW	σ^2_a : 0.20				0.44
	σ^2_e : 0.23				
	σ^2_c : 0.03				
	σ^2_p : 0.46				

ADG3: Lifetime average daily gain
FDINT: Daily feed intake
LEANL: Lean meat percentage based on real time ultrasound measurements
LMW: Lean meat weight of back leg

[1] on diagonal: heritabilities and c^2 effects

[2] above diagonal: genetic correlation (first row), environmental correlation (second row) and phenotypic correlation (third row)

In conclusion, although covariances between traits were obtained from bivariate analyses, no significant change was observed for multitrait analyses. Therefore in this situation where animals were randomly chosen and not selected, multitrait analyses have no benefits in comparison to bivariate analyses. However, the use of the heritabilities and genetic correlations obtained from bivariate analyses when constructing selection indices requires the matrix of

variance components to be positive definite. In order to modify estimates of genetic parameters Hayes and Hill (1980) proposed a procedure called "bending". This method was further developed by Essl (1991) who uses some prior knowledge of the population parameter in order to obtain an appropriate bending factor.

6.4 Discussion of traits

The planned direction of a breeding programme is defined by the breeding objective which should relate to the economic value of animal production. Selection criteria on the other hand are traits that assist the breeder to achieve the breeding goal. Their usefulness is dependent on genetic variances and covariances between traits and practical aspects of measuring these traits. In this project 36 traits were analysed and it is not practical to use all traits in a breeding programme. It is therefore necessary to decide which traits should be included in a recording programme and to discuss their use as selection criteria.

6.4.1 Production traits

Production traits analysed in this study included three growth rate traits, feed intake, feed conversion ratio and lean meat growth. Heritability estimates for these traits were mostly within the range of literature estimates. However, heritabilities were lower than the expected range for average daily gain recorded in the test station (ADG2) and feed conversion ratio (FCR). The possible influence of a short testing period of four weeks, without allowing pigs to adapt to the new environment prior to testing, was discussed. This leads to a higher environmental variation for average daily gain but not for feed intake. It can therefore be concluded that feed intake was not as much affected by the testing procedure (Chapter 5.1). In contrast, average daily gain and subsequently feed conversion ratio showed an increased environmental variation which might be caused by differences in gut fill at test start and test end. To overcome this problem a longer test period is therefore required. The dependence of feed conversion ratio on average daily gain can be explained by results from Simm et al. (1987) who found that a trait which is a combination of other traits is dominated by the component trait with the highest coefficient of variation.

Average daily gain is the most used production trait in breeding programmes. Estimates of heritabilities and litter effects obtained for Large White and Landrace pigs differed substantially. In addition to heterogenous variances between breeds, Klassen (1992) found heterogenous variances between herds for average daily gain in Landrace. In Australia,

breeders currently base their breeding decisions on within herd evaluations. With the development of an across herd evaluation (McPhee et al., 1995; Bunter, 1996 pers. comm.) heterogenous variances have to be taken into account in order to avoid selecting animals from more variable herds. Meuwissen et al. (1996) developed a multiplicative method to account for heterogenous phenotypic variances between herds which was applied by Reverter et al. (1996) in beef cattle for ultrasonic carcase measurements. Although correlations between estimated breeding values with and without correction for heterogeneity were greater than 0.97 for all traits, substantial re-rankings of smaller herds were observed for some traits after heterogenous variances had been taken into account.

Cost of feed accounts for 56 % of total costs in Australia (PRDC/APC, 1995). This shows the importance of an efficient pig production. Genetic improvement of feed efficiency has been discussed widely (Gunsett, 1984; Gunsett, 1987; Cleveland and Schinckel, 1988; Bereskin, 1990) and direct selection for feed conversion ratio has been shown to be less effective than selection for a linear index of the two components traits. (Gunsett, 1984). These results were confirmed in a recently completed selection experiment (Cameron, 1994; Cameron and Curran, 1994b). Responses in lean meat growth rate and lean feed conversion ratio were greater with selection on lean growth rate under ad libitum feeding than with selection on lean feed conversion ratio. There was no response in daily feed intake with selection on lean growth rate, but there was a reduction in daily feed intake with selection on lean feed conversion ratio.

Selection should therefore focus on growth rate and feed intake for production traits. However, other factors including possible genotype by environment interactions and genetic correlations with other traits have to be taken into account. Growth rate measured before the test station (ADG1) and within the test station (ADG2) are different traits. This is reflected in a genetic correlation of 0.32 (Table 5-6) between these two traits and it also becomes apparent in their genetic correlations with leanness (Table 5-8). Two factors contribute to the differences between these two growth rate traits. Firstly, animals were group penned before they entered the test station and single penned in the test station. Secondly, these growth rate traits were measured during different growing periods and differences in feed intake capacity in relation to maximum protein deposition as discussed in chapter 5.2.4 need to be considered. The development of electronic feeders allows group penning of pigs during their stay in the test station which led to an increase in genetic correlations between growth traits measured on farm and within test stations in the study by Merks and van Oijen (1994).

In contrast to literature values (Table 2-19) growth rate from three to 18 weeks is favourably correlated with leanness of the carcase (Table 5-8). Although pigs were fed ad libitum, their

feed intake capacity is not sufficient from three to 18 weeks to meet their protein deposition potential. This data set only included boars which have a higher protein deposition capacity than gilts and barrows (Campbell and Taverner, 1988) and this favourable relationship between growth rate and lean meat percentage might therefore not exist in gilts. In addition, the amount of protein in the diet influences the genetic relationship between growth rate and lean meat content (Stern, 1994). The genetic correlation between growth rate and lean meat content was negative for pigs fed a diet with a high protein content and positive for pigs fed a diet with a low protein content. These factors have to be taken into account when it is decided which genetic correlation should be used in a breeding programme. In this project, genetic correlations between life time average daily gain and leanness traits were not significantly different from zero. With the availability of leaner genotypes and the use of entire boars in Australia, it is suggested that this estimate be used in breeding programmes in contrast to literature values.

Feed intake is positively genetically correlated with backfat measurements (Table 5-8). This antagonistic relationship between feed intake and carcase traits is not new and Brandt (1987) suggested a restricted index for feed intake in order to avoid further deterioration of feed intake. This approach however does not take into account the level of feed intake in relation to the maximum protein deposition capacity. It was shown in chapter 5.2 that average daily gain before the test station is favourably correlated with lean meat content of the carcase but average daily gain in the test station is unfavourably correlated with lean meat content. This is an indication that feed intake is below the optimum feed intake for the maximum protein deposition in the earlier growing period while in the later stage of the growing period, feed intake exceeds the maximum protein deposition. Therefore feed intake needs to be considered in relation to the pig's potential for protein deposition.

A biological model based on the linear plateau relationship between protein deposition and food intake (Whittemore and Fawcett, 1976) (see Figure 2-1), was used by de Vries and Kanis (1992) to estimate economic weights for feed intake capacity. Economic weights were positive when feed intake was below the maximum protein deposition and negative in the situation when feed intake exceeded protein deposition. This model assumed a constant protein gain during the entire growing period. Results from chapter 5.2 indicate that this assumption is not valid all the time. However, de Vries and Kanis (1992) argue that increase in protein deposition in the first half of the growing period followed by a decrease in the second half of the growing period gives the same average protein deposition. Development of daily or weekly changes in protein deposition is therefore not necessary and it was recommended to estimate population averages of protein deposition from nitrogen balance experiments with a sufficient

number of animals which received different amounts of food varying from just above maintenance to ad libitum. The development of electronic feeders which are used to measure feed intake will allow easier collection of this information. In a subsequent paper, Kanis and de Vries (1992) derived selection indices to optimize selection for feed intake capacity. It was suggested that in the long term, a minimum amount of fat is necessary to guarantee sufficient meat quality. This implies that the optimum level of feed intake capacity is not at the point where maximum protein deposition is reached but at a higher feed intake capacity. In the present study however, feed intake has a genetic correlation of 0.66 with pH45. Although relationships to other meat quality traits were not significant different from zero they indicate that a higher feed intake is associated with a higher incidence of DFD meat. This relationship was confirmed by de Vries et al. (1994b) who suggested that it might result from higher maintenance requirements. Animals with higher maintenance requirements could have faster glycogen depletion before slaughter, and therefore a higher risk of DFD meat.

6.4.2 Carcase traits

In the past, breeding programmes have mainly been focusing on selecting for leaner pigs. Good response has been achieved which is due to high heritabilities of these traits and the ability to measure carcase traits on the live animal. Heritability estimates are higher for real time ultrasound measurements than for measurements taken with the Hennesy Chong machine on the carcase. This difference is most important for recording muscle depth. The heritability estimate was 0.21 for real time ultrasound showing that this measurement can be included as a further selection criterion. In contrast, muscle depth recorded with the Hennesy Chong machine is not heritable and in many cases reliable estimates of correlations with other traits could not be obtained.

Estimates of genetic correlations between real time ultrasound muscle depth and backfat measurements are low. In contrast, genetic correlations between muscle depth and weight of the back leg and weight of the ham are moderate, opening the possibility of selecting indirectly for the two weight measurements. Although ham is a valuable part of the carcase, possible benefits of increasing ham weight due to a higher carcase market value have to be compared with disadvantages in meat quality. In contrast to backfat measurements and lean meat percentage, which have low unfavourable genetic correlations with the ultimate meat quality traits colour of the *m. longissimus dorsi* (CLD) and drip loss percentage (DLP), lean meat weight of the back leg has a moderately unfavourable correlation with these meat quality traits (r_g = 0.22 for CLD; r_g = 0.36 for DLP).

This unfavourable relationship between a high ham weight and meat quality traits is economically important in the further processing of hams. The analysis of ham yield showed that ham yield is reduced for high ham weights which might be caused by a higher PSE incidence in these hams. In the future, meat quality of pork will become more important and therefore it might not be desirable to further increase ham weight.

With the selection for higher leanness and higher ham weights, optimum levels might have been reached in these traits. To further improve the carcase value, other parts of the carcase have to be analysed including the middle of the carcase. Estimates of genetic correlations between middle yield and other traits showed that middle yield was increased for PSE meat. It was discussed that this relationship might be due to the processing procedure and might not be applicable to other processing procedures when middles are defatted and derinded, for example. In Australia, it is anticipated that to further increase the value of the middle, the lean meat content of the middle should be increased. Although this opens the possibility to use the middle for other products, barbecue meat for example (Fewson et al., 1990), it also might influence the yield of the middle. The genetic relationship between PSE meat and yield of the middle found in this study was due to this specific situation with the processing procedure having the main influence. Further selection for leanness in middles and other processing procedures might lead to unfavourable relationships between PSE meat and bacon yield.

6.4.3 Meat quality traits

The importance of meat quality in Australia became apparent in a survey conducted by the Pig Research and Development Corporation (PRDC, 1993). In that survey, 30 % of all pigs developed PSE and the total costs for the pig industry were estimated to be A$23 m annually. Large White and Landrace have different heritability estimates for colour measurements and drip loss percentage (Chapter 5.1) and the higher estimates in Landrace might be due to a higher incidence of the halothane gene in this breed. Therefore, a first step to improve meat quality is the reduction of the halothane gene. However, even without the halothane gene in a population, the meat quality traits colour and drip loss percentage still have a moderate genetic variation which could be used to genetically improve meat quality. In contrast, heritability estimates for pH measurements were low for both breeds and this together with a low additive genetic variance will limit possible response in these traits. The slaughter day effect accounted for 20 % of the total variation for colour and drip loss measurements and 40 % of pH measurements. Therefore, the genetic improvement of meat quality has to be accompanied by an improvement of the slaughter environment.

Although pH45 has a low heritability and genetic correlations are moderate between colour of the *m. longissimus dorsi* and drip loss percentage (r_g = -0.23 with CLD; r_g=-0.44 with DLP; Table 5-4) it has the benefit of being measured shortly after slaughter. Since many carcasses are marketed on the slaughter day, it is often not possible to take meat quality measurements 24 hours after slaughter. However, it is crucial for this measurement that pH is taken exactly 45 minutes after slaughter and any variation in time period after slaughter will bias this measurement. pH45 was taken directly before the carcase entered the chiller. A second measurement place in addition to the grading station was therefore required. To overcome this problem, research is currently underway in Australia to develop the use of the reflectance value obtained from the Hennesy Chong grading machine (Myler, 1995). This measurement does not require any additional measurements and it is therefore very inexpensive. Li et al. (1989) and Kern et al. (1990) investigated the use of reflectance value to measure meat quality. It was concluded that the reflectance value is an indicator of meat quality. However, a time period of at least 30 minutes but ideally 40 to 45 minutes after slaughter should be kept when taking this measurement.

pH24 has a low heritability as well as low phenotypic standard deviation which limits the possible response in this trait. In addition, pH24 is highly correlated with colour of the *m. longissimus dorsi* and drip loss percentage (Table 5-9) and does not provide a substantial amount of additional information to these traits. Genetic correlations with production and carcase traits are not significantly different from zero (Table 5-10, Table 5-11) and no correlated response is expected in this trait. Taking into account that the coefficient of variation for this trait is 40% for the slaughter day it can be concluded that pH24 can be neglected in breeding programmes. This is further confirmed by Glodek et al. (1993) who found no genetic relationships between pH24 and palatability characteristics.

Meat quality is currently not paid for but a high drip loss is of direct economical importance to the processing industry due to the weight loss during processing. Recording of drip loss percentage in this project was labour intensive and therefore costly (A$6 per pig, O'Shea, 1995 pers. comm.). The high genetic correlation between colour of the *m. longissimus dorsi* (CLD) and drip loss percentage of 0.80 indicates the use of colour as a selection criterion. The use of drip loss percentage and colour as selection criteria would be expensive based on measurement techniques used in this project. These techniques require the cut of the carcase and drip loss percentage even requires a whole chop weighing approximately 500 grams. An alternative colour measurement would be the measurement with Fibre Optic Probe (FOP) which does not require a meat surface as required by the Minolta Chromamometer but instead has a sonde that is injected into the meat and carcasses are left intact.

The significance of intramuscular fat in breeding programmes is based on its favourable relationship to eating quality (Cameron 1990b; Lo et al., 1992; de Vol et al., 1988). However, an intramuscular fat content of 2.5 % is required to obtain an improvement in eating quality (de Vol et al., 1988). Both white breeds, Large White and Landrace, are below this value with a mean of 1.7%. Given the standard deviation of 0.58 and heritability of 0.35 genetic progress in this trait is possible. In addition, selection for intramuscular fat content might be supported by a single gene affecting this trait which was identified in Meishan crossbreds by Janss et al. (1994).

Intramuscular fat content was determined by ether extraction and Near Infrared. These measurements require a meat sample of the *m. longissimus dorsi* and requirements in time and costs of these measurements prohibit taking these measurements in practical situations. However, Wilson et al. (1992) used image analysis of ultrasonic scans to measure intramuscular fat content in vivo. The development of such a measurement technique in pigs would make the measurement of intramuscular fat content on the breeding animal feasible.

6.4.4 Reproduction traits

Reproductive performance of the sow was described through litter size, litter birth weight, average piglet weight at birth and 21 day litter weight. Litter size is the reproductive trait mostly used in breeding programmes. Although litter size has a low heritability, good response can be achieved for this trait due to the high phenotypic variation (Haley et al., 1988).

The possible response in litter size in theory stands in contrast to the lack of response in litter size, although annual response of one to two percent was achieved in number of piglets weaned (de Vries and Kanis, 1993). Possible reasons might be that the selection emphasis has not been on litter size but on growth rate and backfat. Litter size is negatively correlated with average daily gain and negative indirect response in litter size with selection for growth rate can be expected. In contrast, litter weight at birth as well as average piglet weight at birth are favourably correlated with growth rate and backfat and an indirect response in these traits might have been achieved. A higher average piglet weight at birth is associated with a reduced mortality (Rydhmer et al., 1992) thus leading to a higher number of piglets weaned. Litter size and average piglet birth weight are negatively correlated which might explain the lack of genetic improvement for litter size in practice.

Genetic improvement of 21 day litter weight is limited by a low heritability. Tholen et al. (1996b) found that this trait is mainly influenced by the number of piglets after cross fostering and the length of the time period between farrowing and weighing. These management factors can not always be well explained by the model which might lead to a decrease in heritabilities. To obtain better response for 21 day litter weight it is therefore necessary to limit variation in these fixed effects which implies restrictions on cross fostering practices. However, in practice it might not always be possible to change the management system. In addition, cross fostering practices might have some systematic effects which leads to bias in the genetic evaluation. In many herds small piglets are put on to gilts while heavier piglets from gilts are taken away. This was indicated in this study by an unusual negative genetic correlation between average piglet weight at birth and 21 day litter weight in the first parity. An alternative would then be to only obtain EBVs for boars. These EBVs would be obtained from information from their female relatives and bias due to management system might be smaller for the boar EBV since it is based on the average of all female relatives while the individual sow EBV is very much influenced by these management practices. Possible drawbacks of this approach are a longer generation interval and a reduced accuracy for this EBV. In general, benefits of improving 21 day litter weight would have to be compared with costs of recording this trait and it has to be determined whether indirect selection through litter birth weight or average piglet weight at birth is to be preferred.

Finally, 21 day litter weight is recorded as an indirect measurement of milking and mothering ability of the sow. An American study (Sauber et al. 1994, cited in Pettigrew , 1995) found an increase in milk production in sows that had been selected for leanness and therefore correlated response from selection on leanness might be expected. Although no estimates were obtained between 21 day litter weight and carcase traits, estimates of genetic correlation between litter birth weight and average piglet weight at birth were favourable. These two traits were measured three days after farrowing for the later part of the data and were therefore influenced by the milk production of the sow thus supporting these findings. Pettigrew (1995) suggested that common physiological conditions such as high concentration of growth hormone or IGF-1 might contribute to both lean meat growth and milk production.

6.5 Implications

So far traits have been discussed in regard to their genetic variation and genetic relationship to each other. The emphasis in this project has been on meat quality and different scenarios for including meat quality traits in breeding decisions will be compared. To combine traits in the

breeding objective, traits are weighted accordingly to their economic weight. Possible ways of calculating economic weight were reviewed by Fewson (1993) and James (1993) and are mostly derived from profit functions. Generally it is assumed that non-linear relationships between traits and profit are negligible (Fewson, 1993). However, Hovenier et al. (1993) showed that this assumption does not hold for meat quality traits. Performance in meat quality traits has an optimum range with threshold values beyond which the product is not acceptable or accepted at a lower price. Based on a marginal profit function approach (Hovenier, 1993) economic weights of meat quality traits are dependent on the population mean. The population mean in Hovenier et al. (1994) is in close agreement with the Australian situation and economic weights for meat quality traits as well as production traits were taken from Hovenier et al. (1994). Economic weights for litter size were provided by Luxford (1996, pers. comm.). Litter size was included in the breeding objective since genetic relationships with growth rate were significantly different from zero. It was discussed previously that number born alive in the first parity should be considered a different trait than number born alive in later parities. Tholen et al. (1996b) found an unfavourable relationship between litter size in the first parity and longevity which is the reason for it's lower economic weight in comparison to litter size in the second parity. Genetic correlations were set to zero between litter size and meat quality traits due to the low magnitude and inconsistency of estimates. In order to obtain a positive definite covariance matrix, a bending program of Essl based on Essl (1991) was used.

To compare selection procedures, four options were evaluated for a terminal sire line and a maternal line. The first option considered only production traits which consisted of growth rate, lean meat percentage, feed intake and ham weight (ADG, LEAN, FDINT, LMW) for the terminal sire line. In contrast, ham weight was not included in the maternal line breeding objective but litter size was considered in this breeding objective. The same traits that were in the breeding objective were also included in the selection index for each line. Meat quality traits and litter size were neglected in this option. In option two it is assumed that meat quality traits can not be measured on the animal but are considered by including them in the breeding objective in addition to the traits that were already used in option one. The only practical measurements of meat quality traits are pH45 and colour and option three evaluated the benefits of including these two traits as selection criteria while option four also included intramuscular fat content measured on the live animal as a selection criterion. This last option was based on the availability of a measurement for intramuscular fat content on the live animal using video image analysis. It was assumed that production traits which are measured on the live animal are available for the individual, its parents and 25 half sibs. Carcase and meat quality information was only available on five half sibs of the animal while information on litter size was obtained from the dam as well as three half sibs of the individual. This structure

represents the breeding structure of Bunge Meat Industries and summarizes the information that is available when the animal is selected.

Results for the different options are presented in Table 6-2 for the terminal sire line and in Table 6-3 for the maternal line along with economic weights for each trait in the breeding objective and the correlation between index and breeding objective. Comparing the terminal sire line with the maternal line shows that a higher growth rate in the terminal sire line is accompanied by a reduction in litter size. In addition, more emphasis is put on high ham weight in this line with the consequence of a stronger unfavourable effect on meat quality traits. However, option one will lead to inferior meat quality in both lines. By including meat quality traits in the breeding objective (second option) only colour of the *m. longissimus dorsi* is improved. The meat quality traits pH45, drip loss percentage and intramuscular fat content still decline, although to a lesser extent than in option one. In the third option, information on pH45 and colour obtained from five half sibs in the abattoir is included. This leads to a darker colour of -0.186 and -0.26 (Table 6-2, Table 6-3) while drip loss percentage will still be increased by 0.231 and 0.175 along with a reduction in intramuscular fat content of -0.015 and -0.013 % in both lines. Genetic change in other production traits is not significantly influenced by including pH45 and colour in the selection index in contrast to including intramuscular fat content in the selection index (option four). This leads to a slight increase in intramuscular fat content of 0.002 and 0.007 % and a further improvement in meat quality traits but is also accompanied by a reduced improvement in average daily gain.

For the terminal sire line little changes in the overal objective (ΔG_{total}) are existent between option one to option three (Table 6-2). While no extra costs are involved in including meat quality traits in the breeding objective (option two) costs of measurement have to be considered in option three. The only larger improvement is achieved with option four. For the maternal line options four and two have the highest aggregate value (Table 6-3) confirming results for the terminal sire indices that meat quality traits could be improved by including them in the objective which is enhanced by using measuring intramuscular fat content as a selection criteria.

Table 6-2 Breeding objective traits with economic values per fattening pig, genetic superiority in natural units after one round of selection, correlation between index and breeding objective (r_{IH}) and financial changes for production (ΔG_P), meat quality (ΔG_{MQ}) and total index (ΔG_{total}) for different options for a terminal sire line

Trait	economic weight per fattener	Option 1	Option 2	Option 3	Option 4
ADG	0.262	13.24	14.59	14.58	14.42
LEAN	3.10	0.65	0.52	0.52	0.52
FDINT	-0.064	0.008	0.013	0.013	0.013
LMW	7.50	0.114	0.108	0.107	0.104
pH45	0.00	-0.008	-0.005	-0.004	-0.003
CLD	0.00	0.111	0.20	-0.186	0.018
DLP	-2.25	0.294	0.250	0.231	0.230
IMF	9.90	-0.018	-0.015	-0.015	0.002
NBA_1	0.00	-0.155	-0.171	-0.170	-0.167
NBA_2	0.00	-0.061	-0.068	-0.068	-0.066
r_{IH}		0.62	0.56	0.56	0.57
ΔG_P		6.34	6.24	6.23	6.17
ΔG_{MQ}		-0.84	-0.71	-0.67	-0.50
ΔG_{total}		5.50	5.53	5.56	5.67

Option one: Breeding objective and index traits: ADG, LEAN, FDINT, LMW
Option two: As option one and in addition DLP, IMF in breeding objective
Option three: As option two and in addition pH45 and CLD in index
Option four: As option three and in addition IMF in index

These results show two important points. Firstly, selection for production traits will lead to inferior meat quality traits. Considering meat quality traits in the breeding objective will reduce this deterioration but in contrast to Hovenier et al. (1994) no improvement of meat quality traits is achieved yet. Hovenier et al. (1993) pointed out that economic weights have a large influence on these results and are dependent on the population level. It is therefore necessary to derive economic weights for all traits in the breeding objective for the Australian situation. This is of particular importance for breeders who are not able to obtain information on meat quality traits from the abattoir. An alternative might be measurements of meat quality on the live animal. Due to animal welfare considerations methods using muscle biopsies are not acceptable. However, analysis of real time ultrasound images might be an alternative to obtain information on meat quality on the live animal. Secondly, given genetic correlations between litter size and production traits estimated in this project litter size should be analysed in a

multitrait analysis. However, this relationship was estimated between sows and their offspring which represents only a proportion of the population and might influence this estimate of genetic correlation. Therefore these parameters need to be confirmed through other data sets

Table 6-3 Breeding objective traits with economic values per fattening pig, genetic superiority in natural units after one round of selection, correlation between index and breeding objective (r_{IH}) and financial changes for production (ΔG_P), meat quality (ΔG_{MQ}), reproduction ($\Delta G_{Repr.}$) and total index (ΔG_{total}) for different options for a maternal line

Trait	economic weight per fattener	Option 1	Option 2	Option 3	Option 4
ADG	0.262	9.42	10.40	10.13	9.96
LEAN	3.10	0.58	0.43	0.42	0.41
FDINT	-0.064	0.005	0.009	0.009	0.009
LMW	0.00	0.086	0.075	0.073	0.070
pH45	0.00	-0.007	-0.004	-0.003	-0.002
CLD	0.00	0.083	-0.015	-0.26	-0.033
DLP	-2.25	0.268	0.202	0.175	0.174
IMF	9.90	-0.017	-0.013	-0.013	0.007
NBA_1	3.50	0.177	0.20	0.20	0.20
NBA_2	4.00	0.212	0.24	0.24	0.23
r_{IH}		0.34	0.30	0.30	0.31
ΔG_P		4.26	4.05	3.96	3.87
ΔG_{MQ}		-0.77	-0.58	-0.52	-0.32
$\Delta G_{Repr.}$		1.47	1.66	1.66	1.62
ΔG_{total}		4.96	5.13	5.10	5.18

Option one: Breeding objective and index traits: ADG, LEAN, FDINT, NBA_1, NBA_2
Option two: As option one and in addition DLP, IMF in breeding objective
Option three: As option two and in addition pH45 and CLD in index
Option four: As option three and in addition IMF in index

6.6 General conclusions

This work provides a complete set of genetic parameters for reproduction, production, carcase and meat quality traits which can be used in genetic evaluation programmes in Australia. However, differences in feeding regimes and slaughter procedures will have to be taken into account. It was shown that meat quality traits are moderately heritable and further research has to address the question of how to incorporate meat quality in breeding programmes in regard to the Australian situation. Special emphasis will have to be put on possibilities of measuring meat quality traits on the live animal.

Another area of high importance is efficient lean meat growth. Due to the test procedure, results for feed efficiency are not applicable to other situations but show the need of further research in this area. Aspects that should be investigated are feed intake capacity in relation to maximum protein deposition and possible difference in genetic parameters for different sexes.

This data set also gave the opportunity of estimating genetic parameters between reproduction traits and other performance traits. It was shown that litter size is negatively correlated with average daily gain which might explain the lack of genetic improvement in this trait since evaluation programmes assume no genetic relationship between these two traits. Significant relationships were also found between litter birth weight and average piglet weight at birth and other performance traits. This is an indication to analyse reproduction traits in a multivariate analysis in evaluation programmes.